

COMMUNITY ORGANIZATION OF ARBOREAL BIRDS IN SOME OAK WOODLANDS OF WESTERN NORTH AMERICA¹

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Abstract. Community organization of the arboreal birds in two oak woodlands of western North America was examined during the course of two breeding seasons. A "natural experiment" comparing the arboreal avifaunas inhabiting oak woodlands of similar tree structure in northeastern Sonora, Mexico (referred to as Purica), and in the central coastal mountains of California, USA (referred to as Carmel), was used to address questions concerning (1) variables that account for variation in foraging behavior, (2) overall similarity in foraging behavior of the two avifaunas, (3) partitioning of resources within each avifauna, (4) guild structure, (5) foraging heights, (6) changes in foraging behavior between sites, and (7) complementarity in resource use during foraging.

At Purica there were 15 breeding species, and at Carmel 10 species. Foraging technique, portion of the tree, perch substrate and height, and the substrate from which food was derived during foraging were quantified with the aid of an audio metronome. The first three axes in a Principal Components Analysis (PCA) accounted for ≈75% of the variation in foraging behavior at both sites, and were associated with technique, food site, and height. The rank order of the PCA loadings for all foraging variables on each PCA axis was highly correlated between Purica and Carmel, indicating that the overall pattern of foraging at both sites was very similar despite differences in avifaunal composition, density, and consuming biomass.

Analysis of species breadth and overlap during foraging indicated that at both sites foraging specialization does not connote a decreased potential for species interactions. In addition, estimates of community breadth and overlap indicated that technique and food site were the most important foraging parameters in community organization at both sites.

Three methods were used to develop the guild classification used in this paper: reciprocal averaging ordination, cluster analysis, and discriminant function analysis. At Purica five guilds were recognized: foliage gleaners, bark gleaners, bark probers, air salliers, and ground salliers. At Carmel four guilds were recognized: foliage gleaners, bark probers, air salliers, and ground salliers. In terms of relative guild consuming biomass (CB), foliage gleaners and bark gleaners at Purica together constitute 34% of the community. Interestingly, at Carmel a distinct bark gleaning guild is absent, and foliage gleaners constitute 32% of the community's CB. The proportion of community CB contributed by the other guilds was significantly different between sites. Although the possible functional roles performed within each community were similar (based on the kinds of guilds present), their guild structures were significantly different (based on the distribution of guild CB within each avifauna).

The foraging space used by each of the guilds and the entire community was examined in detail. Foraging height of the birds was generally not related to the tree profile, although at both sites bark probers derived most of their food from upper heights, foliage gleaners mostly from intermediate to upper heights, and ground salliers perched at intermediate heights. In contrast, air salliers at Purica usually perched at lower heights, while at Carmel they used upper heights most frequently. At Purica 50% of the compensatory shifts in foraging were consistent with predictions of competition-based hypotheses, whereas at Carmel none of the predictions was verified. Interspecific complementarity of resource use was demonstrated only marginally in air salliers at Purica.

It is concluded that (1) the foraging behavior of some species at Purica, especially air salliers, is consistent with predictions from competition theory, although a lack of interspecific complementarity indicates that the competitive forces are rather weak, (2) at Carmel, opportunism appears to be more important in affecting the pattern of foraging behaviors, (3) other factors, especially ground cover, shrub density, and the local weather, have influenced foraging behavior and community structure at both sites, (4) similarity between sites in avian community structure is a consequence of the similarity in tree structure, whereas differences between sites probably result from short-term behavioral flexibility in microhabitat use in response to differences in prey distribution and abundance, and (5) interspecific competition is not a prerequisite for resource partitioning.

Key words: arboreal birds; California; community organization; community structure; competition; foraging; guild; insectivorous birds; niche breadth; niche overlap; niche shifts; resource complementarity; resource partitioning; Sonora, Mexico.

¹ Manuscript received 19 January 1982; revised 5 June 1982; accepted 14 June 1982.

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INTRODUCTION

Studies of resource partitioning and the evolution of foraging strategies in birds (e.g., Morse 1971, Rabenold 1978, Eckhardt 1979, Sherry 1979) have contributed to understanding the structure and organization of avian communities. Interspecific competition was cited as the predominant factor influencing resource use in many studies (e.g., Cody 1974, Diamond and Marshall 1976, Ford and Paton 1976, Jones 1977, Alatalo and Alatalo 1979, Williams and Batzli 1979). In contrast, other investigations provided data suggesting that adaptations of species to particular features of the habitat, and opportunism, were more important in structuring communities (e.g., Hespenheide 1964, Ashmole 1968, Crome 1978, Wiens and Rotenberry 1979, Rotenberry 1980). Determinants of avian foraging behavior, however, can rarely be ascribed to a single factor (Pearson 1977b, Karr 1980), and probably vary depending on the species mix (Villeumier and Simberloff 1980) and resource characteristics (Wiens 1977).

