COMMUNITY ORGANIZATION OF RIPARIAN BREEDING BIRDS: RESPONSE TO AN ANNUAL RESOURCE PEAK

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ABSTRACT.—Spatial distribution, foraging behavior, and diets of 12–13 insectivorous bird species were measured during two breeding seasons in a cottonwood- and willow-dominated riparian forest in Arizona. Spatially, no negative associations existed between any species in either year. Although foraging behavior varied considerably, diets overlapped broadly, even between members of different foraging guilds. Eight species preyed heavily on cicadas (38–80% of diet). Sampling of emerging cicadas in cottonwood-willow habitat indicated that numbers exceeded the metabolic needs of the bird community by as much as tenfold. Peak cicada numbers coincided with fledging young in all eight species. We propose that this seasonally superabundant and predictable resource permits coexistence without niche segregation and may, in part, explain the high density and diversity of ecologically similar breeding birds in desert riparian communities. It appears that niche variables such as bill shape and foraging behavior may not be true predictors of actual resource use within a community. Assumptions of resource-based interspecific competition among breeding birds are not supported. *Received 4 May 1981, accepted 1 October 1981.*

AMONG the forces that operate to shape and maintain patterns of avian community organization, competition for limited resources (e.g. food) has been frequently invoked as a primary selective force (MacArthur 1972, Cody 1974, Cody and Diamond 1975). Such competition has rarely been unequivocally demonstrated for birds. An essential assumption behind competition theory is that resources are in short supply. Although White (1978) argued that all organisms are limited by an inadequate supply of nitrogenous foods, this has not been properly demonstrated for many bird communities. Recently, strong criticism of the application of competition theory in community ecology has been expressed (Wiens 1977, Conner and Simberloff 1979), and older arguments against competition are not resolved (e.g. Andrewartha and Birch 1954).

Measurements of avian diets are lacking in most community studies involving resource use. Instead, diets are most often inferred from morphological (Schoener 1974, Hespenheide 1975) or behavioral measures (MacArthur 1958, Cody 1974, Rabenold 1978). The few studies that have examined actual resource use emphasized the inadequacies of such inferences and have not supported the premises of the competition argument (e.g. Wiens and Rotenberry 1979, Rotenberry 1980a). Furthermore, resource-availability patterns are poorly known in even the most well-studied communities.

In the deserts of western North America, riparian forests (the alluvial floodplain and its attendant vegetation) have been shown to be of great ecological importance to bird populations (Carothers et al. 1974, Anderson and Ohmart 1977, Stamp 1978). These ecosystems typically support extremely high densities and diversities of breeding bird species and provide vegetationally and geographically well-defined systems for study.

Riparian systems, like other temperate forests, undergo marked seasonal changes in primary and secondary productivity. It might be predicted that the avian community present during the period of peak productivity would be structured in part by aspects of that resource peak.

We studied an avian community on a large riparian forest plot over two complete breeding seasons. The general approach of the study was to examine densities, microhabitat preferences, foraging behaviors, and diets of all diurnal insectivorous species on the plot. This report documents a response within this bird community to a summer resource peak and discusses the evolutionary consequences of

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this response in light of existing community theory.

METHODS

Study area.—A 20-ha plot was established in a continuous forest stand along the Bill Williams River near its delta at Lake Havasu in Yuma County, Arizona, elevation 100 m. The dominant tree species are cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*), with a patchy understory of exotic salt cedar (*Tamarix chinensis*), cattails (*Typha latifolia*), and bulrushes (*Scirpus* spp.). Daily temperature varied from −6°C to 33°C in early spring, and from 8°C to 43°C in summer. Other details are described in Rosenberg (1980).

Density and breeding phenology.—We gridded the 20-ha plot at 20-m intervals with surveyor's tape and marked each grid point with a coordinate number. Detections of all territorial breeding species were recorded on daily field maps from January through July 1977 and February through August 1978. We gave special attention to locating nests, following known pairs, and determining territorial boundaries. All parts of the grid received approximately equal coverage. We determined the number of pairs and the relative territory size from the composite of field maps for each season.

In addition, we assigned each bird detection its closest grid coordinate number from the daily field maps. Totals of 1,482 bird detections in 1977 and 1,800 detections in 1978 of 12 species were used in this analysis. Associations between pairs of bird species were tested separately for each season based on the frequency of co-occurrence at each of the 281 points. The Cramer's V statistic was calculated as:

$$V = \frac{ad - bc}{(mnrs)^{\frac{1}{2}}},$$

where a, b, c, and d are the observed cells of a 2 × 2 contingency table, and m, n, r, and s are the row and column totals, respectively (Pielou 1977: 201). This is essentially a correlation coefficient and its significance was tested by simultaneously computing "χ^2," which approximates a Chi-square distribution with one degree of freedom.

Foraging behavior.—We observed foraging by birds on the study plot and in similar forest stands along the Bill Williams River. A foraging observation was defined as an actual attempt to procure prey, and we recorded the following data for each observation: bird species, foraging method, height of bird in tree, tree species, tree height, branch diameter, portion of tree, substrate from which prey was captured, and type of prey (if observed). All states of foraging measures are listed and defined in the Appendix. A total of 2,122 observations of 12 species was included in this analysis.

Frequencies and proportions of all states of all foraging measures were computed by subprogram CROSSTABS in SPSS (Nie et al. 1975). We present data for the two seasons combined.

The degree of overlap between species pairs (i, j) for each foraging measure was calculated as:

$$O_a = \frac{\Sigma\, p_{ia} p_{ja}}{(\Sigma\, p^2_{ia})(\Sigma\, p^2_{ja})},$$

where p_{ia} and p_{ja} are the proportional use of resource state "a" by species i and j, respectively (Pianka 1974, May 1975).

To assess the combined effects of overlap in several foraging measures, two additional matrices were computed. The first represents the total overlap in foraging behavior and is the average of overlaps for each species pair in foraging method, substrate, and branch diameter. Because these measures were reasoned to be correlated, the summation-alpha approach (Cody 1974) appeared satisfactory. Similarly, the second matrix represents the total overlap in foraging space and is the average of overlaps in use of tree species and tree portion multiplied by the overlap in foraging height. The use of product-alpha (Cody 1974) seemed appropriate in the case of foraging height, because this measure introduced conditions that were independent of other space measures, i.e. two species that did not overlap in foraging height could not overlap in overall foraging space. The hazards of this approach were discussed by May (1975), but these matrices seemed to represent a realistic approximation of the patterns of similarity within this bird community. We performed a group average clustering on these matrices to construct dendrograms for visual display (Cody 1974).

