ORDINATIONS OF HABITAT RELATIONSHIPS AMONG BREEDING BIRDS

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IN an attempt to express habitat relationships in a new way, I have applied two methods of multivariate analysis to a large set of data pertaining to the habitats of 46 species of common breeding birds. The question asked was: How do these species distribute themselves with respect to the structure of the vegetation? This required (1) devising field techniques that would give quantitative measurements of the vegetation within the breeding territories of individual birds, (2) analyzing these by species in order to obtain a sample of the characteristic habitat dimensions of the species niche, (3) reconstructing the relationships among the species according to their relative habitat separation, and (4) considering the ability of the vegetational variables to describe differences among habitats mathematically.

Data were gathered in the spring and summer of 1967 in Arkansas. The vegetation was sampled in 0.1-acre circular plots, using singing male birds as the centers of the circles. The statistical procedures used which were principal component analysis and discriminant function analysis provided a tool for describing bird distribution objectively as ordinations of continuously-varying phenomena along gradients of vegetational structure. The relative positions of the species were located within multidimensional "habitat space." The relationship between this approach and studies involving ordinations of plant and animal communities is discussed.

FIELD METHODS

Estimates of the characteristics of the structure of the vegetation were obtained by means of sampling one 0.1-acre circular plot within the territory of each singing male bird. A 0.1-acre is a large enough area (radius 37 feet) that it should include an adequate sample of the vegetation. It is convenient to have a circular plot with its center at a singing perch selected by a territorial bird. This might give a biased view of habitat for species which occur in open areas and choose singing perches in places very different from their foraging areas, but this objection is minimized in the forest (including most of the species considered here).

The sampling technique was a modification of the range-finder circle method recommended by Lindsey, Barton, and Miles (1958) as a very accurate and efficient procedure. The range-finder itself was found to be unnecessary. Instead, I suspended a brightly colored yardstick at or below the spot where a territorial male bird was singing. This was sighted by holding at armslength a second yardstick having a mark equal to the length of the first when viewed from the perimeter of the circle. This proved to be an accurate and efficient way of determining whether I was within the area to be sampled. A total of 401 0.1-acre circles was measured in the territories of 46 species. No attempt was made to remain within a fairly uniform stand. In fact as many habitat types as

TABLE 1

FIFTEEN VARIABLES OF THE STRUCTURE OF THE VEGETATION CONSIDERED IN THE ANALYSIS OF 0.1-ACRE PLOTS SHOWING THE CORRESPONDING SYMBOLS USED IN TABLES 2 AND 3

1	% GC	Per cent ground cover divided by 10
2	S/4	Number of shrub or tree stems less than 3 inches DBH per two armslength transects (0.02 acres) divided by 4
3	SPT	Number of species of trees
4	% CC	Per cent canopy cover divided by 10
5	CH	Canopy height divided by 10
6	T_{3-6}	Number of trees 3 to 6 inches DBH
7	T_{6-9}	Number of trees 6 to 9 inches DBH
8	T_{9-12}	Number of trees 9 to 12 inches DBH
9	T_{12-15}	Number of trees 12 to 15 inches DBH
10	$T_{>15}$	Number of trees greater than 15 inches DBH
11	CH × S	Canopy height × shrubs (variable 2 × variable 5)
12	CH × T_{3-9}	Canopy height × trees 3 to 9 inches DBH [variable 5 × variables (6 + 7)]
13	CH × $T_{>9}$	Canopy height × trees greater than 9 inches DBH [variable 5 × variables (8 + 9 + 10)]
14	T^2_{3-9}	Number of trees 3 to 9 inches DBH squared [square of variables (6 + 7)]
15	$T^2_{>9}$	Number of trees greater than 9 inches DBH squared [square of variables (8 + 9 + 10)]

possible were sampled. Data were obtained in eighteen different counties in various parts of Arkansas. In the few cases in which two species were singing in the same 0.1-acre circle, data for that circle were used to describe one observation of each of the species. In the subsequent analysis data from the circles were organized by species of bird, regardless of where the data were obtained.

Each tree greater than three inches in diameter at breast height (DBH) within the circle was identified to species and the size class was recorded. The same sighting stick mentioned above was graded on the other side for three-inch size-class estimates of tree diameters. Calibrations on the stick were determined by using the formula $S = \sqrt{(aD^2)/(a + D)}$, where S is the graduation on the stick, a is the armlength of the observer, and D is the diameter at breast height (Forbes, 1955).

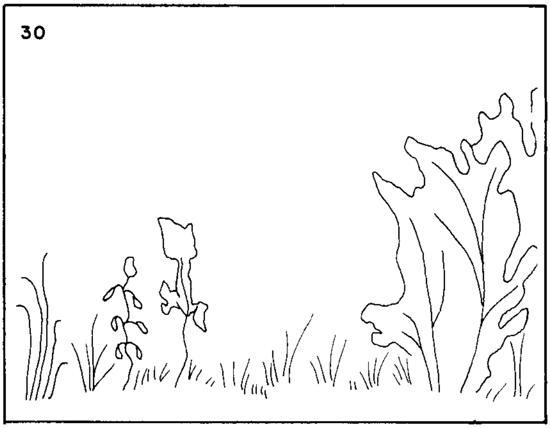
To estimate shrub density, two armlength transects together totalling 0.02 acres were made across the circle and the number of stems intersected that were less than three inches DHB was recorded. An estimate of ground cover was made by taking 20 plus-or-minus readings for the presence or absence of green vegetation sighted through a sighting tube 1.25 inches in diameter held at armslength. An estimate of canopy cover was made by taking 20 plus-or-minus readings for the presence or absence of green leaves sighted directly upwards on alternate steps of a transect of the circle. The average height of the canopy was measured with a clinometer. After some practice a level of efficiency was reached whereby the field data for one 0.1-acre circular plot could be obtained in 15 to 20 minutes of effort. A more detailed description of this sampling technique is given elsewhere (James and Shugart, 1970).

