

DISTRIBUTION OF SUMMER BIRDS ALONG A FOREST MOISTURE GRADIENT IN AN OZARK WATERSHED¹

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Abstract. Vegetational and physical habitat factors were measured in 110 0.05-ha circular plots around singing ♂♂ of eight bird species in a small watershed in northwestern Arkansas during June and July 1973. Sixty birdless plots were similarly sampled in the driest and most moist areas of the watershed to determine a forest moisture gradient. Principal component analysis of the combined avian community habitat data determined that the forest moisture gradient is important in the distribution of the birds, although multiple analysis of variance showed that no one factor can account for the significant distribution. Principal component analysis of the individual species determined the unique characteristics of the realized niches of each species. An ordination of the species using linear discriminant function analysis of the 60 forest samples was similar to the ordination based on the bird distribution, but suggests that other factors are determining the precise distribution of the birds. No species shows a great affinity for the drier forest, although Tufted Titmice seem able to utilize the moist and dry forests equally. The Hooded Warbler, Ovenbird, and Acadian Flycatcher have shorter niche widths than early arriving migrants and permanent residents and can be considered obligatory moist forest species. The results show that the moist forest is of great importance to the avian community and reasons for the lack of birds in the dry forest are discussed.

Key words: Arkansas; birds; community; forest moisture gradient; habitat selection; multivariate analysis; niche width; ordination; realized niche.

INTRODUCTION

Since early works by Lack (1933) and Moreau (1934) concerning habitat selection in birds, much research has led to the conclusion that the configuration of the vegetation is of prime importance (MacArthur and MacArthur 1961; MacArthur et al. 1962; Hildén 1965; Bendell and Elliott 1966; Ficken and Ficken 1966; Cody 1968; Wiens 1969; James 1971; Orians 1971; Zimmerman 1971; Anderson and Shugart 1974). Wiens (1973) summarizes the present viewpoint by stating that vegetational structure is ecologically important to birds in many ways, such as providing display perches, shelter and nest sites, and suitable foraging areas. This in turn may lead to many beneficial results, including increased number of offspring produced (Carrick 1963) and decreased competition among species (Kendeigh 1945; Balda 1969).

Species react to certain proximate factors that ensure ultimate factors essential to the survival of the organism will be satisfied (*for review see* Immelmann 1973). James (1971) used the term "niche-gestalt" to refer to those proximate factors of the ecological niche which elicit the settling response in birds. The ecological niche is conceptualized as a multidimensional space (or hypervolume) that incorporates all the resources a species requires to survive and reproduce, but a species usually exists in a realized niche, some subset of the ecological niche (Hutchinson 1958). Recently, Whittaker et al. (1973) argued for strict defini-

tions for habitat and niche, habitat referring to the "physical and chemical environment" or "environmental variables with an extensive spatial component" and niche referring to "variables by which species in a given community are adaptively related" or "intensive or local environmental variables." However, niche variables intergrade into habitat variables and microhabitat variables can be considered niche variables (Whittaker et al. 1975). Since birds react to and partition vegetation primarily on an intracommunity level, the vegetational habitat should be considered part of the niche (James et al. 1975). Thus the vegetational characteristics of the avian territories measured in this watershed community constitute a habitat component of the species niche and will be referred to as the habitat niche. Other studies have likewise considered the habitat as part of the niche. For example, Whittaker et al. (1973) state that James (1971) correctly ordines avian habitats, although James (1971) states that she is concerned with "characteristic habitat dimensions of the species niche."

In this study, aspects of the different niche-gestalts that are associated with a forest moisture gradient were determined by sampling a variety of habitat characteristics that potentially relate to the niche-gestalts of the different avian species. These habitat characteristics were then correlated to a forest moisture gradient which was determined from the forest stand itself (as in other studies such as Turner [1935] and Whittaker and Niering [1965]). In the process, habitat niche differences between species were detected. The actual forest moisture gradient was determined by sampling in the seemingly driest and most

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TABLE 1. Avian species sampled

Common name	Abbreviation	Scientific name	Sample size
Downy Woodpecker	DW	<i>Dendrocopos pubescens</i>	8
Acadian Flycatcher	AF	<i>Empidonax virescens</i>	12
Tufted Titmouse	TT	<i>Parus bicolor</i>	19
White-breasted Nuthatch	WN	<i>Sitta carolinensis</i>	9
Blue-gray Gnatcatcher	BG	<i>Polioptila caerulea</i>	15
Red-eyed Vireo	RV	<i>Vireo olivaceus</i>	19
Ovenbird	OB	<i>Seiurus aurocapillus</i>	14
Hooded Warbler	HW	<i>Wilsonia citrina</i>	14

moist areas (defined by vegetation) of the watershed. This gradient was compared to the gradient determined from the avian distribution and the importance of the actual forest moisture gradient to the avian distribution was determined.

