

BREEDING BIRD DISTRIBUTION IN CHIHUAHUAN
DESERT HABITATS

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ABSTRACT—During late spring and early summer of 1985, we studied community composition and distributional patterns of breeding birds on a bajada in southern New Mexico. Twenty-eight species were found, of which the 13 more common were examined in detail. We compared mean densities of all species among four transects and among three physiognomically distinct habitats. Comparisons between transects yielded a few significant differences that cannot be attributed to features of the habitat, but significant variation among habitats was found for most species. Bivariate correlations between bird abundances and vegetation suggested a positive relationship between grassland birds and an increase in plant cover in open areas and between scrub birds and the increase in diversity of plant life-forms. Similar relationships were found between the multivariate axes resulting from principal component analysis of plant-cover data and both bird species richness and diversity.

Since the early 1950s, the role of vegetation as a factor underlying structure and composition of avian communities has been widely recognized (Vander Wall and MacMahon, 1984). In the New World, several aspects of this relationship have been studied in a variety of ecological situations, including xeric environments such as the warm deserts of North America (Hensley, 1954; Dixon, 1959; Maze, 1966; Raitt and Maze, 1968; Austin, 1970; Tomoff, 1974; Raitt and Pimm, 1974, 1976; Whitmore, 1975; Vander Wall, 1980; Vander Wall and MacMahon, 1984). Nevertheless, with a few exceptions (Tomoff, 1974; Vander Wall, 1980; Vander Wall and MacMahon, 1984), studies of desert birds include mostly comparisons of habitats or vegetation types without analyzing in detail discrete variables contained within such broad ecological divisions.

In the Chihuahuan Desert, presence of gently sloping alluvial fans (bajadas) produces a range of microhabitats due to a gradient of soils from coarse alluvium at the base of mountains (Barbour et al., 1980) to clays and clay loam at the bottom of the watershed (W. Whitford, pers. comm.). As pointed out by Vander Wall and MacMahon (1984) for the Sonoran Desert, the short length of these gradients provides a unique opportunity to study the relationship of vegetation to distributional patterns of avian communities.

The aim of this study was to compare species composition and densities of the avian community in several major habitats along one of these bajadas. In addition, we sought to identify relationships between several vegetation components to the distribution and abundance of breeding birds along this elevational gradient.

MATERIALS AND METHODS—The study was conducted on the Long Term Ecological Research (LTER) enclosure located at the southern end of the Jornada del Muerto Plain in Dona Ana Co., New Mexico (32°30'N, 106°45'W); elevation ranges from about 1,420 to 1,480 m. The enclosure (approximately 150 ha) had been protected from grazing since 1981; it extended from the base of Summerford Mountain to the lowest part of its watershed (playa) and corresponded to one of the U.S. International Biological Program Desert Biome validation sites.

Visual inspection of the bajada revealed three major vegetation types: an upper grassland near the base of the mountain; a band dominated by creosotebush (*Larrea tridentata*) in the middle of the bajada; a lower band of open habitat dominated by forbs. Dominant perennial plant species in these habitats, respectively, were: *Bouteloua eriopoda*, *Erioneuron pulchellum*, and *Eragrostis lehmani*; *L. tridentata*; and *Xanthocephalum* sp., *Zinnia grandiflora*, *Sphaeralcea subhastata*, *Croton potsii*, *Cassia bauhinoidea*, and *Perezia nana* (G. Cunningham, pers. comm.).

We established four parallel transects along the ba-

jada. The middle two were the LTER permanent sampling lines, which were 70 m apart and contained 80 stations each, spaced 30 m. The other two transects were marked along the enclosure fences. The southeasternmost of those two transects (2,310 m) had 77 stations, and the other 65 (1,950 m).

To delimit the major habitats, we chose the stations for which there were gaps of ≤ 60 m without creosotebush cover as the upper and lower boundaries of the middle habitat. This procedure resulted in a total area for the three major habitats as follows: for the lower open habitat (basin slope), 43.74 ha; for the central bajada (creosotebush), 26.46 ha; for the upper grassland (piedmont), 11.34 ha.