Measurements of 10 vegetational variables were made in each 0.1-acre circle (first 10 items in Table 1). To facilitate handling the data, percentage values for ground cover and canopy cover and the values for canopy height in feet were divided by ten. The number of shrub stems intersected in two transects was divided by four. The last five items in Table 1 are multiples of the first 10. These were used in the discriminant function analysis to determine whether variables were interacting in such a way that their combinations were more highly correlated with the specificity of bird habitats than were the originally measured variables.

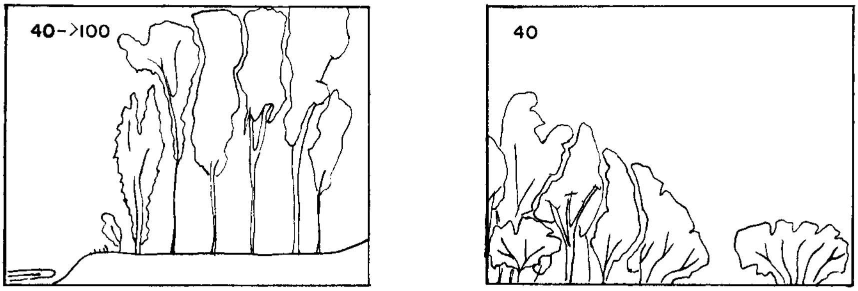
THE NICHE-GESTALT

The assumptions underlying both the field methods and the analysis are somewhat different from those used in other recent studies of avian habitats. In the latter the experimental unit is generally the avian community. Analysis is of study plots large enough to support several coexisting species, and this permits interpretations concerning diversity, resource division, and the relative width of ecological niches (MacArthur and MacArthur, 1961; MacArthur and Pianka, 1966; MacArthur, Recher, and Cody, 1966; MacArthur and Levins, 1967; Cody, 1968; Wiens, 1969; and others). In the present study the advantages of community approach are sacrificed in favor of the opportunity to view habitat relationships among a large number of species occurring in a large geographic area as if each were dependent up a specific life form or configuration of vegetational structure. The experimental unit is the basic life form of the vegetation that characterizes the habitat of each particular species. Measurements from territories are organized by species without regard for which other species occurred nearby. This approach can be defended only if one assumes that predictable relationships exist between the occurrence of a bird and of its characteristic vegetational requirements. I have called this basic configuration of the ecological niche, the *niche-gestalt.*

It is not required that this configuration is directly meaningful to the bird, but this hypothesis could be tested by presenting it with different configurations to see whether it recognizes them as appropriate (see Klopfer, 1963, 1965; Wecker, 1963, 1964; Harris, 1952). Inherent in the term *gestalt* are the concepts that each species has a characteristic perceptual world (the Umwelt of von Uexküll, 1909), that it responds to its perceptual field as an organized whole (the Gestalt principle, see Köhler, 1947), and that it has a predetermined set of specific search images (Tinbergen, 1951). This is



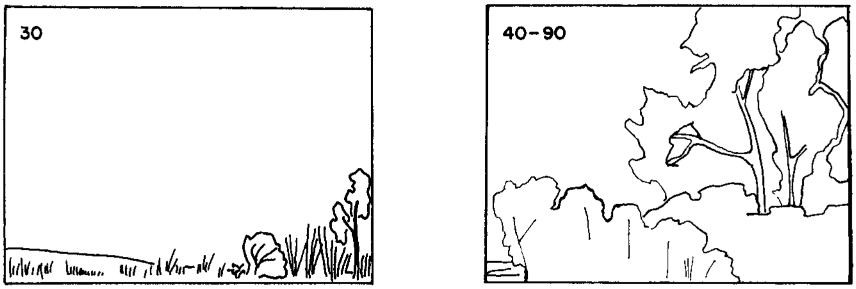
BELL'S VIREO



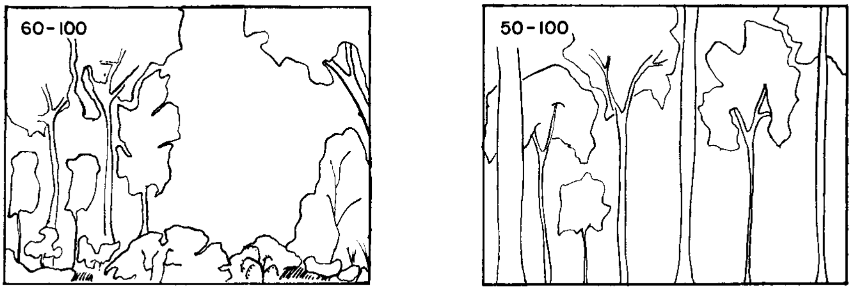
WARBLING VIREO WHITE-EYED VIREO

YELLOW-THROATED VIREO RED-EYED VIREO

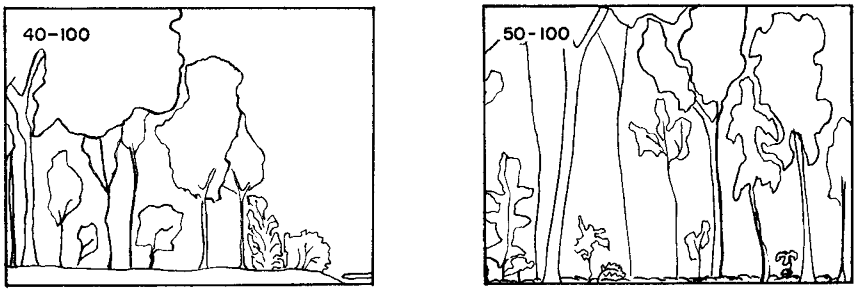
FIG. 1. Outline drawings of the niche-gestalt for five species of vireos, representing the visual configuration of those elements of the structure of the vegetation that were consistently present in the habitat of each. Numbers give the vertical scale in feet.