STUDY AREA

Leatherwood Creek, a small tributary that joins the Buffalo River near Ponca, Newton County, Arkansas, was chosen as the study area. At the time of the study, the watershed was owned by the Nature Conservancy but has been subsequently purchased by the National Park Service for inclusion in the Buffalo National River. The creek flows northwestward and drops ≈ 300 m in its 4-km course (James 1972), which makes the cove ideal for studying the adjacent slopes. The dominant tree species on the dry slope are post oak (*Quercus stellata*) and black hickory (*Carya texana*) whereas large Carolina beeches (*Fagus grandifolia*) which represent a relic mesophytic forest (Braun 1950) dominate the moist slope. Mockernut hickory (*Carya tomentosa*) and sweet gum (*Liquidambar styraciflua*) are important secondary species on the moist slope, while white oak (*Quercus alba*), shagbark hickory (*Carya ovata*), and sugar maple (*Acer saccharum*) occur on both slopes, but more commonly on the moist slope.

METHODS

Sampling

Stewart and Aldrich (1951) demonstrated that the removal of singing male birds in a forest resulted in a replacement at the same site by other singing males of the same species. This habitat-site specificity justifies using a singing bird as the center of sampling plots (James 1971) since the site will reflect the niche-gestalt of the species, not a random occurrence of an individual. A total of 110 samples was obtained between

22 June and 31 July 1973 for the eight most common singing species in the watershed (Table 1).

The vegetation surrounding each singing male was analyzed using the technique of James and Shugart (1970), but additional physical factors were measured to produce a multidimensional characterization of the habitat niches. Twenty-five habitat factors listed in Table 2 were calculated for each plot. From the center of each plot, four orthogonal transects were chosen in the directions of the random positions of the cross hairs of a sighting tube (James and Shugart 1970). Each transect was 12.4 m long, the radius of an 0.05-ha circular plot. While pacing the transect away from the center, 10 random sighting tube readings were taken for ground cover and canopy cover respectively. Sighting a piece of vegetation through the cross hairs was considered a positive score. Returning to the center, all stems (any living vegetation <7.6 cm in diameter at breast height [dbh]) that intersected the outstretched arms of the investigator were counted. All trees (vegetation >7.6 cm dbh) within the plot were classified by species and were recorded into tree trunk diameter classes using a reach stick (Forbes 1955). The tallest vegetation in each quadrant of the plot was measured using a clinometer. A compass bearing determined the general orientation of the slope within the plot and two factors were derived from this reading by making a linear scale from 0° to 180° . For the first factor, north was considered 0° and south 180° , while for the second, east was considered 0° and west 180° . Thus a reading of due southwest (225°) would be 135° on both axes. Ten randomly selected leaves were collected in an air-tight bag and were dried to constant weight in a vacuum oven and percent leaf moisture calculated.

The final 13 habitat factors listed in Table 2 pertain to the most common eight species of trees found in the watershed. Five species were divided into two groups (<22.9 cm dbh and >22.9 cm dbh) to discover any differences in the importance of small and large trees of the same species. So few large trees of the other three species were encountered that they were not so divided. The use of tree species as habitat factors was not construed to mean that tree species per se are important to the birds, but rather that each tree species has a more or less distinctive configuration that may be important to a certain bird species. Moreover, several trees may share common characteristics, such as high, closed canopy, which may attract one species of bird to those tree species.

In order to characterize the actual forest moisture gradient that existed in the watershed, 30 plots (0.05 ha each) were sampled in the most moist and 30 plots were sampled in the driest areas of the watershed using tree species as indicators of the moisture gradient. These birdless plots represented the maximum differences in vegetation on the adjacent slopes and were used to ordinate the bird plots along the forest moisture gradient.

TABLE 2. First principal component correlations between the 25 habitat factors and the individual species, dry and moist forest samples, combined species, and combined forest samples. Correlations in bold type highlight important relationships (the importance increasing as correlations approach ± 1.00) and blanks indicate no data. Percent total variance (based on 100%) refers to the amount of variance accounted for in each principal component analysis. Abbreviations as in Table 1

