AVIAN AND VEGETATION COMMUNITY STRUCTURE AND THEIR SEASONAL RELATIONSHIPS IN THE LOWER COLORADO RIVER VALLEY

BERTIN W. ANDERSON

ROBERT D. OHMART

AND

JAKE RICE

ABSTRACT.—Records of vegetation density and seasonal bird species richness, densities, and diversities for 78 line transects along the lower Colorado River were examined to: (1) isolate seasonal and spatial patterns of avian community variation; (2) determine relationships between patterns of attributes in avian communities and vegetation characteristics; and (3) evaluate effects of different spatial levels of investigation. Principal components analysis of foliage density and diversity measures revealed two important, independent patterns of variation among transects. Avian density was usually independent of, and more regularly arranged than, diversity within each season.

Regression of principal components, derived from principal components analysis of avian community attributes on vegetation components, showed that avian density was more closely related to variation in the vegetation than was avian diversity. Avian community attributes outside the breeding season were more highly correlated with the vegetation measures than were those for communities during the breeding season. Vegetation density and diversity were both important predictors of avian community measures at the habitat level but accounted for little of the variation in bird communities at the transect level.

Additional principal components analyses using the combined avian and vegetation data evaluated at the habitat level produced results similar to those found at the transect level. When we analyzed vegetation and avian community variables together, results were similar to previous findings. The additional studies reinforced the findings of the first analyses, although when evaluating habitat data, avian and vegetation variables were more closely associated than when the analysis was conducted using a more local spatial scale.

Several generalizations were possible. For example, common summer visitors in mature cottonwood-willow (*Populus fremontii-Salix gooddingii*) habitats differed ecologically from species visiting structurally simpler cottonwood-willow habitats in summer. The general similarities among habitats when considering resident avian species contrasted with the differences when species present only part of the year were considered.

Many important factors determining the occurrence and abundance of avian species probably act outside the breeding season, at least in temperate regions (Fretwell 1972, Willson 1974). Furthermore, ecologists disagree on exactly how species theoretically use temporally or spatially patchy habitats, as well as how species actually do use patchy habitats (MacArthur and Levins 1964, Emlen 1966, MacArthur and Pianka 1966, Fretwell 1972, Wiens 1976). These temporal and spatial differences clearly play an important role in species distributions, but avian distribution, diversity, and abundance have received little systematic investigation in a variety of contiguous habitats. Furthermore, comparable relationships of bird community and vegetation attributes have not been clearly demonstrated at different spatial and temporal levels. This is especially important, because if studies at different levels produce different findings, generality of conclusions from a single study is questionable.

Diverse types of birds use riparian habitats along the lower Colorado River. These include several common resident insectivores and a number of other insectivores that visit the area in summer, some for several months. In addition, there are several winter visitors, including insectivores and granivores. The changing species composition of the avian community using riparian vegetation, combined with the demography of populations of individual species, produces an overall avian

community of substantial spatial and temporal complexity. Analyses presented here attempt to resolve a portion of those complex and dynamic ecological interactions into empirically specifiable patterns.

We examine here three questions concerning the relationship of avian diversity and abundance to habitat and consider the effects of spatial and seasonal variation. What is the pattern of variation in bird species diversity (BSD), species richness, and avian density among habitats and seasons? What is the relationship of vegetation to these patterns of variation in avian communities? Do studies at different spatial levels of analysis produce similar patterns and relationships?

METHODS

BIRD AND VEGETATION CENSUS METHODS

The study was conducted in riparian vegetation of the lower 443 km of the Colorado River along the California-Arizona border. We established 78 transects 900 to 1,600 m long by chopping narrow paths (0.75–1.3 m wide) through a variety of vegetation types. Transects were placed so that they passed through stands of vegetation relatively homogeneous in plant species composition and vertical foliage profile, with length being 1,600 m unless the stand was too small for such a line. Orientation of a transect was determined by that of the stand and was independent of the river orientation.

We measured foliage density at heights of 0.15, 0.60, 1.50, 3.00, 4.50, 6.00, 7.50, 9.00 m, and every 3.00 m thereafter, following MacArthur and MacArthur (1961). Mean distance to vegetation at each layer was calculated at 36 points along the 900-m transects and at 66 points along the 1,600-m transects and then converted to foliage density per stratum (MacArthur and MacArthur 1961). Vegetation measurements therefore included: foliage densities at the layers 0–0.6 m, 1.5–3.0 m, and >4.5 m; total density; and foliage height diversity (FHD; after MacArthur and MacArthur 1961).

We recognized six riparian plant communities using dominant vegetation as a criterion: cottonwood-willow (*Populus fremontii-Salix gooddingii*), honey mesquite (*Prosopis glandulosa*), screwbean mesquite (*P. pubescens*), salt cedar (*Tamarix chinensis*), arrowweed (*Tessaria sericea*), and salt cedar-honey mesquite mixture (Anderson et al. 1977). We subdivided communities into six structural types based on vertical distribution of the foliage (Fig. 1). All of these profiles (I–VI, Fig. 1) differed significantly ($P < 0.01$, using a two-tailed Z-test) from all of the others in at least one of the
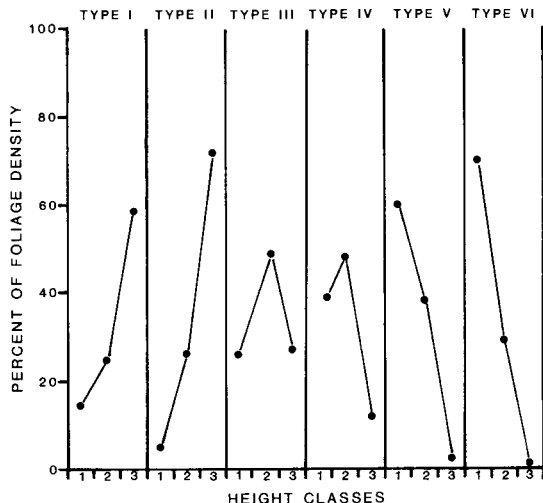

FIGURE 1. Foliage density profiles by proportion of total foliage density occurring at various strata in Colorado River riparian vegetation. Height classes: 1 = 0.15–0.6 m; 2 = 0.6–4.5 m; and 3 = >4.5 m.

three vertical positions. This classification yielded 36 possible habitat types, each differing from the others by average vertical profile, dominant vegetation, or both. Twenty-three of these habitat types actually occurred along the Colorado River.

The census data included here are from March 1976 to March 1977, representing the first full year of data from all transects. We censused birds three times per transect per month using a modification of the Emlen (1971) technique (Anderson et al. 1981). Censusing was done in the morning during periods of peak bird activity. Bird detections were recorded at lateral distances up to 125 m, so the censused area included about 20 ha for 900-m transects and 40 ha for 1,600-m transects.

We determined avian density (DEN) for each transect. The number of different species (NUMSP) found in a given habitat type represented a measure of species richness. We calculated BSD using the formula BSD $= -\Sigma\, p_i \ln p_i$, where p_i is the proportion constituted by species i of all birds seen on a given transect or in a given habitat type.

Two additional bird community measures were used to accommodate seasonal densities of doves (*Zenaida* spp.). Doves breed in large numbers in riparian habitats in summer but obtain only about 10% of their food from riparian vegetation (Anderson and Ohmart, unpubl. data). Including a species with such high ephemeral densities relative to most other bird species might bias density and diversity values in those transects where doves were found. We therefore calculated additional diversity (BSD 10) and density (DEN 10) measures, using 10%

TABLE 1.   Avian densities for 23 habitat types for five seasons along the lower Colorado River.