YELLOWTHROAT REDSTART



HOODED WARBLER BLACK-AND-WHITE WARBLER



PARULA WARBLER OVENBIRD

FIG. 2. Outline drawings of the niche-gestalt for six species of warblers, representing the visual configuration of those elements of the structure of the vegetation that were consistently present in the habitat of each. Numbers give the vertical scale in feet.

FIG. 3. Marsh at the edge of Lake Sequoyah, five miles east of Fayetteville, Washington Co., Ark., where Bell's Vireos and Yellowthroats had breeding territories.

assumed to be at least partially genetically determined, but is surely also modifiable by experience and subject to ecological shift under varying circumstances. Whereas the community approach is sensitive to shifts in habitat due to such factors as competition for resources, the present approach is an attempt to define relationships among birds based upon the basic life forms of the vegetation which each species requires. Since the geographic range of every species is unique and since species are uniquely adapted to utilize certain aspects of their environment, I hope the reader will agree that this approach is justified.

The outline drawings (Figs. 1 and 2) are examples of visual descriptions of the life forms of the vegetation that were consistently present in the habitats of the species in question. These were made by comparing notes and photographs of each 0.1-acre circle where a species occurred and by selecting *only* the features in common. Conversely, if definable niche-gestalt units occur, it should be possible to discover as many of these units as there are pairs of breeding birds in any one place. For example the vegetational configuration in the drawings for the Bell's Vireo (Fig. 1) and the Yellowthroat (Fig. 2) can be identified in a photograph of a place where both occurred (Fig. 3). Likewise the configurations which characterize the habi-

FIG. 4. Vegetation along the Mulberry River, five miles east of Cass, Franklin Co., Ark., where pairs of White-eyed Vireos, Redstarts, and Parula Warblers were nesting.

tats of the White-eyed Vireo (Fig. 1), American Redstart, and Parula Warbler (Fig. 2) can be identified in Figure 4; a territorial male Red-eyed Vireo (Fig. 1), Hooded Warbler, and Ovenbird (Fig. 2) were each present where Figure 5 was photographed.

An attempt will be made to reconstruct relationships between species-specific niche-gestalt units from the quantitative data and to view them in multidimensional "habitat space." Of course this space also contains gradients in types of food, nest-sites, microclimate, etc. Although these variables are undefined in the present study, they would have to be included in a thorough analysis of the ecology of adaptation.

RESULTS

Correlations Among Vegetational Variables.—The vegetational variables are highly interrelated. In the correlation matrix (Table 2) all values of *r* greater than 0.39 are significant at $\alpha = 0.01$ (44 df). The first column, percentage of ground cover, is negatively correlated with all of the other variables. The second column, an estimate of shrub density, has a different pattern of variation from the last eight columns, which are all characteristics of trees. Shrub density varies concordantly with the number of small trees

FIG. 5. Upland mesic forest at Cherry Bend, Franklin Co., Ark., in the Ozark National Forest, where Red-eyed Vireos, Ovenbirds, and Hooded Warblers had breeding territories.

and also with the number of species of trees and canopy cover. But shrub density varies independently of canopy height and trees greater than six inches DBH. Correlations between the number of species of trees per unit area, percentage of canopy cover and canopy height are particularly highly related to each other and to tree density by size classes (last five columns). This means that for a 10 × 46 data matrix of mean values of each vegetational variable for each species (see next section), a large amount of the variation is statistically attributable to these variables. Although there appears to be redundancy in the five interrelated variables for number of trees by size classes (last five items in Table 2), it will be shown in a later section that each contributes significantly to the statistical description of habitat differences among the species of birds.

PRINCIPAL COMPONENT ANALYSIS

Morrison (1967) defines principal components as those linear combinations of the responses which explain progressively smaller portions of the total sample variance. The components can be interpreted geometrically as the variates corresponding to the principal axes of the scatter of observations in space. If a sample of N trivariate observations had the ellipsoidal scatter

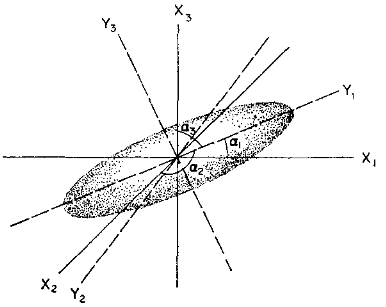


FIG. 6. Principal axes of trivariate observations (redrawn from Morrison, 1967).

plot shown in Figure 6, the swarm of points could be defined as having a major axis Y_1 and less well defined minor axes Y_2 and Y_3. If Y_1 passes through the sample mean point its position can be determined by its orientation with regard to the original response axes (angles a_1, a_2, a_3). The major axis passes through the direction of maximum variance in the points and represents a continuum of the first principal component of the system. The importance and usefulness of the component can be measured by the proportion of the total variance attributable to it. If this proportion is high, then it would be reasonable to express the variation in the data set along a single continuum rather than in N-dimensional space. The second principal component represents that linear combination of the responses that is orthogonal (perpendicular) to the first and has the maximum variance in this direction. The variances of successive components sum to the total variance of the responses. The advantage of the analysis is that it can take

TABLE 2

CORRELATION MATRIX (r) FOR 10 VEGETATIONAL VARIABLES

$N = 46$

	% GC	S/4	SPT	% CC	CH	T_{3-6}	T_{6-9}	T_{9-12}	T_{12-15}	$T_{>15}$
% GC										
S/4	-0.44**									
SPT	-0.67**	0.54**								
% CC	-0.76**	0.55**	0.80**							
CH	-0.51**	0.23	0.72**	0.77**						
T_{3-6}	-0.63**	0.54**	0.92**	0.76**	0.60**					
T_{6-9}	-0.58**	0.25	0.80**	0.79**	0.76**	0.81**				
T_{9-12}	-0.52**	0.06	0.61**	0.61**	0.63**	0.57**	0.77**			
T_{12-15}	-0.59**	0.15	0.69**	0.63**	0.65**	0.61**	0.68**	0.77**		
$T_{>15}$	-0.45**	0.16	0.66**	0.62**	0.81**	0.47**	0.55**	0.43**	0.48**	

