GUILDS AND COMMUNITY ORGANIZATION: ANALYSIS OF AN OAK WOODLAND AVIFAUNA IN SONORA, MEXICO[1]

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ABSTRACT.—Community organization of an oak woodland breeding avifauna was studied in Sonora, Mexico. Species were classified into guilds by quantifying foraging behavior, based on investigator-defined resource classes, and subjecting these data to cluster analysis. From this analysis five guilds were recognized: foliage gleaning, wood gleaning, wood probing, air sallying, and ground sallying. Within each resource class all guilds foraged in a significantly different manner, except for air and ground salliers.

Species within guilds were most often separated by food-site and perch height. Use of height classes by the avian community was significantly different from the quantity of tree vegetation per height class. Differential height utilization generally resulted from gleaning and probing guilds foraging at upper heights and sallying guilds foraging at lower heights. Ecological separation within and among guilds is discussed and related to community organization in this oak woodland avifauna. When the guild structure of this community is compared to other oak woodland avifaunas, a decrease in foliage gleaners of nearly 2.5-fold and a 6.4-fold increase in salliers occur from Oregon to Sonora, Mexico. Utility of the guild approach is discussed in relation to some prominent questions raised by results of the above comparison concerning (1) foraging plasticity in species coexistence and (2) change in community structure over time and between geographic locations. *Received 18 September 1979, accepted 14 December 1979.*

TWO factors appear to be of major importance in influencing avian foraging behavior. Habitat characteristics largely determine the number of bird species and individuals that may exploit available resources and survive in that habitat (Odum 1945, MacArthur et al. 1962, Johnson 1975, Pearson 1975, and others), and biotic interactions may alter individual foraging characteristics and contribute to partitioning of exploitable resources (Svärdson 1949, MacArthur 1958, Crowell 1962, Baker and Baker 1973, Pearson 1977, and others). The interaction of these factors often leads to equivocal results in studies in community ecology, especially analyses of community structure and organization (see Wiens 1977).

Community organization is the focus of much current ecological interest, although no widely accepted working definition exists for the term "community." Most definitions include some notion of arbitrary spatial boundaries as a criterion in delimiting communities (e.g. MacArthur 1971), ignoring the importance of interspecific coevolutionary interactions (Connell and Slatyer 1977, see also Ricklefs 1973: 590). The definition of MacMahon et al. (1978: 702) seems the most precise and satisfies theoretical considerations: "Groups of interacting populations, among which no gene exchange is taking place, but whose demography or gene pools are affected by the interaction, are termed communities." The study of communities, in practice, usually will require spatial and temporal boundaries; interactions, because seldom observed, usually must be inferred. Arbitrary boundaries may be imposed so long as the investigator can discern population and community attributes that result from interactions across those boundaries.

Community organization implies attributes concerned with species occurrence and their interactions, e.g. abundance, diversity, succession, stability, and spatial, tem-

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[1] Send reprint requests to J.A.M.

poral, and trophic relationships. Abundance and diversity are measures of community structure, while succession and stability are concepts pertaining to long-term patterns of community change and persistence. Organization is here deemed to be those aspects of a community that pertain to its functioning, i.e. spatial, temporal, and trophic interactions of populations within the defined community (cf. Whittaker 1975: 362).

Interspecific interactions are of particular interest in light of a developing theory of the guild in ecology. A guild may be considered a subset of the community in which individuals use a similar class of resources in a similar manner (Root 1967); this does not imply that guild members use all aspects of their environment similarly. In community analyses, grouping species into guilds is attractive for two reasons. First, because guild members are the most likely potential competitors, it is appropriate to study competitive interactions and resource partitioning within a guild framework (Willson 1974; Pearson 1975, 1977; Feinsinger 1976). Second, reduction of species numbers and interspecific interactions into fewer functional units would enable easier recognition of possible organization (Botkin 1975, MacMahon 1976).

Knowledge of organizational processes is fundamental in understanding coexistence in multi-species communities; we hope that the approach adopted herein towards this goal will have heuristic value. This paper is an attempt at applying the above ideas in describing the organization of an avian community from an oak woodland in northeastern Sonora, Mexico. For pragmatic reasons this study was restricted (from a total of 37 breeding birds in this habitat) to the arboreal component (12 species) of the community, i.e. those species using some part of a tree in the majority of their food capture. Use of foraging substrates in trees, foraging technique, and rate of foraging were quantified for each species. These data were then used to divide species into guilds. The resulting guild structure may then conveniently be used to elucidate interactions of component species and thus serve as an index of organization in this community. Recently Holmes et al. (1979) have used a similar approach to elucidate partitioning and to enhance understanding of community structure in forest bird communities.

MATERIALS AND METHODS

Study area.—Oak woodlands occur throughout northeastern Sonora, Mexico, forming a belt between ~1,300 m and 1,600 m in elevation (Marshall 1957). At its lower elevation, the woodland grades into savanna and grassland, while at higher elevations it grades into pine-oak forests (White 1948). The study site was located in the eastern foothills of the Sierra la Purica (30°35′N, 109°43′W), ~1,500 m in elevation, 120 km south of the international border at Douglas, Arizona. During the study period, mean minimum and maximum temperatures were 5.2°C and 25.5°C, respectively; precipitation was 0.3 mm (based on Douglas, Arizona, Fire Department recordings for the National Climatic Center).