Habitat[b]	Total avian density[a] in no. birds/40 ha				
	Spring	Summer	Late summer	Fall	Winter
CW I	274 (217)	173 (156)	318 (318)	411 (411)	201 (198)
CW II	298 (277)	638 (290)	356 (235)	230 (230)	247 (247)
CW III	159 (116)	508 (339)	294 (212)	381 (381)	235 (233)
CW IV	193 (159)	348 (226)	312 (218)	167 (161)	159 (159)
CW V	84 (67)	246 (134)	213 (172)	107 (102)	71 (67)
CW VI	134 (131)	167 (136)	186 (157)	161 (128)	173 (167)
HM III	180 (150)	483 (232)	344 (276)	183 (183)	171 (171)
HM IV	200 (166)	360 (182)	216 (154)	316 (308)	191 (185)
HM V	178 (161)	210 (130)	112 (98)	207 (206)	147 (119)
HM VI	194 (182)	220 (128)	120 (104)	226 (226)	153 (153)
SC I	23 (23)	124 (101)	141 (135)	99 (99)	28 (28)
SC II	146 (136)	290 (193)	213 (183)	165 (165)	153 (153)
SC III	75 (55)	503 (238)	362 (177)	268 (267)	529 (529)
SC IV	101 (81)	316 (156)	296 (239)	129 (129)	137 (137)
SC V	39 (28)	241 (98)	187 (155)	105 (103)	51 (49)
SC VI	54 (50)	131 (86)	89 (75)	110 (110)	112 (112)
SH IV	89 (83)	226 (157)	280 (140)	171 (95)	245 (187)
AW IV	111 (91)	295 (170)	184 (151)	177 (176)	104 (104)
SM II	202 (150)	948 (330)	676 (371)	142 (140)	112 (104)
SM III	103 (85)	344 (165)	337 (222)	203 (190)	147 (107)
SM IV	201 (160)	286 (181)	106 (77)	356 (257)	151 (124)
SM V	92 (70)	147 (116)	123 (113)	144 (136)	59 (58)
SM VI	—[c] (—)[c]	97 (69)	89 (80)	225 (212)	163 (155)

[a] Values in parentheses recalculated with only 10% doves observed.
[b] As described in text. CW = cottonwood-willow, HM = honey mesquite, SC = salt cedar, SH = salt cedar-honey mesquite, AW = arrowweed, SM = screwbean mesquite.
[c] Not censused.

of the observed dove population as a correction.

Strictly transient species included those that neither bred nor wintered in the riparian habitats. These species were excluded from the analyses. Their sporadic occurrences and brevity of stay rendered them impossible to census accurately. Their large variability in density over a brief period should also minimize their contribution to community organization at the temporal level of entire seasons and habitats.

On the basis of the birds' breeding and migration activity, we recognized five seasons: summer (May–June–July); late summer (August–September); fall (October–November); winter (December–January–February); and spring (March–April). All calculations for bird community measures were based on averages of the six to nine censuses per transect per season.

ANALYTICAL METHODS

Data from other studies reveal that it is common for vegetation measures (FHD and density at various strata) to be interrelated (e.g., James 1971; Whitmore 1975, 1977; Smith 1977; Rice 1978). We used principal components analysis (PCA) of the five different vegetation measures for the 78 transects or 23 habitat types to delineate major trends in vegetation configuration found among the sample units. The PCA identifies linear patterns of correlated change among several variables (in this case, vegetation measures; in our other analyses, seasonal bird community measures) and arranges each sample unit (transect or habitat) along the trend represented by the principal component (PC). In our study, Varimax rotations were used to improve the biological interpretability of the ordination axes (Cooley and Lohnes 1971).

Bird communities varied not only among different sites but also seasonally at the same site. We used PCA to examine the extent to which relationships among bird community attributes in different habitat types were consistent over the seasons. In the analysis, five bird community measures for five seasons yielded 25 variables, across either 78 transects or 23 habitat types. Resulting components represented trends of variation in bird density, diversity, and richness across transects or habitat types that were either consistent over several seasons or intercorrelated among several bird community measures. The important principal components (i.e., those with eigenvalues greater than 1.0) potentially represented biological trends with as much information about bird community structure as any single original measure contained (Cooley and Lohnes 1971). Each variable received a factor loading on each principal component. Those variables with the highest loadings, positive or negative,

TABLE 2. Bird species diversities for 23 habitat types for five seasons along the lower Colorado River.

Habitat[b]	Total bird species diversity[a] calculated on no. of individuals				
	Spring	Summer	Late summer	Fall	Winter
CW I	2.75 (2.75)	2.83 (2.76)	2.51 (2.51)	2.29 (2.29)	2.61 (2.56)
CW II	2.27 (2.16)	2.12 (2.83)	2.29 (2.57)	2.20 (2.20)	2.43 (2.43)
CW III	2.53 (2.80)	2.85 (3.29)	3.01 (3.24)	2.49 (2.49)	2.49 (2.50)
CW IV	3.11 (3.22)	2.71 (3.07)	2.99 (3.22)	2.98 (2.93)	2.57 (2.57)
CW V	1.99 (1.94)	2.00 (2.18)	2.67 (2.64)	2.64 (2.59)	1.97 (1.88)
CW VI	2.68 (2.64)	2.79 (2.77)	2.86 (2.86)	2.43 (2.52)	2.40 (2.33)
HM III	2.71 (2.73)	2.03 (2.67)	2.46 (2.38)	2.77 (2.77)	2.36 (2.36)
HM IV	2.80 (2.87)	2.12 (2.81)	2.59 (2.80)	2.58 (2.54)	2.48 (2.42)
HM V	2.69 (2.64)	2.32 (2.70)	2.72 (2.70)	2.44 (2.42)	2.21 (2.21)
HM VI	2.56 (2.50)	2.26 (2.71)	2.48 (2.45)	2.30 (2.29)	1.91 (1.91)
SC I	2.46 (2.42)	2.67 (2.61)	2.70 (2.66)	2.52 (2.52)	2.38 (2.38)
SC II	2.17 (2.09)	2.50 (2.73)	1.83 (1.71)	1.91 (1.91)	1.54 (1.54)
SC III	2.07 (2.16)	2.04 (2.54)	1.82 (2.12)	2.26 (2.24)	1.55 (1.55)
SC IV	1.72 (1.61)	1.85 (2.16)	2.40 (2.31)	2.39 (2.39)	1.90 (1.90)
SC V	2.54 (2.69)	1.93 (2.61)	2.50 (2.39)	2.63 (2.59)	2.20 (2.13)
SC VI	2.41 (2.34)	2.44 (2.68)	2.80 (2.80)	2.58 (2.58)	2.11 (2.11)
SH IV	2.24 (2.17)	2.53 (2.62)	1.54 (2.75)	1.87 (2.41)	1.86 (1.84)
AW IV	2.45 (2.49)	2.33 (2.68)	2.55 (2.47)	2.51 (2.50)	2.25 (2.25)
SM II	2.63 (2.82)	1.79 (2.76)	1.85 (1.90)	2.55 (2.52)	2.40 (2.34)
SM III	2.54 (2.53)	2.15 (2.73)	2.39 (2.44)	2.77 (2.73)	2.40 (2.62)
SM IV	2.63 (2.74)	2.51 (2.79)	2.77 (3.07)	2.41 (2.41)	2.64 (2.72)
SM V	2.46 (2.58)	2.73 (2.74)	2.53 (2.45)	2.72 (2.65)	2.49 (2.44)
SM VI	—[c] (—)[c]	2.22 (2.19)	2.47 (2.36)	1.53 (1.41)	1.74 (1.64)

[a] Values in parentheses recalculated with only 10% doves observed.
[b] As described in text and Table 1.
[c] Not censused.

on a principal component were used to interpret that principal component.