We conducted 62 bird censuses from 16 May to 19 July 1985. The beginning of fieldwork was determined by the presence of territorial breeding birds and ended with the arrival of the first migrants and the dispersal of juveniles. We sampled two transects on every date, the order being inverted on subsequent dates. To avoid counting the same bird at more than one transect on the same date, an uncensused transect line was left between the two transects being surveyed on each date. The first census on a given date started immediately after sunrise (around 0600 h) and the second at about 0730 h. All censuses lasted approximately 60 min.

Birds seen within a 45-m perpendicular distance on either side of each transect were counted. Only birds that were actually using the habitats at the moment of the observation were recorded; passing individuals or flocks were ignored. Since visibility was exceptionally good in the area, we assumed that counts represented an accurate estimate of the total number of birds present, although some incubating birds may not have been detected during a census for some nests that were distant from the transects. However, most nests that were occupied during the survey were close enough to the transect line so that the observer could flush incubating birds during each census.

Vegetation measurements were made in late July and early August. At each station of the outside transects, we measured plant cover on a 30-m line perpendicular to the transect and centered on it (after Canfield, 1941). For the two LTER transects, similar cover measurements were taken and provided by personnel of the project.

We grouped all plants into grasses, forbs, cacti, and shrubs and also considered individually some species, namely *Yucca elata*, creosotebush, mormon tea (*Ephedra* sp.), and mesquite (*Prosopis glandulosa*). Means for all line-intercept variables were compared both between habitats and between transects by means of separate oneway analyses of variance, using pairwise least significant difference (LSD) comparisons on ranks established from the raw data. Habitat ordination was made by means of principal component analysis (PCA) for the line intercept based on 302 sampling points.

Mean bird densities were compared between habi-

tats also by the LSD method. Bird habitat selection was studied using Spearman rank correlations between abundance of particular species and vegetation variables along transects (after Rotenberry and Wiens, 1980). Habitat selection by birds was further investigated by ordination of bird species based on mean habitat vectors (after James, 1971, and Rotenberry and Wiens, 1980).

Bird species diversity was calculated for each habitat using Hill's (1973) numbers. All correlations and multivariate analyses were made using the Statistical Analysis System (SAS Institute Inc., 1985a, 1985b).

RESULTS—Comparison of Major Vegetation Types—Some variation of plant cover was found among transects (Naranjo, 1986). Most differences were due to unequal horizontal distribution of major habitats, so the transects can be considered a set of replicates.

In a comparison of means between habitats (Table 1), the basin slope was dominated by forbs and was intermediate in total plant cover. Shrub cover, mostly mormon tea, was lowest in this habitat. Grass cover also was high but intermediate to the other habitats. The middle part of the bajada had the highest shrub and creosotebush cover, and the lowest total plant and grass cover. The piedmont had the highest total cover, dominated by grasses, with intermediate forb cover, and the highest cover of cacti, yucca, and mesquite.

Habitat Ordination—The first three axes of the PCA explained 78.7% of the variability in the data set (Table 2). The first component reflected a gradient from sites with dense shrubs and much bare ground to sites dominated by grasses and forbs resulting in high total plant cover. The gradient can be viewed as a decrease in patchiness of plant life forms as, for example, from the creosotebush band to the basin slope.

The second component reflected a gradient of increase in creosotebush and a decrease in both grasses and forbs, showing an increase in patchiness of the vegetation. Sites with high scores on this axis were either at the middle of the bajada or near arroyos.

Because of the high loadings on the third component of both cacti and mesquite, plants that typically are found in scattered clumps or patches across the area, this axis reflected the spatial heterogeneity (patchiness) of the habitat. The relatively high positive loading of forbs suggests that this gradient represents change in vegetation with

TABLE 1—Mean values of vegetation variables on each habitat. Within rows, means with the same letter are not significantly different ($P > 0.05$).

