

HABITAT PARTITIONING IN A COMMUNITY OF PASSERINE BIRDS

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Since the concept of the niche was brought into the forefront by G. E. Hutchinson (1957), many ecologists have sought to analyze niche relationships in natural communities. The quest for quantification has led to numerous field studies from which huge quantities of ecological data have been amassed, much of it concerned with birds (e.g. MacArthur 1958, Hespeneide 1971, Willson 1974). One problem in such studies is to visually synthesize relationships from complex data matrices. Several techniques have been developed to address this problem. One such technique is ordination. Briefly stated, 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 (Bray and Curtis 1957). Classically, ordinations have been restricted to plant complexes but ecologically meaningful ordinations can be constructed of animal data as well (e.g. James 1971, Whitmore 1975a).

Additional operational problems are listed by Green (1971): (1) there is a practical limit to the number of environmental parameters which can be measured, and (2) many of the parameters measured are likely to be highly correlated (redundant), and some may be relatively invariate or irrelevant. The use of multivariate statistical analyses, especially those techniques which reduce the number of variables to a more easily visualized set, can help provide answers to these last 2 problems. Combining ordination with multivariate statistics can give insight into all of the above problems (e.g. James 1971, Whitmore 1975a). Once the position of the birds along environmental gradients has been established, generalizations can be made about their relationships with each other and other species.

The purpose of this study was to quantify the relationships of a community of passerine birds in an attempt to ascertain which variables are important in habitat selection, to develop an ordination along environmental gradients, and to determine the range of habitat use.

STUDY AREA AND METHODS

The Virgin River Valley is located in the southwest corner of Utah, northwest corner of Arizona, and southeast tip of Nevada at about 37°N 113°W. Lower Sonoran desert surrounds the valley on 3 sides and the Pine Valley Mountains border on the north. The Valley is an isolated oasis from the rather harsh surrounding environment and the density of birds in it is quite high. I collected data in the streamside vegetation along Santa Clara Creek to the Virgin River and along the Virgin River to Zion National Park. The area is characterized by stands of mature Fremont cottonwood (*Populus fremontii*), large

clumps of tamarix (*Tamarix pentandra*), and isolated patches of sand bar willow (*Salix exigua*). Much of the river valley is heavily planted with alfalfa (*Medicago sativa*) and numerous species of fruit, nut, and ornamental trees. The rivers and streams of the area usually flow year round, though excessive removal of water for irrigation or unusually low rainfall will sometimes cause drought in August and September.

Avifaunal investigations in the valley have been primarily restricted to species accounts, most notable those of Behle (1943), Wauer and Russel (1967), and Wauer (1969). Much collecting, under the direction of W. H. Behle, has been done in the valley and surrounding areas.

Vegetational data were collected between 1 May and 30 June 1973 using a modification of the range finder circle method described by James and Shugart (1970). I measured 10 vegetational variables in a 0.04 ha circular plot around each singing, territorial male bird encountered while walking along the river. Habitats for 421 individuals of 24 species of passerine birds were measured. Table 1 lists the passerine species I encountered.

In order to determine which variables were important in species' separation, the data were subjected to stepwise discriminant analysis (Dixon 1970), a multivariate statistical technique. The underlying theory for the use of the discriminant function in ecology is discussed elsewhere (Green 1971, 1974, James 1971, Whitmore 1975a) and will not be considered here. The stepwise adaptation of the discriminant analysis allows for insertion of each variable in a stepwise manner based on its ability to achieve discrimination between species. The order of insertion determines the order of importance in group separation.

When dealing with an n-dimensional data matrix, interpretations may be more meaningful if the number of axes can be reduced to a number which can be easily visualized. Principal component analysis (PCA) can be used to accomplish such a task. PCA produces linear combinations of the original variables in such a manner as to explain progressively smaller portions of the total variance in the data. This total variance is the sum of the variances for each of the variables. The first axis is constructed so that linear combination of variables represents the greatest amount of response variance. The second axis, which is orthogonal to the first, represents the second greatest amount of variance. The third represents the third greatest amount and so on. The sum of the variance of components is the total variance. The data were subjected to PCA in order to produce an ordination along vegetational gradients.