We regressed major bird principal components (BPCs) on vegetation principal components (VPCs) to examine the extent to which the relative position of each transect or habitat type on the BPCs was correlated with its position on VPCs. Because the relationship of bird diversities and densities to vegetation might not be linear, we used a step-wise regression of the major VPC scores and each VPC score raised to the second, third, and fourth power. This regression allowed us to detect nonlinear associations between bird communities and the vegetation supporting them (Meents et al. 1981, 1982, 1983). Although such a step-wise method produces an overall Type I error rate greater than the error rate of each step (in our case 0.05), our interpretation stresses the variance in bird community attributes accounted for by the VPCs, rather than the level of statistical significance of any particular relationship. Comparison of the VPCs and amount of variance explained in regressions of BPCs on VPCs between transect and habitat levels of analyses allows consideration of the importance of spatial scale in avian community studies.

We repeated PCA on a data set that included bird community variables as well as the five vegetation measures for each habitat during all five seasons in an effort to reveal any subtle bird-vegetation relationships which might have been overlooked to this point. PCs from such analyses would reveal covarying vegetation and bird community trends during seasons with the strongest relationship.

RESULTS

Differences between habitats were apparent when any single bird community attribute was considered (Tables 1–3). For example, bird species richness measures had their highest values in cottonwood-willow habitats. Differences in bird species richness between cottonwood-willow and other habitats varied seasonally, however, and seasonal differences also varied depending on which habitats were being compared. Finally, structural configuration of a habitat clearly affected attractiveness of the area to various bird species. For example, cottonwood-willow type III habitat had much higher richness values in summer and late summer than did any other habitat. In spring, however, the number of species found in this habitat was comparable to the number of bird species using most honey mesquite habitats. Riparian birds apparently did not differ much in their use of salt cedar habitats. Relatively few species used these areas (as evidenced by lower richness values in salt cedar than in most other habitats), and we found little variation in the number of species recorded in the six

TABLE 3.   Species richness for 23 habitat types along the lower Colorado River.

Habitat[a]	Species richness (no. species/40 ha)				
	Spring	Summer	Late summer	Fall	Winter
CW I	21	29	26	21	28
CW II	24	25	24	21	20
CW III	23	44	43	36	26
CW IV	39	33	41	34	21
CW V	11	15	27	21	14
CW VI	22	23	27	24	24
HM III	27	28	27	24	19
HM IV	30	22	27	27	23
HM V	26	23	24	25	20
HM VI	25	22	19	22	15
SC I	13	21	23	18	12
SC II	12	25	8	12	8
SC III	17	20	13	18	16
SC IV	6	19	27	20	12
SC V	15	18	24	22	13
SC VI	13	20	25	22	20
SH IV	17	24	26	21	25
AW IV	20	20	19	22	19
SM II	24	27	27	23	19
SM III	22	25	31	28	22
SM IV	26	22	22	30	21
SM V	18	21	24	23	17
SM VI	—[b]	12	15	21	12

[a] As described in text and Table 1.
[b] Not censused.

structural types of salt cedar (Table 3). Clearly, investigations of avian communities must consider both seasonal and habitat factors. Other community measures such as total avian density would disclose different temporal patterns of habitat use.

When selected pairs of bird community attributes were considered, significant interrelationships appeared. For example, overall species richness and diversity correlated positively with each other in summer ($r = 0.449$, $P < 0.05$). Cottonwood-willow communities usually attracted both the richest and most diverse assemblages of species. The correlation between richness and bird species diversity closely paralleled each other across the six structural types of cottonwood-willow. In contrast, variation in densities of doves among different structural types in salt cedar habitat led to markedly different diversities but little variation in richness.

Patterns became even more complex than the foregoing when seasonal variation was included. Summer and winter bird community richness measures were significantly correlated ($r_{richness} = 0.576$, $P < 0.05$), but diversity measures were not ($r_{diversity} = 0.350$, $P > 0.05$). However, in winter, richness and diversity measures were highly positively correlated ($r = 0.627$, $P < 0.01$, all df = 76). Relationships between different community types also differed in avian community attributes across

seasons being examined. Relationships between avian community attributes across seasons are obviously complex. Bird-vegetation associations are superimposed upon this complexity. We attempt to unveil this complexity with principal components analysis.

ANALYSIS OF VEGETATION STRUCTURE

Both levels of investigation (habitat and transect levels) extracted two independent components (VPCs) from the five vegetation measures (Fig. 2). The variables showing a high degree of association with a component loaded higher on that component. At the transect level VPCI arranged transects by foliage density from those with sparse vegetation to those with dense vegetation. All foliage density measures made substantial positive contributions to this component, with density from 0 to 0.6 m making the smallest contribution. A negative association between differences in ground and canopy vegetation was emphasized more in the habitat-level analysis. Habitats were arranged from sparse to dense, and areas with dense vegetation overall supported sparse ground vegetation.

In both analyses VPCII arranged areas from low FHD to areas of high FHD. The strata of vegetation contributing most to this trend differed between the two levels, however. At the transect level, increasing FHD reflected increases in canopy and decreases in ground vegetation. At the habitat level, the contribution of intermediate stratum vegetation (1.5–3.0 m) to FHD was most important.