To test for actual differences between species for each foraging measure, we compared the distributions of the state frequencies of each measure for goodness-of-fit using G_H (Sokal and Rohlf 1969: 575). The lack of a significant difference between two species is assumed to imply a biologically important overlap. When the statistical significances associated with different degrees of overlap between species are compared directly, the biological relevance of each approach can be assessed.

Diet/morphology.—During July and August 1978, 106 birds of 13 species were collected from riparian forest stands similar to the study plot, and their esophagi and stomachs were immediately preserved in a formalin solution. We recorded age, sex, weight, bill size (exposed culmen, depth, and width), wing chord, fat condition, and condition of molt for each specimen. A reference series of skins was prepared.

Esophageal and stomach contents were dried and weighed, and their volumes determined. Length, frequency, and percent-volume of each individual prey item were recorded. All arthropod prey were identified to order and many were identified to family. Identifiable insect parts contributed to the percent-volume of that category but not to its frequency.

TABLE 1. Densities and breeding characteristics of 13 species of birds on a riparian forest plot. Species names are followed by abbreviations used in subsequent tables and figures. Density is based on estimates from two breeding seasons. Solid line indicates duration of stay; F indicates timing of fledging of broods.

			Breeding chronology							
Species	Code	Density (n/40 ha)	January	February	March	April	May	June	July	August
Yellow-billed Cuckoo *(Coccyzus americanus)*	YC	28–30					—	—	F	—
Common Flicker *(Colaptes auratus)*	CF	2–4	—	—	—	—	F	—	F	—
Gila Woodpecker *(Melanerpes uropygialis)*	GW	36–40	—	—	—	—	F	—	F	—
Ladder-backed Woodpecker *(Picoides scalaris)*	LW	28–36	—	—	—	—	F	—	—	—
Wied's Crested Flycatcher *(Myiarchus tyrannulus)*	WF	20–24					—	F	—	—
Ash-throated Flycatcher *(Myiarchus cinerascens)*	AF	4–6		—	—	—	F	—	F	—
Verdin *(Auriparus flaviceps)*	VN	20–24	- -	- -	- -	—	—	F	F	—
Common Yellowthroat *(Geothlypis trichas)*	YT	80				—	F	F	—	—
Northern Oriole *(Icterus galbula)*	NO	64–80		—	—	—	F	F	F	—
Summer Tanager *(Piranga rubra)*	ST	24				—	—	F	F	—
Blue Grosbeak *(Guiraca caerulea)*	BG	4				—	—	F	—	—
Abert's Towhee *(Pipilo aberti)*	AT	50–56	—	—	F	F	—	F	F	—
Song Sparrow *(Melospiza melodia)*	SS	80–100	—	—	—	F	—	—	F	—

Unidentified parts were not included in volumetric analysis.

The importance of selecting relevant categorical divisions in the computation of diet diversity and overlaps has been emphasized by Hespenheide (1975) and others. Because a majority of insect orders shows consistent features of form, habit, and catchability, this level was used in most cases to group prey items in this study. A few families (e.g. Cicadidae), which were frequently identified and were considered sufficiently different from others in their order, comprised distinct categories. We considered soft-bodied larvae of several orders as one group and all spiders as another. Overlap matrices were prepared for all species pairs, as described. We also grouped prey items into 10-mm size classes for computation of prey size overlaps, as above. The G_H statistic was used to test for differences in the mean prey-size and prey-taxa frequency distributions of each species pair, as was done for foraging measures. Percent-volume data were not appropriate for such comparisons.

From the morphological measurements, the ratio of the values of each measure for any pair of species was used as an index of similarity. Overall morphological similarity for each species pair was the average of the similarity values for each measure. We performed group average clustering on the matrix of similarity values, as for foraging overlaps.

RESULTS

Density amd breeding phenology.—Table 1 lists the breeding densities (n/40 ha) and summarizes the breeding biology for the 13 species in this study. Densities were nearly identical

TABLE 2. Summary of spatial associations among 12 riparian bird species in 1977 and 1978. + = significant positive association (Cramer's V; $P < 0.05$); ○ = no association; n = number of grid points where a species occurred each season. Species codes from Table 1.

			1977											
	n		108	152	99	109	22	46	49	136	143	24	25	72
	n	Species	YC	GW	LW	WF	AF	VN	YT	NO	ST	BG	AT	SS
	72	YC		○	○	○	○	○	○	+	○	○	○	○
	144	GW	○		+	+	+	○	○	○	○	+	○	○
	133	LW	○	+		○	○	○	○	○	○	○	○	○
	114	WF	+	+	○		○	+	+	○	○	○	+	○
1	38	AF	○	○	○	○		+	○	○	○	○	○	○
9	32	VN	○	○	○	○	+		○	○	○	○	○	○
7	93	YT	+	+	+	○	○	○		○	+	○	○	○
8	148	NO	○	+	+	+	○	○	+		○	○	○	○
	95	ST	+	○	○	○	○	○	+	○		○	○	○
	11	BG	○	○	○	○	○	○	○	○	○		○	○
	84	AT	○	○	○	○	○	○	○	+	○	○		○
	136	SS	○	○	○	+	○	○	○	+	○	○	○	

in both seasons and are presented as a range of values, representing breeding adults. Five species were permanent residents on the plot. The Verdin (*Auriparus flaviceps*) is a resident in the region but was only a summer visitor to the study area. All species except the Common Flicker (*Colaptes auratus*) nested on the plot. Flickers used saguaro cacti (*Carnegiea gigantea*) in the adjacent desert for nesting but regularly foraged in the riparian forest. This species, however, was not detected frequently enough on the plot to be included in the spatial analysis.