Vegetational resource use was calculated by dividing each of the measured variables into discrete units. For example, canopy cover was divided into 10, 10% classes and the number of individuals in each species present in each class was determined. After the development of resource matrices for each of the 4 most important variables as determined by stepwise discriminant analysis, I calculated vegetational resource use values using the procedures described by Colwell and Futuyma (1971) for expanded matrices.

RESULTS

Discriminant analysis.—Results of the stepwise discriminant analysis have been presented elsewhere (Whitmore 1975a).

Prior to calculating the discriminant functions the stepwise discriminant analysis program performs a multivariate analysis of variance (MANOVA) among the species based on the measured variables. The advantage of such an analysis is that it not only accounts for the variate but also the covariate

TABLE 1

LIST OF PASSERINE SPECIES ENCOUNTERED IN THE VIRGIN RIVER VALLEY FROM 1 MAY TO 30 JUNE 1973 GIVING SYMBOLS USED IN FUTURE TABLES AND FIGURES

| | | |
|-----|-------------------------|--|
| WK | Western Kingbird | (<i>Tyrannus verticalis</i>) |
| AF | Ash-throated Flycatcher | (<i>Myiarchus cinerascens</i>) |
| * | Black Phoebe | (<i>Sayornis nigricans</i>) |
| WF | Willow Flycatcher | (<i>Empidonax traillii</i>) |
| * | Western Flycatcher | (<i>Empidonax difficilis</i>) |
| * | Western Wood Pewee | (<i>Contopus sordidulus</i>) |
| HW | House Wren | (<i>Troglodytes aedon</i>) |
| BW | Bewick's Wren | (<i>Thryomanes bewickii</i>) |
| * | Rock Wren | (<i>Salpinctes obsoletus</i>) |
| BGN | Blue-gray Gnatcatcher | (<i>Poliotilta caerulea</i>) |
| * | Phainopepla | (<i>Phainopepla nitens</i>) |
| WV | Warbling Vireo | (<i>Vireo gilvus</i>) |
| * | Orange-crowned Warbler | (<i>Vermivora celata</i>) |
| LW | Lucy's Warbler | (<i>Vermivora luciae</i>) |
| YW | Yellow Warbler | (<i>Dendroica petechia</i>) |
| AW | Audubon's Warbler | (<i>Dendroica coronata auduboni</i>) |
| YT | Common Yellowthroat | (<i>Geothlypis trichas</i>) |
| YBC | Yellow-breasted Chat | (<i>Icteria virens</i>) |
| MW | MacGillivray's Warbler | (<i>Oporornis tolmiei</i>) |
| WW | Wilson's Warbler | (<i>Wilsonia pusilla</i>) |
| * | Yellow-headed Blackbird | (<i>Xanthocephalus xanthocephalus</i>) |
| RWB | Red-winged Blackbird | (<i>Agelaius phoeniceus</i>) |
| BHC | Brown-headed Cowbird | (<i>Molothrus ater</i>) |
| * | Hooded Oriole | (<i>Icterus cucullatus</i>) |
| BO | Bullock's Oriole | (<i>Icterus galbula bullockii</i>) |
| * | Summer Tanager | (<i>Piranga rubra</i>) |
| BHG | Black-headed Grosbeak | (<i>Pheucticus melanocephalus</i>) |
| BG | Blue Grosbeak | (<i>Guiraca caerulea</i>) |
| IB | Indigo Bunting | (<i>Passerina cyanea</i>) |
| LB | Lazuli Bunting | (<i>Passerina amoena</i>) |
| * | House Finch | (<i>Carpodacus mexicanus</i>) |
| LG | Lesser Goldfinch | (<i>Spinus psaltria</i>) |
| * | Rufous-sided Towhee | (<i>Pipilo erythrophthalmus</i>) |
| AT | Abert's Towhee | (<i>Pipilo aberti</i>) |
| SS | Song Sparrow | (<i>Melospiza melodia</i>) |

* Not included in analyses since the sample was less than 5.

relationships among habitat variables (Anderson and Shugart 1974). The regular assumptions required for statistical tests are needed here and are considered to be met based on the multivariate central limit theorem (Morrison 1967). A total of 276 species comparisons can be made from 24 different species; of these all but 4 were significantly different ($p < .01$). These 4