Interpretation of the position of individual transects would be unnecessarily detailed, owing to the number of individual cases. But placements of individual habitats are biologically interpretable, and we identified consistent patterns of difference between habitats on the two VPCs. Vegetation structural types I and II were clearly differentiated from type III, and types I, II, and III from types IV, V, and VI, on VPCI (horizontal axis, Fig. 3), with I and II having the greatest canopy density. Structural types IV, V, and VI were similar on VPCI but were in general differentiated on VPCII (vertical axis, Fig. 3). FHD and intermediate densities decreased from types IV to V to VI within each habitat. Types I to III were similar to each other on this component. Habitats with the same vertical structure differed in this measure, with cottonwood-willow consistently scoring higher than other habitats of the same vertical structure and with salt cedar usually scoring next. Therefore, the relative relationships of plant communities differing by dominant tree species showed the same trends in change across structural types, but the struc-
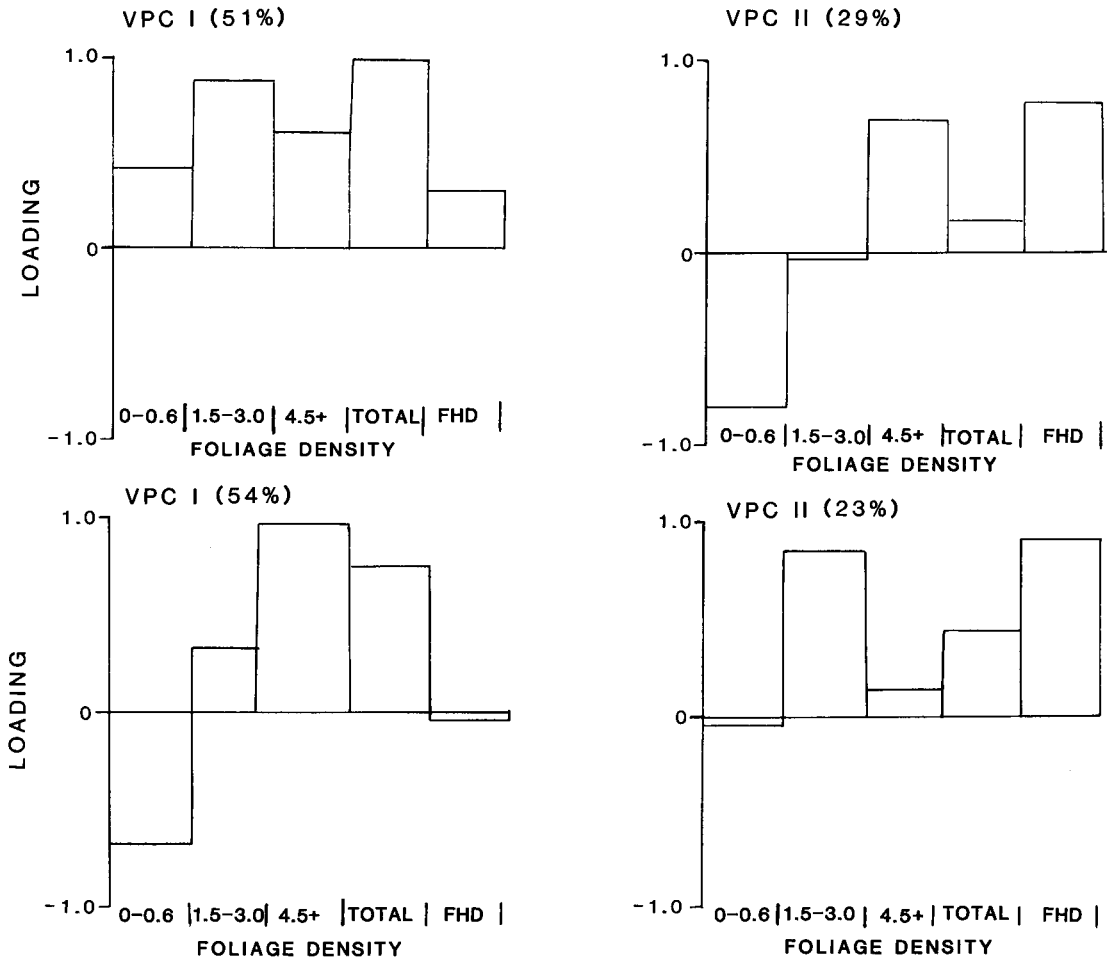
FIGURE 2.   Variable loadings on the first two principal components of vegetation data from 72 individual transects (top graphs), and from 23 habitats (bottom graphs). Horizontal axes for each season are the five vegetation measures and vertical axes are component loadings. Percent of total variation accounted for by each principal component is given.

tural types differed in absolute position on each axis.

AVIAN COMMUNITY STRUCTURE—TRANSECT LEVEL

The PCA of seasonal avian density, diversity, and richness measures produced seven bird principal components (BPCs). BPCI (Fig. 4) represented variability (i.e., had factor loadings ≥ 0.5) among transects in fall and winter avian density; BPCII represented summer and late summer density variation; and BPCIII represented spring density variation. Spring diversity differences also contributed to BPCIII. Species richness loaded on each of these factors, indicating that for all seasons transects with high densities of birds also had large numbers of species. These components, all arranging density and richness variation among transects, together accounted for 63%

of the total variability among transects in the avian community measures.

The four remaining PCs all emphasized diversity differences among transects. BPCIV represented spring and fall patterns of diversity; BPCV, late summer trends in diversity; BPCVI, winter diversity patterns; and BPCVII, summer diversity patterns.

AVIAN COMMUNITY STRUCTURE—HABITAT LEVEL

At the habitat level, PCA of bird community measures of different seasons yielded six independent trends of variation. These components accounted for 88% of the variation in avian community measures between habitat types (Fig. 5).

BPCI represented a gradient across habitats in diversity during late summer, fall, and winter (i.e., diversity measures tended to load at

FHD AND FOLIAGE DENSITY 1.5 – 3.0m

CW III
CW IV   HM III
SC IV   SM III
SM IV   CW I
CW V
HM IV
SH IV
SC III   SC I   SM II
SC V
SM V
AW VI
CW VI
HM V
SC VI   CW II
SC II
HM VI
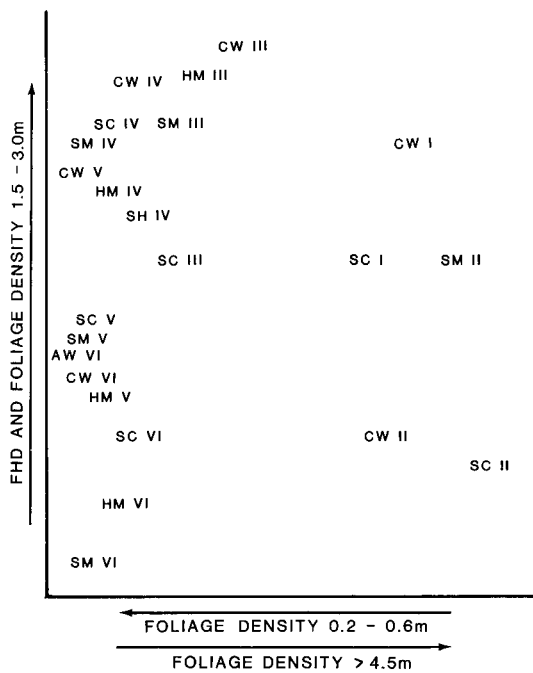SM VI

FOLIAGE DENSITY 0.2 – 0.6m

FOLIAGE DENSITY > 4.5m

FIGURE 3. Component scores of the 23 habitats on principal components I (horizontal axis) and II (vertical axis) of the vegetation data. CW = cottonwood-willow, SC = salt cedar, HM = honey mesquite, SM = screwbean mesquite, AW = arrowweed, SH = salt cedar-honey mesquite mix.

0.5 or more). BPCII identified variation among habitats in bird densities from summer and late summer. BPCIII reflected differences among habitats in both spring and fall density. Fall diversity contributed negatively to the third component as well. This indicated that in fall when densities were high, diversities were low (as indicated by negative loadings from -0.5 to -1.0). BPCIV represented bird diversity measures in spring and summer, BPCV arranged habitats by their variation in winter densities, and BPCVI arranged habitats by summer diversity measures.

Biologically, each gradient extracted by the analysis indicated that habitats which were high (or low) in one of the attributes loading high on that BPC would be high (or low) for all other attributes and seasons loading high on that component. For example, cottonwood-willow habitats had relatively high species richness in late summer (BPCI, Fig. 5). BPCIII was an exception; the negative contributions of fall diversity measures implied interaction of two ecological factors. First, habitats which were selected (or avoided) in spring tended to be selected (or little used) in fall as well. Also, in fall but not in spring there were a few exceptionally abundant species that depressed

diversity measures. Otherwise, groups of bird species showed similar patterns of habitat use for seasons which ordinated together on the various components.

Much of the value of these components is that the relative position of transects or habitats on individual components directly reflect many of the complex relationships discussed in the initial part of the results. For example, in the habitat analysis, cottonwood-willow communities had high scores on BPCI, indicating generally high BSD from August to February. Structurally complex habitats (types I, II, and III) tended to have high scores on BPCs II and III, indicating that such communities attracted many birds (high densities) from March to October. Similarly, ecological relationships of bird communities in various habitats for any season can be much more readily viewed by appropriate graphical displays of the positions of habitats on components.