Habitat factors	DW	TT	WN	BG	RE	OB	HW	AF	DS	MS	CS	CF
Trees 7.6–15.2 cm dbh	-.18	-.12	-.01	-.77	-.67	-.67	-.51	-.55	-.51	.77	-.39	-.49
Trees 15.2–22.9 cm dbh	.35	-.45	-.37	-.41	-.18	-.23	-.62	-.57	.35	.80	-.25	-.30
Trees 22.9–38.1 cm dbh	.52	.04	-.32	-.45	-.02	.45	-.05	-.62	.57	.34	-.04	-.09
Trees >38.1 cm dbh	-.14	.76	.40	.76	.68	-.18	.80	.64	-.77	-.71	.51	.40
Total stems	-.27	-.27	.65	-.36	-.23	.07	-.28	.15	-.46	-.12	-.06	.73
Ground cover (%)	.38	-.19	-.11	.23	.38	-.28	-.57	-.09	-.22	.04	.05	.01
Canopy cover (%)	.88	.85	.81	.87	.86	.49	.07	.44	.57	-.23	.80	.93
Average tree height	.72	.67	.67	.80	.76	.18	.68	-.15	.36	.23	.64	.94
Leaf moisture (%)	.80	.66	.27	.65	.72	.29	-.26	-.32	.59	-.15	.56	.87
North-south bearing	-.88	-.52	-.38	.22	-.74	.90	.05	-.27	-.70	-.60	-.39	-.83
East-west bearing	-.84	-.50	-.84	-.66	-.78	-.90	-.59	-.51	.38	.60	-.70	-.94
White oak <22.9 cm dbh	.38	.02	.01	-.30	-.51	-.32	.11	-.32	.47	.15	-.19	-.27
White oak >22.9 cm dbh	.37	-.12	-.12	-.12	-.24	.18	-.70	-.70	.65	-.10	-.11	-.25
Shagbark hickory—total	.05	.05	-.23	-.28	-.23	-.38	-.81	-.51	.39	.36	-.18	-.07
Sugar maple—total	.11	.11	-.00	-.00	.21	-.09	.06	-.21	.62	-.06	.18	.40
Post oak <22.9 cm dbh	-.92	-.76	-.49	-.61	-.64				-.24		-.76	-.86
Post oak >22.9 cm dbh	-.81	-.66	-.49	-.73	-.70				-.40		-.70	-.74
Black hickory—total	-.86	-.76	-.49	-.58	-.56				-.39		-.71	-.82
Mockernut <22.9 cm dbh	.62	.45	.50	.19	.36	.09	-.32	-.73		.65	.31	.55
Mockernut >22.9 cm dbh	.29	.46	.89	.33	.35	.49	.34	-.66		.26	.36	.51
Beech <22.9 cm dbh	.34	.45	.72	.28	.27	.43	.33	-.23		-.03	.29	.56
Beech >22.9 cm dbh		.50	.81	.73	.57	.64	.72	.95		-.86	.54	.69
Sweetgum <22.9 cm dbh	.36	.16	.81	.35	.40	.57	.25	.28		.58	.36	.54
Sweetgum >22.9 cm dbh	.34		.83	.35	.41	.50		-.32		.54	.33	.54
Dead trees—total	.57	.28	-.42	.35	-.11	-.01	.43	-.40	-.43	-.15	-.05	-.48
Total variance (%)	32.4	23.4	29.5	25.8	27.0	20.5	23.0	24.0	24.9	21.7	20.1	38.3

Statistical analysis

Principal component analysis (PCA) (Anderson 1958; Morrison 1967) is a multivariate technique that has become quite useful in ecological research. Unlike most correlation techniques, it elucidates underlying factors without any a priori assumptions concerning which factors are important and is recommended when applied to sample sets of relatively limited ranges of community differences (Gauch and Whittaker 1972). The 25 habitat factors for all 110 avian plots were collectively subjected to PCA to discover habitat niche relationships among species. (Different sample sizes [Table 1] could influence the results of this analysis since PCA is somewhat weighted towards larger data sets. However, this influence is considered minimal and the sample sizes reflect absolute numbers of singing males in the watershed.) The habitat data for each species were next subjected to PCA separately so that the differences in importance of habitat factors could be compared and contrasted between species.

An ordination was constructed by plotting the mean principal component scores for each species from the first two principal components. Confidence ellipses of 1% were drawn around each mean using the method of Rao (1966), simply to highlight differences between species at the sacrifice of showing broad overlap that would be evident if 95% confidence ellipses were used (e.g., Gipson et al. 1974). This does not necessarily imply that the species are symmetrically distributed

around their mean score, but see the discussion concerning the use of ellipses to characterize niche dimensions in Green (1974).

Multivariate analysis of variance (Morrison 1967; Cooley and Lohnes 1971) with step-down analysis (Bargmann 1962) was used to determine if a significant difference existed between groups based on the vegetational characteristics, and what vegetational factors were accounting for the observed difference. However, to perform this multivariate statistical technique, the variance between the groups should be stabilized, a process requiring that the number of habitat factors be less than the number of observations per group. Thus, it was decided that all tree species factors plus dead trees be eliminated, lowering the number of factors from 25 to 11. The Downy Woodpecker and White-breasted Nuthatch had <12 observations and were deleted from this analysis.

Box's (1949) test showed that the variance between the remaining six species was not stable (homogeneous). A variance-stabilizing program based upon Box and Cox (1964) and Andrews et al. (1971) was used to produce power transformations for each habitat factor which reduced the *F* value with 330 and 9,424 degrees of freedom from 1.18 to 1.07, very close to the value of 1.00, that would signify homogeneous variance. This process is analogous to normalization of the covariance matrices. (Since the variance-stabilizing program requires nonzero numbers, a near-zero value [0.00001] was added to all variables.)

