FLYCATCHER HABITAT SELECTION IN THE EASTERN DECIDUOUS FOREST

HENRY A. HESPENHEIDE

RESTRICTION of breeding or foraging activities by a bird species to a particular habitat is termed habitat selection. Habitat is usually defined in terms of plant communities, especially those of different structural characteristics, rather than floristic composition (MacArthur and MacArthur, 1961). Ten species of flycatchers (Tyrannidae) are typical of North America east of the Great Plains: Eastern and Gray Kingbirds (*Tyrannus tyrannus* and *T. dominicensis*); Great Crested Flycatcher (*Myiarchus crinitus*); Eastern Phoebe (*Sayornis phoebe*); Yellow-bellied, Acadian, Traill's and Least Flycatchers (*Empidonax flaviventris, E. virescens, E. traillii,* and *E. minimus*); Eastern Wood Pewee (*Contopus virens*); and Olive-sided Flycatcher (*Nuttalornis borealis*). Although a few of these show geographic replacement (the Kingbirds, and especially the Acadian and Least Flycatchers; see Hespenheide, 1969), most of them show distinct preferences of breeding habitat. Two are restricted to boreal forests (Yellow-bellied and Olive-sided Flycatchers), three are found in open (unforested) situations (the Kingbirds and Traill's Flycatcher), one is found along streams or near man-made structures at forest openings (Phoebe), and four are found primarily in deciduous forest types (Great Crested, Acadian and Least Flycatchers, and Pewee). In the case of members of the genus *Empidonax*, habitat is one of the best aids to the identification of breeding individuals (Peterson, 1947: 148). On the other hand, of the three small eastern forest flycatchers, combinations of the Wood Pewee and Acadian Flycatcher (Kendeigh, 1944; Johnston and Odum, 1956), Wood Pewee and Least Flycatcher (Kendeigh, 1948; Martin, 1960), and even all three species (Bond, 1957) have been recorded together in breeding bird censuses of forests chosen by the investigators to be reasonably uniform in structure and floristic composition.

MacArthur et al. (1962, Figure 4) showed that a given species tends to be associated with a foliage density profile of a given type, and that this profile can be simplified into the proportions of vegetation in three more or less closely-defined layers. Colquhoun and Morley (1943) have also demonstrated recognition of three layers of vegetation by birds of temperate deciduous forests on the basis of winter feeding behavior. These conclusions suggest techniques for testing the habitat preferences of forest species such as the flycatchers discussed above.

Although it is not clear whether vegetation density is the factor actually

 The Auk, 88: 61–74. January 1971

measured behaviorally by the birds MacArthur et al. (1962) studied, the birds distribute themselves as if they were doing so. The behavioral bases of habitat selection have been reviewed by Hildén (1965) and Klopfer and Hailman (1965). This study has concentrated on describing the results of such selection, rather than the means by which it is obtained.

METHODS

Data on habitats occupied by the smaller eastern forest flycatchers were collected during the breeding seasons of 1965, 1966, and 1967 at sites in North Carolina, Virginia, New Jersey, Ohio, Michigan, and Wisconsin (see Description of Sites). Singing territorial male birds were located and watched for variable periods of time on at least two different days for a given individual, to determine the extent of the singing territory. Nests were located when possible. All sampling was restricted to forests of uniform structure, insofar as visually ascertainable. Territories of birds that exploited obvious discontinuities in the forest—forest edges or large breaks in an otherwise uniform canopy—were not used. The restriction to uniform habitats is required for the type of sampling used, and was found to exclude only territories of the Pewee, discussed in detail below. Once the territory was defined and a nest located or not, a 100-foot long transect was laid entirely within the area used by the birds. The compass direction of the transect was determined by twirling a straight object and using the direction it assumed when it came to rest as the direction of the transect, presumably random. If found, the nest served as the midpoint of the transect, unless knowledge of the bird's activity indicated it should be at or toward one end (determined before establishing direction). The zero end of the transect was determined by coin toss.