TABLE 2
CORRELATION MATRIX (r) FOR 10 VEGETATIONAL VARIABLES $N = 24$

| | SPT ¹ | T-7 | T-15 | T-22 | T-30 | T-38 | % SD | % CC | CHM |
|------|------------------|-------|-------|-------|--------|-------|-------|--------|-------|
| SPT | | | | | | | | | |
| T-7 | 0.65* | | | | | | | | |
| T-15 | 0.74* | 0.83* | | | | | | | |
| T-22 | 0.78* | 0.85* | 0.90* | | | | | | |
| T-30 | 0.69* | 0.40* | 0.59* | 0.68* | | | | | |
| T-38 | 0.63* | 0.21 | 0.34* | 0.47* | 0.83* | | | | |
| % SD | -0.09 | 0.28 | 0.01 | 0.01 | -0.22 | -0.30 | | | |
| % CC | 0.78* | 0.64* | 0.62* | 0.66* | 0.61* | 0.60* | -0.10 | | |
| CHM | 0.85* | 0.39* | 0.44* | 0.55 | 0.66* | 0.74* | -0.29 | -0.81* | |
| % GC | -0.32 | -0.18 | -0.30 | -0.25 | -0.39* | -0.33 | -0.28 | -0.17 | -0.20 |

¹ See key to abbreviations of variables in Table 3.

* Significant at $p < 0.05$.

will be discussed later. It is remarkable that 10 measured variables can separate 272 of the possible 276 species pairs, especially since the environment is restricted and low in plant diversity. Whitmore (1975a) presented a 2-dimensional ordination along the first 2 discriminant function axes and compared those results with those of James (1971).

Principal component analysis.—Since PCA is usually based on a correlation matrix, it is of value to examine the correlations among the vegetational variables. As can be seen in Table 2 many of the variables are highly correlated. Values greater than 0.34 are significant ($p < .05$). James (1971) found many similar vegetational correlations in a study in Arkansas. Percent ground cover is negatively correlated with all other variables. This corresponds to going from the high biomass forested areas, cottonwood and tamarix stands, to the low biomass open areas, alfalfa and open field. The highest correlations are found among the 3 classes of middle and small sized trees, possibly corresponding to the isolated willow and tamarix stands. The 2 classes of large trees are positively correlated due to the presence of several sizes of large cottonwoods. Canopy cover and canopy height are also positively correlated. Other positive correlations occur between the number of species of trees and the number of trees in each of the size classes. Thus, tree species number per unit area is positively correlated with vegetational diversity. Shrub density is not strongly correlated with any of the other variables, indicating rather uniform distribution throughout the study area. It is, however, correlated positively with small trees, again corresponding to the clumps of willow and tamarix, and correlated negatively with the large tree variables and ground cover.

TABLE 3
SUMMARY OF THE RESULTS OF THE PRINCIPAL COMPONENT ANALYSIS OF EACH OF 10
VEGETATIONAL VARIABLES FOR 24 SPECIES OF PASSERINE BIRDS

| | Correlations With Original Variables Component | |
|--|---|-------|
| | I | II |
| Number of Species of Trees (SPT) ¹ | -0.65 | -0.14 |
| Number of Trees 7.6-15.2 cm DBH (T-7) | -0.54 | 0.42 |
| Number of Trees 15.2-22.9 cm DBH (T-15) | -0.65 | 0.23 |
| Number of Trees 22.9-30.4 cm DBH (T-22) | -0.71 | 0.10 |
| Number of Trees 30.4-38.1 cm DBH (T-30) | -0.64 | -0.36 |
| Number of Trees > 38.1 cm DBH (T-38) | -0.53 | -0.58 |
| Percent Shrub Density (% SD) | 0.01 | 0.74 |
| Percent Canopy Cover (% CC) | -0.49 | -0.22 |
| Canopy Height in Meters (CHM) | -0.43 | -0.48 |
| Percent Ground Cover (% GC) | 0.75 | -0.16 |
| Percentage of Total Variance Accounted for | 56.56 | 16.87 |
| Cumulative Percentage of Total Variance Accounted for | 56.56 | 73.43 |

¹ Abbreviations for variables used in Tables 2 and 4.