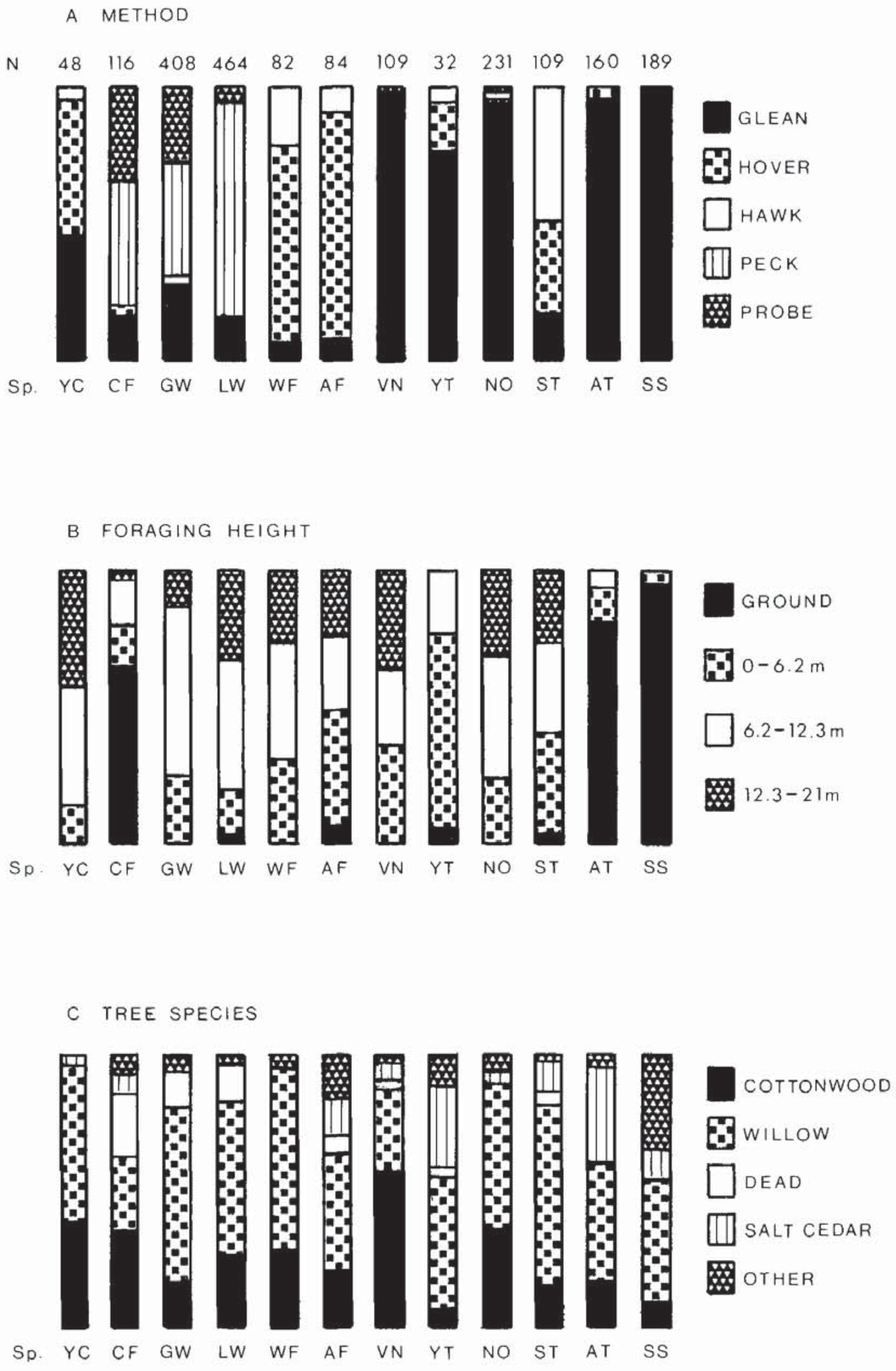
If bird species were dividing space so that they were avoiding or in some way excluding one another, species pairs should have occurred together less frequently than by chance in a given season. No significant negative associations were found for any species pair in either year (Table 2). Nine significant positive associations were found in 1977, however, and 16 in 1978. With 66 comparisons, as many as four positive and four negative associations would be expected if the species were distributed at random with respect to one another (Kirk 1968: 197). It can be concluded, then, that there was a tendency for some species such as cavity nesters to be clumped together on the plot, although the pattern of positive association was not consistent.

Foraging behavior.—Species-specific use patterns for each foraging measure are illustrated in Fig. 1. Qualitatively, three major functional groupings of species were recognized. These groups may be termed foraging guilds (Root 1967).

The two species of woodpeckers foraged primarily on bark, on larger branches (e.g. trunks), and in the inner portion of trees. Abert's Towhees (*Pipilo aberti*) and Song Sparrows (*Melospiza melodia*) foraged on the ground. The Common Flicker foraged primarily like other woodpeckers, but it also fed on the ground.

The remaining seven species can be generally grouped into a canopy-feeding guild. All tended to use leaves as a substrate and to feed on the outer portions of trees. This group can be divided further into specialist gleaners [Verdin, Common Yellowthroat (*Geothlypis trichas*), and Northern Oriole (*Icterus galbula*)] and those that tend to hover or hawk for prey [Yellow-billed Cuckoo (*Coccyzus americanus*), two flycatchers, and Summer Tanager (*Piranga rubra*)]. Sufficient foraging data for the Blue Grosbeak (*Guiraca caerulea*) were not obtained. Anecdotal observations, however, suggest that this species also hovered and gleaned from foliage.

Average niche overlaps and their associated levels of statistical significance between all species pairs for each measure were presented by Rosenberg (1980). A summary of these relationships is presented in Table 3. In general,


A METHOD
N 48 116 408 464 82 84 109 32 231 109 160 189
Sp. YC CF GW LW WF AF VN YT NO ST AT SS
GLEAN
HOVER
HAWK
PECK
PROBE
B FORAGING HEIGHT
Sp. YC CF GW LW WF AF VN YT NO ST AT SS
GROUND
0−6.2 m
6.2−12.3 m
12.3−21 m
C TREE SPECIES
Sp. YC CF GW LW WF AF VN YT NO ST AT SS
COTTONWOOD
WILLOW
DEAD
SALT CEDAR
OTHER