Vegetation density was then measured in the manner of MacArthur et al. (1962). From a table of random numbers (Dixon and Massey, 1957; Hoel, 1962), 20 points along the transect were determined and measured for vegetation density in the layers 0–2 feet, 2–20 feet, and above 20 feet above the ground as follows: For the lower two layers, a pole was moved vertically above the point, and the number of leaves intersected was counted. For the layer of vegetation above 20 feet, a 135-mm lens was directed at the canopy and the resultant image focused on a translucent plastic screen marked with a grid of 10 $\times$ 10 squares. The equivalent number (per cent) of squares totally unobscured by leaves was then used to estimate from a table the number of equal areas of leaves above the point (see MacArthur and MacArthur, 1961, for derivation of the formula relating leaf density to canopy cover). After the 1965 season measurement of the 0 to 2-foot layer was abandoned as irrelevant to the flycatchers, and only the leaves of woody species higher than 2 feet above ground were counted (see Discussion). This allowed graphic consideration of absolute as well as relative density in the layers used by the birds (cf. MacArthur et al., 1962; and Discussion).

DESCRIPTION OF SITES

North Carolina (June 1965).—Acadian Flycatcher (4 transects)—Three sites were in deciduous forest types near Wake Forest, Wake County, of which two were in stream bottoms and one in upland; the other site, just west of Durham in the Duke University Forest, was a mixed pine-maple stream bottom. Wood Pewee (1 transect)—The site was in Wake Forest in a young pine stand.

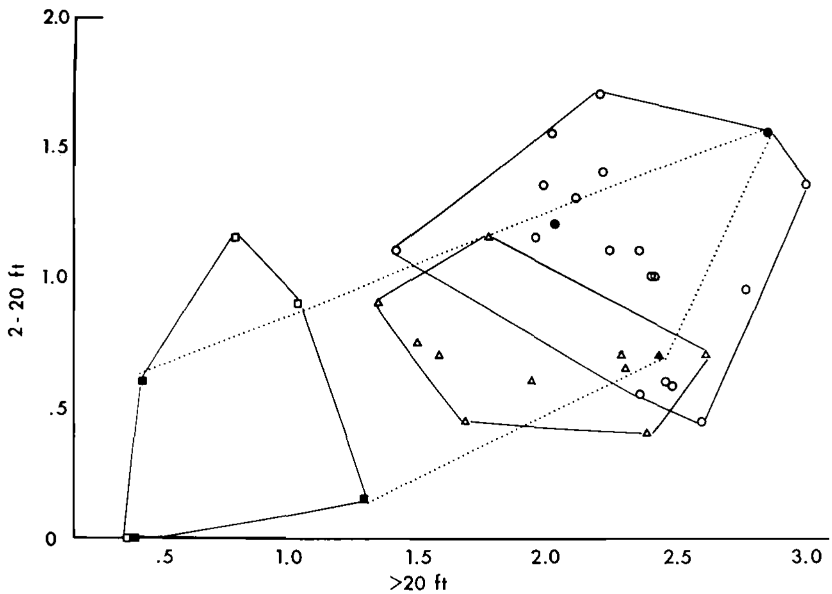

Figure 1. Habitat preferences of four forest flycatchers with respect to vegetation density in understory and canopy layers of the forest. Axes marked in the average number of leaves above a point; each point on graph represents a transect through a different nesting territory. Flycatcher species include the Wood Pewee (squares), Least Flycatcher (triangles), and Acadian Flycatcher (circles). Filled points indicate presence of the Crested Flycatcher. Outermost points of each species joined by a line, broken for the Crested Flycatcher. See text for details of measurement.

Virginia (June 1965, 1966).—Acadian Flycatcher (5 transects)—All sites were in the southern portions of the cities of Chesapeake and Virginia Beach (formerly Norfolk and Princess Anne Counties) along their mutual border; two were in gum swamps (*Nyssa aquatica*), two in successionally advanced pine stands more or less heavily undergrown with hardwoods, and one in an upland woods of oak and mixed hardwoods. Wood Pewee (1 transect)—The site, located as above, was a stand of mature pines and hardwoods near a golf course; undergrowth had been removed, but the site was not on the course.

