HABITAT ORDINATION OF PASSERINE BIRDS OF THE VIRGIN RIVER VALLEY, SOUTHWESTERN UTAH

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During the past 20 years much attention has been placed on defining habitat preferences of bird species and habitat differences between or among species. Focus has been both on closely related species groups (Sibley 1954, Dilger 1956, MacArthur 1958, Selander 1964) and entire communities (Bond 1957, Beals 1960, Cody 1968, James 1971). The theory that individual animals seek out a certain spot in the environment based on specific search images, early experience, genetic make-up or a combination of these factors is widely discussed in the literature (see Klopfer 1963, 1970). The environmental configuration of the selected sites has been termed the "niche gestalt" by James (1971). It has also been demonstrated, both theoretically and quantitatively in the field, that no two species can occupy the same niche for any prolonged period of time (Gause 1934, Hutchinson 1959, MacArthur 1968, 1970). It is the purpose of this study to determine quantitatively the spatial configuration of a group of passerine birds in their environment through the use of an ordination technique, to determine which habitat variables are most responsible for the separation of the species and to compare these results with those of a similar study (James 1971).

DATA COLLECTION AND METHODS OF ANALYSIS

Data were collected between 1 May and 30 June 1973, in the Virgin River Valley of southwestern Utah. The study area included the Santa Clara Creek from the Shivwits Indian Reservation to its junction with the Virgin River, along the Virgin River to Zion National Park and parts of Ash Creek at its junction with the Virgin River. The area is characterized by stands of dense tamarix (*Tamarix pentandra*), large clumps of mature Fremont cottonwood (*Populus fremontii*) and scattered patches of sand bar willow (*Salix exigua*). Much of the river valley is planted with alfalfa. In isolated marsh areas bull rush (*Scirpus americanus*), cattail (*Typha* sp.) and similar species may be found.

I collected data in a manner similar to that of James and Shugart (1970) using a modification of the range finder circle method. Data were collected from 0.1-acre (0.04-ha) circular plots with a singing territorial male bird as the center of the circle. The biases of this type of sampling are discussed elsewhere (James 1971) and are not considered important here. The variables measured for each plot are listed in Table 1. Percent canopy cover, percent ground cover and percent shrub density were all measured by taking about 20 sightings along transects from the center of the territory to its periphery, a distance of 11.3 m. Trees were divided into five 3 inch (7.62 cm) size classes and were measured directly at breast height using a graduated stick held at arms length. Tree species was also recorded. I measured canopy height using the modified Boy Scout method which uses a mirror held perpendicular to the tree, parallel

TABLE 1

SUMMARY OF THE VARIABLES ENTERED BY THE DISCRIMINANT FUNCTION PROGRAM AND THEIR RESPECTIVE F-VALUES

Step	Variable Entered	F-Value
1	Percent Canopy Cover	53.99
2	Percent Shrub Density	21.82
3	Number of Trees 3–6 inches (7.62–15.24 cm) DBH	19.18
4	Percent Ground Cover	17.86
5	Number of Trees 6–9 inches (15.24–22.86 cm) DBH	6.74
6	Number of Trees > 15 inches (38.1 cm) DBH	7.11
7	Number of Trees 9–12 inches (22.86–30.40 cm) DBH	4.52
8	Canopy Height in feet (meters)	4.14
9	Number of Trees 12–15 inches (30.4–38.1 cm) DBH	3.80
10	Number of Species of Trees	1.92

to the ground. Upon approaching the tree with the hand held mirror outstretched, the point where the crown of the tree first appears is marked and the distance from the point to the tree plus 3 feet (0.91 m) is the estimated height of the tree. A total of 421 samples was taken for 24 species of passerine birds (Table 2).

I subjected the data to stepwise discriminant function analysis, a multivariate statistical technique. Lately multivariate analysis has been used as a tool to analyze the spatial configuration of organisms in the environment and to determine which variables are important in their separation (Cody 1968, James 1971, Green 1971, 1974).

Summarizing the discussion of discriminant function analysis from Sokal and Rohlf (1969) will give the basic ideas behind this statistical tool. Supposing habitat relationships for two different species of birds are desired and several characters, x_1, x_2, $x_3 \ldots$, are measured for each one. Although the means of x_1 for the two species are dissimilar, they may not be sufficiently different to distinguish significantly between the two species. The same is true for the second and third characters and so on. Discriminant function analysis computes a new variable, Z, which is a linear function of the measured variables. The function is of the type

$$Z = a_1x_1 + a_2x_2 + a_3x_3 \ldots$$

which is the equation of a line cutting across the intermixed cluster of points representing the two species. This function is constructed in such a way that as many as possible of the members of one population have high values of Z and as many as possible of the members of the other have low values, so that Z serves as a much better discriminant of the two populations than do each of the measured variables taken separately. The assumptions for the valid use of discriminant analysis are discussed by Green (1971) and are considered to be met in this study. My data were analyzed using the BMD-07M stepwise discriminant analysis computer program (Dixon 1967). The program also computes F statistics between pairs of species based on the variables measured.