Variable	Plant cover (cm)		
	Basin slope	Creosote-bush	Piedmont
Grasses	433.0 B	184.6 C	1,061.4 A
Forbs	1,044.0 A	433.0 B	529.0 B
Cacti	0.8 B	7.8 B	78.3 A
Yucca	15.3 B	9.7 B	44.7 A
Creosote	14.1 B	726.1 A	22.5 B
Mesquite	3.6 B	6.1 B	29.3 A
Mormon tea	58.3 A	22.4 B	68.9 A
Total shrubs	76.3 C	758.7 A	171.6 B
Total cover	1,557.4 B	1,385.2 C	1,850.0 A

increasing distance from the base of Summerford Mountain.

From these interpretations, we conclude that, in spite of some local variation, the origins of the three axes roughly correspond, respectively, to the creosotebush, the basin slope, and the piedmont.

Bird Species Composition, Distribution, and Abundance—Twenty-eight species of birds were included in the sample (Table 3), of which only 11 were confirmed as breeding on the bajada. Some species were clearly visitors from neighboring habitats: the rocky slopes of Summerford Mountain (Say's phoebe, rock wren, canyon wren, canyon towhee, rufous-crowned sparrow) or areas with some tree cover or dense mesquite, such as the neighboring New Mexico State University College Ranch headquarters and the playa fringe (Gambel's quail, ladder-backed woodpecker, western wood-pewee).

For more detailed analyses, we chose the 13 species that were found with an overall frequency of at least 24%. In general, densities of birds were low but consistent enough to permit inferences on habitat preferences for most species (Table 4).

The only species found exclusively in only one habitat were rufous-crowned sparrow in the piedmont and eastern meadowlark in the basin slope. All other species were distributed throughout the habitats, but most showed a definite peak of abundance in a particular habitat or a gradual decrease along the bajada, e.g., ash-throated flycatcher and house finch.

Black-throated sparrow was the only species to reach its highest densities in the creosotebush band; the other species occurred in very low num-

TABLE 2—Factor loading of the line intercept principal components; only factors with eigenvalues >0.9 are shown.

Variable	Component		
	I	II	III
Grass cover	0.41	0.16	0.38
Forb cover	0.39	-0.23	-0.49
Shrub cover	-0.37	0.52	-0.16
Cacti cover	0.08	0.20	0.64
Creosote cover	-0.40	0.47	-0.20
Mesquite cover	0.08	0.19	0.25
Total cover	0.43	0.42	-0.20
Bare ground	-0.43	-0.42	0.20
Eigenvalue	3.11	2.01	1.18
Proportion	0.39	0.25	0.15
Cumulative	0.39	0.64	0.79

bers in this habitat. The basin slope was the habitat with highest densities of scaled quail, mourning dove, western kingbird, northern mockingbird, loggerhead shrike, and eastern meadowlark; their mean densities in this area were significantly different from those in other habitats. Mean densities of cactus wren and Scott's oriole were not significantly different among habitats.

Habitat Preference—Calculation of Spearman rank correlation coefficients for the 302 sampling stations, using mean bird densities and vegetation measurements, yielded a total of 38 significant correlations for 11 species of birds (30% of all possible correlations; Table 5), and densities of both cactus wren and northern mockingbird did not have any significant correlation with measured variables. Based on these correlation coefficients, the community can be divided initially into open-habitat and scrub birds. The first group included scaled quail, mourning dove, western kingbird, eastern meadowlark, and rufous-crowned sparrow, species which had significant negative correlations with shrubs, creosotebush, or both. Densities of ash-throated flycatcher, crissal thrasher, Scott's oriole, and black-throated sparrow correlated significantly and positively with the same variables, and these species can be considered scrub birds. Abundances of loggerhead shrike and house finch were correlated with variables other than shrubs and creosotebush, indicating preferences for sites with specific plant characteristics (respectively, presence of tall yuccas and dense grass cover).

TABLE 3—Frequencies, common and scientific names, and species' codes of birds recorded on the study area. Nomenclature and sequence follows the A.O.U. checklist, 6th edition (1983).