PREDICTIONS OF BIRD COMMUNITY ATTRIBUTES FROM VEGETATION ATTRIBUTES

Overall ability to predict bird community scores from vegetation component scores lacked power at the transect level (Table 4). Only May to September densities (BPCII) had more than one-sixth of their variance predicted from the VPCs. The analyses indicated that BPC measures were related to overall vegetation density (VPCI) and specifically to canopy density and FHD (VPCII). In BPCs IV–VII, all of which relate to BSD aspects of community structure at various seasons, the canopy density-FHD component was significantly correlated with a BPC twice, whereas the total density component was significantly correlated with a BPC once. In the first two avian community components, reflecting differences in bird community densities and richness, both vegetation components were significant predictors and accounted for comparable amounts of variation. Spring density and diversity (BPCIII) were not related to any VPC.

Regressions naturally accounted for more of the variation in factor scores at the habitat level, because by combining transects into habitats some of the variation was lost. The best predictor of scores for BPCI was VPCII, the FHD measures, to the third power (Table 5). This implies that both small increases in FHD when it is low, and small increases in FHD when it is already high, have greater effects on BSD than changes in FHD at intermediate values.

Foliage density also predicted fall and winter BSD, bringing the cumulative between-habitat
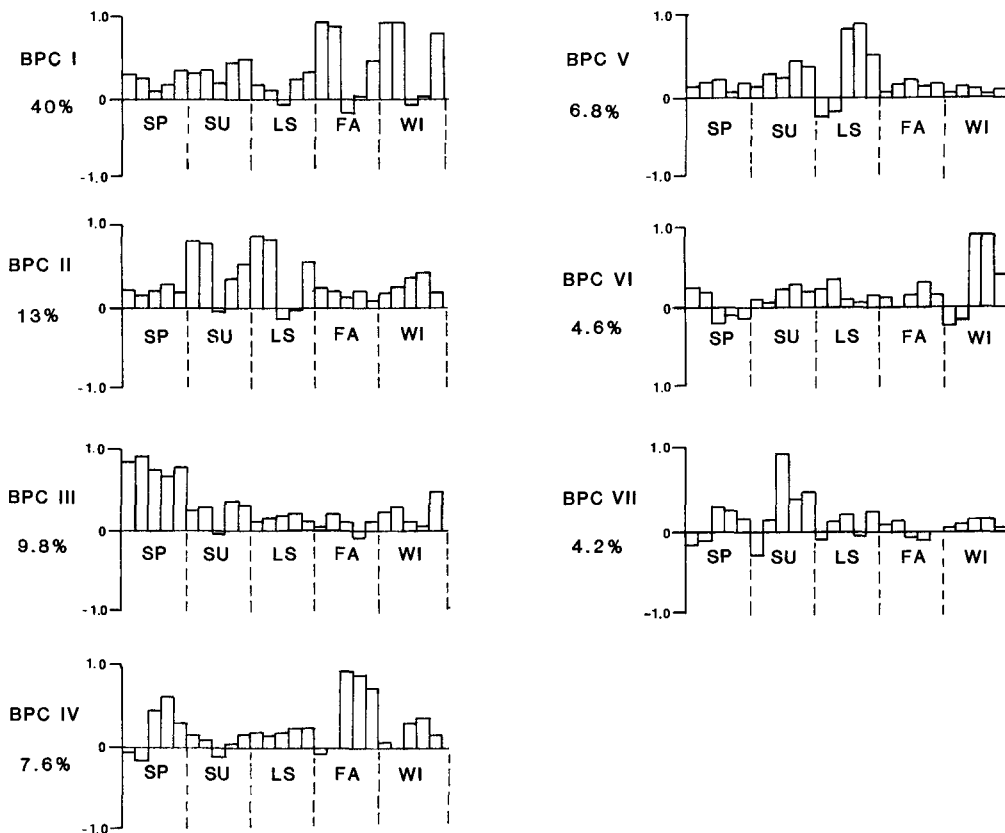
FIGURE 4. Variable loadings on the first seven principal components of the bird community data from 72 individual transects. Horizontal axes are bird community variables: SP = spring, SU = summer, LS = late summer, FA = fall, and WI = winter. For each season the five bird community measures, in order, are: bird density (DEN); DEN with 10% doves; bird species diversity (BSD); BSD with 10% doves; and number of species.

variance of BPCI accounted for to 58%. Over-all, fall and winter diversity measures increased within increasing foliage density. Avian diversity changed most with moderate foliage densities and was greatest when the foliage was spread among the middle and upper strata.

Over half of the differences in summer bird densities among habitat types, as measured by BPCII, were correlated with differences in foliage density among habitats. As the canopy became denser and as ground vegetation became sparser, density of summer birds increased. VPCII was also significantly related to summer bird density but accounted for little additional variance.

The effect of spring and fall migrants on density and diversity was measured by BPCIII. This correlated significantly with only the vegetation density component (VPCI). The complex curvilinearity of the relationship implies an increase in bird community measures with an increase in canopy density or a decrease in ground-level vegetation.

Differences in breeding season BSD among habitats, as measured by BPCIV, were not significantly predicted by either vegetation component. Apparently variations among habitats in spring and summer bird diversity are not closely related to differences among habitats in vegetation density or FHD measures. Differences in winter density (BPCV) among habitats were significantly related in complex curvilinear ways to both vegetation components. Functionally, details of the curvilinear relationship imply that ground vegetation had more effect than canopy vegetation. The last major bird community component, representing summer diversity differences, was not predicted significantly by any VPC.

COMBINED ANALYSIS

Major trends in avian community organization may be closely related to some vegetation attributes but not necessarily to the principal independent trends in vegetation variation extracted by the PCA. For this reason we conducted a PCA from the combined bird and
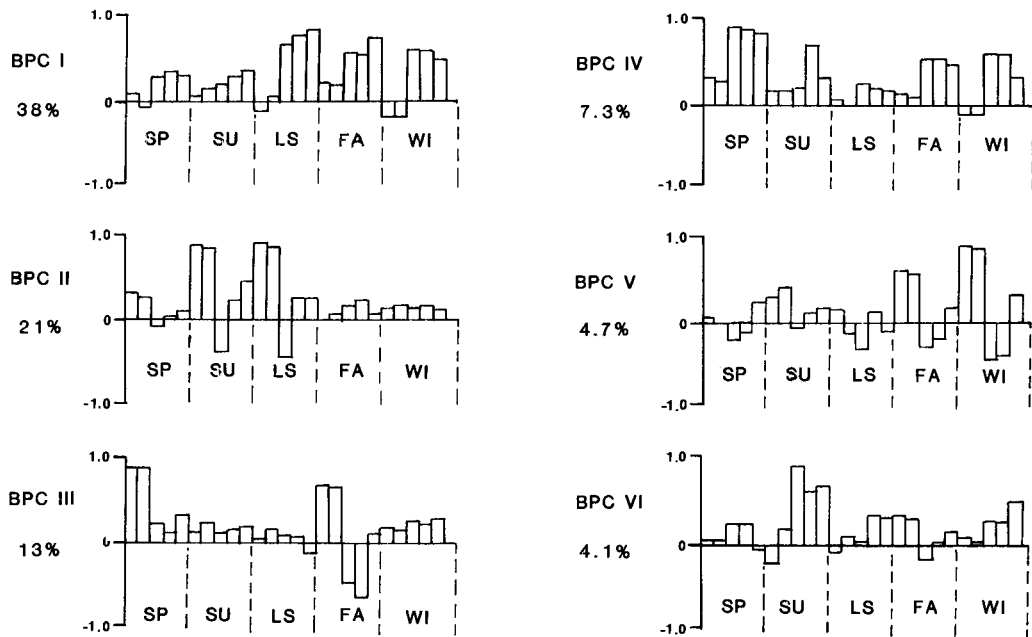
FIGURE 5.   Variable loadings on the first six principal components of the bird community data from 23 habitats. Abbreviations and arrangement as in Figure 4.

vegetation data from the 23 habitat types. This produced seven vegetation-bird principal components (VBPCs). These components (Fig. 6), in general, provided results similar to the previous results.