The dominant tree species was Emory oak (*Quercus emoryi*), which, together with the infrequent Mexican blue oak (*Q. oblongifolia*), forms an open, park-like woodland. Individual *Q. emoryi* began dropping leaves on 6 April 1977. Flowering occurred shortly thereafter, so at any given time numerous trees were in various stages of leaf development or flowering (cf. Balda 1970). A few cacti (*Opuntia engelmannii, O. spinosior*) were interspersed throughout the woodland, along with the subtree *Chilopsis linearis*. Ground cover consisted mostly of grasses, with many herbaceous perennials and annuals scattered throughout. The study area is currently being intensively grazed by cattle.

Vegetation sampling.—Vegetation was sampled using methods modified from James and Shugart (1970). Ten 0.05-ha circles were randomly established on the 10-ha plot used for bird censusing. Vertical distribution of tree foliage and wood was sampled using line transects originating at the center of each circle. An aluminum rod marked in 1.5-m divisions was placed vertically at 700 points along a 1,000-m long transect, with presence or absence of foliage or wood recorded for each vertical stratum. From these

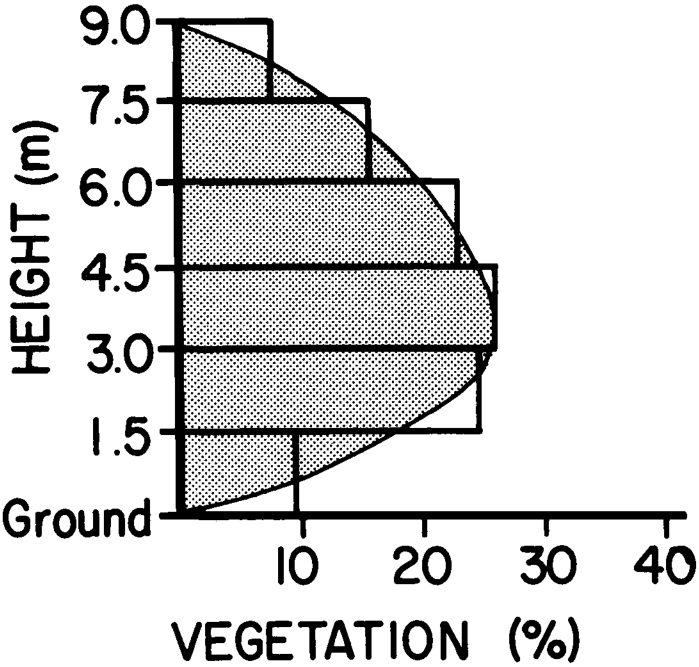

Fig. 1. Percent vegetation per height class. Shaded area, drawn by eye, represents "typical" tree profile used in Fig. 3.

measurements, the percent of tree vegetation within 1.5-m height classes (hereafter termed tree profile) was determined (Fig. 1).

Censusing and foraging.—A modified spot-map method (Kendeigh 1944) was used on the 10-ha plot from 28 March to 1 May 1977 to ascertain which species were actively breeding. Ten censuses were conducted during the study period between 0600 and 0900 MDT.

Foraging behavior was quantified using a metronome technique developed by Wiens et al. (1970). This method employs an audio metronome that "beeps" at 15-s intervals, each "beep" serving as an indicator for the observer to record data (see below). These data are time-dependent, violating the statistical assumption of independence when testing for significance. For species that actively pursue prey on trees, however, the 15-s time interval seemed adequate to insure independence of consecutively recorded behaviors. Metronome data were collected from 0600 to 1800 MDT daily, with individual recordings of a single bird limited to 2-min periods to reduce sampling bias.

Data were gathered only from individuals actively foraging. During observation periods, the following subjectively determined components of foraging behavior were recorded: time of day; species; sex (when determinable); portion of vegetation used for activity, defined as inner (a vertical axis extending from the tree's base to its top and including, and 1 m away from, the trunk), outer (the outermost periphery of the tree and extending 1 m inwards towards the tree's center), and middle (that region between inner and outer portions); perch site, i.e. the perch from which foraging was initiated, estimated as twig (<1.25-cm diameter), branch (≥ 1.25 cm, ≤ 15.0 cm), trunk (>15.0 cm), and ground; food site, i.e. the site from which food was obtained, defined as foliage (including flowers), twig, branch, trunk, ground, and air; vertical height of perch site (1.5-m height classes); and foraging technique, defined as gleaning (taking food from a surface), probing (taking food from beneath a surface), and sallying (taking food after flying from a perch). The metronome was not used for individuals that used sallying as a foraging technique. Instead, each sally was used as the indicator to record the above data. For convenience, each major component of foraging (i.e. portion, perch site, food site, height, and technique) is hereafter referred to as a Foraging Category (FC), e.g. technique FC.

Stopwatches, and estimates (by eye) of distance traveled and number of stops made by an individual were used to quantify species' foraging rate (Cody 1974: 39–40).

Analysis.—Density (pairs/10 ha) was calculated from census data for each species. Within each FC,

TABLE 1. Bird densities and guild membership.