Common name	Scientific name	Code	Frequency ²
American kestrel	<i>Falco sparverius</i>		1.6
Scaled quail ¹	<i>Callipepla squamata</i>	SCQU	51.0
Gambel's quail	<i>Callipepla gambelii</i>		3.2
Mourning dove	<i>Zenaida macroura</i>	MODO	79.0
Greater roadrunner	<i>Geococcyx californianus</i>		6.4
Lesser nighthawk ¹	<i>Chordeiles acutipennis</i>		6.4
Ladder-backed woodpecker	<i>Picoides scalaris</i>		1.6
Western wood-pewee	<i>Contopus sordidulus</i>		1.6
Say's phoebe	<i>Sayornis saya</i>		9.6
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>	ASHT	32.0
Western kingbird ¹	<i>Tyrannus verticalis</i>	WEKI	88.0
Horned lark	<i>Eremophila alpestris</i>		6.4
Cactus wren ¹	<i>Campylorhynchus brunneicapillus</i>	CAWR	83.0
Rock wren ¹	<i>Salpinctes obsoletus</i>		8.0
Canyon wren	<i>Catherpes mexicanus</i>		3.2
Black-tailed gnatcatcher	<i>Poliophtila melanura</i>		4.8
Northern mockingbird ¹	<i>Mimus polyglottos</i>	MOCK	87.0
Crissal thrasher	<i>Tyrannus dorsale</i>	CRTH	24.0
Loggerhead shrike ¹	<i>Lanius ludovicianus</i>	LOSH	45.0
Pyrrhuloxia	<i>Cardinalis sinuatus</i>		3.2
Canyon towhee	<i>Pipilo fuscus</i>		9.6
Rufous-crowned sparrow ¹	<i>Aimophila ruficeps</i>	RUCR	27.0
Chipping sparrow	<i>Spizella passerina</i>		3.2
Black-throated sparrow ¹	<i>Amphispiza bilineata</i>	BLTH	100.0
Eastern meadowlark	<i>Sturnella magna</i>	EAME	24.0
Brown-headed cowbird	<i>Molothrus ater</i>		13.0
Scott's oriole ¹	<i>Icterus parisorum</i>	SCOR	75.0
House finch ¹	<i>Carpodacus mexicanus</i>	HOFI	45.0

¹ Either active nests or fledglings observed.

² Frequency = (trips on which species was observed ÷ total number of censuses) × 100.

The low values of the coefficients in all cases suggest that each vegetation variable per se is not a strong predictor of abundances of birds and that an additional set of variables may be needed to support inferences of breeding-habitat preferences of birds in the Chihuahuan Desert. For this reason, another correlation analysis was done using mean bird densities for groups of five stations (1.35 ha) and yucca variables (Naranjo, 1986). Of 117 possible correlations, only nine (7.7%) were significant, suggesting some might be due to chance alone. However, the positive, significant correlations of cactus wren with four of nine yucca variables can be indications of definite preferences of this bird for particular features of the habitat.

Additional confirmation of habitat preferences was achieved by ordination of locations of birds. Using the ordination space previously created for

the sampling sites (based on vegetation measurements alone), mean values for all variables at the sites where each species was present were incorporated into the PCA equation to calculate species scores. Following this procedure, the 13 species were ordinated on the line intercept variables (Fig. 1).

Along the first principal component (gradient of decreasing creosotebush cover), the species were scattered in a manner that supports the separation of two subsets of the community based on the previous correlation analyses. From left to right, the desert-scrub species are replaced by the open-habitat birds, but the two groups are not distinctly separated.

The short range of variation along the second axis occupied by birds in comparison with the total range of variation of the site scores (−3.09 to 4.75), as well as the lack of any definite pattern

TABLE 4—Comparisons of mean densities of birds between the three major habitats. Mean density = number of birds per hectare; for each species, means with same letters are not significantly different ($P > 0.05$).