** Significant at $\alpha = 0.01$.

TABLE 3
SUMMARY OF THE RESULTS OF THE PRINCIPAL COMPONENT ANALYSIS OF MEAN VALUES OF EACH OF 10 VEGETATIONAL VARIABLES FOR 46 SPECIES OF BREEDING BIRDS

	Component			
	I	II	III	IV
Percentage of total variance accounted for	64.8	12.5	7.7	4.9
Cumulative percentage of total variance accounted for	64.8	77.3	85.0	89.9
Correlations to original variables				
% GC	-0.77	0.21	0.15	0.53
S/4	0.46	-0.83	0.04	0.03
SPT	0.93	-0.16	0.03	0.17
% CC	0.91	-0.17	0.06	-0.12
CH	0.84	0.25	0.35	0.01
T_{3-6}	0.87	-0.25	-0.14	0.29
T_{6-9}	0.89	0.16	-0.12	0.25
T_{9-12}	0.76	0.41	-0.34	0.01
T_{12-15}	0.80	0.30	-0.27	-0.13
$T_{>15}$	0.71	0.22	0.62	-0.07

N-dimensional data and reduce it to a few new variables which account for known amounts of the variation in the original set.

In the present case, the basic ten vegetational variables (first 10 items in Table 1) are used as coordinates of a hypothetical ten-dimensional space. Each of the 46 species of birds has a position in this space according to the mean values of the variables for the 0.1-acre circles measured. This complex situation is analyzed so that a few new variables, the principal components are derived. The principal component analysis is summarized in Table 3.

The first or major component accounts for 64.8 per cent of the total variance and is highly correlated with all of the original variables. All values are positive except percentage of ground cover. The highest correlations are with number of species of trees per 0.1-acre, percentage of canopy cover, number of small trees, and canopy height. Species found where ground cover is high and where there are few shrubs and trees would be expected to have low values of the first component. Species found in mature forests, where ground cover is low and there are many trees of various species and sizes, would be expected to have high values of this component.

The second principal component accounts for an additional 12.5 per cent of the total variance (Table 3). Correlations between it and the original variables show that it represents an inverse interaction between medium-sized trees and shrub density. Species inhabiting dense shrubs would have low values of this component. Species found where there are medium-sized trees and few shrubs would have high values of the second component. The third component accounts for 7.7 per cent of the variance in addition to that already explained. It represents parkland, the presence of large trees with the absence of smaller ones. The fourth component, representing 4.9 per cent of the variance is most closely associated with ground cover. By means of these four newly-computed variables, it has been possible to account for 89.9 per cent of the variation in the original data set. The analysis has derived a parsimonious description of the dependence structure of the multivariate system.

Now it is possible to reconstruct the habitat relationships among these species using the components as coordinates. Figure 7 is a three-dimensional view of the position of each species listed in Table 4 along the axes of the first three principal components. The horizontal axis, representing the first component, has separated the species fairly regularly from open-country birds on the left found in places having high ground cover and few trees (Prairie Warbler, Bell's Vireo, Yellow-breasted Chat, Brown Thrasher) to birds on the right found in well-developed shaded forests (Ovenbird, Red-eyed Vireo, Wood Thrush). In the center along this axis falls a group of species that show remarkable latitude in their choice of habitat (Cardinal, Brown-headed Cowbird, Blue-gray Gnatcatcher). The axis of the second principal component extends backwards from species found in shrubs and low trees (Catbird, White-eyed Vireo, Kentucky Warbler) in the foreground toward species found where there is limited understory (Prothonotary Warbler, Robin, Red-headed Woodpecker). The axis of the third component extends vertically from species not dependent on large trees to those requiring large trees. The highest circles are for the Baltimore Oriole and Hooded Warbler.

Distances between species in Figure 7 represent ecological differences in "habitat space." Consider the positions of the five species of vireos. Their major separation is accomplished along the axis of the first principal component in the order Bell's, Warbling, White-eyed, Yellow-throated, and Red-eyed. This ordering corresponds to increases in the following: number of species of trees per unit area, percentage of canopy cover, number of small trees per unit area, and canopy height (see legend for Fig. 7). Along the axis of the second component (bases of the vertical lines) the same species fall in the order White-eyed, Red-eyed, Bell's, Warbling, and Yellow-throated. This axis is defined as increasing number of medium-sized trees and/or decreasing shrub density. Along the axis of the third component (height of circles) the