Common name	Scientific name	Abbreviation	Pairs per 10 ha	Percent of community	Guild
Acorn Woodpecker	*Melanerpes formicivorus*	AW	3[a]	8.1	Wood probe
White-breasted Nuthatch	*Sitta carolinensis*	WN	3	8.1	Wood glean
Bewick's Wren	*Thryomanes bewickii*	BW	6	16.2	Wood glean
Scott's Oriole	*Icterus parisorum*	SO	2	5.4	Wood glean
Bridled Titmouse	*Parus wollweberi*	BT	5	13.5	Foliage glean
Bushtit	*Psaltriparus minimus*	BU	2	5.4	Foliage glean
Lucy's Warbler	*Vermivora luciae*	LW	3	8.1	Foliage glean
Ash-throated Flycatcher	*Myiarchus cinerascens*	AF	4	10.8	Ground sally
Eastern Bluebird	*Sialia sialis*	EB	2	5.4	Ground sally
Dusky Flycatcher	*Empidonax oberholseri*	DF	2	5.4	Air sally
Vermilion Flycatcher	*Pyrocephalus rubinus*	VF	1	2.7	Air sally
Cassin's Kingbird	*Tyrannus vociferans*	CK	4	10.8	Air sally

[a] Represents number of Acorn Woodpeckers encountered in groups divided by 2 for concordance with other species pairs.

66 pair-wise comparisons were made for the 12 species in the community. Based on the number of observations, a G-test (Sokal and Rohlf 1969) was used to test for significant differences in foraging among species ($P < 0.01$, unless stated otherwise). The number 5 was added to each datum in tests of significance to eliminate cell frequencies less than 5, which would skew the value of G upwards (Sokal and Rohlf 1969). Breadth and overlap (Colwell and Futuyma 1971) of resource use were calculated for each species. Cluster analysis was used to classify species into guilds based on interspecific similarity; resemblance coefficients are based on Euclidean distances, while clustering by the unweighted pair-group method (Sokal and Sneath 1963) is based on arithmetic averages.

RESULTS

Censusing and foraging.—Total bird-species density (Table 1) was 37 pairs per 10 ha. The 4 most abundant species, representing 3 of 4 foraging techniques, were the Bridled Titmouse (gleaning), Bewick's Wren (gleaning and probing), and Cassin's Kingbird and Ash-throated Flycatcher (sallying). Balda (1970) found the Bridled Titmouse, Bewick's Wren, and Ash-throated Flycatcher to be the three most abundant arboreal species in an oak woodland in the Chiricahua Mountains, Arizona.

Foraging data for all species, upon which the following results are based, are presented in the Appendix. Species breadth and overlap for each FC are not included here but are available from the authors upon request.

Guilds.—Technique and food-site FC's were combined in a cluster analysis from which the 75%-level of relative similarity on the resulting dendrogram was subjectively used to determine guilds (Fig. 2). Five guilds are recognized: foliage gleaning (Bridled Titmouse, Bushtit, Lucy's Warbler), wood gleaning and probing (White-breasted Nuthatch, Bewick's Wren, Scott's Oriole; hereafter referred to as wood gleaning), wood probing (Acorn Woodpecker), air sallying (Cassin's Kingbird, Dusky and Vermilion flycatchers), and ground sallying (Eastern Bluebird, Ash-throated Flycatcher). Individual technique and food-site cluster analysis cophenetic matrices are strongly correlated ($r = 0.91$ and 0.95, respectively) to the combined cophenetic matrix. A discriminant function analysis using a posteriori guilds as the grouping variable correctly classified 100% of the species, corroborating the effectiveness of cluster analysis and use of the 75%-level of relative similarity in designating guilds. Of the possible 50 pair-wise interguild comparisons per FC (G-test; Table 2), only one is not significantly different: air vs. ground salliers in technique. Interestingly,

TABLE 2. Guild and community ("all species") use of foraging categories. Values are summed species percent use of each category. Number of foraging observations given in parentheses. Columns total 500%.

		Guild				
Foraging category	All species (3,010)	Foliage glean (796)	Wood glean (846)	Wood probe (386)	Air sally (635)	Ground sally (347)
Technique						
Glean	44.1	98.0	60.4	9.3	0.0	0.3
Probe	22.2	0.3	39.4	85.5	0.6	0.0
Sally	33.7	1.7	0.2	5.2	99.4	99.7
Portion						
Outer	36.2	44.6	9.2	7.5	69.4	53.9
Middle	42.5	50.4	43.4	60.9	30.6	23.9
Inner	16.6	4.5	40.4	31.6	0.0	0.0
Ground	4.7	0.5	7.0	0.0	0.0	22.2
Perch Site						
Twig	54.2	83.4	11.8	1.8	98.6	67.4
Branch	27.5	15.5	48.3	63.5	1.4	11.8
Trunk	13.8	0.6	32.9	34.7	0.0	0.0
Ground	4.5	0.5	7.0	0.0	0.0	20.8
Food Site						
Foliage	23.7	76.0	5.7	3.9	7.1	0.0
Twig	6.7	14.3	9.6	0.5	0.6	0.0
Branch	22.1	7.3	44.1	61.1	0.0	0.0
Trunk	13.4	0.6	33.2	29.3	0.3	0.3
Ground	17.6	1.8	7.4	1.0	26.0	81.8
Air	16.5	0.0	0.0	4.2	66.0	17.9
Height (m)						
Ground–1.5	21.1	1.0	17.0	7.8	43.3	51.0
1.6–3.0	12.9	11.7	14.2	0.8	19.8	13.5
3.1–4.5	15.6	18.3	16.7	12.7	9.3	21.9
4.6–6.0	21.0	27.0	28.8	28.0	4.6	10.4
6.1–7.5	23.4	36.7	21.2	36.0	13.5	2.0
7.6–9.0	6.0	5.3	2.1	14.7	9.5	1.2

when only technique and food-site FC's are used to describe guilds, almost complete separation in all foraging axes is achieved.