While the importance of vegetation structure in avian ecology is firmly established (e.g., Willson 1974, Roth 1980), the influence of resource characteristics and interspecific interactions on foraging behavior is still unsettled. Habitats with similar vegetation architecture in different geographic locations and inhabited by different resident birds afford a "natural experiment" where the effects of resource characteristics and interspecific interactions may be distinguished from those of vegetation architecture in structuring avian communities. Classifying species into guilds (Root 1967) on the basis of foraging behavior provides a framework for examining these effects within the community, and their potential impact on community structure (Willson 1974, Pearson 1975, Feinsinger 1976, MacMahon 1976, Landres and MacMahon 1980). Part of the difficulty in generalizing about community patterns and processes is a lack of congruity in the use of certain ecological terms. In this study we limit the analysis to a taxonomic assemblage which we refer to as an avian community. We recognize that other distantly related taxa (e.g., reptiles or mammals) may affect avian foraging behavior and may therefore be members of the community; a preliminary analysis of these effects is given below. Also, we differentiate between the terms structure: any characteristic or attribute of the community that can be described at a given time, and organization: the interactions of organisms both with other organisms and the physical environment that, over time, influence community structure.

Oak woodlands of western North America extend from the interior of Mexico north to the state of Washington, USA. Stands of various oak species may be found within this range that, while similar in tree structure, are inhabited by different resident birds, satisfying the conditions for the type of "natural experiment" described above. Two study sites were selected for their similarity of tree structure and dissimilarity

of avifaunas; one in northeastern Sonora, Mexico, the other in the coastal mountains of central California, USA.

Various aspects of avian foraging behavior have been studied in oak woodlands by previous workers. Root (1967) examined the foraging, diet, and morphology of species in the foliage gleaning guild at sites adjacent to those of this study. Also in California the coexistence of tyrannid flycatchers (Verbeek 1975), ecological complementarity of some parids (Hertz et al. 1976), and seasonal changes in guild foraging (Wagner 1981) were studied. In Oregon, Anderson (1970) examined seasonal change in guild composition and foraging, and in southern Arizona, Austin and Smith (1972) studied the "foraging niche" of winter flocks. To date no studies have compared widely separated oak woodlands in an attempt to address questions on interspecific competition, resource partitioning, and community organization.

This paper examines various factors potentially influencing avian community structure in oak woodlands. The following questions, and some hypotheses derived from competition theory (e.g., Cody 1974, Pianka 1978) to test the often assumed importance of interspecific competition in determining community structure, will be examined:

- 1) Which variables account for the greatest amount of variation in foraging behavior in these oak woodland bird communities? Are the same variables important in different avian communities that inhabit woodlands of similar tree structure?

- 2) How similar is the overall pattern of foraging behavior in different avian communities that inhabit oak woodlands of similar tree structure?

- 3) How are foraging substrate resources partitioned within each avian community?

- 4) How similar are the guild structures of different avian communities that inhabit oak woodlands of similar tree structure?

- 5) Do species and genera common to different avian communities that inhabit oak woodlands of similar tree structure exhibit changes or shifts in foraging behavior? Can such changes in foraging be attributed to particular features of the habitat, or to interspecific competition?

In addition, factors related to differences in geographic location of the study areas, such as (1) climate and its effect on the arthropod fauna, (2) biogeographical and evolutionary histories, (3) predation and competition from distantly related organisms, and (4) chance events, may also affect community patterns and will be examined by drawing on the available literature.

STUDY AREAS

Purica

Oak woodlands occur throughout Sonora, Mexico, forming a belt from ≈1300 to 1600 m in elevation (Marshall 1957). Study plots were located in the eastern