The results of the PCA are summarized in Table 3. The first component accounts for 56.6% of the variance in the original data. Percent ground cover shows a high positive correlation with the first axis. Species of birds having high values on this axis occur where there is high ground cover. The first axis also shows negative correlations with the measured variables for trees. Therefore, this axis represents a gradient starting with the forested areas with low ground cover and proceeding to open areas with high ground cover, i.e. going from cottonwood stands to alfalfa fields. The second axis, which accounts for an additional 16.9% of the variance, is correlated positively with shrub density and small trees and negatively with large trees and canopy height. This corresponds to a gradient going from areas of tall trees, if trees are present at all, with low shrub density to areas of high shrub density and no large trees. A 2-dimensional plot is presented in Fig. 1.

Species in the lower left of this ordination, e.g. Bullock's Oriole, Yellow Warbler, Audubon's Warbler, and Black-headed Grosbeak, are those associated with high canopy cover and many trees. Ground cover and shrub density are low in this area of the ordination. A species such as the Warbling Vireo would be expected to be found in areas with the same amount of canopy cover and ground cover as the Bullock's Oriole, but with increased shrub density. A group of 5 species; Yellow-breasted Chat, Red-winged Blackbird,

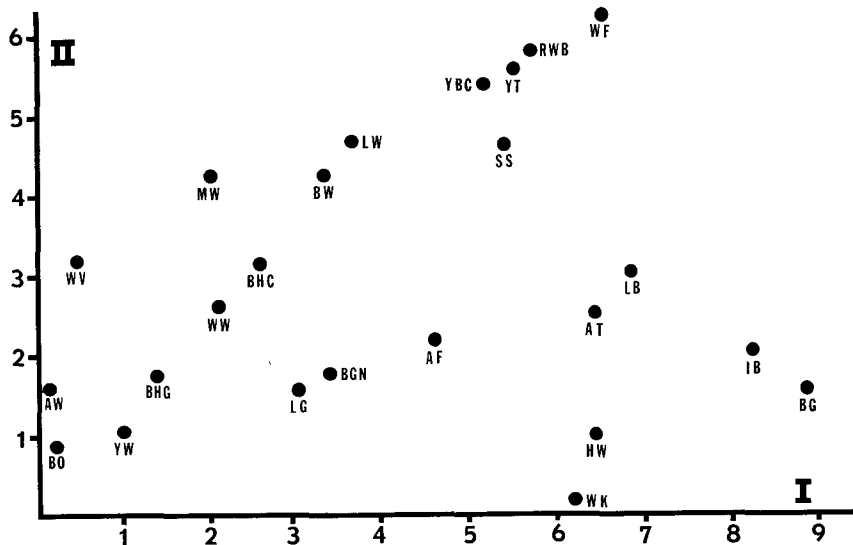


FIG. 1. Two-dimensional ordination of bird species along the first and second principal component axes. The first, horizontal, axis accounts for 56.6% of the response variance and second, vertical, axis accounts for an additional 16.9%. Increasing values on the first axis correspond to an increase in ground cover and a decrease in the numbers of trees. Increasing values on the second axis represent an increase in shrub density. Species' names are abbreviated as in Table 1.

Yellowthroat, Song Sparrow, and Willow Flycatcher, is located on the upper end of both axes. These are high shrub density species with little canopy cover and moderate ground cover in their territories. Six species cluster in the lower right corner of Fig. 1. These species are found in either open country or the alfalfa fields as evidenced by their positions on axis I. If these 6 species are considered a separate habitat guild, then a regression line ($r = .77$) can be drawn through the remaining 18. This line can be viewed as a third gradient and corresponds to going from densely forested areas with low ground cover (lower left), to dense shrub areas with moderate ground cover (upper middle). Therefore, 3 separate gradients are apparent on this 2-dimensional ordination, thus increasing its value.