Foliage gleaners are all quite similar in their foraging behaviors, exhibiting the narrowest foraging breadth (Table 3) by concentrating their activities on twigs and foliage in the outer and middle portions of the tree (see Table 2). All three species use significantly different food sites and heights, although Lucy's Warbler and the Bushtit are not differentiated in either portion or perch-site FC's (Table 4). These latter two species are the most closely matched pair in the community. In contrast, foliage gleaning *Dendroica* (MacArthur 1958) and *Parula* (Morse 1967) warblers were separated mostly by portion and height during foraging. This difference in

TABLE 3. Mean foraging breadth and overlap of guilds. Values calculated from data in Table 2.

Guild	Breadth	Overlap
Foliage glean	0.1615	0.1800
Wood glean	0.3122	0.1973
Wood probe	0.2060	0.1697
Ground sally	0.1728	0.1486
Air sally	0.1680	0.1455

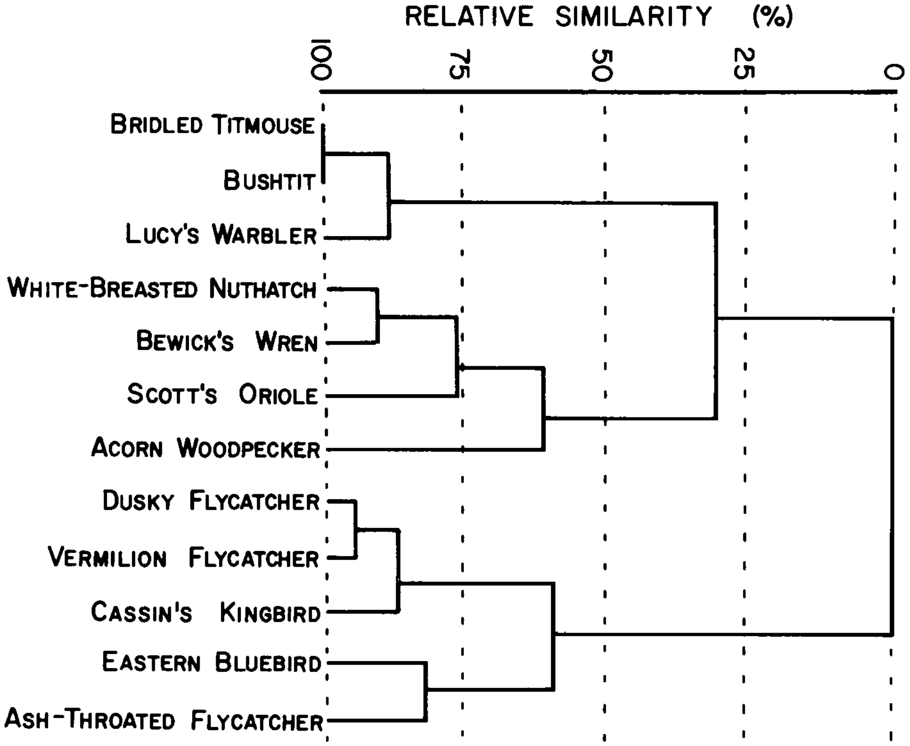

Fig. 2. Cluster analysis dendrogram showing interspecific affinities (guilds) from combined technique and food-site foraging data. Cophenetic correlation coefficient = 0.944. See text for explanation of relative similarity levels.

separation of foraging is probably due to a restriction of foliage to the periphery of the trees in this study.

Wood gleaners exhibit a significantly greater (Mann-Whitney U test, $P < 0.05$) mean foraging breadth (Table 3) than foliage gleaners and air and ground salliers and exhibit the greatest overlap, although the overlap values are not significantly different. These species move rapidly (Table 5) over the middle and inner portions of the tree, searching mostly branches and trunks (see Table 2). The White-breasted Nuthatch and Bewick's Wren constantly jabbed their bills into bark crevices and often tapped lightly, dislodging small pieces of bark. Scott's Oriole was often seen gleaning insects from foliage and small branches and feeding at the same sap holes

TABLE 4. Intraguild species comparisons. Data are mean G-values from pair-wise species comparisons within each guild. Wood-probing guild excluded from analysis. * = significance at $P < 0.01$.

Guild	Foraging category				
	Technique	Portion	Perch site	Food site	Height
Foliage glean	3.50	35.92*[a]	15.86*[b]	44.11*	83.84*
Wood glean	5.38	46.35*	107.78*	127.97*	79.78*
Air sally	1.53	89.47*	0.26	43.45*	198.69*
Ground sally	0.31	121.33*	80.69*	56.62*	251.39*

[a,b] Only two of three pair-wise comparisons significant; see text for explanation.

TABLE 5. Timed foraging behavior. Data are averaged values from species within each guild.

Guild	*n* (s)	$\bar{x}$ speed (cm/s)	$\bar{x}$ distance per move (cm)	Time stationary (%)	Duration $\bar{x}$ stop (s)
Foliage glean	2,334.3	8.84	26.52	79.75	2.4
Wood glean	2,549.6	9.75	35.66	61.82	2.4
Wood probe	1,157.6	4.27	28.35	88.77	5.7
Air sally	5,167.3	30.18	106.98	87.26	26.6
Ground sally	3,499.5	13.72	44.59	87.37	27.8

used by Acorn Woodpeckers (see Stephans 1906, and below). All three species differ significantly in their use of portion, height, perch, and food-site FC's (Table 4).