RESULTS AND DISCUSSION

The importance of the individual habitat characteristics as predictors of which bird species will occupy a particular environment is summarized in Table 1. This table is based on Bargman's extension of the discriminant analysis program which computes the relative importance of variables in their ability to distinguish between populations. All 10 variables (Table 1) contribute to the separation of the species although the contributions of the first four are considerably greater than the others. The most important variable, percent canopy cover, has been found to be of principal importance in several previous studies (see James 1971) and, therefore, its rank as number one is not surprising. The placement of shrub density as the second most important variable and the number of trees 3–6 inches (7.62–15.24 cm) diameter breast height as the third most important variable is of interest. These characteristics reflect the scattered stands of cottonwoods, separated by dense tamarix and young willows in my study area. Different bird species occur in these two types of habitat within the area and this results in the importance of these two variables as separating devices.

The alfalfa grown on the farms surrounding the rivers also affects the bird species present. Many species which actively defend territories in the riparian community often forage for food in the fields surrounding it. As a result their defended territories are in the periphery of the streamside vegetation and often contain part of the cropland. This causes percent ground cover to be an important variable for species separation.

Two variables of minor importance here, the number of tree species and the canopy height, were of major importance in the study by Frances James (1971). This is, however, not a discrepancy in the study methods nor techniques but a reflection of geographic differences. James worked in the deciduous forest of Arkansas where many species of trees with differing heights are likely to be found in any one sample, whereas my study is essentially restricted to two species of trees, each of similar height. The homogeneity of height in my study area is due, in part, to the extreme intolerance to shade of *Populus fremontii*, making growth of young trees difficult in mature stands. The difference in variable importance between the Utah and Arkansas study areas demonstrates a principle of this particular method of analysis in that the importance of variables is determined by the nature of the environment and should likely change from one area to the next.

Figure 1 presents a linear arrangement or ordination of the bird species along the first discriminant axis. High values on this axis indicate more heavily forested areas whereas low values indicate more open areas with higher ground cover.

TABLE 2

A COMPARISON OF THE JAMES (1971) AND WHITMORE ORDINATIONS ON THE FIRST DISCRIMINANT AXIS[1]

	Arkansas James Ordination		Utah Whitmore Ordination
3.2	Prairie Warbler (*Dendroica discolor*)	1.80	Blue Grosbeak (*Guiraca caerulea*) *
5.6	Bell's Vireo (*Vireo bellii*)	2.20	Indigo Bunting (*Passerina cyanea*) *
6.5	Brown Thrasher (*Toxostoma rufum*)	2.57	Western Kingbird (*Tyrannus verticalis*)
6.7	Yellowthroat (*Geothlypis trichas*) *	2.91	Lazuli Bunting (*Passerina amoena*)
8.0	Field Sparrow (*Spizella pusilla*)	2.97	Red-winged Blackbird (*Agelaius phoeniceus*)
8.1	Blue Grosbeak (*Guiraca caerulea*) *	3.07	Abert's Towhee (*Pipilo aberti*)
8.3	Eastern Kingbird (*Tyrannus tyrannus*)	3.17	House Wren (*Troglodytes aedon*)
8.8	Chat (*Icteria virens*) *	3.28	Willow Flycatcher (*Empidonax traillii*)
9.0	Chipping Sparrow (*Spizella passerina*)	3.54	Ash-throated Flycatcher (*Myiarchus cinerascens*)
12.9	Rufous-sided Towhee (*Pipilo erythrophthalmus*)	3.94	Chat (*Icteria virens*) *
14.2	Orchard Oriole (*Icterus spurius*)	4.34	Song Sparrow (*Melospiza melodia*)
15.4	Indigo Bunting (*Passerina cyanea*)	4.63	Yellowthroat (*Geothlypis trichas*) *
19.8	Robin (*Turdus migratorius*)	4.89	Bewick's Wren (*Thryomanes bewickii*)
22.3	Common Grackle (*Quiscalus quiscula*)	4.91	Bullock's Oriole (*Icterus galbula bullockii*) *
25.4	Cardinal (*Cardinalis cardinalis*)	5.01	Lucy's Warbler (*Vermivora luciae*)
25.6	Red-headed Woodpecker (*Melanerpes erythrocephalus*)	5.20	Blue-gray Gnatcatcher (*Polioptila caerulea*) *
25.9	Catbird (*Dumetella carolinensis*)	5.30	MacGillivray's Warbler (*Oporornis tolmiei*)
26.1	Kentucky Warbler (*Oporornis formosus*)	6.04	Black-headed Grosbeak (*Pheucticus melanocephalus*)
26.2	Blue-gray Gnatcatcher (*Polioptila caerulea*) *	6.79	Lesser Goldfinch (*Spinus psaltria*)
27.0	Brown-headed Cowbird (*Molothrus ater*) *		
28.9	Red-bellied Woodpecker (*Centurus carolinus*)		
29.6	Louisiana Waterthrush (*Seiurus motacilla*)		
30.0	Baltimore Oriole (*Icterus galbula galbula*) *		
31.6	Blue Jay (*Cyanocitta cristata*)		
32.2	Warbling Vireo (*Vireo gilvus*) *		
32.4	Prothonotary Warbler (*Protonotaria citrea*)		
32.7	White-eyed Vireo (*Vireo griseus*)		
34.3	Carolina Chickadee (*Parus carolinensis*)		
34.4	American Redstart (*Setophaga ruticilla*)		
36.4	Yellow-billed Cuckoo (*Coccyzus americanus*)		
36.6	Crested Flycatcher (*Myiarchus crinitus*)		
36.8	Eastern Wood Pewee (*Contopus virens*)		