New Jersey (1965).—Wood Pewee (4 transects)—All sites were in the pine barrens region of Burlington County, two in the Wharton Tract below Atsion, one in Lebanon State Forest, and one between these two areas. Two were in essentially pure tracts of pine, one in the oak climax, and one in mixed pine and oak.

Ohio (June 1966).—Acadian Flycatcher (5 transects)—All sites were in the Wayne National Forest near the Burr Oak Campground, Athens County. All were in more heavily wooded ravines in mixed hardwood forests (in ravines, primarily beech-maple).

Michigan (June 1966).—Least Flycatcher (6 transects)—Five sites were in the Lake Michigan Campground of Hiawatha National Forest, Mackinac County, the other a few miles to the northeast. Four of the transects were in mixed oak-maple-birch woods, two others in nearly pure stands of paper birch.

TABLE 1
ACADIAN AND LEAST FLYCATCHERS: DISCRIMINANT FUNCTION ANALYSIS OF VEGETATION DENSITY IN NESTING TERRITORIES[1]

Acadian Flycatcher				Least Flycatcher			
	No. leaves[2]				No. leaves		
Pair	2–20 feet	20+ feet	X′[3]	Pair	2–20 feet	20+ feet	X′
1965.1	11	47.2	55.9	1966.1	12	38.8	48.3
.2	31	57.2	81.6	.2	14	45.8	56.8
.3	22	28.3	45.7	.3	18	26.9	41.1
.4	24	40.7	59.6	.4	15	30.0	41.8
.5	22	44.9	62.3	.5	14	52.3	62.3
.6	20	48.1	63.9	.6	8	47.7	54.0
.7	23	39.1	57.2	1967.1	14	31.6	42.6
.8	22	47.2	64.6	.2	23	35.5	53.6
.9[4]	11.6	49.7	58.9	.3	9	33.6	40.7
1966.1	19	55.4	70.4	.4	13	46.1	56.3
.2	31	40.4	64.8	.5	14	48.7	59.7
.3	9	51.9	59.0				
.4	26	42.3	62.8				
.5	34	44.2	71.0				
1967.1	27	60.2	81.5				
.2	28	44.4	66.5				
.3	12	49.2	58.7				
.4	27	39.8	61.1				
.5	20	48.2	64.0				

[1] Variance ratio (F, with 2 and 27 degrees of freedom) = 19.70123; $P_F < 0.001$.
[2] Total number of leaves intersected or estimated for all 20 points.
[3] $X' =$ discriminant function $= 132.429X$, where $X = 0.0059567x_{2-20} + 0.0075512x_{20+}$.
[4] Only 19 points sampled; adjusted to 20 points for comparison.

Wisconsin (June 1967).—Acadian and Least Flycatchers (5 transects each)—All sites were in Devil's Lake State Park, Sauk County, in mixed hardwood forests of oak, maple and poplar. Understory, especially in territories of Acadian Flycatchers, was occasionally dense, with either witch hazel or young maples.

RESULTS

Data from the 36 transects are presented in Figure 1, expressed as the average number of leaves above a randomly selected point in each of the two upper layers of the three vegetation layers distinguished by MacArthur et al. (1962). The three species sampled directly are seen to occupy different areas of the two-dimensional vegetation density space. The Wood Pewee occurs in woods with a low density of vegetation, the Least Flycatcher in more densely vegetated habitats, and the Acadian Flycatcher in still more heavily vegetated forests, although the Least and Acadian Flycatchers overlap somewhat in their habitat preference. No territories of the Crested Flycatcher were sampled directly, with transects chosen for a given breeding pair of the species, but the presence of the species in the territories of the other three was recorded. The Crested Flycatcher occurs in habitats used by each of the other three species, implying that it does not select habitat with respect to the other three flycatchers.