The wood-probing Acorn Woodpecker exhibited the second highest mean foraging breadth (Table 3, though not significantly different from other guilds). It was also the slowest moving bird in this study (Table 5), spending most of its time on large diameter perches in the middle and inner portions of the tree (see Table 2). This species was often seen chiseling and feeding at ~1-cm diameter irregularly spaced holes, many of which were copiously exuding sap. Whether only sap or both sap and insects attracted to the sap were exploited is unknown, although Acorn Woodpeckers have been observed sap-sucking in California oak woodlands (MacRoberts and MacRoberts 1976, W. Koenig pers. comm.).

Air salliers exhibit narrow foraging breadth and overlap (Table 3), perching almost exclusively on twigs (see Table 2). Cassin's Kingbird generally foraged from the topmost dead twigs of trees, usually sallying upwards. In contrast, the other two flycatchers typically foraged at low heights from dead twigs protruding beneath the canopy, sallying to both air and ground. Although all three species employ the same foraging technique, Cassin's Kingbird exploits a markedly different range of resources. These species all differ significantly in their use of portion, food site, and height FC's (Table 4), although Hespenheide (1964) observed species of *Tyrannus* to be separated by habitat rather than by foraging tactics.

Ground salliers possess intermediate foraging breadth (Table 3), using lower and middle heights and all but the inner portions of the tree (see Table 2). The Eastern Bluebird perches almost exclusively on twigs, whereas the Ash-throated Flycatcher is the only species in the community with extensive use of the ground (37.2%) as a perch site. From its ground perch, the bird typically sallies 1–2 m to catch flying or crawling arthropods. This behavior is in contrast to previous foraging records (e.g. Bent 1942, Marshall 1957) in which this species is described as sallying from low perches in foliage to capture aerial prey or as hovering to capture prey crawling on foliage. These two species differ significantly in their use of portion, height, perch, and food-site FC's (Table 4).

Published foraging accounts of foliage gleaners (Marshall 1957, Dixon 1961, Ficken and Ficken 1968, Hertz et al. 1976), wood gleaners (Stephans 1906, Miller 1941, Marshall 1957, Stallcup 1968), the wood prober (MacRoberts and MacRoberts 1976, W. Koenig pers. comm.), air salliers (Bent 1942, Marshall 1957, Hespenheide 1964), and ground salliers (Thomas 1946, Bent 1949, Marshall 1957) from diverse habitats and communities closely match observed foraging behaviors of species in this oak woodland study, except for the Ash-throated Flycatcher mentioned above.

A Mann-Whitney *U* test was used to test for differences within the community (Table 2, all species) in use of foraging categories with arcsine transformed percent

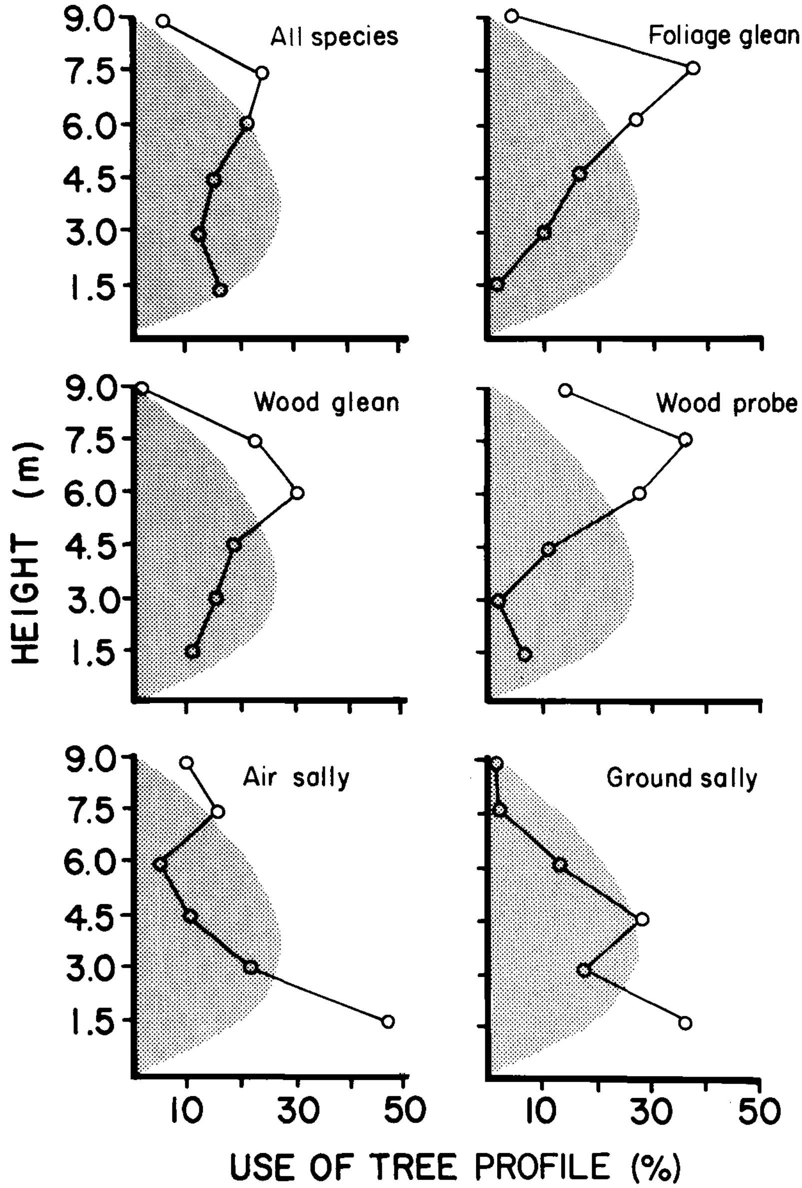

Fig. 3. Height use of the tree profile by the community ("all species") and guilds. Shading represents "typical" tree profile (see Fig. 1). Solid line represents percent of perch height observations of guilds per height class.