[1] The scales of the ordinations are not the same due to different transformations of the data but increasing values represent habitats of increasing biomass in both studies. Species marked with an asterisk are found in both ordinations.

TABLE 2 (continued)

Arkansas James Ordination		Utah Whitmore Ordination	
38.7	Scarlet Tanager (*Piranga olivacea*)	7.02	Warbling Vireo (*Vireo gilvus*) *
39.0	Hooded Warbler (*Wilsonia citrina*)	7.30	Brown-headed Cowbird (*Molothrus ater*) *
39.1	Tufted Titmouse (*Parus bicolor*)	7.68	Wilson's Warbler (*Wilsonia pusilla*)
39.5	Downy Woodpecker (*Dendrocopos pubescens*)	9.01	Yellow Warbler (*Dendroica petechia*)
39.8	Black and White Warbler (*Mniotila varia*)	9.57	Audubon's Warbler (*Dendroica coronata auduboni*)
40.1	Yellow-throated Vireo (*Vireo flavifrons*)		
40.9	White-breasted Nuthatch (*Sitta carolinensis*)		
41.5	Parula Warbler (*Parula americana*)		
41.7	Wood Thrush (*Hylocichla mustelina*)		
41.8	Ovenbird (*Seiurus aurocapillus*)		
43.0	Carolina Wren (*Thryothorus ludovicianus*)		
43.2	Red-eyed Vireo (*Vireo olivaceus*)		
43.3	Acadian Flycatcher (*Empidonax virescens*)		

A two-dimensional plot of the first and second discriminant axes is presented in Figure 2. The same generalizations hold true for the first axis here as in Figure 1. The second axis represents variation in shrub density. For example, the Bullock's Oriole lies midway on the first axis indicating moderate values of ground cover, and total number of trees, but it lies at the upper end of the second axis indicating an extremely low shrub density value. At the other extreme the Willow Flycatcher lies in the area of high shrub density on the second axis and in the area of moderate numbers of trees on the first axis.

Interesting comparisons can be made among the eight species of birds ordinated along the first discriminant axis both here and in the study by James (see Figs. 1 and 2 and Table 2). The Indigo Bunting, Blue Grosbeak, Yellow-breasted Chat and Yellowthroat all lie in the lower half of both graphs. James defines low to high values on her axis as going from open country to forest, low biomass to high biomass and xeric to mesic conditions, not unlike those described for my first discriminant axis. There is a difference in order of species between the two ordinations which can be partially explained by the presence of different species in the study areas. For example, the Indigo Bunting is a new species in southwestern Utah and several instances of interspecific competitive interactions have been reported for it with