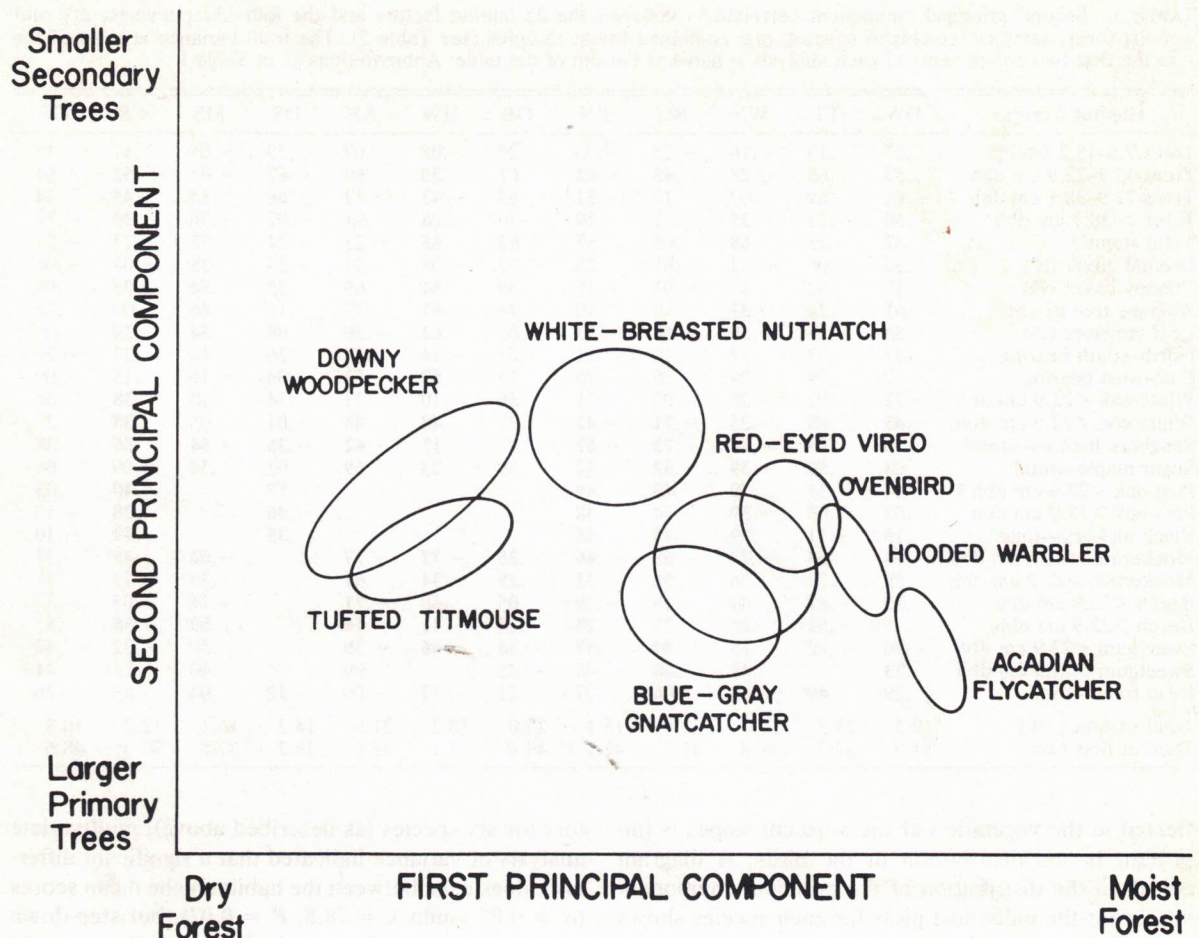


FIG. 1. Ordination of the avian habitat niches represented by 1% confidence ellipses obtained from principal component analysis of the combined avian data.

Linear discriminant function analysis for separating two multivariate normal populations with unequal covariance matrices (Anderson and Bahadur 1962) was used to maximize the difference between the moist and dry forest samples for the subset of 11 habitat factors. Linear discriminant function analysis combines the variance observed in all variables and reduces it to one new variable which can distinguish the groups better than any one of the original variables (Sokal and Rohlf 1969). As James (1971) points out, PCA shows relative positions within a hypervolume, whereas discriminant function analysis maximizes the distance between groups. The habitat data for all 110 avian plots were multiplied by the discriminant weights obtained for each factor from the forest sample analysis and the products were summed to produce a single discriminant score for each plot. These discriminant scores were subjected to the variance-stabilization program after all scores had been divided by 10 to reduce magnitude and had 5 added to eliminate negative numbers. These transformed data were analyzed using one-way analysis of variance with Duncan's

multiple range (Steele and Torrie 1960) to assess the significance of the mean score distribution along the discriminant axis.

RESULTS

Community habitat niche relationships

By combining all the avian species data into one PCA, the vegetational characteristics of the adjacent slopes in the watershed that are important to the avian community were identified (CS in Table 2). Percent canopy cover, average tree height, percent leaf moisture, and trees >38.1 cm dbh, especially Carolina beeches, have high positive correlations for the first component and characterize the moist forest situations. Post oaks and black hickories plus a southward compass bearing have high negative correlations and represent the dry forest condition. Comparing these results with the correlations for the birdless forest samples (CF in Table 2), it is evident that similarities exist between the important habitat factors for the avian species and the forest moisture gradient. Thus it appears that a forest moisture gradient re-

TABLE 3. Second principal component correlations between the 25 habitat factors and the individual species, dry and moist forest samples, combined species, and combined forest samples (see Table 2). The total variance accounted for in the first two components of each analysis is listed at bottom of the table. Abbreviations as in Table 1