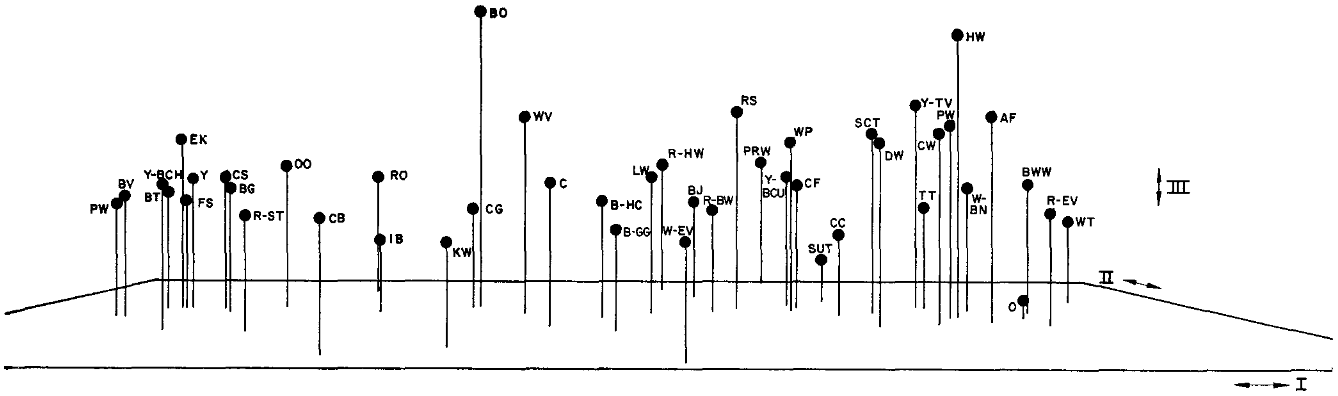


FIG. 7. Three-dimensional ordination of the distribution of 46 species of birds according to the first three principal components of their habitat relationships. The first component, extending from left to right and accounting for 64.8 per cent of the total variance, is highly correlated with all the vegetational variables measured but mainly with increasing number of species of trees, percentage of canopy cover, number of small trees, and canopy height. The second principal component, extending from front to back and accounting for an additional 12.5 per cent of the variance, represents an increasing number of medium-sized trees and/or decreasing shrub density. The third component, extending from low to high and accounting for 7.7 per cent of the variance, represents the presence of large isolated trees. The total variance explained by this ordination is 85 per cent. Symbols for the species are given in Table 4.

TABLE 4

LIST OF SPECIES IN ALPHABETICAL ORDER GIVING SYMBOLS USED IN FIGURES 7 AND 9

AF	Acadian Flycatcher	(*Empidonax virescens*)
BG	Blue Grosbeak	(*Guiraca caerulea*)
B-GG	Blue-gray Gnatcatcher	(*Polioptila caerulea*)
B-HC	Brown-headed Cowbird	(*Molothrus ater*)
BJ	Blue Jay	(*Cyanocitta cristata*)
BO	Baltimore Oriole	(*Icterus galbula*)
BT	Brown Thrasher	(*Toxostoma rufum*)
BV	Bell's Vireo	(*Vireo bellii*)
BWW	Black-and-White Warbler	(*Mniotilta varia*)
C	Cardinal	(*Richmondena cardinalis*)
CB	Catbird	(*Dumetella carolinensis*)
CC	Carolina Chickadee	(*Parus carolinensis*)
CF	Crested Flycatcher	(*Myiarchus crinitus*)
CG	Common Grackle	(*Quiscalus quiscula*)
CS	Chipping Sparrow	(*Spizella passerina*)
CW	Carolina Wren	(*Thryothorus ludovicianus*)
DW	Downy Woodpecker	(*Dendrocopos pubescens*)
EK	Eastern Kingbird	(*Tyrannus tyrannus*)
FS	Field Sparrow	(*Spizella pusilla*)
HW	Hooded Warbler	(*Wilsonia citrina*)
IB	Indigo Bunting	(*Passerina cyanea*)
KW	Kentucky Warbler	(*Oporornis formosus*)
LW	Louisiana Waterthrush	(*Seiurus motacilla*)
O	Ovenbird	(*Seiurus aurocapillus*)
OO	Orchard Oriole	(*Icterus spurius*)
PW	Prairie Warbler	(*Dendroica discolor*)
PAW	Parula Warbler	(*Parula americana*)
PRW	Prothonotary Warbler	(*Protonotaria citrea*)
RS	American Redstart	(*Setophaga ruticilla*)
RO	Robin	(*Turdus migratorius*)
R-BW	Red-bellied Woodpecker	(*Centurus carolinus*)
R-EV	Red-eyed Vireo	(*Vireo olivaceus*)
R-HW	Red-headed Woodpecker	(*Melanerpes erythrocephalus*)
R-ST	Rufous-sided Towhee	(*Pipilo erythrophthalmus*)
SCT	Scarlet Tanager	(*Piranga olivacea*)
SUT	Summer Tanager	(*Piranga rubra*)
TT	Tufted Titmouse	(*Parus bicolor*)
W-BN	White-breasted Nuthatch	(*Sitta carolinensis*)
W-EV	White-eyed Vireo	(*Vireo griseus*)
WP	Eastern Wood Peewee	(*Contopus virens*)
WT	Wood Thrush	(*Hylocichla mustelina*)
WV	Warbling Vireo	(*Vireo gilvus*)
Y	Yellowthroat	(*Geothlypis trichas*)
Y-BCH	Yellow-breasted Chat	(*Icteria virens*)
Y-BCU	Yellow-billed Cuckoo	(*Coccyzus americanus*)
Y-TV	Yellow-throated Vireo	(*Vireo flavifrons*)

TABLE 5

RESULTS OF THE DISCRIMINANT FUNCTION ANALYSIS AND STEP-DOWN PROCEDURE

The computed coefficients (w) for the formula $\overline{D} = \Sigma w_i \bar{x}_i$, and the ranking of the vegetational variables (x) are given in the order of their respective power to separate the species of birds by habitat. Each variable had a significant ability to separate the species in addition to that separation already achieved by all the variables above it on the list.

Rank	Original order of variable	Vegetational variable (x)	Computed weight (w)	*F*-ratio*
1	4	Percentage canopy cover	2.0197	46.05
2	5	Canopy height	1.5305	16.58
3	3	Number of species of trees	0.5807	9.76
4	12	Canopy height × trees 3–9 inches DBH	–0.0954	4.73
5	13	Canopy height × trees larger than 9 inches DBH	0.0803	5.23
6	2	Shrub stems/0.02-acre	0.3091	11.28
7	11	Canopy height × shrubs	–0.0131	6.51
8	6	Trees 3–6 inches DBH	1.1134	5.47
9	1	Percentage ground cover	–0.2861	7.24
10	14	Trees 3–9 inches DBH squared	0.0117	5.01
11	7	Trees 6–9 inches DBH	–0.2592	4.80
12	9	Trees 12–15 inches DBH	2.2260	4.88
13	8	Trees 9–12 inches DBH	2.8539	4.37
14	10	Trees larger than 15 inches DBH	2.9848	5.87
15	15	Trees larger than 9 inches DBH squared	–0.2284	6.39

* All *F*-ratios are significant at $\alpha = .001$.