data (Sokal and Rohlf 1969). Although gleaning is used most often, no significant differences occur among foraging techniques. Use of the outer and middle portions of the tree are significantly greater ($P < 0.05$) than exploitation of the inner portions and the ground. Use of twig and branch perch sites is significantly greater ($P < 0.05$) than use of trunk and ground sites, respectively. Although twigs are exploited nearly twice as often as branches, use of twigs is not significantly different. No significant differences occur among use of food sites, though twigs are exploited much less than other sites. No significant differences occur among use of foraging heights.

Foraging-height use by each guild (Fig. 3) is significantly different from the average tree profile (*G*-test, $P < 0.01$). In addition, there is a marked difference in height use between sallying guilds and guilds that derive their food from trees. Foliage gleaners, wood gleaners, and the wood prober spend 69.0%, 52.1%, and 78.7% of their time from 4.5 m to 9.0 m, respectively. Tree profile at this height range is 43.6% (Fig. 1), indicating greater species use than proportional tree availability. Air and ground salliers spend more time from ground to 3.0 m (63.1% and 64.5%, respectively) than the percent tree profile (32.1%) at these heights. Greater use by air salliers from 6.0 to 9.0 m is due to preferential use of these heights by Cassin's Kingbird. In ground salliers, two distinct peaks (at 1.5 m and 4.5 m) depict preferential use by Ash-throated Flycatcher and Eastern Bluebird, respectively. By pooling species height utilizations (Fig. 3, all species), community use is found to be significantly different ($P < 0.01$) than the average tree profile. Compared to the tree profile, species usage from 1.5 to 6.0 m is 19.6% less that expected, while usage from ground to 1.5 m and from 6.0 to 9.0 m is 11.7% and 7.8% more than expected, respectively.

Timed foraging behavior is presented in Table 5 as mean values for each guild. Species within guilds that derive their food from trees move an average 8 cm/s (30 cm per move), stopping frequently for short periods ($\bar{x} = 3.5$ s). Of these, wood gleaners exhibit a trend in moving the quickest and spend less time stationary. In contrast, salliers move an average 22 cm/s (757 cm per move), stopping frequently for long periods ($\bar{x} = 27.2$ s). Air salliers move significantly quicker (Mann-Whitney *U* test, $P < 0.01$) than ground salliers, especially Cassin's Kingbird, which flies an average 21.8 m per sally. "Gleaning" and "flycatching" guilds of birds from the Colorado Rocky Mountains (Eckhardt 1979) exhibit patterns of movement during foraging similar to the corresponding guilds from this study.

Discussion

Community studies employing guild analyses frequently involve circular reasoning. From many foraging axes a few are subjectively chosen for quantification. The relevancy of axes depends upon the observer's knowledge of the organisms studied. As a result of defining these foraging axes, species are divided into guilds. The subsequent analysis can yield meaningful information about community organization, but only to the extent that chosen axes are important in "real life" species interactions. Typically in community studies overlap in resource use is quantified and patterns of partitioning elucidated, with competition evoked as a causative mechanism. Such community patterns may result from current competitive interactions, but, until documentation of resource bases and manipulative experiments are completed, this assumption is untenable. That 49 of 50 pair-wise interguild comparisons per FC (Table 2) are significant in this study corroborates our initial assumption that technique and food site foraging axes are important components in the orgnization of this community; this does not imply that competition along these axes is producing the observed partitioning.

Though not based on a rigorous statistical framework, cluster analysis presents a hierarchial grouping of species that may possess biological significance; in the analysis of this community, several levels of guild abstraction occur (Fig. 2) that may be present in any community. At 0% similarity, all species may be included in the ecologically trivial "tree using, arthropod eating" guild (a result of how the study community was defined). A finer level of resolution (25% similarity) yields the "tree using" and "air using" guilds, which probably represent broad adaptive strategies determined by the substrate (i.e. trees) and habitat (Morse 1971). Little or no information on functional relationships is obtained from this level of grouping. The next level (50% similarity) includes "air using" and divides "tree using" into "gleaning" (predominantly from foliage) and a combination of "gleaning and probing" (predominantly from wood). The highest level of abstraction recognized here (75% similarity) includes foliage gleaners, divides "gleaning and probing" into wood gleaning and wood probing, and divides "air using" into air sallying and ground sallying. It is probably within this level that species interactions play a role in modifying patterns of foraging behavior (see Bock 1972), especially during periods of reduced resource availability, i.e. "ecological crunches" (Wiens 1977) when competition is likely to be most intense.

From the preceding analysis, the guild structure of this community is suggested to result from a division of broad adaptive strategies (tree and air using) into detailed strategies (foraging techniques), from which species may be divided into guilds based on patterns of microhabitat foraging preferences. Ecological partitioning in this community can be attributed mostly to differing adaptive strategies among guilds, indicative of evolutionary commitment to the physical structure of the habitat (see Holmes et al. 1979). Microhabitat foraging use by guild members, representative of ecological expediency, may be the only area where competitive interactions are likely to be of importance in structuring communities.