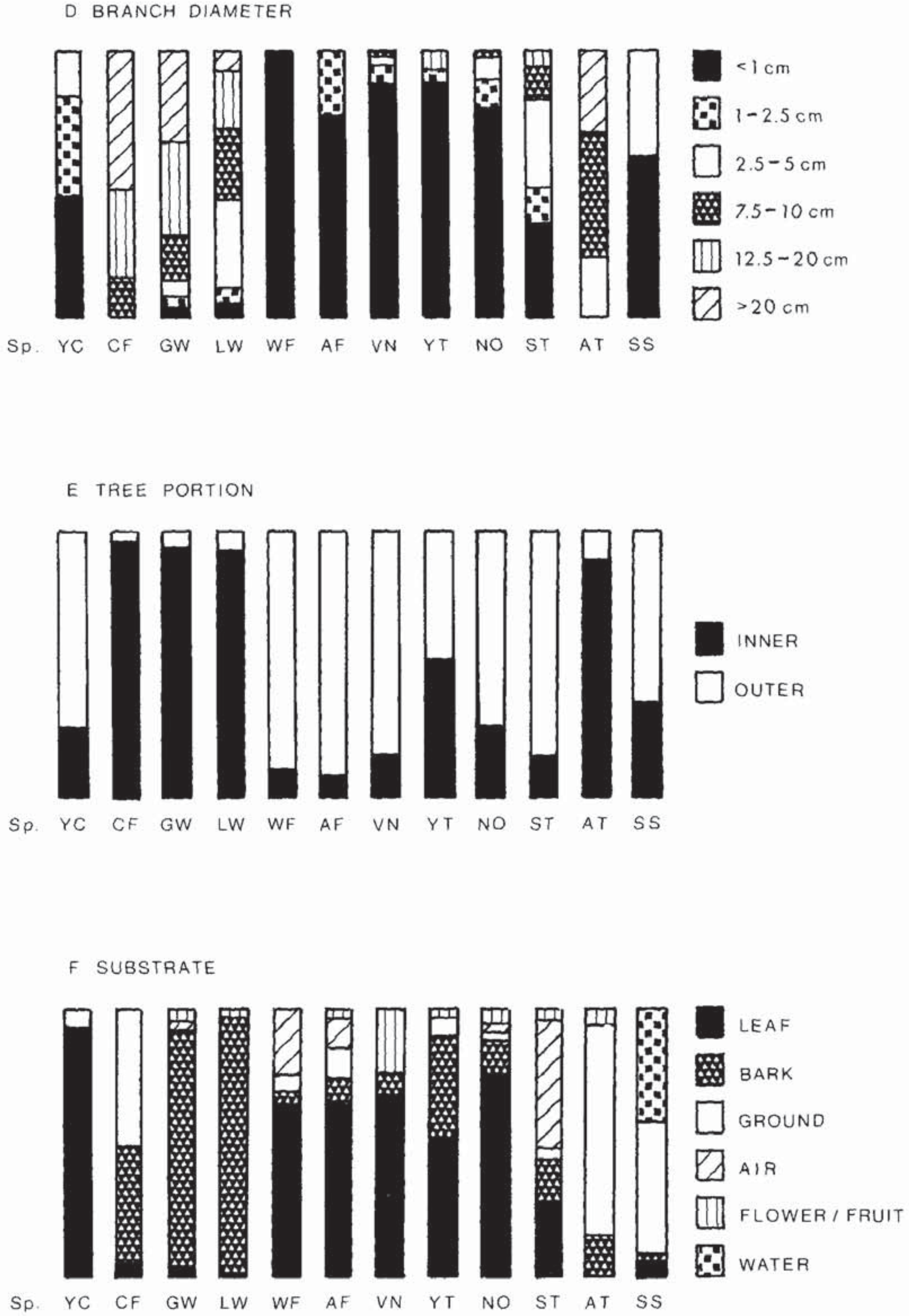


Fig. 1. Foraging behavior of 12 riparian birds for six measures (A–F). Bars indicate percentage of observations. Sample size (N) applies to all measures. Species codes from Table 1.

TABLE 3. A demonstration of the lack of significant differences among 12 riparian birds on three measures of foraging behavior (above diagonal) and three measures of foraging space (below diagonal). M = method, B = branch size, S = substrate, H = height, T = tree species, P = tree portion. Species codes from Table 1.

Species	YC	CF	GW	LW	WF	AF	VN	YT	NO	ST	AT	SS
YC		—	—	—	BS-	BS-	S—	BS-	BS-	B—	—	—[a]
CF	—		MB-	—	—	—	—	—	—	—	—	—
GW	—	P—		S—	—	—	—	—	—	—	—	—
LW	HT-	P—	HTP		—	—	—	—	—	—	—	—
WF	HTP	—	H—	H—		MBS	B—	B—	B—	—	—	—
AF	P—	—	—	—	HP-		B—	B—	BS-	—	—	—
VN	HTP	—	—	—	HP-	HP-		MB-	MBS	—	M—	M—
YT	P—	—	—	—	—	HT-	P—		MBS	—	M—	M—
NO	HTP	—	H—	H—	HTP	HP-	HP-	P—		—	M—	M—
ST	HTP	—	—	H—	HTP	HTP	HP-	P—	HTP		—	—
AT	—	HP-	P—	P—	—	—	—	T—	—	—		M—
SS	P—	—	—	—	P—	P—	P—	P—	P—	P—	H—	

[a] Song Sparrows rarely used branches; their use of this measure was not tested.

pairs with the highest calculated overlaps in each matrix (usually >0.900) did not differ significantly. All differences stated below were significant ($P < 0.05$).

As described, overlap matrices for the six foraging measures were combined into two sets of overlap patterns: one for foraging behavior and one for foraging space (Fig. 2). In general, the clustering of species paralleled the previous separation into three guilds, although membership by several species was now less clear.

Behaviorally, the most similar species were within the canopy-feeding guild. The two congeneric flycatchers were statistically inseparable in all three behavioral measures. Both fed primarily by snatching insects from foliage during short flights through the canopy. The Northern Oriole, Verdin, and Common Yellowthroat were specialist leafgleaners and did not differ in eight of nine possible comparisons. The Yellow-billed Cuckoo was intermediate in behavior between these two groups, whereas the Summer Tanager differed from all species except the cuckoo on all measures.

The Gila (*Melanerpes uropygialis*) and Ladder-backed woodpeckers (*Picoides scalaris*) were similar only in their use of bark as a substrate; they differed with respect to foraging method and branch size. The Common Flicker differed from the Ladder-backed Woodpecker in all measures but differed from the Gila Woodpecker only with respect to substrate. The two ground foragers used identical foraging methods but used different substrates; the Song Sparrow often gleaned insects from the surface of shallow standing water, whereas the Abert's Towhee gleaned from dry ground and litter.

With respect to foraging space, again the greatest overlap was within the canopy-feeding guild. The Northern Oriole, Wied's Crested Flycatcher (*Myiarchus tyrannulus*), and Yellow-billed Cuckoo did not differ in any spatial measure. The Verdin and Summer Tanager differed only in regard to tree species use. The two flycatchers overlapped less spatially than behaviorally, with the Ash-throated Flycatcher (*Myiarchus cinerascens*) foraging more in salt cedar. Overall, there were fewer differences in spatial than in behavioral measures within this guild (43 versus 29), and there was a nonsignificant tendency for these to be complementary ($r = -0.323$, $P \gg 0.05$). The Common Yellowthroat was widely separated spatially from the other foliage feeders and from all other species as well.

The two woodpeckers were inseparable in all spatial measures. The Common Flicker's foraging space was most similar to the Abert's Towhee's, with no differences in foraging height or use of the inner portion of trees. The Song Sparrow and Abert's Towhee did not differ in foraging-height distributions and were widely separated from most other species.