Warbling and Yellow-throated Vireos have higher positions than the others, indicating that they require the presence of higher trees. These relationships can be checked by considering the drawings in Figure 1 in the order that the species fall along the respective axes. The same procedure can be applied to the six species of warblers for which the niche-gestalt is outlined in Figure 2.

Although the species in Figure 7 are fairly evenly distributed, several appear to be more isolated than the others, and these are birds that are not widely distributed in Arkansas in the breeding season. The Baltimore Oriole occurs in summer only in places having very large trees with clearings below. These are in towns and farmyards in the southern parts of the state and along river banks. Warbling Vireos are confined to cottonwoods (*Populus*) and willows (*Salix*) along major rivers or adjacent to them. Hooded Warblers occur in upland and lowland situations but only in the most mature mesic forests.

I do not want to exaggerate the validity of specific relationships. This analysis is based on mean values of the vegetational variables without regard for their variance. Sample sizes by species are small, and data pertain to a limited area of the breeding range of each. Nevertheless, a complex environmental situation has been reduced to a manageable mathematical and diagrammatic structure.

DISCRIMINANT FUNCTION ANALYSIS AND STEP-DOWN PROCEDURE

The entire data set, values of 15 vegetational variables (Table 1) for 401 tenth-acre circular plots representing the habitats of 46 species of birds was subjected to a type of multivariate technique known as Fisher's classical method of discriminant function analysis (Fisher, 1936, 1938). This procedure computes an equation that is constructed in such a way that it defines a linear axis through the data set which maximizes the differences among populations. The new axis (D) serves as a better discriminant than do any of the variables taken singly (Sokal and Rohlf, 1969). The result is a set of discriminant function coefficients ($w_1, w_2, \ldots, w_p$) for the 15 vegetational variables which maximizes the *F*-ratio of the corresponding univariate one-way analysis of variance applied to a linear combination of the multivariate measurements. The average value of the discriminant function for a species can be expressed as

$$\overline{D} = \Sigma w_i \bar{x}_i$$

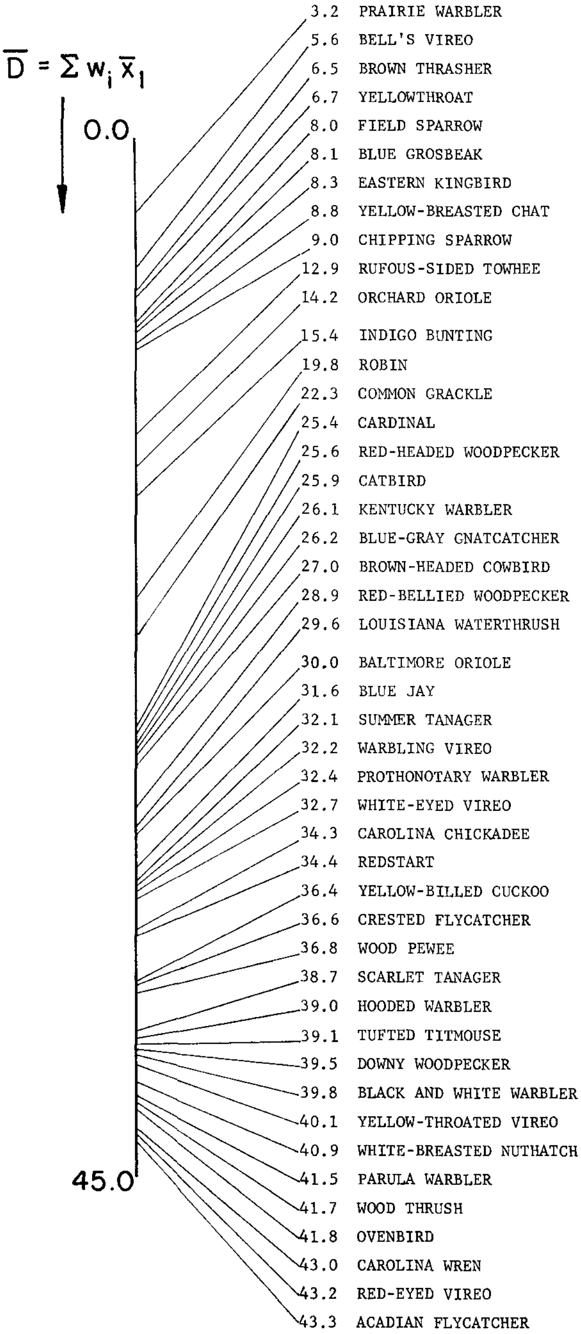
where each $\bar{x}$ is the mean of the observations of that variable for that species. For an individual bird,

$$D = w_1(\%GC) + w_2(S/4) + w_3(SPT) \ldots, w_{15}\,(T_{>9})^2$$

The values w for each vegetational variable are given in Table 5.

This method provides an optimum procedure for separating the habitats mathematically and it permits a linear ordering of the species such that their separation on the discriminant function axis is a function of their differences in habitat. The order should be similar to that along the first principal component except that the species should be more evenly distributed along the discriminant function axis. Whereas the principal component analysis described the relative positions of the species in multidimensional space (each component of which is orthogonal to every other but in which differences are not necessarily maximized) the discriminant function analysis maximizes the distances between species in this space. Figure 8 gives the positions of the species along the discriminant function axis.