Discussion

Overlap in breeding habitat between Least and Acadian Flycatchers.—To determine the degree of overlap, or its converse, the degree of separation between the Acadian and Least Flycatchers' choices of nesting habitat, a discriminant function was calculated for all transects of both species. If two species, A and B, differ slightly in each of two characteristics, x and y, a new variable, X, can be calculated by combining x and y so as to maximize the differences between A and B in a single measurement, the "discriminant function." The derivation and use of this technique has been discussed fully by Mather (1951: 152ff) and used by Cody (1968) to discuss differences in habitat preferences by grassland birds; its use in this case is shown in Table 1. The resultant discriminant function X′ is found on analysis to be only slightly more useful than consideration of the 2 to 20-foot measurements alone. One can measure by t-test the probability that a given value of X′ will deviate from the mean of that species by more than half the difference in magnitude between the means of the two species (and thus be "misclassified," or too similar to the other species). Only deviations in the direction of the other mean will result in misclassification; thus the probability of misclassification (P) measured by t is $\frac{1}{2} P_t$. For the discriminant function, t with $(n-3) = 27$ degrees of freedom equals 0.81 and $P_t = 0.42$; the realized misclassification is 4/30 or 0.133, as compared with the expected value of $\frac{1}{2} P_t = 0.21$. The data for the 2 to 20-foot layer alone gives an expected value of misclassification of 0.30 ($t_{(28)} = 0.5145$; $P_t = 0.61$), as compared to a realized misclassification of 5/30 or 0.166.

Measurement of overlap.—The extent of overlap in habitat preference can be calculated from the foliage density measurements expressed as the discriminant function X′. The coefficient α is used here as a measure of overlap. As defined by MacArthur and Levins (1967), α_{ij} is the constant from the Volterra competition equations that measures the competitive effect of an individual of species j on an individual of species i. The index does not presuppose a particular theoretical frequency distribution of effect relative to some continuously variable resource, although interpretations and comparisons are difficult in situations where data do not fit such distributions. MacArthur and Levins have discussed the properties of α in terms of normal distributions and made a number of theoretical predictions on the possibility of invasion of a two species system by a third, intermediate species. Slobodkin (1961: 62ff) has summarized the theoretical results of competition between two species having a known α_{12} (his α) and α_{21} (his β), and carrying capacities K_1 and K_2. From the Volterra equations, the conditions for stable coexistence are that

$$\alpha = \alpha_{12} < \frac{K_1}{K_2} \quad \text{and} \quad \beta = \alpha_{21} < \frac{K_2}{K_1}.$$

The values of α are calculated by MacArthur and Levins' formula

$$\alpha_{ij} = \frac{\sum_n N_{in} \cdot N_{jn}}{\sum_n N_{in}^2},$$

where N_{in} is the proportion of the total number of territories of species i within a given range of discriminant function values n; α_{ji} is calculated in the same manner, with the sum of N_{jn}^2 in the denominator. MacArthur and Levins' index of overlap is identical to that of Morisita as discussed by Horn (1966) in the case where the values of K are equal for the two species.

If the index of overlap is calculated from the resulting frequency distribution of the discriminant function X′, the values for the effect of the Least Flycatcher (l) on the Acadian Flycatcher (a) is $\alpha_{al} = 0.488$; that for the effect of the Acadian on the Least Flycatcher $\alpha_{la} = 0.681$. These values of α can be compared with the appropriate ratios of K if we can estimate carrying capacity. The value of K may be roughly estimated by the reciprocal of territory size. Thus, if $K_a \propto 1/T_a$ and $K_l \propto 1/T_l$, then

$$\frac{K_a}{K_l} \propto \frac{T_l}{T_a} \quad \text{and} \quad \frac{K_l}{K_a} \propto \frac{T_a}{T_l}:$$

Walkinshaw (1966a) gives an estimate for the size of the territory of the Acadian Flycatcher as 2.97 acres (N = 80). For the Least Flycatcher he (1966b) quotes the average value of 0.18 acres as determined for 33 territories by MacQueen (1960) but suggests that territories of birds he has observed (but not measured) as being 1.0–1.5 acres. Martin (1960) gives a territory size of 0.32 (SD = 0.24) for 10 territories in Ontario. If 0.25 acres is taken as an estimate of the territory size of Least Flycatchers, then $K_a/K_l = T_l/T_a = 0.084$ and $K_l/K_a = T_a/T_l = 11.88$. Comparison of these ratios with the empirical values of overlap given above show $\alpha_{la} < K_l/K_a$, but $\alpha_{al} > K_a/K_l$. This indicates that the Least Flycatcher is having a greater effect on the Acadian than expected for a stable equilibrium, and that it ought theoretically to replace it in competitive situations. The competitive relations of these two species are considered below.