Morphology.—Table 4 lists the means and standard deviations of all morphological measures for the 13 species used in this study. The

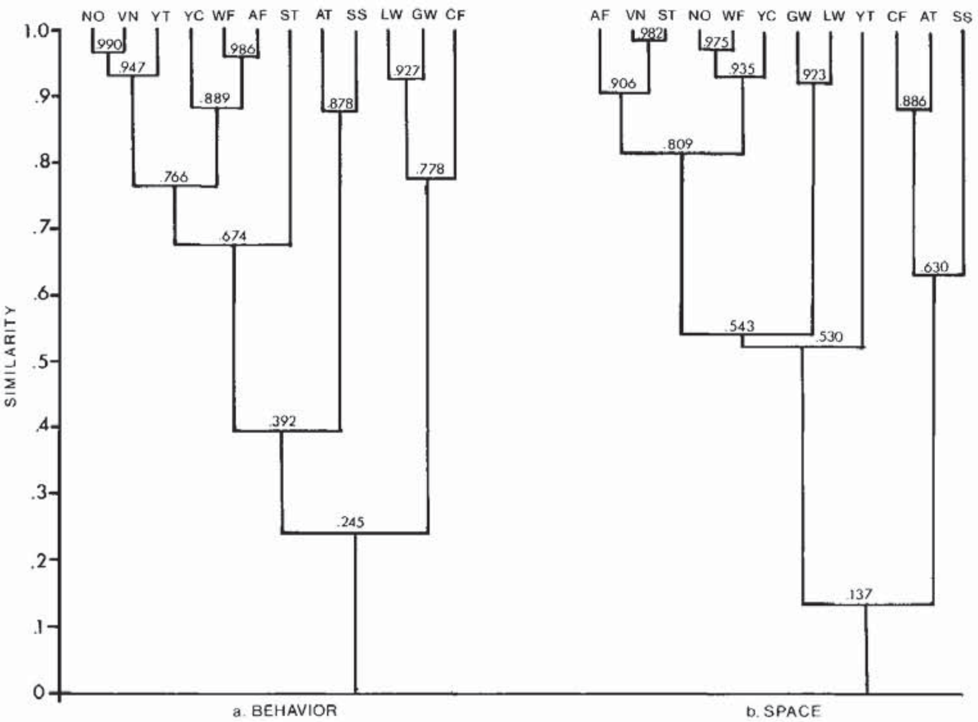


Fig. 2. Foraging similarity among 12 riparian birds. Behavior (a) = average of overlaps in method, branch size, and substrate. Space (b) = average of overlaps in tree species and tree portion multiplied by overlap in height (see text). Species codes from Table 1.

smallest species was the Verdin (6.5 g, 8.4-mm bill length), and the largest was the Common Flicker (110 g, 32.7-mm bill). Seven species were between 27 and 46 g, with bill lengths varying from 15.7 mm to 23.8 mm.

Overall morphological similarity based on ratios of the measures is illustrated in Fig. 3. In general, species were arrayed by body size and bill length, forming three major size groups. The seven medium-sized species dif-

TABLE 4. Morphological means of 13 species of riparian birds. Standard deviations are in parentheses. Bill length is exposed culmen; width and depth measured at nares. Species codes from Table 1.

				Bill		
Species	*n*	Weight (g)	Wing (mm)	Length (mm)	Width (mm)	Depth (mm)
YC	6	66 (4.8)	149 (4.0)	29.3 (0.9)	7.8 (0.3)	8.9 (0.8)
CF	2	110 (2.6)	145 (3.1)	32.7 (2.7)	9.2 (0.1)	8.0 (0.3)
GW	11	62 (6.9)	128 (1.8)	27.4 (2.8)	7.2 (0.6)	7.3 (0.5)
LW	2	33 (3.0)	106 (8.5)	20.4 (0.6)	6.5 (0.2)	5.9 (0.2)
WF	11	38 (11.6)	108 (5.8)	23.8 (2.5)	9.7 (0.6)	8.1 (0.6)
AF	13	27 (1.8)	93 (3.4)	19.0 (0.7)	7.5 (0.4)	6.3 (0.3)
VN	12	6.5 (0.4)	49 (3.1)	8.4 (0.4)	3.7 (0.4)	3.9 (0.4)
YT	10	10 (0.7)	54 (1.3)	11.9 (0.7)	3.6 (0.3)	3.6 (0.4)
NO	10	31 (2.7)	95 (3.0)	18.1 (0.5)	5.7 (0.5)	6.9 (0.4)
ST	7	33 (3.3)	100 (3.7)	20.3 (0.8)	9.4 (0.4)	9.7 (0.4)
BG	9	27 (1.9)	85 (3.6)	16.3 (0.9)	8.5 (0.8)	11.3 (0.8)
AT	10	46 (3.8)	89 (2.8)	15.7 (0.4)	6.7 (0.5)	8.8 (0.4)
SS	10	19 (2.4)	64 (2.1)	11.9 (0.5)	5.4 (0.4)	6.2 (0.3)

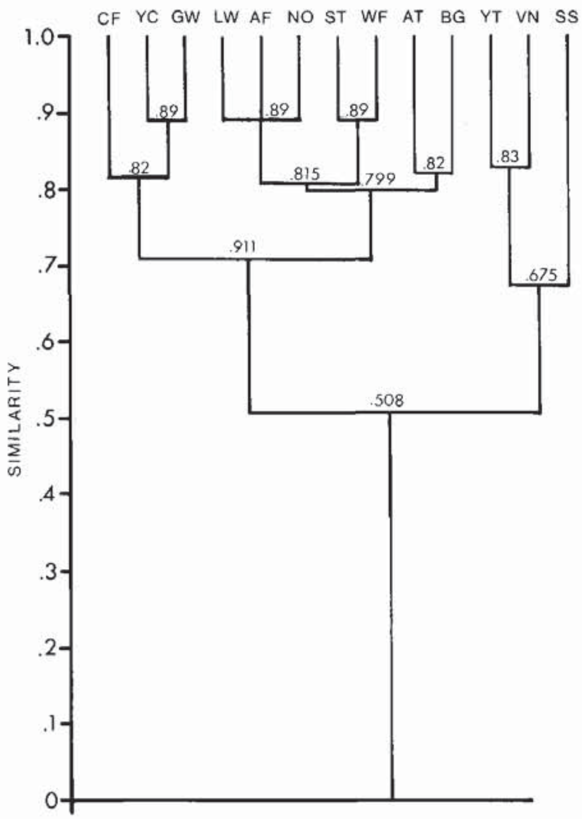


Fig. 3. Morphological similarity among 13 riparian birds. Represents average of ratios of five measures for each species pair (Table 4). Species codes from Table 1.

fered primarily with respect to bill width and depth. The Ladder-backed Woodpecker, Northern Oriole, and Ash-throated Flycatcher had relatively narrow or flattened bills; the Wied's Crested Flycatcher and Summer Tanager had the widest bills, and the Abert's Towhee and Blue Grosbeak had very deep as well as wide bills.