Here a 15-dimensional system has been reduced to one dimension, and all the measurements are accounted for simultaneously. The result is a continuum of vegetational structure along which the mean values of D for each species are located. The linear discriminant function is an expression of a con-


$\overline{D} = \Sigma w_i \bar{x}_i$
0.0
45.0
3.2 PRAIRIE WARBLER
5.6 BELL'S VIREO
6.5 BROWN THRASHER
6.7 YELLOWTHROAT
8.0 FIELD SPARROW
8.1 BLUE GROSBEAK
8.3 EASTERN KINGBIRD
8.8 YELLOW-BREASTED CHAT
9.0 CHIPPING SPARROW
12.9 RUFOUS-SIDED TOWHEE
14.2 ORCHARD ORIOLE
15.4 INDIGO BUNTING
19.8 ROBIN
22.3 COMMON GRACKLE
25.4 CARDINAL
25.6 RED-HEADED WOODPECKER
25.9 CATBIRD
26.1 KENTUCKY WARBLER
26.2 BLUE-GRAY GNATCATCHER
27.0 BROWN-HEADED COWBIRD
28.9 RED-BELLIED WOODPECKER
29.6 LOUISIANA WATERTHRUSH
30.0 BALTIMORE ORIOLE
31.6 BLUE JAY
32.1 SUMMER TANAGER
32.2 WARBLING VIREO
32.4 PROTHONOTARY WARBLER
32.7 WHITE-EYED VIREO
34.3 CAROLINA CHICKADEE
34.4 REDSTART
36.4 YELLOW-BILLED CUCKOO
36.6 CRESTED FLYCATCHER
36.8 WOOD PEWEE
38.7 SCARLET TANAGER
39.0 HOODED WARBLER
39.1 TUFTED TITMOUSE
39.5 DOWNY WOODPECKER
39.8 BLACK AND WHITE WARBLER
40.1 YELLOW-THROATED VIREO
40.9 WHITE-BREASTED NUTHATCH
41.5 PARULA WARBLER
41.7 WOOD THRUSH
41.8 OVENBIRD
43.0 CAROLINA WREN
43.2 RED-EYED VIREO
43.3 ACADIAN FLYCATCHER

tinuum from xeric to mesic situations, from upland to bottomland, from low to high biomass, and from open country to forest associations. Each species of bird has a unique mode of environmental response along this continuum.

A two-dimensional separation of the species was achieved by computing the second characteristic root from the same data (third graph in Fig. 9). This gave new coefficients for the vegetational variables and new average values along a second axis for each species. This second ordination (D_2) proceeds from areas having large isolated trees with relatively open understory to areas having the biomass concentrated in the lower strata, i.e. high shrubbiness or a high number of small trees. For example, the Robin requires isolated trees (low value of D_2) whereas the Catbird requires dense low trees or shrubs (high value of D_2).

The power of the method to separate the species of birds is partly determined by the number of variables considered. Examples using 3, 10 and 15 variables (in the order given in Table 5) show the additional separation that is possible as the number of variables increases (Fig. 9). Compare also with Cody (1968).

Once it has been established that discrimination can be accomplished, i.e. that the species of birds can be separated stochastically according to their habitats, Bargmann's extension (1962) can be used to find a minimal set of variables for discrimination. The method requires an a priori ordering of the variables, then proceeds by selecting a subset and testing the hypothesis that the remaining variables give no additional contribution to the discrimination. This step-down procedure provided a list of the vegetational variables in the order of their respective ability to separate the species of birds. The computed *F*-ratios of Table 5 reflect the power of each variable to separate the species in addition to that separation already achieved by all the variables above it on the list.

Surprisingly, every one of the 15 variables considered had a significant ability to separate the species of birds (Table 5). By far the most powerful were the two which would probably be the most conspicuous visually, percentage of canopy cover and canopy height. These were followed by the number of species of trees, a factor closely related to tree-species diversity. Next came two variables which combined canopy height and some aspect of tree density: canopy height times trees three to nine inches DBH, and canopy height times trees greater than nine inches DBH. The next three variables were related to the density of shrubs or small trees: shrub density,

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FIG. 8. Ordination of the habitats of 46 species of birds along a linear discriminant function.

canopy height times shrub density, and trees three to six inches DBH. After ground cover the last six variables, although still highly significant, were probably those that are least conspicuous in the visual configuration of the habitat. They were measurements of tree density by size class.

This does not mean that all 15 variables are required to maximally separate any two species, but only that all are required to separate some species from all of the others. It should also be possible to define other variables that would give additional separation.

DISCUSSION

The value of multivariate methods to analyze sets of dependent variables has been exploited widely in systematics under the name of numerical taxonomy (Sokal and Sneath, 1963). That the methods are equally useful in ecology is suggested by several recent applications to ecological data. Examples include cluster analyses of forests (West, 1966), the characteristics of the life history of beetles (Fujii, 1969), and of climatic variables (Johnston, 1969); principal component analysis of stands of vegetation (Orloci, 1966; Austin, 1968; Swan et al., 1969; and others) and of grain bulk ecosystems (Sinha et al., 1969); discriminant function analysis of habitats of grassland birds (Cody, 1968).

The assumptions underlying the present study are conceptually related to the individualistic concept of distribution described by Gleason (1926) for plant species. This was extended by workers at the University of Wisconsin who developed the continuum concept of plant distribution and devised mathematical procedures for its expression (Curtis and McIntosh, 1951; Bray and Curtis, 1957; Beals, 1960; and others). These studies show that in a series of stands any particular species has distinct conditions for optimum development and that to consider species as organized into discrete communities is to exaggerate the dependence between them.

Bond (1957) demonstrated that the continuum concept has usefulness in analyzing bird distribution. He concluded that "the importance of the life form and physical features of the habitat in the distribution of birds, the occurrence of similar bird species in similar life form situations in different biomes, the indistinctness of boundaries between units, all suggest that the unitary nature of community categories should be questioned." A comparison between the one dimensional ordination in Figure 8 extracted by discriminant function analysis with the position of the same species of birds along the plant continuum described by Bond (ibid.) shows many similarities. Whether the differences are due to the difference between the two methods of analysis, the difference between Wisconsin and Arkansas, or to differences in habitat preferences of the populations is not evident.