Geographic differences in habitat preference.—Because the Acadian and Least Flycatchers show a narrow overlap in both habitat and distribution,

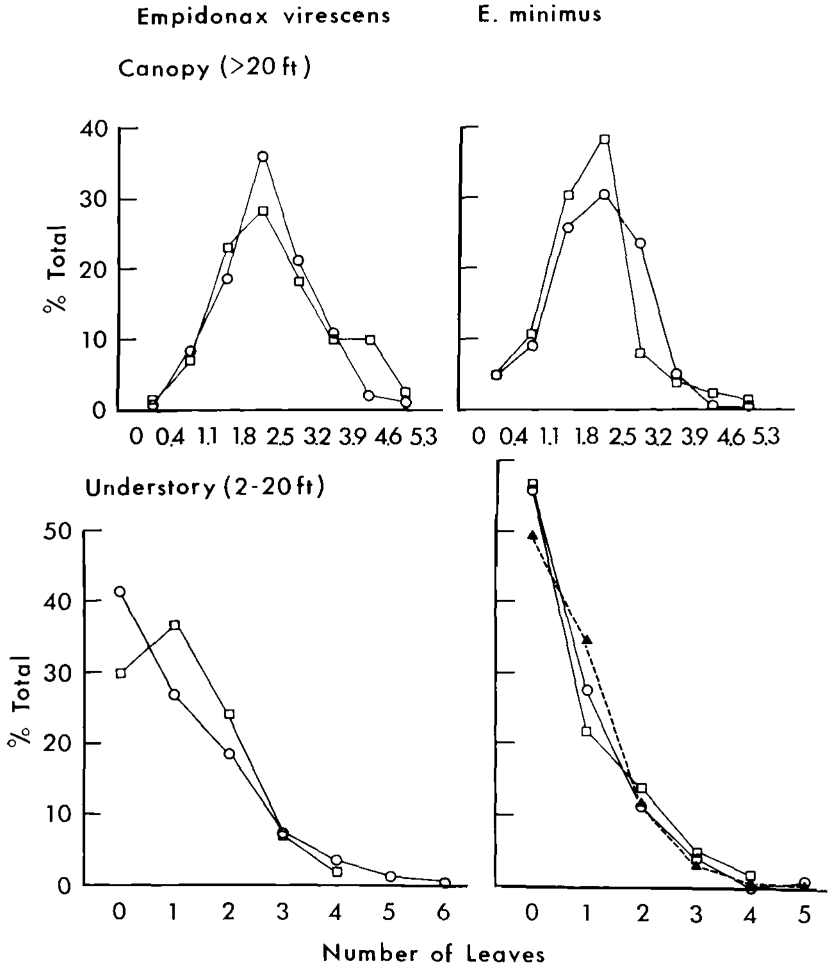

Figure 2. Comparisons of distributions of leaves above random points in nesting territories of Least and Acadian Flycatchers in (open squares) and out (open circles) of zone of overlap. Filled triangles are Poisson distribution for Least Flycatcher understory data. See text for analysis.

habitat preferences in and out of the zone of overlap were examined in detail, to determine whether either species showed changes in, or sharpening of, habitat preferences in the presence of the other, as predicted above on theoretical grounds. Quantitative measurement of the extent of overlap in the geographic ranges of the two species (Hespenheide, 1969) showed such overlap to be extremely small, a result confirmed by the author's difficulty in locating populations of either species within the zone of overlap in northern Illinois and southern Wisconsin. The area chosen for study was Devil's Lake State Park in Wisconsin, where transects were run in five territories of each species. The frequency distributions of the number of leaves above individual points could then be compared with distributions from transects run outside the zone of overlap (Upper Michigan for the Least Flycatcher; Ohio and the southeast for the Acadian Flycatcher). This is done in Figure 2 for each species and for each of the two layers.