Diet.—Contents of 106 stomachs, representing midsummer diets of 13 species, were used for this study. The small sample size for the Common Flicker and Ladder-backed Woodpecker prevents conclusive analysis; they were included for completeness, however.

Distribution of size classes in the diets is shown in Fig. 4. The largest and smallest species (Common Flicker and Verdin) were specialists on the smallest size class, illustrating the danger of inferring prey size indirectly from bill measurements. The most frequently eaten size class among the larger species was 21–30 mm. All these species, except the Yellow-billed Cuckoo, ate very small insects as well.

There was much overlap among both the larger and smaller bird species with respect to prey size (Fig. 5a). Within each group, the canopy-foraging summer visitors were nearly inseparable statistically (Table 5). Among permanent residents and the other two foraging guilds, the only nonsignificant difference was between the Gila Woodpecker and the Abert's Towhee.

Distribution of prey types in the diets of the 13 species is shown in Fig. 6. Eight species preyed heavily on cicadas. Among these birds, grasshoppers were an important food for the Yellow-billed Cuckoo, Blue Grosbeak, Abert's Towhee, and possibly the Northern Oriole. Summer Tanagers were the only birds to feed on bees and wasps, and Gila Woodpeckers ate many ants. Abert's Towhees fed heavily on beetles, and the two flycatchers took a wide variety of food items in addition to cicadas.

The smaller bird species fed on a variety of soft-bodied prey, primarily spiders and larvae of several insect orders. The small samples of Common Flicker and Ladder-backed Woodpecker stomachs suggest that their diets may have been very different from most other species. Of the three species sometimes referred to as granivores, the Song Sparrow and Abert's Towhee ate very few seeds, and the nine stomachs of Blue Grosbeaks contained none.

Overlaps in diet are illustrated in Fig. 5b for percent-frequency distributions. Among the eight species that preyed upon cicadas, 23 of 28 pairs did not differ significantly in diet (Table 5). Among the remaining five species, only two of 10 species pairs were different: the Verdin with both the Common Yellowthroat and Song Sparrow.

DISCUSSION

Species usage patterns indicated a high degree of overlap with respect to both space and food. Although diet samples were small, these are believed to be adequate for most species, based on the small variation in individual diets and their correspondence with field observations. Wiens and Rotenberry (1979) similarly justified small samples as being reasonable inventories of avian diets.

The failure of avian species to avoid or ex-

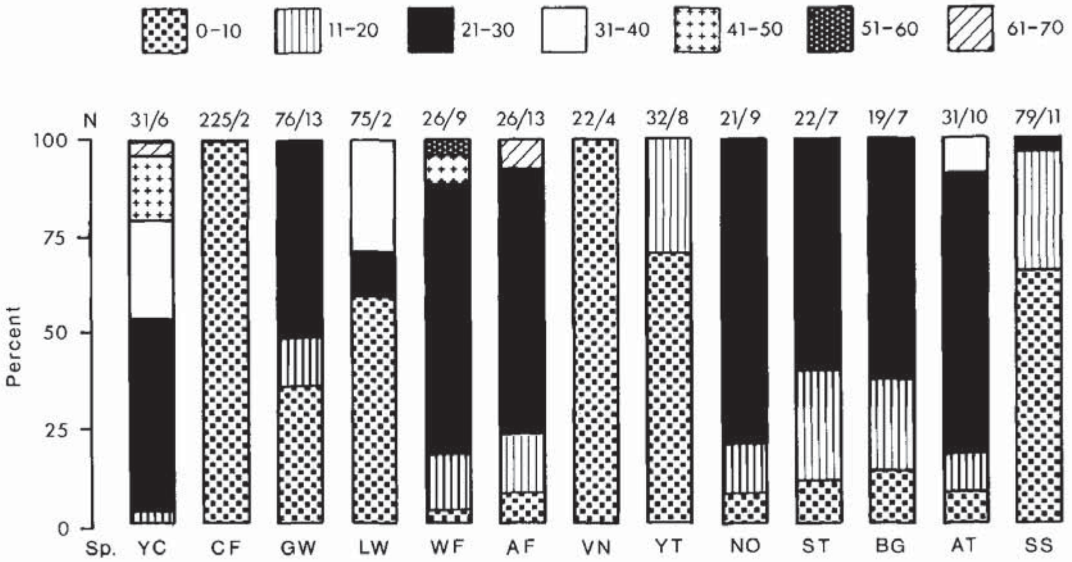


Fig. 4. Prey size distributions of 13 riparian birds. N represents number of food items/number of stomachs. Species codes from Table 1.

clude one another spatially suggests that, for each species, microhabitat selection on the study plot was independent of the other species present. The lack of distinct microhabitat preferences among these species (Rosenberg et al. MS) further suggests that spatial partitioning was unnecessary. An assumption of interspecific competition is not necessary to explain the observed spatial distribution.

In nearly every study investigating actual resource use among a community of breeding birds, a high level of dietary overlap has been

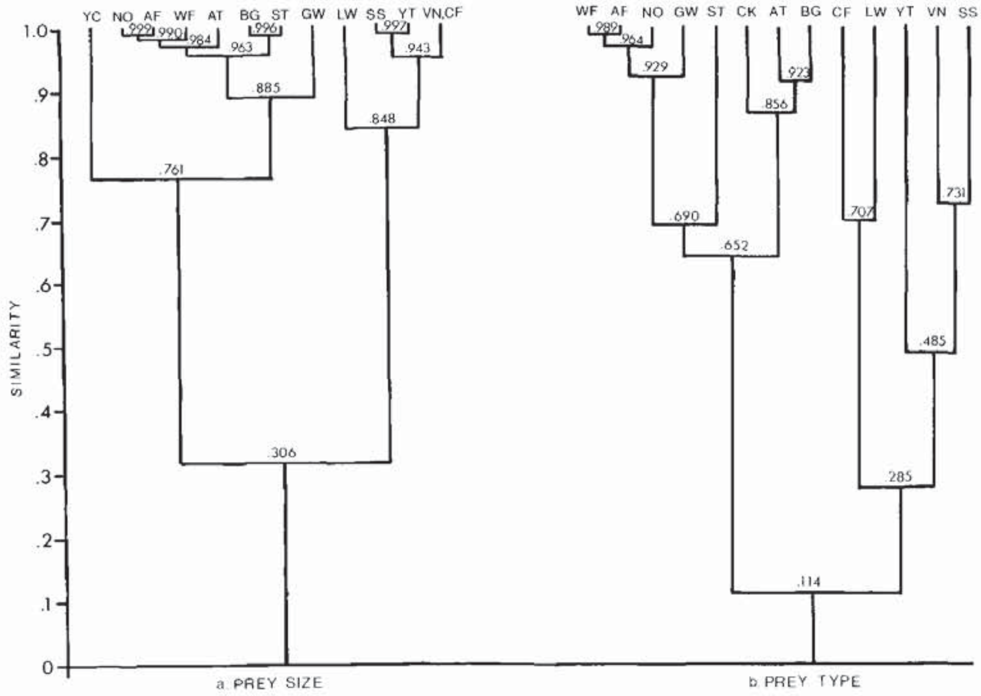


Fig. 5. Similarity in prey size (a) and diet (b) among 13 riparian birds. Overlaps based on percent-frequency distributions. Species codes from Table 1.