Habitats on component I of the combined analysis (VBPCI) were arranged in order of differences in avian density from summer and late summer and a bipolar change in vegetation density, negative for low vegetation, and positive contributions from other heights. The variables with substantial contributions and the arrangement of cases on the component corresponded closely to BPCII and VPCI at the habitat level. VBPCII of the combined analysis corresponded to BPCI, ordering habitats by species richness and diversity during the nonbreeding season. FHD, as well as low and intermediate density contributed more than other vegetation variables to this component.

VPCIII corresponded to BPCIII, the density differences from spring and fall. None of the vegetation measures loaded heavily on this component. VBPCIV represented differences among habitats in winter densities of birds. Again, no vegetation measures contributed substantially to this component. VBPCV arranged BSD in summer among habitats. The only vegetation measure contributing to this component was vegetation density at low strata, such that communities of structural types I and VI, with well-developed understory vegetation, tended to have high BSD.

Spring, summer, fall, and winter BSD loaded heavily on component VI. Vegetationally, FHD contributed most to this component. This component, relating species diversity to foliage diversity across most of the year, represents the aspect of community organization so extensively studied by avian ecologists. Notably, it was one of the smallest components in our analysis.

The above point is emphasized by component VII of the combined analysis. Here none of the avian community variables contributed much, but FHD and intermediate vegetation density both had high loadings. Thus, most of the variation in FHD among habitats was not associated with changes in avian community measures. Many of the relationships between FHD and avian communities may have been extracted by previous components, but the communality (for a given variable, proportion of variance accounted for, calculated by summing squares of factor loading on PCs) of FHD increased from 0.316 with six combined components to 0.825 with seven components. This 2.6-fold increase in the communality of FHD means that much of the differences among habitats in FHD was not matched by linear changes in the avian community.

DISCUSSION

PATTERNS OF VARIABILITY IN VEGETATION STRUCTURE

Foliage density and foliage diversity showed largely independent patterns of variation

TABLE 4. Regression statistics of relationships of bird community principal components (BPCs) to individual transect vegetation principal components (VPCs) arranged in decreasing order of variation accounted for. R^2 = proportion of variance accounted for, F = F-statistic.

BPCs	Contributing VPCs	R^2	F
I	$(VPCI)^2$, VPCII	0.113	4.70*
II	VPCII, VPCI	0.345	19.49**
III	No significant relationships		
IV	$(VPCI)^2$, $(VPCII)^2$, VPCII	0.157	4.52*
V	No significant relationships		
VI	No significant relationships		
VII	$(VPCII)^3$	0.058	4.64*

* $P < 0.05$; ** $P < 0.005$.

among habitat types. The habitat level analyses may have combined slightly heterogeneous stands, but the overall interpretation of structure of the vegetation was little altered by a change in scale. Habitat types I, II, and III were differentiated from each other and from IV–VI by foliage density (VPCI), whereas, types IV, V, and VI were differentiated from each other by foliage diversity (VPCII). Therefore our habitat level identifies plant structural types that are statistically distinct. Used cautiously, in light of the two statistically independent dimensions of change in vegetation, the structural categories can be thought of as distinct habitats.

Each type of habitat had a predominant plant species such as honey mesquite or salt cedar. The relationships of the dominant plant species to the vegetation components were also straightforward. The structural types with different dominant plants consistently showed the same relative positions on the two components, but the absolute positions varied substantially. Therefore, in comparing vegetation attributes between sites, one should specify both the dominant species and the vertical configuration.

That both structure and species composition of the vegetation are important aspects of habitat quality is hardly novel to ecologists. It is important, however, that their relationships to the bird communities remained distinct through extensive quantitative analyses. The-

oretical ecologists and practicing management personnel often search for a single index of habitat attributes which will relate well to bird use of the habitat. Our findings argue against the likelihood of success in this quest. The importance of a broader statistical approach to elucidating bird-vegetation relationships becomes clear below.

PATTERNS OF SPATIAL AND SEASONAL VARIATION IN BIRD COMMUNITY ATTRIBUTES

When bird community measures from adjacent seasons covaried on a single PC, consistent use of the vegetation between seasons was implied. We found that in the absence of migratory species which breed in the area, fall and winter species diversities and richness covaried (BPCI); spring and summer diversities also covaried between habitats. The results show that habitats with a given diversity in spring had the same diversity in summer and habitats with a given diversity in fall had the same diversity in winter, but fall and winter differed from spring and summer, possibly because of influx of winter visitors with different ecological requirements from those of summer visitors.

At the transect level, the same general patterns were found, although spring and summer correspondence in avian diversity was not apparent. Hence the complex community patterns shown in the initial sections of this paper

TABLE 5. Regression statistics of relationships of bird community principal components to habitat type principal components. R^2 = proportion of variance accounted for, F = F-statistic.

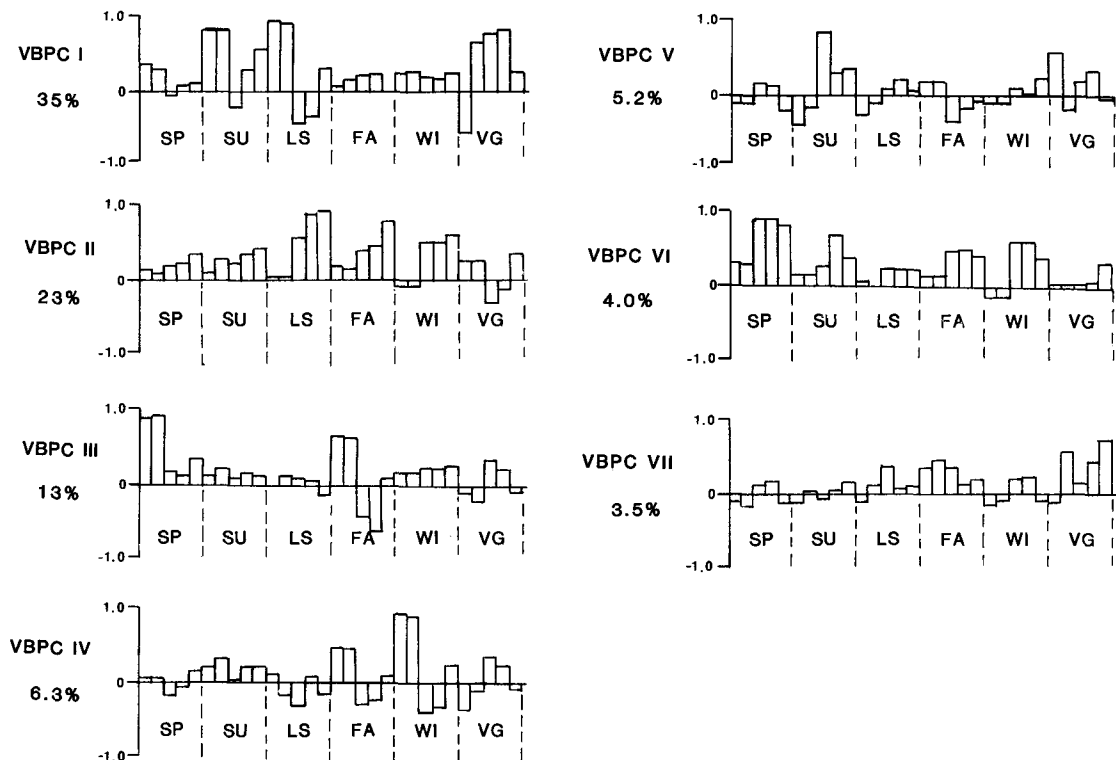| BPCs	Contributing VPCs	R^2	F
I	$(VPCII)^3$, VPCI, $(VPCI)^3$	0.578	8.22**
II	VPCI, VPCII	0.591	13.70**
III	VPCI, $(VPCI)^4$, $(VPCI)^2$	0.379	3.66*
IV	No significant relationships		
V	$(VPCI)^4$, $(VPCII)^2$, $(VPCI)^2$	0.611	9.40**
VI	No significant relationships		

* $P < 0.05$; ** $P < 0.005$.