Species ¹	Basin slope		Creosote		Piedmont	
	Mean	SD	Mean	SD	Mean	SD
SCQU	0.12 A	0.33	0.00 B	0.00	0.04 B	0.12
MODO	1.41 A	1.70	0.33 B	0.48	0.18 B	0.31
ASHT	0.01 B	0.03	0.04 AB	0.08	0.11 A	0.23
WEKI	0.26 A	0.15	0.08 B	0.25	0.04 B	0.09
CAWR	0.11 A	0.08	0.02 A	0.07	0.23 A	0.40
MOCK	0.15 A	0.09	0.05 B	0.11	0.05 B	0.13
CRTH	0.02 A	0.03	0.02 A	0.07	0.03 A	0.11
LOSH	0.05 A	0.08	0.02 B	0.07	0.01 B	0.06
RUCR	0.00 B	0.00	0.00 B	0.00	0.24 A	0.49
BLTH	0.51 B	0.71	0.57 A	0.44	0.59 B	0.52
EAME	0.01 A	0.03	0.00 B	0.00	0.00 B	0.00
SCOR	0.13 A	0.11	0.12 A	0.26	0.08 A	0.23
HOFI	0.00 C	0.00	0.06 B	0.14	0.08 A	0.20

¹ See Table 3 for species' codes.

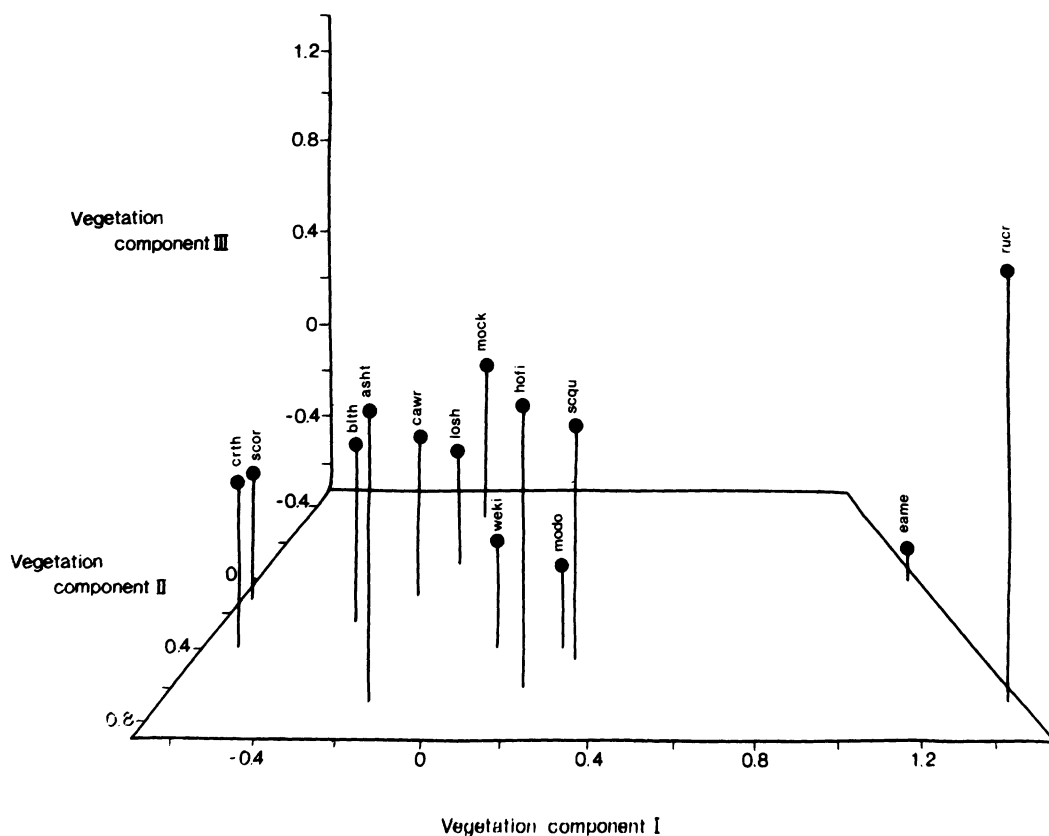


FIG. 1—Bird-species ordination based on mean vegetation vectors; axes are interpreted in the text. See Table 3 for species' codes.