To consider the density of leaves above 20 feet first, the mean number of leaves is found significantly different between the two species, all transects considered together ($t_{(597)} = 4.3906$, $P_t < 0.001$; see Mather, 1951: 55ff). Comparisons of mean values within each species in and out of the zone of geographic overlap show no significant differences in either species (Least Flycatcher, $t_{(218)} = 0.5001$, $0.60 < P_t < 0.70$; Acadian Flycatcher, $t_{(377)} = 1.2316$, $0.30 > P_t > 0.20$). It is interesting that the direction of difference in each mean in the area of overlap is away from the mean of the other species, although the differences are not themselves significant.

The distribution of leaves above points in the understory in all cases suggests, but is infrequently equivalent to, a Poisson distribution. If the leaves in the forest are distributed at random, an assumption made by the sampling technique, the number of samples with 0, 1, 2, 3 . . . or n leaves above randomly chosen points should conform to a Poisson distribution. Goodness of fit to a Poisson distribution is measured by a Chi-square test with (N – 2) degrees of freedom (in the following discussion the probability of a given value of Chi-square for, say, 3 degrees of freedom will be symbolized as P_3).

The aggregate data for each of the two species are significantly different from a random (Poisson) distribution (for the Least Flycatcher, $0.01 > P_3 > 0.001$; for the Acadian Flycatcher, $0.02 > P_4 > 0.01$). In fact, the distribution of leaves in any given forest is probably usually not random, with the variance characteristically exceeding the mean, indicating a tendency to clumping. In the slash plots sampled by MacArthur et al. (1962, Figure 1), leaves above 240 points in a layer 2–15 feet above the forest floor were significantly nonrandom in distribution ($0.05 > P_{2 \text{ or } 3} > 0.02$). If the transects in and out of the region of overlap are considered separately for each species, only two of the four subsamples are significantly nonrandom (Acadian Flycatcher outside the region of overlap, $P_5 < 0.001$; Least Flycatcher in the region of overlap, $0.02 > P_3 > 0.01$). Two subsamples were not significantly different from a Poisson distribution (Acadian Flycatcher in overlap region, $P_4 > 0.90$; Least Flycatcher outside overlap region, $0.20 > P_3 > 0.10$). The tendency of less diverse sampling areas to show a closer agreement to randomness suggests that lumping of samples may obscure local approximation of leaves to a random distribution.

Comparison of subsamples of understory leaf numbers within and between species yields one interesting result. Although Least and Acadian Flycatchers show significantly different distributions between species in and out of the zone of geographic overlap ($P < 0.001$), and Least Flycatchers show no significant differences between in and out of the overlap zone ($0.50 > P_3 > 0.30$), the Acadian Flycatcher does show a difference between overlap and nonoverlap transects ($0.05 > P_4 > 0.02$; see Figure 2). This difference is not large compared with the differences between the species; it is in the direction away from the preference of the Least Flycatcher. It is noteworthy that the change in preference occurs in the Acadian Flycatcher rather than the Least, since the analysis of overlap, above, predicted replacement of the Acadian Flycatcher by the Least in competitive situations.

Other studies of habitat selection.—Although several studies have demonstrated successions of bird communities that parallel the successions of plant communities toward a local climax situation, most have been based on the floristic composition of the plant communities (Kendeigh, 1944, 1948; Johnston and Odum, 1956; Martin, 1960; Haapanen, 1965, 1966), rather than on physical characteristics of the vegetation. Karr (1968) and Henry S. Horn (pers. comm.) have demonstrated that vegetation density is correlated with successional changes in floristic composition. Using successional stages following strip mining in Illinois, Karr (1968, Figure 3) has also demonstrated that the diversity of birds is proportional to the density of vegetation through succession. However the pattern and structure of vegetation in Karr's (1968: 350) small number of census areas seems to have been complex so that the preferences of particular bird species cannot be readily assessed.