FIGURE 6. Variable loadings on seven principal components of the combined bird and vegetation data from 23 habitats. First five variables on horizontal axis for each season are as in Figure 4. VG = vegetation measures in the following order: foliage density 0.15–0.6 m; foliage density 0.6–4.5 m; foliage density >4.5 m; total foliage density; and foliage height diversity (FHD). Vertical axes as in Figure 2.

were resolved into fewer, more comprehensible, patterns of community organization, but dynamic seasonal aspects of community organization remain. Differences in avian use of the vegetation in seasons outside of the breeding season are possibly due to seasonal dispersal schedules. This is consistent with several predictions from recent models of avian population ecology, especially those of Fretwell (1972), but is inconsistent with the common practice of studying avian community ecology solely during the breeding season.

Habitats differed in bird densities and diversities in winter much more than they did in summer at both levels of analysis. Lack of clear relationships between birds and habitats in the breeding season may reflect the presence of a superabundant food supply, at least for insectivorous birds (Anderson et al. 1982, Rosenberg et al. 1982). This would demand less habitat differentiation by birds, other factors, such as nest site availability, being equal.

At the transect level, breeding season species diversity was the least regular of all the avian community aspects measured. In fact, even after the seventh component was included, the communality of summer BSD 10 was still the

lowest of all variables studied, indicating that much of the variability in this measure was still unaccounted for.

AVIAN COMMUNITY–VEGETATION COMMUNITY RELATIONSHIPS

At the habitat level, nonbreeding-season attributes of avian communities were more closely related to vegetation parameters than were breeding-season attributes. More between-habitat variance in fall-winter diversity (BPCI) was accounted for by vegetation components than was variance in spring or summer diversity (BPCIV, Table 5). Comparing winter density variation (BPCV) to that of spring and summer (BPCs II and VI) showed that nonbreeding season densities tended to be at least as closely related to vegetation attributes of habitats as breeding season densities. Furthermore, density-related components (BPCs II and VI) were consistently more correlated with vegetation factors than were diversity components (BPCs I and IV).

There are several possible reasons why fall and winter avian communities were more closely attuned to attributes of the habitat than was the spring or summer avian community.

Winters can be harsh, usually with several frosts and cold nights. Insects are also less available in the fall and winter (Anderson et al. 1982), while being superabundant in summer (Rosenberg et al. 1982). In some habitats (e.g., cottonwood-willow), certain kinds of insects (e.g., leafhoppers, Cicadellidae) are plentiful and seemingly readily available (Rosenberg et al. 1982), yet virtually unused by birds. Competition for food does not seem to be a plausible explanation for the observed distribution of insectivorous birds at such times. The lack of competition (food is abundant everywhere) perhaps partly negates habitat discrimination by birds in summer. Most overwintering visitors are present in the area for a longer period than are breeding season visitors, and this may lead to more precise adaptations to habitats (selection pressures are greater). For example, some of the most abundant winter species, such as the White-crowned Sparrow (*Zonotrichia leucophrys*), Ruby-crowned Kinglet (*Regulus calendula*), Yellow-rumped Warbler (*Dendroica coronata*), and Phainopepla (*Phainopepla nitens*), are present for five or six months. In contrast, most breeding visitors are here for only three or four months (e.g., Yellow-billed Cuckoo, *Coccyzus americanus*; Yellow-breasted Chat, *Icteria virens*; Blue Grosbeak, *Guiraca caerulea*; Lucy's Warbler, *Vermivora luciae*; and White-winged Dove, *Zenaida asiatica*), at a time when insects are superabundant. Some birds, such as Lucy's Warbler, leave the area shortly after the onset of extremely hot summer conditions.

At the transect level of analysis, unlike the habitat level, breeding season density and diversity were more predictable from vegetation factors than were nonbreeding season densities and diversities. Even though the differences in explained variance were sometimes relatively large (11 to 35% for density BPCs I and II, Table 4), explained variance for diversity (BPCs VI and VII) was low (0 to 5%). These values were much lower than the level of predictability consistently found in the habitat analyses. Again, densities were consistently more predictable than diversities from vegetation factors.

We also found indications that the emphasis placed on relating avian community structure to FHD may not apply in our study area. At the habitat level, where bird community attributes were most highly correlated with VPCs, the latter were significant predictors of avian community PCs 11 times. FHD contributed substantially to only three of these correlations. Among habitats, none of five correlations between avian diversity and vegetation was exclusively an FHD-related vegetation factor. At the transect level, FHD (VPCII) was a significant predictor five times, compared to three for the foliage density component.

Nonlinear powers of vegetation components often were good predictors of avian community components. This finding supports arguments of several ecologists (Colwell and Futuyma 1971, Hurlbert 1971, Willson 1974, Dyer 1978) that species are not equally sensitive to all changes in a particular aspect of the habitat at all times. For example, in the habitat analysis, avian diversity from late summer to winter was greatly influenced by small changes in FHD at very high or very low FHD values but was influenced little by changes at intermediate values. The same is true of the relationship of summer avian densities to FHD.

IMPORTANCE OF SPATIAL AND TEMPORAL LEVELS

Comparing the outcomes of the two levels of analysis revealed several similarities. At both levels, foliage density and diversity measures usually loaded on separate components. Fall and winter community attributes were generally predictable, among both transects and habitats, as reflected by their correlation with VPCI. During periods of greatest migratory and dispersal activity (spring and fall), BPCIV of the transect analysis and BPCIII of the habitat analysis, loaded together in both analyses. More detailed comparison shows that BPCII of both analyses stressed the same attributes, summer and late summer density of birds. Also, the last component selected in both levels of analysis was one arranging sites by their summer BSD.

The two analyses were not wholly alike; at the transect level, richness measures consistently loaded with density measures, implying that many species were attracted to sites that also supported large populations of birds. This relationship was not found at the habitat level, where richness loaded instead with diversity. At the latter scale, differences because of the densities of a few species (i.e., doves and possibly other flocking species) must be the major source of between-habitat density differences. The greater regularity of density differences among transects, represented by the contribution of density measures to the first three components and diversity measures only to later components, was also not seen at the habitat level. Among habitat BPCs, I, III, and IV stressed diversity measures, and II, III, and V stressed density measures. Analysis at the habitat level stressed similarities among seasons much more than did that at the transect level.

Four of seven transect level components emphasized mainly community attributes of single seasons (BPCs III, V, VI, and VII), whereas, at most two of the habitat BPCs (V and VI) emphasized attributes of any single season.

When details of the factor structures are contrasted, differences abound. Fall and winter density variation was more predictable than diversity at the transect level, whereas, diversity was more predictable at the habitat level. Spring density and diversity loaded together at the transect level (BPCIII) but separately at the habitat level (BPCs III and IV). Summer and late summer community attributes were almost wholly independent of fall and winter attributes at the transect scale, but at the habitat scale, they were associated on at least two BPCs (I and IV).