TABLE 5.—Significant Spearman correlation coefficients for mean densities of birds versus plant cover. Variable codes as follow: EPHEd = *Ephedra* sp., LARRE = *Larrea tridentata*, PROSO = *Prosopis glandulosa*, Shrub = total shrub cover, Total = total plant cover, BAREC = bare ground. In all cases, $n = 302$ and $P < 0.05$.

Bird	Plant cover									
	Grass	Forbs	Yucca	Cacti	EPHEd	LARRE	PROSO	Shrub	Total	BAREC
Scaled quail						-0.14		-0.16		
Mourning dove	0.18	0.25				-0.27		-0.34		
Ash-throated flycatcher	0.11	-0.17	0.13	0.14			0.20	0.16		
Western kingbird			0.14			-0.17		-0.17		
Crissal thrasher								0.18		
Loggerhead shrike			0.14	-0.12						
Rufous-crowned sparrow	0.34	-0.18		0.24	0.15	-0.11			0.18	-0.18
Black-throated sparrow		-0.27				0.27		0.26		
Eastern meadowlark	0.20	0.12			-0.12			0.14		-0.14
Scott's oriole	-0.16				0.21					
House finch	0.13	-0.15					0.20			

in the distribution of the different species along it, makes this axis more difficult to interpret. However, the closeness of species scores to the middle of the axis might indicate a choice of sites where the vegetation includes more than only creosotebush.

Five species are clearly separated from the others on the third component. Scaled quail, ash-throated flycatcher, house finch, and rufous-crowned sparrow reached high values on this gradient of increasing spatial heterogeneity and cover of both mesquite and cacti. Eastern meadowlark, having the lowest score on this axis, also separated from the rest of the community.

A Spearman rank correlation analysis between mean bird densities and site factor scores (Table 6) was conducted to obtain additional confirmation of the relationships between the multivariate ordination axes and bird abundances (after Rotenberry and Wiens, 1980). Of 39 possible correlations, 18 (51.2%) were significant. Only densities of cactus wren, crissal thrasher, and loggerhead shrike were not correlated with the ordination axes. The second component alone (gradient of increasing creosote cover) contributed to variation in abundance of eight species of birds, while the other two explained variation of five species each (three in common).

DISCUSSION—Species Composition, Distribution, and Abundance—Species composition along the bajada was very similar to that found in previous studies on sites in the Chihuahuan Desert (Dixon, 1959; Maze, 1966; Raitt and Maze, 1968; Raitt and Pimm, 1974, 1976; Reitzel, 1982; Pieper et al., 1983). The high proportion of grassland species in this area is attributable to the continuity of the bajada with typical desert grassland. As several authors have noted (Raitt and Pimm, 1974, 1976; Meents, 1979; Pieper et al., 1983), during summer, the avifauna of the Chihuahuan Desert scrub is more similar to that of the desert grassland than to those of other North American warm deserts. The low abundances of all species in our study also agree with previous studies, and, thus, we can consider the Chihuahuan Desert as depauperate when compared to more complex North American ecosystems.

Not only were most avian species widely distributed across the study area in all three main habitat types, but active nests of several species were likewise found in a variety of situations in each habitat. This contrasts with the observation

TABLE 6—Spearman correlation coefficients for mean densities of birds versus factor scores of sites (principal component analysis based on plant-cover data); only significant correlations are shown ($n = 302$).

Species	Principal component		
	I	II	III
Scaled quail		-0.12*	
Mourning dove	0.17*	-0.32***	
Ash-throated flycatcher		0.17**	0.17**
Western kingbird		-0.15**	
Northern mockingbird		-0.15**	
Rufous-crowned sparrow	0.21***	0.18**	0.28**
Black-throated sparrow	-0.16**	0.23***	0.12*
Eastern meadowlark	0.17**		-0.17**
Scott's oriole	-0.18**		
House finch		0.19***	0.11*

* $P \leq 0.05$.
 ** $P \leq 0.025$.
 *** $P \leq 0.001$.

of Raitt and Maze (1968) who found that nests of all birds but mourning dove, lesser nighthawk, and black-throated sparrow were restricted to arroyo habitats. An explanation for such a striking difference between two areas, which are not very far apart, is, undoubtedly, related to the presence of clumps of mesquite and widespread yuccas in our study area. Those plants were confined to arroyos in the study area of Raitt and Maze (1968).