For the one case in which a large number of relatively uniform floristic successional stages have been numerically ranked on a logical basis, information is also available on their relative use by birds (Curtis and McIntosh, 1951; Bond, 1957). These studies of the plant and bird communities were made in southern Wisconsin, within the area of overlap of the Least and Acadian Flycatchers. McIntosh (1958) describes the development of the Continuum Index, which is based on the relative importance of several tree species as measured by their size, density, and relative frequency. Bond (1957), using an indirect measure of relative abundance comparable to that used for the plants, censused 64 individual wooded stands for which the plant Continuum Index had been measured. Figure 3 shows the distribution of the four eastern forest flycatchers with respect to these ordered stands; the distributions of the average Importance Values for the birds are expressed as unit curves, to correct for differences in relative abundance between species. The Crested Flycatcher occurs with little noticeable pref-

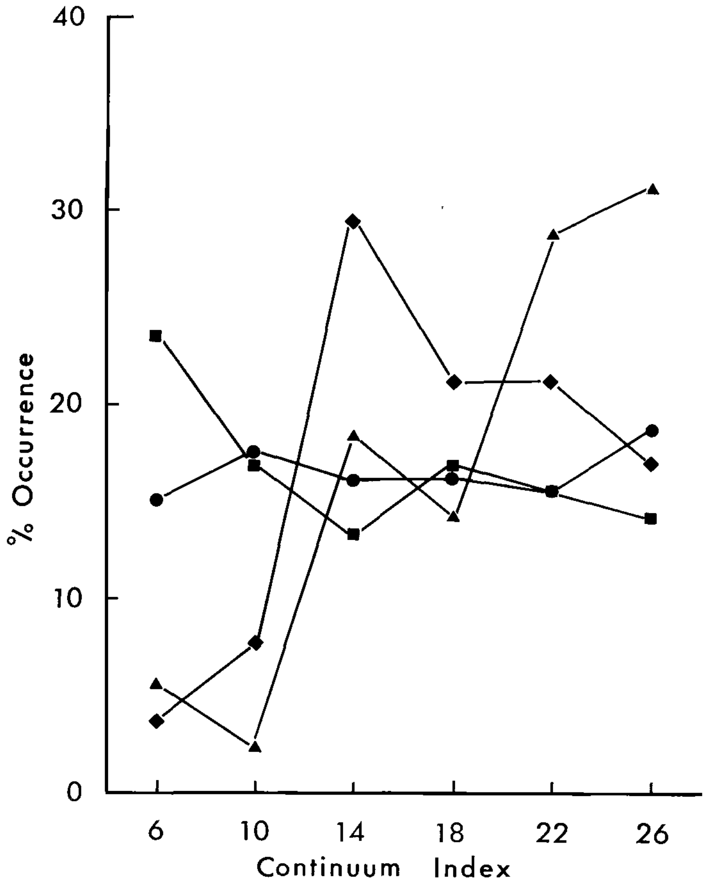

Figure 3. Relative occurrence of flycatchers in a continuum of forest types; data from Bond (1957). Species include Crested Flycatcher (squares), Wood Pewee (circles), Least Flycatcher (diamonds), and Acadian Flycatcher (triangles). Higher Continuum numbers indicate denser vegetation; see text.

erence for more open (low Continuum Index) or less open (high Continuum Index) forest types (Curtis and McIntosh, 1951: 489). On the other hand, Least Flycatchers are most common at intermediate Index values and the Acadian Flycatcher at very high values, indicating a difference in preference similar to that found in this study (Figure 1). The occurrence of the Pewee, like the Crested Flycatcher in all parts of the Continuum in approximately equal abundance, is in apparent contradiction to the results of this study (cf. Figure 1) and will be considered further.

Breckenridge (1956) showed that the Least Flycatcher prefers forests of intermediate openness in the understory, but his measurements were made only in terms of this one species and are not of use for comparison with other flycatchers. It should be noted that his technique is similar to that of MacArthur et al. (1962), but measures openness rather than closedness.