In this study the addition of a third PCA axis adds little new information in that only 11.2% more variance is accounted for and there are no strong correlations with the original variables. The 4 most important variables, as determined by the stepwise discriminant program, are all accounted for by the first and second principal component axes. Therefore, discussion of

TABLE 4
SPECIES HABITAT USE VALUES OF THE 4 MOST IMPORTANT VARIABLES¹

| Species | % CC ² | % SD | T-7 | % GC |
|-----------------|-------------------|------|------|------|
| BO ³ | .208 | .511 | .274 | .563 |
| WK | .383 | .376 | .256 | .393 |
| AF | .513 | .344 | .303 | .464 |
| BHC | .328 | .678 | .626 | .403 |
| LB | .399 | .310 | .256 | .457 |
| BC | .245 | .288 | .276 | .356 |
| YW | .342 | .255 | .332 | .310 |
| AW | .263 | .300 | .379 | .362 |
| WW | .193 | .440 | .430 | .560 |
| IB | .317 | .376 | .274 | .390 |
| YT | .201 | .385 | .428 | .399 |
| YBC | .437 | .546 | .358 | .378 |
| MW | .351 | .356 | .364 | .325 |
| LW | .253 | .413 | .422 | .379 |
| AT | .416 | .443 | .327 | .361 |
| BHC | .372 | .658 | .463 | .257 |
| GHN | .378 | .593 | .497 | .605 |
| RWB | .392 | .365 | .309 | .354 |
| HW | .410 | .341 | .309 | .331 |
| BW | .408 | .667 | .523 | .475 |
| WF | .179 | .271 | .311 | .334 |
| LG | .391 | .219 | .435 | .309 |
| WV | .393 | .310 | .470 | .436 |
| SS | .362 | .223 | .435 | .285 |

¹ Calculated by formulae in Colwell and Futuyma (1971).

² See key to abbreviations of variables in Table 3.

³ See key to abbreviations of species' names in Table 1.

species' distributions along gradients constructed using PCA will be confined to the first 2 axes.

Habitat resource use.—Values for resource matrices constructed from the 4 most important variables are found in Table 4. Most of these values are less than 0.5, indicating that the species are restricted in habitat use. Those species that show consistently low values and with a low mean value for the 4 resource use determinations, may be termed habitat specialists. Included in this designation are the Blue Grosbeak, Yellow Warbler, Willow Flycatcher, Lesser Goldfinch, and Song Sparrow. Species with high resource use values, are relative habitat generalists. They include the Black-headed Grosbeak, Yellow-breasted Chat, Brown-headed Cowbird, Blue-gray Gnatcatcher, and Bewick's Wren. Some species, e.g. Bullock's Oriole, Lazuli Bunting, and Wilson's Warbler, are high in 1 variable and low in others.

DISCUSSION

Certain aspects of the ecological distribution of species in the Utah study area lend themselves to comparisons with previously published data. For this reason the following species or groups of species will be examined in more detail.

Indigo Bunting and Blue Grosbeak.—One of the 4 species' pairs that were found to be not significantly different by the MANOVA was the Indigo Bunting and the Blue Grosbeak. In a table presented by Shugart and James (1973) only moderate overlap between these species was recorded, the Blue Grosbeak being found solely in clonal persimmon field plots while the Indigo Bunting was scattered throughout several habitat types, most notably forest edges. Stewart and Kantrud (1972) found the Blue Grosbeak in the Coteau Slope of North Dakota while the Indigo Bunting was found in the Coteau Slope and Northeastern Drift Plain. In 2 types of ordinations, James (1971) found moderate separation between the species. Using the same techniques, discriminant analysis and principal component analysis, I found little separation between the species. In my study the Blue Grosbeak was one of the most restricted in habitat use (Table 4). Therefore, in the Virgin River study area their habitat use was almost indistinguishable. Even though species specific habitat differences were not detected it is reasonable to assume that the 2 might take different sized food items, based on bill size alone. In other southwestern studies (Dixon 1959, Raitt and Maze 1968, Austin 1970, Carothers et al. 1974) Indigo Buntings were not observed. Whitmore (1975b) suggests that the Indigo Bunting is new in Utah, coming from the southeast approximately 30 to 40 years ago. Perhaps as a result of interspecific competition with its congener, the Lazuli Bunting, it may be forced into a suboptimal habitat, therefore causing overlap with the Blue Grosbeak.

Bewick's Wren and Song Sparrow.—Although these species seem to require river lowlands with dense vegetation and cover (Behle 1943), as in the previous pair of species, effective partitioning may be carried out by means of different food preferences and feeding behavior. Two other pairs of birds indistinguishable in habitat preference, House Wren and Western Kingbird, and Abert's Towhee and Ash-throated Flycatcher, also differ behaviorally and in food selection.