TABLE 5. Nonsignificant differences in prey size (S) and prey type (T) among 13 riparian birds. Species codes from Table 1.

Species	YC	CF	GW	LW	WF	AF	VN	YT	NO	ST	BG	AT	SS
YC		—	—	—	S	—	—	—	—	—	—	—	—
CF	—		—	—	—	—	S	—	—	—	—	—	—
GW	—	—		—	—	S	—	—	S	—	S	S	—
LW	—	—	—		—	—	S	—	—	—	—	—	—
WF	T	—	T	—		S	—	—	S	S	S	S	—
AF	—	—	T	—	T		—	—	S	S	S	S	—
VN	—	—	—	—	—	—		S	—	—	—	—	S
YT	—	—	—	—	—	—	T		—	—	—	—	S
NO	T	—	T	—	T	T	—	—		S	S	S	—
ST	T	—	—	—	T	T	—	—	T		S	S	—
BG	T	—	—	—	T	T	—	—	T	T		S	—
AT	T	—	—	—	T	T	—	—	T	T	T		—
SS	—	—	—	—	—	—	T	—	—	—	—	—	

discovered. This is true for such diverse groups as shorebirds (Holmes and Pitelka 1968), blackbirds (Orians and Horn 1969), finches (Pulliam and Enders 1971), owls (Herrera and Hiraldo 1976), grassland insectivores (Wiens and Rotenberry 1979), and riparian insectivores (this study). These findings are in contrast to theoretical predictions of resource allocation and limiting similarity and would most likely be considered exceptions to the "general rule" by these models. As pointed out by Wiens (1977), however, there is no justification in assuming a priori that resource-based competition exists or even that a community is at equilibrium with respect to resource use.

It is often suggested that high dietary overlap, especially among breeding birds, most often results from temporary superabundances of food. The magnitude and duration of these superabundances are rarely measured, however.

Arthropod sweep samples from the study area (Anderson and Ohmart unpubl. data) indicate a peak in biomass and numbers in May. This peak is made up of mostly tiny insects (e.g. Cicadellidae), however, that are apparently unrepresented in the avian diets. Although a July–August peak in larger insects such as Orthopterans can be shown, abundant prey such as Cicadidae, ants, and termites were generally absent from sweep samples.

Because cicadas were so important to a large segment of the bird community, including several similarly sized and potentially competing species, the question of food abundance was addressed using data from Glinski and Ohmart (1981). These consisted of successive weekly counts of cicada exuvia in cottonwood-willow-salt cedar habitat along the San Pedro River in southeastern Arizona in summer 1978. The species of cicada (*Diceroprocta apache*) was the same as on our study plot, and qualitative comparisons of habitat and cicada populations (noise levels) suggest that these data are relevant to the present study.

Cicada numbers peaked at nearly 700,000 per 40 ha on 21 July and declined steadily until late August (Fig. 7). The average number of adult cicadas emerging through the sampling period was 250,000 per 40 ha per week. We feel that these numbers, superimposed on the sweep-sample data, indicate the availability of large insects to birds in midsummer.

Daily expenditures of birds were estimated using the equation $DDE = 11.87$ (mass$^{0.608}$) (Walsberg 1980) for all species that preyed heavily on cicadas (Table 6). The energy needed to maintain this segment of the bird community was estimated as 200,019 kJ per 40 ha per week. Assuming the metabolizable energy from insects to be 4.94 kJ/g (Ricklefs 1974) and using a weight of 1.5 g for a live cicada and a 0.92 efficiency for birds (Thompson and Grant 1968), the energy gained per cicada was calculated as 6.82 kJ. If all these species depended entirely on cicadas for food (a conservative assumption), then approximately 29,328 cicadas were needed each week. This is far fewer than were present in any week during which stomach samples were taken. Because cicadas are conspicuous and easy to catch by a variety of methods, it is reasonable to assume that most

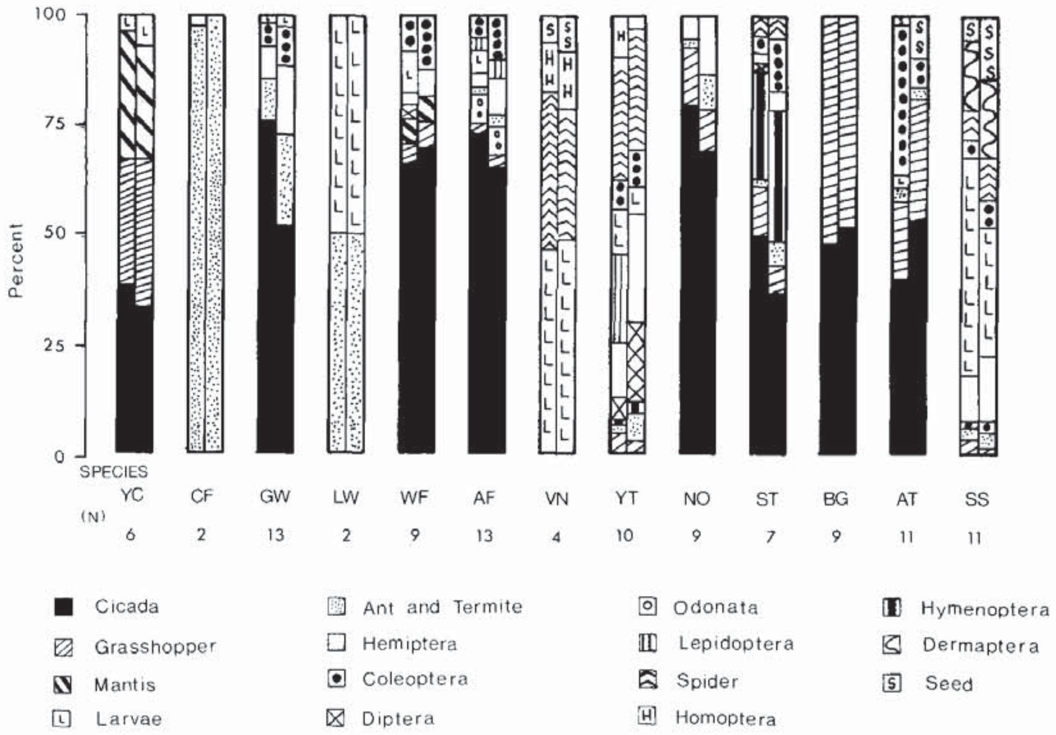


Fig. 6. Diets of 13 riparian birds in summer. Percent-volume on left; percent-frequency on right. Species codes from Table 1.

flying adult cicadas were readily available to birds.