Habitat factors	DW	TT	WN	BG	RE	OB	HW	AF	DS	MS	CS	CF
Trees 7.6–15.2 cm dbh	-.23	.13	-.16	-.25	-.36	.20	-.08	.07	.39	-.05	.41	.15
Trees 15.2–22.9 cm dbh	.55	.65	-.28	-.45	-.62	.67	-.35	-.60	.67	-.01	.62	.54
Trees 22.9–38.1 cm dbh	-.61	.59	.07	.12	-.51	.65	-.43	.42	-.66	.53	.45	.54
Trees > 38.1 cm dbh	-.50	-.27	-.35	.17	.40	.30	.28	.63	-.07	-.06	-.39	-.72
Total stems	.57	-.23	.68	.06	.57	-.83	.65	-.23	-.21	-.77	-.27	-.21
Ground cover (%)	.32	-.06	-.33	.01	.25	-.77	-.08	-.11	-.25	.35	-.04	-.08
Canopy cover (%)	-.10	.02	-.12	-.03	-.18	.39	.54	.69	.52	.50	.03	.09
Average tree height	-.61	.24	-.37	.18	.10	.74	-.61	.77	.15	.46	.09	.08
Leaf moisture (%)	.54	.26	-.59	-.58	-.33	-.03	-.62	-.30	-.08	.54	.29	.06
North-south bearing	.13	-.03	.31	-.10	.11	-.07	-.14	.52	.26	.18	-.27	-.29
East-west bearing	-.12	.29	.24	-.26	-.28	.13	.57	.53	-.04	-.18	.15	.09
White oak <22.9 cm dbh	-.72	.03	-.38	-.07	-.21	.36	.10	.21	.34	.10	.38	.38
White oak >22.9 cm dbh	-.43	.68	-.25	-.71	-.42	.27	.48	.43	-.01	.05	.38	.37
Shagbark hickory—total	.15	.59	-.24	-.72	-.67	.47	.13	-.42	-.36	-.54	.56	.38
Sugar maple—total	.08	.50	-.39	-.52	-.32	.59	.23	.69	.02	.34	.09	.06
Post oak <22.9 cm dbh	.14	-.11	.79	.45	.49				.77		-.40	-.03
Post oak >22.9 cm dbh	.03	.03	-.59	.34	.48				-.46		-.28	-.17
Black hickory—total	.16	-.11	.79	.45	.45				.35		-.39	-.10
Mockernut <22.9 cm dbh	.44	.64	-.24	-.65	-.46	.35	-.72	-.27		-.51	.49	.31
Mockernut >22.9 cm dbh	-.59	.25	.26	-.56	-.31	.39	-.34	.64		-.26	.13	.11
Beech <22.9 cm dbh	.73	-.51	.44	-.19	-.19	.05	.50	-.71		-.71	-.05	-.22
Beech >22.9 cm dbh		-.51	.28	.27	.28	.24	.41	.14		.09	-.50	-.51
Sweetgum <22.9 cm dbh	.30	-.02	.28	.49	.37	-.34	.46	-.39		.50	-.32	.42
Sweetgum >22.9 cm dbh	.73	.41	.40	.48	-.32	-.32		-.09		.46	-.24	.41
Dead trees—total	.29	.49	-.40	.04	-.07	.21	-.17	-.06	-.12	.04	.45	-.26
Total variance (%)	19.5	14.3	19.3	15.3	15.1	20.0	18.2	21.6	14.3	16.1	12.2	10.3
Total of first two	51.9	37.7	48.8	41.1	42.1	40.4	41.1	45.6	39.2	37.8	32.3	48.6

flected in the vegetation of the adjacent slopes is important in the distribution of the birds. A diagram based on the distribution of the principal component scores for the individual plots for each species shows that this interaction between the moist and dry forest situations separates the species quite well (Fig. 1). The Downy Woodpecker, Tufted Titmouse, and White-breasted Nuthatch show an affinity for the dry forest, while the Acadian Flycatcher and Hooded Warbler favor the mesic situation with the Blue-gray Gnatcatcher, Red-eyed Vireo, and Ovenbird in an intermediate position.

In the second principal component, ordering of the species changes and the species are more closely grouped (Fig. 1). The correlations for this component are lower than for the first (Table 3) and smaller secondary tree species have the highest positive correlations, while the larger primary tree species have the highest negative correlations. Although this component is not as well defined as the first one, it does seem to represent relative tree size. The Downy Woodpecker and White-breasted Nuthatch show an affinity for mixed deciduous stands with smaller trees, while the Acadian Flycatcher favors larger trees, primarily the Carolina beeches (Fig. 1). The other species form an intermediate group showing no affinity for either extreme.

Despite showing differences in the habitat niches, PCA offers no information on whether these differences are significant. Using transformed habitat fac-

tors for six species (as described above), multivariate analysis of variance indicated that a significant difference does exist between the habitat niche mean scores ($\alpha = 0.05$, $-\ln \lambda = 78.8$, $P = 0.02$), but step-down analysis indicated that no single habitat factor could account for the difference observed. However, in other studies, several (Posey 1974) or all (James 1971; Whitmore 1975) habitat factors were in themselves enough to characterize the significant differences ($\alpha = 0.05$). Since the differences in habitat niches cannot be explained by any one factor, the species must react to two or more factors collectively, thus lending support to the concept of niche-gestalt.