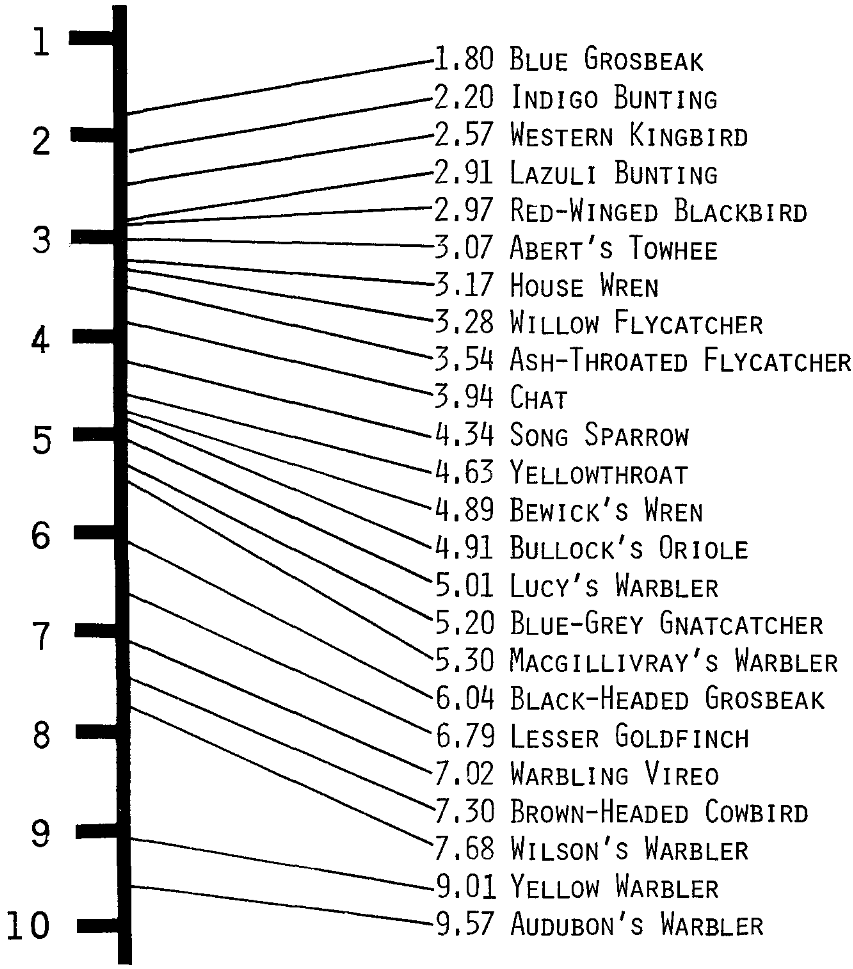

FIG. 1. Ordination of 24 Passerine species along the first discriminant function axis. Low values indicate areas of high ground cover and low canopy cover whereas high values indicate the more densely forested areas. 51.28% of the dispersion is accounted for by this axis.

its congener, the Lazuli Bunting (Whitmore, in press). This probably has an effect on the positioning of the two species along environmental gradients and could show up in a comparison of ordinations in areas of allopatry, such as Arkansas, and sympatry, such as Utah. Further research is currently being carried out in hopes of answering questions such as this.

As in my ordination, the Blue-Gray Gnatcatcher is found near the center

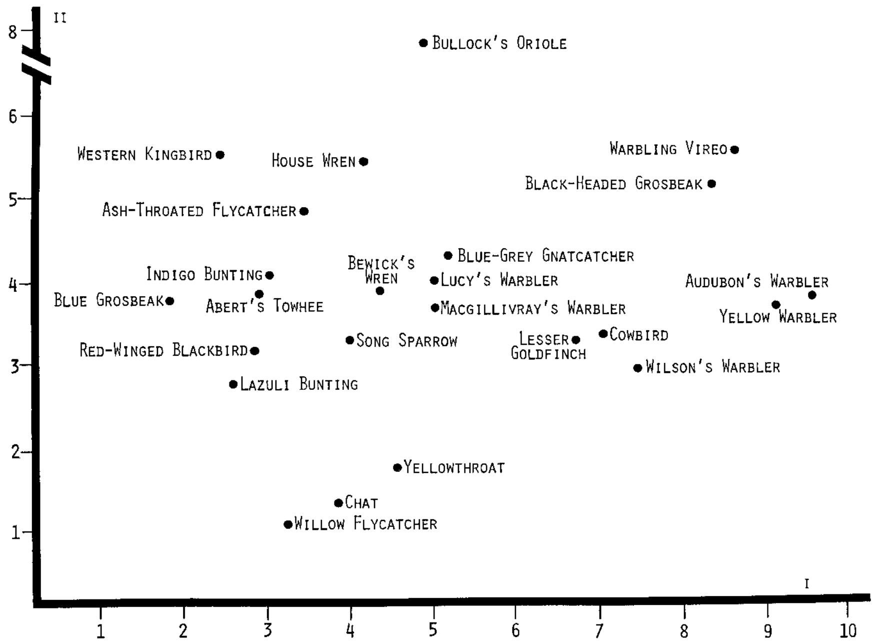

FIG. 2. A two-dimensional ordination using the first (I) and second (II) discriminant function axes. The first or horizontal axis is the same as in Figure 1. High values on the second axis correspond to the presence of large trees whereas low values indicate the absence of large trees. The second axis accounts an additional 18.10% of the dispersion for a total of 69.38% for the figure.