The habitat of the Wood Pewee.—The occurrence of Wood Pewees throughout the continuum of forest types studied by Bond (Figure 3), as well as their inclusion in most censuses of breeding forest birds, seems to contradict the findings of this study that Pewees occur only in very open habitats (Figure 1), and not in the denser forests inhabited by Least and Acadian Flycatchers. On the other hand, six transects run in nesting territories of Pewees might be thought too few from which to generalize. The reason for the small number of Pewee transects is that, early in the summer of 1966 it was discovered that Pewee territories rarely met the criterion of being situated in an area of uniform, regular coverage of vegetation. For example, of about 15 pairs of Pewees in southeastern Ohio, none was unambiguously found to use a uniform woods of any sort. Of the 9 best-known pairs, 5 pairs occurred in groves or narrow lines of trees in otherwise agricultural settings; 2 pairs were associated with openings in otherwise unbroken canopied forest (both where large trees had been selectively logged out); 1 with a few large, open trees that bordered an open, brushy stream, and 1 with a few emergent trees over a brushy, slash-cut understory. Of the rest, not investigated closely, 3 seemed to be associated with the forest margin, 2 with openings or margins, and 1 unknown. Similarly of 5 territories in which transects were not run in southeastern Virginia (two nests), 2 were in second growth pines (5 of the 6 transects that were run were taken in pine habitats), and 3 were obviously using forest margins. All pairs found in central North Carolina (one nest) were also in open pine woods or in scattered trees or stands of trees in yards of homes. Nine pairs of Pewees observed in Upper Michigan were all associated with openings, and most of the six nests found were also at or near an opening. Only after this pattern emerged of association of Pewees with discontinuities in the vegetation was it realized that at least three of the six Pewees sampled for vegetation density also had relied on openings or edges for feeding. In situations where the Pewee nests in more or less uniform vegetation, the canopy layer is always incomplete, and often sparse besides, as in the case of the several pine habitats. The bird feeds high in the trees as a rule, and will even occur in forests with a dense understory up to 15 or 20 feet in height, providing the broken canopy layer is itself sufficiently high above the understory. Situations of this sort were seen in southeastern Virginia (dense cane thicket under open pines) and Wisconsin (dense maple saplings under open, advanced oak second growth). In these cases, even the 2 to 20-foot layer of MacArthur et al. (1962)

becomes irrelevant in the way that the 0 to 2-foot layer is irrelevant to other flycatchers.

It therefore appears that the Pewee is primarily an "edge" species, in its restriction to forest margins or openings. Because it requires trees for nesting and feeding perches, one is tempted to think of it as a forest species, hence its regularity in forest breeding bird censuses, such as those of Bond (1957) and others.

The absence of Wood Pewees from closed canopy situations and the restriction of Acadian Flycatchers to forests with both closed canopy and dense understory leaves a range of deciduous forest types uninhabited by small flycatchers. Extensive areas of this sort were seen in southeastern Ohio, where the upland oak-hickory forests were too open for the one species and too closed for the other.

In any case, there appears to be never more than one species of small flycatcher coexisting with the Crested Flycatcher over extensive areas of habitat, although in any given area any one of three small species might be present. Likewise the smaller Traill's Flycatcher may coexist with the larger Eastern Kingbird. This pattern of one small and one large flycatcher as a maximum for any given habitat suggests that division of food by size is a method of reducing possible competition.

ACKNOWLEDGMENTS

This study began with and has continued to be stimulated by the ideas of R. H. MacArthur and P. H. Klopfer. The practical guidance of W. John Smith and discussions with R. E. Ricklefs have been especially helpful. R. O. Erickson gave advice on statistical treatment of the data. Richard R. Bond provided information from his field notes, while the author's field research has been aided at points too numerous to mention. The author held a National Science Foundation Cooperative Graduate Fellowship for the academic years from 1964 to 1967.

SUMMARY

Measurements of vegetation characteristics in nesting territories of Least and Acadian Flycatchers and Wood Pewees show clear differences in preferred breeding habitat between the Pewee and the other two species, and significant differences, despite overlap, between the Least and Acadian Flycatchers. Apparent changes in preferred habitat by the Acadian Flycatcher in regions of overlap with the Least Flycatcher were in accord with predictions of competitive effect based on overlap data alone. The Wood Pewee was characteristically associated with forest margins or other discontinuities. Crested Flycatchers were found in a wide range of habitats, establishing a pattern of one large and one small flycatcher as a maximum in eastern forests.

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Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Canal Zone. Present address: Biological Sciences Group, Box U-42, University of Connecticut, Storrs, Connecticut 06268. Accepted 17 December 1969.