Habitat Preferences—The artificial separation of two subsets of the community agreed with data from other studies. With the exception of rufous-crowned sparrow, our open habitat birds have been considered as typical components of grassland habitats (Pieper et al., 1983), and their presence on the bajada can be due either to occasional visits to scrub areas or irregular nesting in scrub. All scrub birds so classified by our analyses are more representative of the Chihuahuan Desert scrub proper (Dixon, 1959). Correlations of the densities of ash-throated flycatcher and Scott's oriole with shrub cover agree with those found by Vander Wall and MacMahon (1984), who explained these relationships in terms of increased food availability. The preference for sites with dense creosotebush by black-throated sparrow has been extensively documented by previous studies (Raitt and Maze, 1968; Delesantro, 1978), and that of crissal thrasher for sites with dense shrubs may be related to nest-site availability, as suggested for the curve-billed thrasher (*Toxostoma curvirostre*) by Vander Wall and MacMahon (1984).

Positive correlations among most yucca variables with densities of the cactus wren clearly show a preference for sites with large, mature yuccas that offer enough structural complexity to serve as both nesting sites and feeding places. Further, of 13 nests of the cactus wren found in the study area during this breeding season, all but two were built on yuccas (Naranjo, 1986). This suggests that a lack of suitable nest sites could limit the distribution of this species, as noted by Vander Wall and MacMahon (1984) along a Sonoran Desert bajada. The positive correlation between density of Scott's oriole and number of inflorescences per clump also can be easily understood, since this bird is frequently found feeding on the inflorescences of *Yucca elata*, and usually nests on this plant (Naranjo, 1986).

In the bird ordination, eastern meadowlark and rufous-crowned sparrow were outliers on the first axis (Fig. 1), which is additional evidence that they are occasional visitors from other habitats. The fact that "desert grassland" species are not clearly separated on this ordination axis from more typical desert birds is another indication of the similarity between these two habitats in terms of bird community composition, as noted by Pieper et al. (1983).

The high score of scaled quail on the third axis of PCA agrees with Ligon's (1961) statement that the distribution of this bird is similar to that of mesquite and that it often nests under cacti. The high scores of ash-throated flycatcher, house finch, and rufous-crowned sparrow support Raitt and Maze's (1968) consideration of these species as

breeders of complex desert habitats, such as floodplain thickets and mouths of mountain canyons. Finally, the separation on this axis of eastern meadowlark is consistent with its widespread occurrence in grasslands (Wiens and Dyer, 1975).

The many correlations among abundances of birds and ordination axes (Table 6) strongly indicate preferences of breeding birds for particular habitats along the bajada. These findings agree with those of Rotenberry and Wiens (1980) that a change in horizontal heterogeneity of the vegetation determines a clearcut separation between prairie and scrub birds.

Species Diversity—The interpretation of the community as subdivided into two major groups occupying distinct habitats was further supported by significant correlations between bird species diversity (BSD) and both vegetation variables and ordination axes (Naranjo, 1986). Following Rotenberry and Wiens (1980), Naranjo (1986) obtained positive, significant correlations between indices of BSD and both the first and third principal components of the vegetation ordination. The correlations with the first component (gradient of decreasing patchiness) represent the increase in abundance of grassland birds as cover of both forbs and grasses increases. Correlations with the third component (gradient of increasing heterogeneity of the vegetation) seem contradictory with this interpretation, but variation of bird species composition from point to point indicate increasing densities of scrub and mountain birds as vegetation increases in complexity. In addition, Naranjo (1986) found that bird species richness was positively correlated with both number of equally abundant and very abundant shrubs. This means that the bird community has more species as the habitat increases in patchiness, as predicted by the model of MacArthur et al. (1962) and supported by findings of strong correlations between avian abundances and gradients of both physiognomy and floristic composition of the vegetation on the horizontal plane (Wiens, 1974; Rotenberry and Wiens, 1980; Vander Wall, 1980; Rotenberry, 1985).

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