Individual realized habitat niches

The principal components obtained from the analysis of combined species are dominated by relationships that are exhibited by overall trends across the avian community, habitat characteristics that extend from species to species rather than being confined to a particular avian species. The combined species treatment can show how a community of birds partitioned shared habitat resources. The realized habitat niches for the individual species can be represented by principal components derived from the eight species separately since the analysis will lack this interspecific element.

A comparison between the realized habitat niches of the species explains why no single habitat factor characterized the relationships between the habitat

niches found above in the combined species analysis. An examination of the first principal component for the individual species (Table 2) reveals that, although most species have the same high correlations as the combined species (CS) and combined forest sample correlations (CF), all species have additional high correlations that characterize the individual realized habitat niches. The Downy Woodpecker, Tufted Titmouse, White-breasted Nuthatch, Blue-gray Gnatcatcher, and Red-eyed Vireo share high negative correlations for post oaks, black hickories, and a westerly compass bearing, and high positive correlations for canopy cover and average tree height, but the importance of these habitat factors is different for each species (the significance increasing as the correlations approach ± 1.00). Most of the species share high correlations for southerly compass bearings, percent leaf moisture, and large Carolina beeches. However, high correlations are variable for tree trunk size classes and secondary tree species, again reflecting individual differences in the realized habitat niches and the reaction of the species to the moist to dry forest ordination. The Ovenbird, Hooded Warbler, and Acadian Flycatcher were encountered only in the moist forest as can be told by the absence of post oaks and black hickories (Table 2). They share high positive correlations for large Carolina beeches and high negative correlations for small trees and westerly compass bearings. The Hooded Warbler and Acadian Flycatcher also show a high positive correlation for large trees and a high negative correlation for intermediate size trees, large white oaks, and shagbark hickories. Breckenridge (1956) found Least Flycatchers (*Empidonax minimus*), a close relative of the Acadian Flycatcher, require a closed canopy with an open understory, much like the situation found here for the Acadian Flycatcher, since it shows a contrast between large Carolina beeches and percent canopy cover with almost all other habitat factors. Anderson and Shugart (1974) found the Tufted Titmouse and Blue-gray Gnatcatcher favor an open understory, and the correlations in Table 2 reveal this also.

The important correlations from the second principal component (Table 3) are scattered, with an interaction among the three largest tree trunk size classes existing for all species and secondary tree species also exhibiting some importance. Small Carolina beeches have several high correlations for the White-breasted Nuthatch, Blue-gray Gnatcatcher, and Red-eyed Vireo. Since sampling was conducted only in one watershed, the subtle differences rather than the broad similarities between habitat niches are emphasized, unlike the results of James (1971) and Whitmore (1975) with studies ranging over several habitats.

Distribution along forest moisture gradient

In the previous two sections it has been shown (1) that when habitat niches of forest birds in a watershed

community are analyzed, the forest habitat is partitioned in a way that reflects a cline from dry to moist forest conditions; and (2) that this moisture gradient relationship is not as sharply defined as it could be because there is considerable variation in the realized habitat niches of the various species involved. It is necessary then to eliminate these extraneous elements in isolating the habitat properties and avian responses relating only to the moisture gradient. This can be accomplished by maximizing the differences that exist between the moist and dry forest samples using linear discriminant function analysis (LDFA). The resulting ordination would closely reflect the pure effect of the moisture gradient because the forest habitat samples are strongly biased towards establishing this environmental axis. If this ordination closely matches the one based on the analysis of the actual habitats occupied by the birds (Fig. 1), it can be concluded that this avian community is primarily structured by a moisture gradient. If not, it is assumed that other habitat factors also have a role in determining the community composition and spatial patterns.

In the ordination based on LDFA (Fig. 2), the graduated line at the bottom represents the discriminant axis with the dry forest samples at one extreme ($\bar{x} = -35$) and the moist forest samples at the other ($\bar{x} = 248$). All avian means show a greater tendency towards moist situations than suspected from the ordination based on the avian habitat samples alone (Fig. 1). Several changes in the ordering of the species also are apparent. Most noticeably, the Tufted Titmouse rather than the Downy Woodpecker, exhibits the greatest affinity for the dry situation, and the Hooded Warbler rather than the Acadian Flycatcher shows the greatest affinity for the moist situation. Also, the Red-eyed Vireo is separated from the Blue-gray Gnatcatcher. Each line above the main axis refers to an individual species and each small mark on these lines refers to the score of each sample with the extreme scores numbered. The Tufted Titmouse has the most xeric scores and Red-eyed Vireo also has several xeric scores, showing more affinity for the xeric situation than the Blue-gray Gnatcatcher. The Acadian Flycatcher has one score that is much lower than the others which accounts for its mean being below that of the Hooded Warbler. Note the great dichotomy in the scores with few between 50 and 150. This accounts for the interactions observed between high positive and negative correlations in most of the principal components (Tables 2 and 3) and demonstrates that little, if any, intermediate habitat exists between adjacent slopes in a steep cove. Since the discriminant function maximizes the clinal separation by determining the particular habitat factors that best separate the dry and moist ends of the cline and then stresses those factors in establishing the gradient, the resulting ordination (Fig. 2) is more informative than the principal component ordination (Fig. 1). Since the arrangement of