House Wren and Bewick's Wren.—Inasmuch as Kroodsma (1973) recorded instances of competition between the House and Bewick's wrens in Oregon one might expect similar activity in the Virgin River Valley. I observed 16 House and 20 Bewick's wren territories in my study area and recorded no instances of interspecific territoriality. Behle (1943) states that the House Wren only winters in the lowlands while breeding in the mountains in Utah. This is not consistent with my observations nor those of Wauer and Carter

(1965) who stated that there are several records of the House Wren in the riparian woodland during the breeding season. Habitat use was, however, similar to that reported by Kroodsma (1973) in that the Bewick's Wren was confined to the dense thickets and House Wren occurred where shrub density decreased and grassy substrate increased. This latter point can be noted also by the positions of the species in Fig. 1. As noted in Table 4, the Bewick's Wren has one of the broadest habitat ranges of all the species measured and therefore species' overlap with it is to be expected.

Parulidae.—All 7 species of the family Parulidae observed in the Virgin River Valley fall on or very close to the regression line drawn through the 2-dimensional principal component ordination. With the exception of the chat and yellowthroat, 2 species of different size, the species seem to be evenly distributed along the gradient going from the forested areas to dense shrub zones. Warblers are not found on the gradient going to the open country. A species that Cody (1974) found to be a generalist, the Yellow Warbler, is found here to be one of the most restricted species. This could be due to the high number of warbler species in such a restricted habitat. Carothers et al. (1974) found only 3 warbler species in their study in the riparian habitat of Arizona. As evidenced by the uniform distribution of warblers along the forest-shrub gradient one might think that competition is severe. The presence of large numbers of Audubon's Warblers, the closest warbler on the ordination, could exert a competitive influence on the Yellow Warbler, but I have no direct evidence that they are affecting one another. Behle (1943) and Wauer and Carter (1965) stated that the Audubon's Warbler is an abundant migrant through the Virgin River Valley during April and May but breeds only in the conifers found at higher elevations. I observed them actively countersinging and defending territories through June. Therefore, even if these birds are non-breeding in the area, they probably affect community structure. I do not know if Audubon's Warblers ever left during the breeding season and if they did leave the effect of competitive release on the other warbler species. One explanation for the appearance of many Audubon's Warblers late in the season is that the severe winter of 1972-1973 could have delayed northward migration.

The 2 warblers most closely associated in habitat use are the Common Yellowthroat and Yellow-breasted Chat. As noted from their positions on the ordination, these species inhabit areas of dense shrubs. Both species are rather broad in their habitat use (Cody 1974; Table 4) but differ in body size and foraging behavior. The chat, the larger, feeds primarily by gleaning insects from the foliage of shrubs whereas the yellowthroat often hawks insects from exposed perches or flies to the ground to pick prey out of the grass. In spite

of the closeness of the 7 warbler species in habitat use, I observed few instances of interspecific aggression.

Brown-headed Cowbird.—With the exception of the Ash-throated Flycatcher all of the 24 passerine species analyzed in this paper are known hosts of the Brown-headed Cowbird (Friedmann 1963, 1971). Since the Ash-throated's eastern congener, the Great-crested Flycatcher (*Myiarchus crinitis*) is a known host, I assume that the Ash-throated Flycatcher is also parasitized. To be effective at nest parasitism it should be advantageous for the cowbird to be broad in its range of habitat choices, thus allowing it better access to more nests. Examination of Fig. 1 shows that the Brown-headed Cowbird is centrally located in the ordination and almost equidistant from the ends of the regression gradient. Its mean habitat use value of .438 is one of the highest, indicating broad use of the 4 variables tested. James (1971) states that the Brown-headed Cowbird shows remarkable latitude in habitat use. One might conclude, therefore, that the cowbird, in order to take advantage of as many hosts as possible, is not as restricted as other species in habitat use.