of the James ordination, a condition resulting from the species ability to show remarkable latitude in habitat use (often termed generalism in the literature). This is exemplified by looking at the various measurements obtained for individual birds of this species. For 21 individuals of the Blue-gray Gnatcatcher ground cover ranged from 15–80%, canopy height from 15–51 feet (4.6–15.5 m), canopy cover from 30–80% and shrub density from 10–70%. As a result its final position reflects an average of the extremes and places the bird near the middle of the graph.

In relation to other species present the Warbling Vireo is in an almost identical position on both graphs. In fact, James describes the same habitat as I found them to occur in, streamside cottonwoods (*Populus*) and willows (*Salix*).

I obtained a somewhat higher value for the Brown-headed Cowbird than did James, perhaps because of fewer tree-inhabitating granivorous birds in my study area than hers, resulting in more latitude for the existing species in my area.

Note the position of the kingbirds in the two ordinations. The Eastern Kingbird is very rare in extreme southwestern Utah being replaced by the Western Kingbird. The Western Kingbird is not commonly found in Arkansas. The position of the two in the ordinations is almost identical indicating habitat or ecological replacement as well as geographic replacement. This phenomenon is also apparent in the now conspecific Bullock's and Baltimore orioles. A comparison of the original data in the two studies could be of interest for this species.

As defined by Goodall (1954) and further developed by Bray and Curtis (1957) an ordination is "an arrangement of units in a uni- or multi-dimensional order" as opposed to "a classification in which units are arranged in discrete classes." Whether the units are arranged using discriminant function analysis, principal components, similarity indices, a combination of these, or other techniques matters little if the results can be interpreted ecologically. Beals (1960) constructed an effective ordination using the Bray and Curtis (1957) coefficient of similarity while James (1971) used both principal components and discriminant function analysis. Both studies produced major contributions to the knowledge of avian ecology. Beals (1973) states that the coefficient of similarity ordinations produce results that are "ecologically more easily interpreted." However, ease of interpretation probably lies in familiarity with study sites and birds present, rather than the technique used.

As James (1971) mentions, care should be taken when analyzing the results obtained from ordinations using multivariate analysis since "the choice and number of variables may affect the results." This point is exemplified by examination of Figure 2. It would be a logical assumption that any species lying close to each other on the graph would occur together in nature. This assumption is true for the majority of cases. For example the Yellowthroat, Chat, and Willow Flycatcher are found together both on the graph and in nature. Another set of species commonly found in close association is the Lesser Goldfinch, Brown-Headed Cowbird, Wilson's Warbler, Yellow Warbler and Audubon's Warbler group. The Warbling Vireo and Black-Headed Grosbeak were almost always found together. Some abnormalities do occur in the ordination. Whereas the Indigo Bunting, Abert's Towhee, Bewick's Wren, Song Sparrow and Lazuli Bunting form an associated group in my study area, the Red-Winged Blackbird is seldom found with any of them even though they all have similar positions on the graph. This is brought about in part by the fact that even though the species had similar values of the most important variables, percent canopy cover, percent shrub density, number of trees 3–6 inches (7.6–15.2 cm) DBH and percent ground cover, the method in which percent ground cover data were collected could not distinguish between bare ground and water. Consequently a marsh bird was placed with open shrub species. For ease in comparing my study and that of James the same variables were selected. In my study area other variables that could possibly be of importance include: litter depth, distance from water, the division of shrubs into size classes and others. Whether or not the addition of variables would provide a more effective ordination is unascertainable at this time.

The advantages of this type of analysis include the use of an easily programmable mathematical calculation, graphic results which are ecologically interpretable by a person with only limited knowledge of the technique, ease in comparison with other studies of a similar nature and lastly, according to Green (1971), the observed species diversity can often be explained by the distribution of species on variables which are a small subset of the possible ecological variables.

SUMMARY

A quantitative habitat ordination was carried out on 24 species of passerine birds inhabitating the riparian community of the Virgin River Valley, southwestern Utah. This work was compared to that of a previous study done by Frances James (1971). Many similarities were found between the two studies, including an interesting example of ecological replacements as exemplified by the Eastern and Western Kingbirds. Numerous differences were discussed and possible explanations for their appearance presented.

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