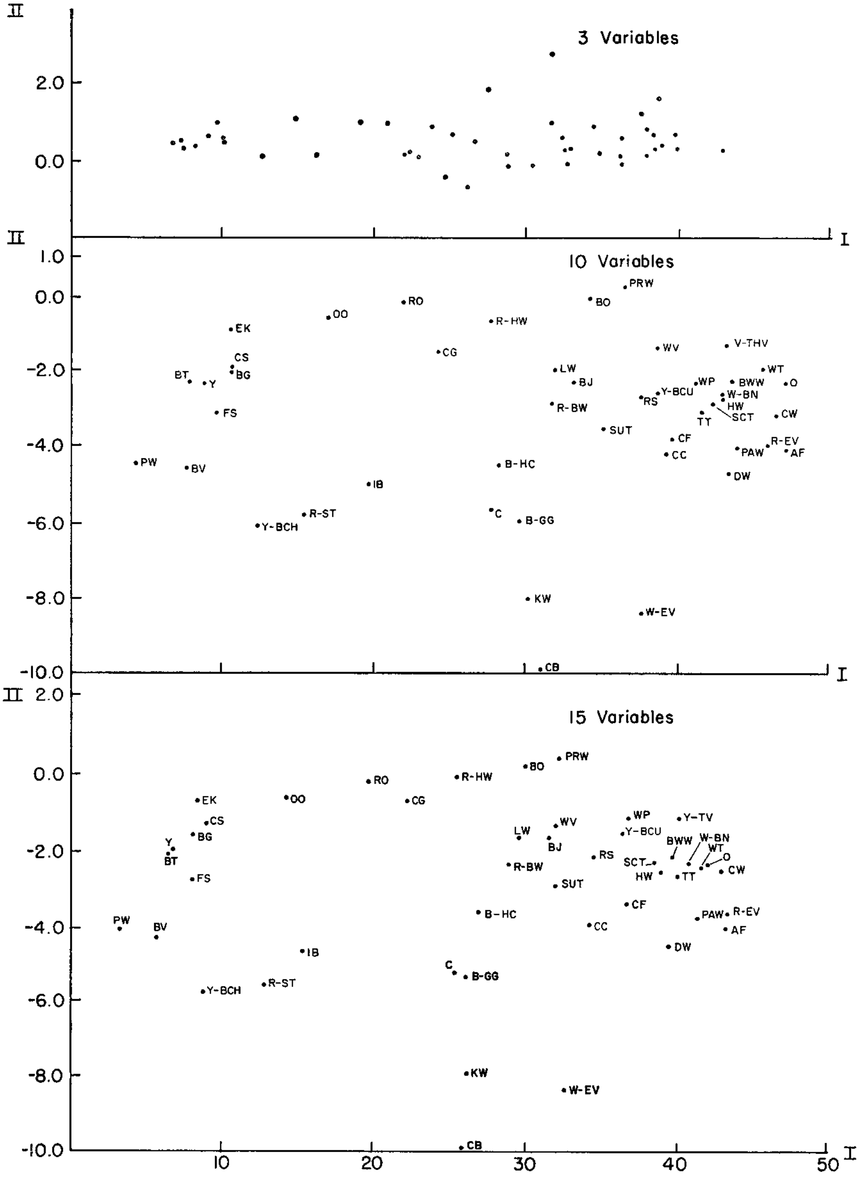

FIG. 9. Two-dimensional ordinations of the habitats of birds representing their positions with respect to the first and second discriminant function axes. Comparisons reveal the additional separation of populations that is possible by consideration of an increasing number of variables. The variables are in the order in which they are listed in Table 5. See sections on Discriminant Function Analysis and Discussion for further explanation.

Beals (1960) extended the application of the continuum concept to bird distribution by constructing a two-dimensional ordination of 24 forest stands based on their avifaunal similarities. He was able to relate this environmental complex to tree species distribution and vegetational structure. Recently the mathematical procedure he used has been criticized on the basis that the method of axis construction is a false estimate of a Euclidean measure of distance, that the axes in multidimensional ordinations are oblique rather than orthogonal (Austin and Orloci, 1966; Orloci, 1966) and that the axes are not objectively selected (Swan et al., 1969). These workers agree that a principal component analysis of a matrix of weighted similarity coefficients between species is not subject to these objections and is the best technique presently available for ordination work.

In the present study the combination of two multivariate methods proved to be more informative than either would have been alone. By considering the species means as individuals and the vegetational variables as attributes, a principal component analysis of the correlation matrix extracted four definable axes which accounted for 90 per cent of the variation in the original data set. A discriminant function analysis of 401 tenth-acre samples representing the habitats of 46 species of birds provided ordinations in which the species were maximally separated according to their habitat relationships. A step-down procedure evaluated the relative power of the 15 vegetational variables to achieve discrimination.

I would like to emphasize the point that the methods used to obtain ordinations are merely objective ways of viewing sets of multivariate data. Their use does not restrict the interpretation of results to the framework of the continuum concept. If the species had appeared as clusters in Figures 7, 8 and 9, one might be justified in interpreting these as belonging to species-groups having similar habitat types. On the other hand, the graphs in Figure 9 reveal the risk involved. The first one, made on the basis of the three most powerful variables for separating the species (canopy cover, canopy height, and number of species of trees per unit area), appears to have clusters of species at each end with a gap in the middle. When additional variables were included in the same program, the cluster on the left disappeared. The open-country birds became spread out along the second axis, but the cluster on the right remained. In other words, the choice and number of variables affect the results to such an extent that caution regarding conclusions is in order.

SUMMARY

Quantitative vegetational data obtained in the breeding territories of 46 species of birds are organized by species as samples of the characteristic life form of the vegetation for each. Examples of outline drawings of the niche-gestalt represent those structural

features of the vegetation that were consistently present where a certain species occurred. Principal components and discriminant functions are used to describe habitat relationships among the species as positions along one-, two- and three-dimensional continua representing gradients in the structure of the vegetation. Although all 15 vegetational variables contributed significantly to the ordinations, the most powerful variables for describing habitat differences were per cent canopy cover, canopy height, and the number of species of trees per unit area. If one considers the vegetation of a geographic area to be a set of continuously-varying phenomena, and if one assumes that bird distribution is at least partly based on species-specific adaptiveness to the resources offered by this heterogeneous structure, then ordination procedures are appropriate methods for its expression.

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