Willow Flycatcher.—Of all of the species in this analysis, the Willow Flycatcher has the lowest habitat use value. This species is confined to areas of shrub density ranging from 70% to 100%. Trees of any size or species seldom occur in its defended territories. Behle (1943) listed this species as a common breeder in the streamside willows throughout the valley and cited numerous specimens collected along the Virgin River and Santa Clara Creek (including 6 collected from one site 3 km southwest of St. George, Utah). This species is now uncommon to rare. A possible explanation for this is habitat change. Christensen (1962) documented the introduction and spread of the shrub tamarix (*Tamarix pentandra*) in Utah. This colonization has taken place at the expense of the willows. The stands of streamside willow discussed by Behle are almost totally gone. In fact, one is hard pressed to find any substantial willow stands along the Santa Clara Creek. Probably tamarix does not provide a suitable nest site for the Willow Flycatcher and as a result the bird has been forced to go elsewhere. Possible evidence for this exists in that Wauer and Carter (1965) observed the species in the remaining willows at the Springdale Ponds area near the mouth of Zion Canyon. Habitat changes such as this are probably responsible for many of the differences in recent observations as compared to the older published data of Behle (1943) and Woodbury et al. (1949).

Blue-gray Gnatcatcher.—Also found near the center of the ordination is the Blue-gray Gnatcatcher. James (1971), Whitmore (1975a), and Kimberly Smith (pers. comm.) observed and discussed the wide range of habitats selected by this species. In a more definitive study, Root (1967) lists many habitats in which the Blue-gray Gnatcatcher may be found and remarks on

the variability of selected sites in various areas of its geographic range. Based on the 4 most important variables, gnatcatchers in the Virgin River Valley had the broadest habitat use of any of the species in the community. My observations of the foraging behavior of this species are consistent with those of Root in that foraging was primarily confined to the foliated portions of the available habitat, most notably the outer most foliage of large mature trees. Hawking for insects was observed, but it was mostly confined to times when gnatcatchers were flying between trees. Occasional sorties low over the alfalfa were also observed, possibly, as mentioned by Root, to catch grasshoppers.

The use of indices such as niche breadth and overlap has been discussed by Cody (1974) but one point should be re-emphasized, that of weighting. The aspect of the Colwell and Futuyma (1971) calculations that make them so valuable is that the species themselves determine the weights of each of the resource states by their positions in the habitat, i.e. their use of each state. This type of calculation effectively eliminates the misconception that each of the subdivisions of the resource matrix is equally important to the species and, therefore, provides a more meaningful interpretation of the data. However, these calculations, to date, have been confined to one resource matrix at a time. What is needed, and is currently being worked on, is an n -dimensional habitat use matrix, i.e. one that will allow simultaneous analysis of several variables. It is possible to combine several variables into one by the construction of an index, such as an importance value, but in this type of statistic much information is lost.

It is frequently reported in the literature (Wiens 1969, James 1971, Anderson and Shugart 1974) that bird species select certain parts of the habitat based on specific search images. But care should be taken in emphasizing habitat keys. Perhaps the perceptual world (niche-gestalt) described by James (1971) is an artifact of the observer, i.e. the ecologist may be recognizing distinct habitats or positions along environmental gradients, but the bird species present may not be capable of the same distinctions or their distinctions may not be equivalent to those of the observer (Vandermeer 1972).

Vandermeer argues that the ecologist will never be able to view the niche through the eyes of a bird, even though the sensory systems are similar. However, if the goal of the ecologist is, as Bronowski (1973) stated, to have the ability to visualize the future and to foresee what may happen, i.e. gain an index of predictability, then placing the species along environmental gradients offers useful insights. Acknowledging the conceptual problems involved, it is still useful to derive axes that allow the scientist to predict the behavior of a species, particularly in respect to the concept of environmental change and its impact on the community. The validity of ordination work can be tested by subsequent field observation.

SUMMARY

Habitat relationships within a community of passerine birds were examined using multivariate statistical techniques and one index of niche breadth here termed "habitat use." Four species pairs were not significantly distinct when analyzed using multivariate analysis of variance. A 2-dimensional ordination along known vegetational gradients was constructed using principal component analysis. A regression line was drawn through this ordination providing a third gradient. Habitat use analysis defined several habitat generalists, including the Blue-gray Gnatcatcher and Brown-headed Cowbird, and several habitat specialists, including the Willow Flycatcher and Blue Grosbeak. Reasons for taking care in discussing avian habitat selection were presented.

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