Although the above calculation is crude, and the additional energy demands of growing young need to be considered, the magnitude of the cicada surplus and the additional abundance of grasshoppers and other prey justify the conclusion of a nonlimiting food supply. This is consistent with Rotenberry's (1980b) conclusion from a more complete bioenergetics study of shrubsteppe birds. Furthermore, cicada irruptions are of annual occurrence in this region, suggesting that this surplus is predictable.

All species exploiting cicadas fledged either their first or second broods in July when food was potentially most abundant. This is indirect evidence of a response to a resource peak. In addition, environmental conditions were possibly most stressful at that time, and most other species of the region breed much earlier.

The consequence of this unlimited resource was the convergence in diet of species differing greatly in behavior and morphology. Most striking was the predation on cicadas by Gila Woodpeckers and Abert's Towhees, two species specialized for bark and ground foraging, respectively. These two species could have "avoided competition" with the similar-sized coexisting species but instead shared in the exploitation of the most abundant prey. A similar pattern has been reported for breeding shorebirds differing greatly in body size and bill morphology (Baker 1977).

Thus, measured niche variables such as bill

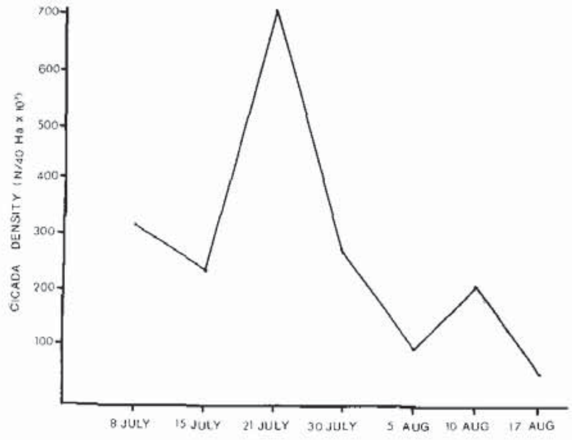


Fig. 7. Density of emerging cicadas in cottonwood-salt cedar habitat during summer 1978. Data from Glinski and Ohmart (1981).

TABLE 6. Energetics of eight medium-sized riparian insectivores. $DEE = 11.87\ \text{mass}^{0.608}$ (Walsberg 1980). Population energy expenditure (PEE) = $DEE \cdot$density. Species codes, densities from Table 1; body mass from Table 4.

Species	*DEE* (kJ/day)	*PEE* (kJ/week/40 ha)
YC	152	30,775
GW	146	38,836
WF	108	16,694
AF	88	3,080
NO	96	46,924
ST	100	16,712
BG	88	1,848
AT	122	45,151
Community		200,019

shape and foraging behavior may not be true predictors of actual resource use within a community, and all community studies that have made such inferences may have drawn spurious conclusions. For example, there is no justification for assuming that coexistence within a community is due to any of the observed differences among the species present. If each individual bird is opportunistically exploiting its environment as efficiently as is necessary to survive and reproduce, irrespective of the presence of other species, then differences may exist within a community, and local interspecific competition need not be invoked as a cause. Indeed such opportunism was implicated by Rotenberry (1980a) as determining relationships among a simple community of arid shrubsteppe birds.

This is not to say that resource limitation and competition could not have been the selection pressures that affected the species-specific differences observed in this and other communities. Selection pressures from competition may only be intermittently important to present-day populations (Wiens 1977). Such selection, however, may still be reflected in current distribution and behavioral repertoires of bird species. The important distinction to be made is between those factors governing the presence of species over large geographic areas through evolutionary time and those that structure short-term, sympatric species interactions.

Until now, we have concentrated heavily on the cicada-eating subset of this community. The remaining smaller species are rather widely separated ecologically, and an apparent peak in small arthropod biomass seems unexploited. In this region, some small insectivores have experienced local extinctions [Yellow Warbler (*Dendroica petechia*), Bell's Vireo (*Vireo bellii*)] or are near the periphery of their breeding range [Bewick's Wren (*Thryomanes bewickii*)]. Thus, this segment of the community is depauperate for reasons probably unrelated to food supply, and discussion of these species can neither refute nor support the above conclusions.

Finally, it should be noted that this discussion has been based only on a period of resource superabundance. Indeed, theory predicts the consequences of such competitive release situations (MacArthur 1972). What is of greater interest is that this may not be a unique or even a rare situation. The evolution of diverse breeding bird communities in response to seasonally superabundant and predictable resources may be quite common, especially in temperate regions. In fact, many communities studied in light of competition models (e.g., MacArthur 1958, Cody 1974) may be examples of such evolution (Rabenold 1978).

Given the abundance and variety of theoretical considerations of community organization, it is clear that empirical evidence lags far behind. Specifically, the exact dietary relationships of species assemblages and the relative seasonal resource productivity of various habitats need to be measured and not inferred. We maintain that such a sound empirical foundation is essential if speculation about community patterns is to be more meaningful.

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APPENDIX. Definitions of foraging measures and states.

Measure	State	Definition
Method	1. Glean	Bird perched; prey captured from surface of substrate
	2. Hover	Bird in flight; prey captured from surface of substrate
	3. Hawk	Both bird and prey in flight
	4. Peck	Bill struck against substrate to expose prey below surface
	5. Probe	Bill enters substrate to capture prey below surface
Foraging height	1. Ground	Ground and litter
	2. 0.0–6.2 m	Understory
	3. 6.2–12.3 m	Mid-canopy
	4. 12.3–21.0 m	Upper-canopy
Tree species	1. Cottonwood	*Populus fremontii*
	2. Willow	*Salix gooddingii*
	3. Dead	Dead cottonwood or willow
	4. Salt cedar	*Tamarix chinensis*
	5. Other	Honey mesquite (*Prosopis glandulosa*), cattails (*Typha latifolia*), etc.
Branch diameter	1. ≤1 cm	
	2. 1.0–2.5 cm	
	3. 2.5–5.0 cm	
	4. 7.5–10.0 cm	
	5. 12.5–20.0 cm	
	6. >20.0 cm	
Tree portion	1. Inner	Larger branches close to and including trunk
	2. Outer	Smaller branches and twigs, containing most foliage
Substrate	1. Leaf	
	2. Bark	
	3. Ground	
	4. Air	
	5. Flower or fruit	
	6. Surface of water	