With these numerous differences at two levels of inquiry, one may legitimately ask which is correct. The competition and selective pressures affecting individuals are better reflected by community properties at the local transect level. Responses by populations to environmental conditions are probably better tracked at a larger scale, as with our habitat inquiries. Some quite different patterns are seen at the two levels of inquiry. Studies should be designed with these scale factors in mind, and unwarranted generalizations should not be made across inappropriate leaps of scale (Wiens 1981).

It appears necessary that studies be conducted over at least an entire year, because patterns of community relationships differ substantially from season to season. In fact, other analyses (Anderson et al. 1981; Rice et al. 1981, 1983, in press) revealed substantial variation between years as well. Spatially, similar patterns of community organization were found in analyses by habitat and by individual transects, but the relative amount of variance attributable to biologically comparable individual components (e.g., BPCs arranging fall and winter density variations, BPCV in the habitat case, and BPCVI in the transect case) differed greatly. In short, there are no grounds for arguing that either pattern is more "real" than the other. Furthermore, the particular order in which PCs sort out should be interpreted cautiously.

Predictions were consistently better at the habitat level than at the transect level in terms of variance accounted for by bird community-vegetation regressions. The pooling process through which this data set was derived from the transect-by-transect data apparently averaged out much of the variability unrelated to bird-vegetation relationships. These gains apparently outweighed the fact that analyses at the transect level were much closer to the level of habitat selection being exercised by individual birds, which we thought initially might lead to greater precision in our bird-vegetation studies.

Our results are consistent with, but of course do not prove, theories stating that bird species face more severe ecological interactions in fall and winter than in spring and summer (Fretwell 1972). Our findings also imply that groups of species use structurally more complex habitats differently than simpler habitats. For example, the avian community of structurally complex, mature cottonwood-willow habitats consists of a group of resident insectivores, including Gila Woodpecker (*Melanerpes uropygialis*), Ladder-backed Woodpecker (*Picoides scalaris*), and Song Sparrow (*Melospiza melodia*). These species are ecologically well differentiated. During the breeding season, however, eight species of common and ecologically similar immigrants, including Yellow-billed Cuckoo, Northern Oriole (*Icterus galbula*), and Summer Tanager (*Piranga rubra*), among others, are superimposed on the resident community (Rosenberg 1981). In structurally simple type VI cottonwood-willow communities, however, the summer community is strongly dominated by Gambel's Quail (*Callipepla gambelii*), Mourning Dove (*Zenaida macroura*), and White-winged Dove, whose use of the habitats differs greatly from that of the resident insectivores, including Abert's Towhee (*Pipilo aberti*), Gila and Ladder-backed woodpeckers, and Verdin (*Auriparus flaviceps*) (Rice et al. 1983).

In addition to the effects of foliage structure, however, the dominant tree species of habitats play an important role in determining the properties of the communities. This role is illustrated by the consistently different positions of some habitats in arrangement of their bird communities. Importance of dominant tree species to avian community structure is contrary to the initial conjectures of MacArthur and MacArthur (1961), but supports recent findings by Rotenberry and Wiens (1980). Had we included the number of each dominant tree species, the shrub composition, and other special elements such as presence of mistletoe (*Phoradendron californicum*) fruit, which is a vital food for Phainopeplas in winter (Anderson and Ohmart 1978), we probably could have increased the amount of variance explained by measures of vegetation. The importance of these habitat attributes is being investigated in other analyses (Rice et al. 1983, unpubl. data).

LITERATURE CITED

ANDERSON, B .W., R. W. ENGEL-WILSON, D. WELLS, AND R. D. OHMART. 1977. Ecological study of southwestern riparian habitat: Techniques and data applicability, p. 146–155. *In* R. R. Johnson [ed.], Importance, preservation and management of riparian habitat. U.S. For. Serv. Gen. Tech. Rep. RM-43, Fort Collins, Colorado.

ANDERSON, B. W., AND R. D. OHMART. 1978. Phainopepla utilization of honey mesquite forests in the Colorado River valley. Condor 80:334–338.

ANDERSON, B. W., R. D. OHMART, AND S. D. FRETWELL. 1982. Evidence for social regulation in some riparian bird populations. Am. Nat. 120:340–352.

ANDERSON, B. W., R. D. OHMART, AND J. RICE. 1981. Seasonal changes in avian densities and diversities, p. 262–264. *In* C. J. Ralph and J. M. Scott [eds.], Estimating numbers of terrestrial birds. Stud. Avian Biol. No. 6.

COLWELL, R. K., AND D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

COOLEY, W. W., AND P. R. LOHNES. 1971. Multivariate data analysis. John Wiley and Sons, New York.

DYER, D. D. 1978. An analysis of species dissimilarity using multiple environmental variables. Ecology 59: 117–125.

EMLEN, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100:611–617.

EMLEN, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323–342.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Monogr. Popul. Biol. No. 5.

HURLBERT, S. H. 1971. The nonconcept of species diversity: A critique and alternative parameters. Ecology 52:577–586.

JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

MACARTHUR, R. H., AND R. LEVINS. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proc. Natl. Acad. Sci. U.S.A. 51:1207–1210.

MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42:594–598.

MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. Am. Nat. 100: 603–609.

MEENTS, J. K., B. W. ANDERSON, AND R. D. OHMART. 1981. Vegetation characteristics associated with Abert's Towhee numbers in riparian habitats. Auk 98:818–827.

MEENTS, J. K., B. W. ANDERSON, AND R. D. OHMART. 1982. Vegetation relationships and food of Sage Sparrows wintering in honey mesquite habitat. Wilson Bull. 94:129–138.

MEENTS, J. K., J. RICE, B. W. ANDERSON, AND R. D. OHMART. 1983. Nonlinear relationships between birds and vegetation. Ecology 64:1022–1027.

RICE, J., R. D. OHMART, AND B. W. ANDERSON. 1983. Habitat selection attributes of an avian community: A discriminant analysis investigation. Ecol. Monogr. 53:263–290.

RICE, J., R. D. OHMART, AND B. W. ANDERSON. In press. Turnovers in species composition of avian communities in contiguous riparian habitats. Ecology.

RICE, J. C. 1978. Ecological relationships of two interspecifically territorial vireos. Ecology 59:526–538.

RICE, J., R. D. OHMART, AND B. W. ANDERSON. 1981. Bird community use of riparian habitats: The importance of temporal scale in interpreting discriminant analysis, p. 186–196. *In* D. E. Capen [ed.], Proceedings of the use of multivariate statistics in studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87.

ROSENBERG, K. V. 1981. Breeding bird community organization in a desert riparian forest. M.Sc. thesis, Arizona State Univ., Tempe.

ROSENBERG, K. V., R. D. OHMART, AND B. W. ANDERSON. 1982. Community organization of riparian breeding birds: Response to an annual resource peak. Auk 99: 260–274.

ROTENBERRY, J. T., AND J. A. WIENS. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: A multivariate analysis. Ecology 61:1228–1250.

SMITH, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810–819.

WHITMORE, R. C. 1975. Habitat ordination of the passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:64–74.

WHITMORE, R. C. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89:253–265.

WIENS, J. A. 1976. Population responses to patchy environments. Annu. Rev. Ecol. Syst. 7:81–120.

WIENS, J. A. 1981. Scale problems in avian censusing, p. 513–521. *In* C. J. Ralph and J. M. Scott [eds.], Estimating numbers of terrestrial birds. Stud. Avian Biol. No. 6.

WILLSON, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017–1029.

The Center for Environmental Studies, Arizona State University, Tempe, Arizona 85287. Received 25 August 1981. Final acceptance 28 April 1983.