Common breeding birds of an oak-juniper woodland from southeastern Arizona (Balda 1969: 411) demonstrated "an exceptionally good fit" in their use of available tree foliage per height class in *Quercus* sp. In contrast, avifaunal use of the tree profile in this Mexican oak woodland was not close (Fig. 3). Species deriving food directly from trees spend a majority of their time at upper heights, not fully using available tree vegetation at intermediate heights. The reason for this discrepancy might be related to two factors. First, an idealized oak tree has a roughly hemispherical shape and thus a greater proportion of foliage, small twigs, and branches at its upper parts. Although intermediate heights exhibit the greatest proportion of the tree profile, much of this is air, affording little opportunity for foraging. Second, height distribution of insects may be disproportionate (possibly due to the greater surface area of foliage and small twigs at upper heights). Salliers perch at lower heights to a greater extent than available tree vegetation. This seems reasonable, because four of five salliers derive much of their food from the ground (see Appendix). Cassin's Kingbird, the one exception, uses upper heights in approximate relation to the tree profile (Fig. 3). Height use by this avian community seems to result generally from use of foliage, twigs, and branches at upper heights by gleaning and probing guilds and use of the ground and twigs at lower heights by sallying guilds.

Our results indicate that the arboreal birds from this oak woodland are organized into a distinct guild structure. Analysis of the guild structure in this community helped clarify the functional relationships of species and thus interpretation of ecological processes important in coexistence. Foliage gleaners exhibit a narrow range of foraging behaviors but overlap species in other guilds extensively; due to their use of a distinctive foraging technique and food site, this overlap is probably eco-

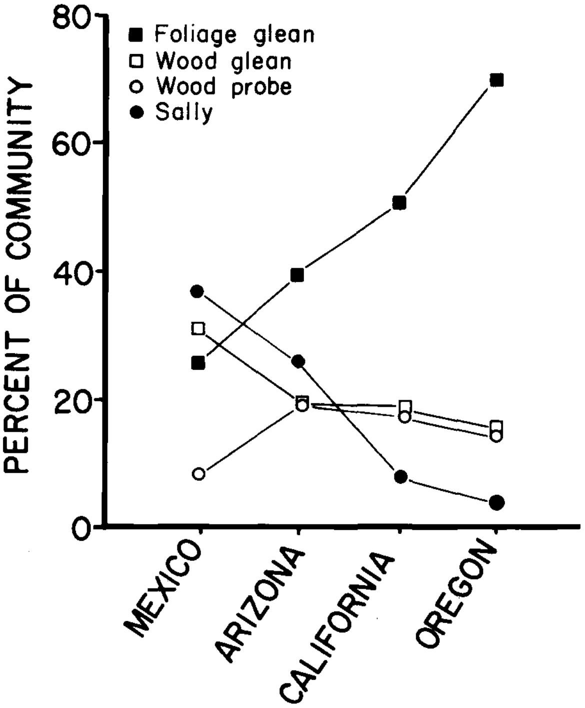

Fig. 4. Comparison of number of species per guild (%) from four sites. See text for explanation of sites and methods.

logically trivial. Wood gleaners have the broadest range of foraging, extensively overlapping those species that acquire food directly from trees. Foliage gleaners are certainly separated from wood gleaners, as is the wood prober with its distinct foraging technique and food source. Wood gleaners and the wood prober exhibit the widest range of microhabitat use, possibly because wood offers a greater variety of places to find suitable food in this habitat and prey may often be hidden from view. Air and ground salliers are similar in patterns of foraging breadth and overlap, e.g. they both overlap foliage gleaners considerably and one another the most. Different food-site selection and foraging technique separate salliers and gleaners; the two sallying guilds are also separated from one another by food-site selection. Due to the large degree of ecological separation between species of different guilds, species interactions may be largely confined to within-guild encounters. Within each guild, species are separated primarily by differences in food site and height. The approach adopted herein also has heuristic value in studies of the effects of competition in structuring communities (e.g. manipulative experiments where a particular resource class that a species is known to use can be eliminated).

Determinants of community organization have been investigated recently by studies of similar though disjunct habitats. For example, resource axes found to be important in avian communities were examined by Cody (1975) in Mediterranean climates on three continents and by Stiles (1978) in Alder (*Alnus*) forests from Central and North America. Similarly, factors contributing to community organization in oak woodlands from Mexico and western North America are currently under investigation (P. Landres MS). Following this same approach, one finds some interesting trends when the present study is compared to (1) Anderson's (1970) study in Oregon white oak (*Quercus garryana*) woodlands (stands 4 and 5 averaged during late spring), (2) Balda's (1970) study from a *Q. emoryi* woodland in southeastern Arizona, and (3) a central Californian Blue oak (*Q. douglassii*) woodland censused during spring 1977 (P. Landres unpubl. data). The number of species per guild, expressed as percent of the community (Fig. 4), is used to make comparisons rather than standardized abundance species pairs$\cdot$guild$^{-1}\cdot 10^{-1}$ ha, because Anderson's (Oregon) and Balda's (Arizona) study sites were nearly four times larger than sites censused in Mexico and California. A conspicuous result of this comparison is that foliage gleaners decrease from Oregon to Mexico nearly 2.5 fold, whereas salliers increase 6.4 fold. The reasons for these patterns are at present obscure. Such patterns raise questions concerning community structure and how species are assembled into guilds: Does admittance to a community depend on specific resource requirements? Is there a relationship between differing guild structures and changes in species diversity? Are species assemblages determinant or random in composition? Do communities "evolve," i.e. how do communities change over time? The following preliminary remarks concerning these questions are given as ideas for further investigation in community studies.