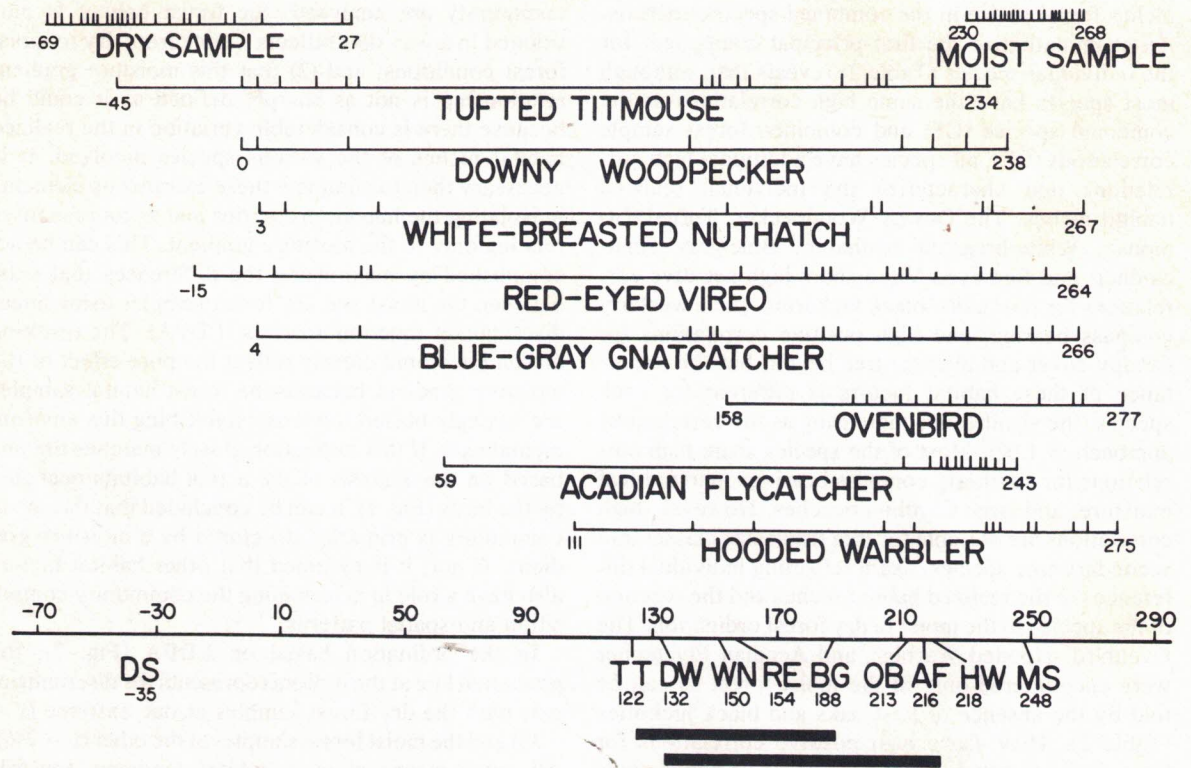


FIG. 2. Ordination of the avian species along the forest moisture gradient determined by the dry and moist forest random samples but having a maximized separation through use of discriminant function. (The short marks are positions of individual samples, the horizontal lines join common samples with extreme values numbered. The bottom line denotes the discriminant axis, the abbreviations show mean positions for bird species and forest samples, and the two heavy bars show common populations from Duncan's multiple range.)

species along this axis is different from the arrangement in the first ordination (Fig. 1), the species are not reacting solely to the actual forest moisture gradient. (This can also be demonstrated by weighting the avian habitat data using directional cosines obtained for PCA of the 60 forest samples [Smith 1975].)

A significant difference between avian mean scores was indicated by one-way analysis of variance, and the two dark lines in Fig. 2 highlight the two groups that differ significantly at the $\alpha = 0.05$ level as indicated by Duncan's multiple range. The first group, composed of the Tufted Titmouse, Downy Woodpecker, White-breasted Nuthatch, Red-eyed Vireo, and Blue-gray Gnatcatcher, utilized both moist and dry situations in the watershed, as can be seen from the sample marks for individual species (Fig. 2). The second group, encompassing all species except the Tufted Titmouse, utilized the moist forest to a greater extent than the dry forest. It would seem that the Tufted Titmouse is able to utilize the dry forest to a greater extent than the other species.

DISCUSSION

Several other workers compared the avifauna of dry and moist forest situations, but most were primarily

interested in avian populations in a wide range of habitats rather than relative habitat utilization between species. Bond (1957) used an index of relative conspicuousness to sample 64 plots in upland forests of southern Wisconsin. The Acadian Flycatcher, Ovenbird, and Red-eyed Vireo were common moist-forest birds, although the Red-eyed Vireo was common throughout the study area. Beals (1960) states that the Red-eyed Vireo is ubiquitous in Wisconsin, with the greatest densities occurring in the moist situations. Bond (1957) further found that the Downy Woodpecker and possibly the Tufted Titmouse were common dry-forest birds, while the White-breasted Nuthatch (leaning towards xeric) and Blue-gray Gnatcatcher were found only in intermediate situations. Shugart and James (1973) likewise encountered the Acadian Flycatcher and the Ovenbird only in the moist forest in their study of ecological succession of breeding bird populations in northwestern Arkansas. The Tufted Titmouse and the Blue-gray Gnatcatcher were found in all forest situations.