(1) Certain threshold levels of resource requirements must be met for a species to become established in a community. Availability of resources for individual use will depend upon the interplay of chance events, habitat characteristics, species interactions, and evolutionary history of the species. Data from this study, when compared with published foraging accounts of the same species (see Results) from other habitats and communities, indicate that species in this oak woodland are to a large degree restricted in their foraging behavior. Such restricted behavior suggests that particular resources need to be available in sufficient quantity for individuals to survive in that community; this does not imply a plethora or scarcity or resources, because both may contribute to a narrow range of resource use. Also relevant is MacArthur's (1972) discussion of the degree of overlap in species resource utilizations affecting entry and persistence of species in communities (e.g. see Werner 1977). In addition, observed similarity in species foraging might result from convergence of behaviorally flexible individuals in response to differing environmental exigencies. In contrast, other studies identified foraging shifts in similar species within different types of communities (e.g. Crowell 1962, Cody 1974). Greater quantification (in number and kind of observations) and experimental manipulations are needed in community studies to investigate further the role of foraging plasticity in species coexistence.

(2) Patterns of community change (e.g. succession, or latitudinal comparisons of communities) may be viewed as shifts in the number and composition of species assemblages (guilds). Communities change in structure over time and between geographic locations. Quantifying changes in the number of species (and individuals or biomass) per guild may provide a means for examining how resources are used in different communities (see Orians 1969). This would allow testing of hypotheses offered to explain such phenomena as latitudinal gradients in bird species diversity (e.g. smaller breadth in resource use during foraging as opposed to a larger overlap in foraging by tropical species and less resource availability in temperate regions). This approach involves some circular reasoning (from species to resources back to

species) and should be used with caution. An advantage of guild analyses is that they contribute to knowledge of resource states used by species and thus provide broader insight into the structuring of communities.

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APPENDIX. Foraging data (%) of species per foraging category. Species abbreviations as in Table 1. Number of foraging observations given in parentheses. Columns total 500%.

	Species											
Foraging category	AW (386)	WN (350)	BW (351)	SO (145)	BT (357)	BU (235)	LW (204)	AF (185)	EB (162)	DF (217)	VF (235)	CK (183)
Technique												
Glean	9.3	60.8	64.5	49.7	96.0	100.0	99.2	0.0	0.6	0.0	0.0	0.0
Probe	85.5	38.6	35.5	50.3	0.0	0.0	0.8	0.0	0.0	0.0	0.0	2.2
Sally	5.2	0.6	0.0	0.0	4.0	0.0	0.0	100.0	99.4	100.0	100.0	97.8
Portion												
Outer	7.5	6.9	11.1	10.3	28.0	57.4	58.7	55.7	51.9	37.0	94.9	75.6
Middle	60.9	43.1	35.3	63.5	61.3	42.6	40.2	4.3	46.2	63.0	5.1	24.4
Inner	31.6	50.0	36.8	26.2	9.5	0.0	1.1	0.0	0.0	0.0	0.0	0.0
Ground	0.0	0.0	16.8	0.0	1.2	0.0	0.0	40.0	1.9	0.0	0.0	0.0
Perch Site												
Twig	1.9	1.4	20.1	16.5	73.5	89.8	93.6	60.1	75.9	98.2	98.1	99.4
Branch	63.5	50.2	33.1	80.7	24.0	10.2	6.4	2.7	22.2	1.8	1.9	0.6
Trunk	34.6	46.1	32.2	2.8	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ground	0.0	2.3	14.6	0.0	1.1	0.0	0.0	37.2	1.9	0.0	0.0	0.0
Food Site												
Foliage	3.8	0.0	4.2	22.8	64.7	74.9	97.0	0.0	0.0	14.3	0.0	7.7
Twig	0.5	1.4	16.4	13.1	16.5	22.5	0.8	0.0	0.0	1.7	0.0	0.0
Branch	61.2	50.4	30.8	61.3	13.5	2.6	2.2	0.0	0.0	0.0	0.0	0.0
Trunk	29.3	45.9	33.0	2.8	1.4	0.0	0.0	0.0	0.6	0.9	0.0	0.0
Ground	1.1	2.3	15.6	0.0	3.9	0.0	0.0	67.6	98.2	35.5	30.6	8.7
Air	4.1	0.0	0.0	0.0	0.0	0.0	0.0	32.4	1.2	47.6	69.4	83.6
Height (m)												
Ground–1.5	7.8	13.4	27.6	0.0	2.2	0.0	0.0	88.6	8.0	28.6	86.0	6.0
1.6–3.0	0.8	16.0	16.5	4.1	17.6	13.0	0.0	6.0	22.2	42.4	8.1	8.2
3.1–4.5	12.7	16.8	10.8	30.3	28.3	19.0	0.0	0.5	46.3	11.5	0.4	18.0
4.6–6.0	28.0	30.9	15.7	55.9	22.7	26.3	35.3	1.1	21.0	7.4	0.0	7.1
6.1–7.5	36.0	22.3	24.8	9.7	22.4	39.7	58.3	2.2	1.9	8.3	2.5	33.9
7.6–9.0	14.7	0.6	4.6	0.0	6.8	2.0	6.4	1.6	0.6	1.8	3.0	26.8