In this study, the Ovenbird and Acadian Flycatcher plus the Hooded Warbler were found only in the moist forest (Fig. 2) and can be considered "obligatory" moist-forest species. The Downy Woodpecker, Tufted

Titmouse, and White-breasted Nuthatch appear to show an affinity for the dry-forest situation (Fig. 1), but only the Tufted Titmouse occurs equally in both moist and dry situations (Fig. 2). The Red-eyed Vireo and Blue-gray Gnatcatcher are found in both situations, but more often in the moist forest. Recently Anderson and Shugart (1974) found similar results in their study of the birds of an eastern Tennessee deciduous forest.

Since the ordination based on the position of the species in the watershed (Fig. 1) does not agree precisely with the ordination based strictly on the actual forest moisture gradient (Fig. 2), other factors besides the forest moisture gradient must also be influencing the distribution of the species. For example, when comparing the habitat niches, the Downy Woodpecker occupies the most xeric situation (Fig. 1), but when comparing avian reactions to the actual forest moisture gradient, the Tufted Titmouse occupies the most xeric situation (Fig. 2). Since the position of the birds are different on each ordination, the ordinations must be emphasizing different habitat factors. Many factors have accounted for the differences, such as the Downy Woodpecker not being encountered in large Carolina beeches (Table 1) or the large number of the Tufted Titmouse samples in the dry situation (Fig. 2). This may reflect other important differences like feeding behavior, the Downy Woodpecker being a trunk gleaner and the Tufted Titmouse a branch gleaner.

A comparison of the size of the confidence ellipses (Fig. 1) is useful. Roughgarden (1972) defines niche width as the variety of resources a population exploits, and given a suite of resource axes, such as in a forest moisture gradient, the niche width of each species is the length of the interval on each respective axis. The Downy Woodpecker, Tufted Titmouse, White-breasted Nuthatch, Red-eyed Vireo, and Blue-gray Gnatcatcher have relatively larger niche widths than the Hooded Warbler, Ovenbird, and Acadian Flycatcher (Fig. 1), the former group being permanent residents and early migrants, the latter late-arriving migrants. This smaller niche width coupled with the small range of discriminant scores (Fig. 2) suggests that the Hooded Warbler, Ovenbird, and Acadian Flycatcher have specific requirements along a forest moisture gradient. Likewise, the other species are able to utilize a greater portion of the available habitat, and recent evidence shows that permanent residents (the Downy Woodpecker, Tufted Titmouse, and White-breasted Nuthatch in this study) are able to utilize north slopes in the summer and south slopes in the winter (Shields and Grubb 1974).

The fact that no species occurred primarily in the post oak-black hickory forest is of great interest. James Karr (personal communication) has suggested that possibly less common species occupy the drier south-facing slopes, but my impression is that all other birds of the watershed with the exception of the

Carolina Chickadee (*Parus carolinensis*) are members of the late migrant group and utilize the moist slopes. The Carolina Chickadee probably resembles closely its congener, the Tufted Titmouse, in its habitat use (Anderson and Shugart 1974; Watt 1975). Shugart and James (1973, Fig. 2) found a great decrease in bird density in the xeric forest and state that this uniform habitat attracts few birds throughout the northwestern Arkansas region. Compared to findings in Georgia (Johnson and Odum 1956), they conclude that forest-edge birds in northwestern Arkansas tend to utilize fields more often than in Georgia, having been conditioned by long contact with prairies in Arkansas. Prairies and arid lands were more extensive in recent times than the present-day distribution and extended through most of northwestern Arkansas (Hubbard 1973). Beilmann and Brenner (1951) present convincing arguments that post oak forests are <150 yr old in the Ozark region, although this has been questioned by Steyermark (1959). The depauperate avifauna of the xeric forest may reflect the recent origin of the dry forest. Due to the more open canopy in these forests, the reduced amount of shade may be a critical factor during the hot summer months. Also, I have observed that insects and soil invertebrates seem to be quite reduced in the post oak forests, thus limiting exploitation by many species.

The technique for choosing the extremes of the forest moisture gradient using a priori assumptions worked well in this situation where little intermediate habitat existed. Gauch and Whittaker (1972) have suggested that "the ecologist should use his understanding" to determine the end points of the ecological axes he is interested in. However, many ecological ordination studies deal with such subtleties that the ends of the cline are not evident. For example, Grigal and Ohmann (1975) would have chosen either spruce-fir or pine as one end of their cline if they had relied on previous studies of the upland plant communities in Minnesota. However, using statistical methods to choose the end point, they discovered that, in fact, white cedar (*Thuja occidentalis*) characterized the climax community. In this study where the ends of the cline were purposely selected, several bird plots were "more mesic" than the forest samples supposedly taken in the most mesic situations. To overcome this difficulty, it is necessary to use PCA and/or other statistical procedures which determine the ends of a cline in the absence of a priori information.

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