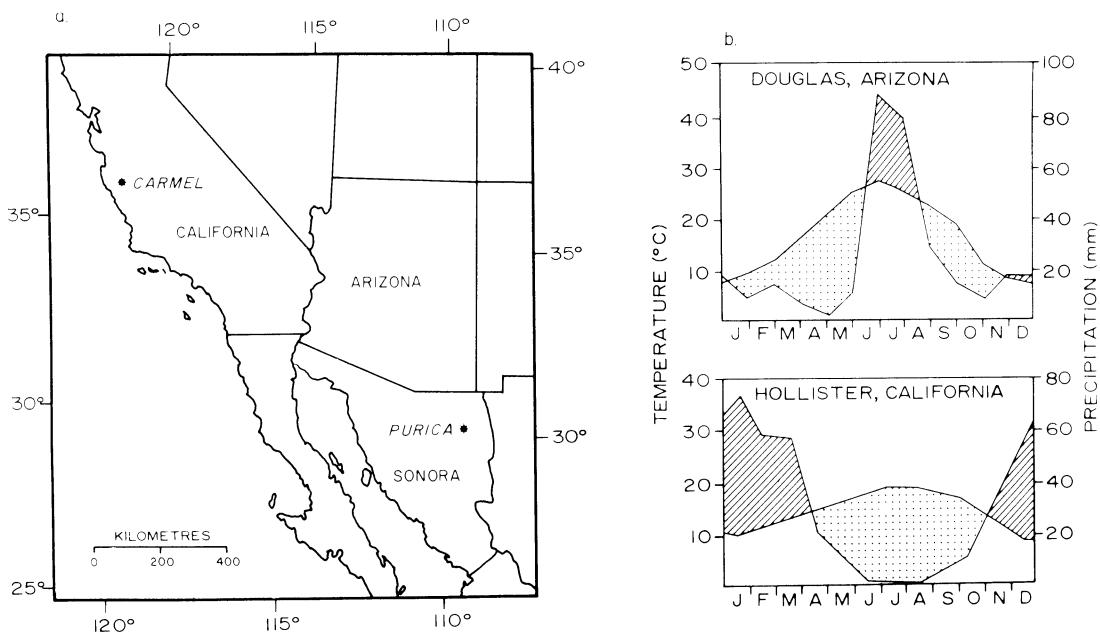


FIG. 1a. Locations of the study sites in southwestern United States and northwestern Mexico. b. Climate diagrams (top from National Climatic Center 1973, bottom from Walter and Lieth 1967) illustrating relatively humid (diagonal lines) and dry (stippling) seasons for sites near Purica (top) and Carmel (bottom).

foothills of the Sierra la Purica, northeastern Sonora, Mexico ($30^{\circ}35'N$, $109^{\circ}43'W$), ≈ 1500 m in elevation, 120 km south of Douglas, Arizona (Fig. 1a; hereafter referred to as Purica). A 10-ha plot was established in late March 1977. Two replicate plots were established in late March 1978.

Emory oak (*Quercus emoryi*) dominated each plot, and with the infrequent Mexican blue oak (*Q. oblongifolia*), formed an open, park-like woodland. Individual *Q. emoryi* began dropping leaves during the first week in April both years; flowering occurred shortly thereafter. Thus, at any time during the study, some trees were in various stages of leaf development or were flowering (cf. Balda 1970). A few cacti (*Opuntia engelmannii*, *O. spinosior*) were interspersed throughout the woodland. The only subtree (<6 m in height) present was desert willow (*Chilopsis linearis*) which occurred along dry river margins; *Mimosa biuncifera* was virtually the only shrub. Ground cover consisted mostly of grasses with interspersed herbaceous perennials and annuals. The study plots were heavily grazed by cattle.

During the study (March through May 1977 and 1978) mean minimum and maximum temperatures were $5.6^{\circ}C$ and 35.4° , respectively. Climatic data for Douglas, Arizona (National Climatic Center 1973) at ≈ 1250 m elevation indicate a typical warm desert climate with predominantly summer rain, and spring and fall drought (see Fig. 1b).

Carmel

In California, between Los Angeles and Trinity counties, park-like oak woodlands occur in foothills

and along valley borders between ≈ 120 and 920 m in elevation (Munz and Keck 1968). Study plots were located at ≈ 540 m elevation in the northern Santa Lucia Mountains ($36^{\circ}26'N$, $120^{\circ}37'W$), Monterey County, California (Fig. 1a; hereafter referred to as Carmel). A 10-ha study plot was established in May 1977. Two replicate plots were established in May 1978.

Each study plot was dominated by pure stands of blue oak (*Q. douglasii*), with an occasional coast live oak (*Q. agrifolia*) and valley oak (*Q. lobata*). The few shrubs present were individuals of currant (*Ribes spp.*), redberry (*Rhamnus crocea*), and poison oak (*Rhus diversiloba*). Ground cover consisted mostly of grasses, except for heavily grazed areas where filaree (*Erodium botrys* and *E. cicutarium*) predominated. Numerous herbaceous perennials and annuals were present. Each of the study plots was moderately to heavily grazed by cattle.

During the study (May through June 1977 and 1978) mean minimum and maximum temperatures were 4.3° and 26.1° , respectively. Climatic data for Hollister, California (≈ 60 km northeast of Carmel [Walter and Lieth 1967]) indicate a typical mediterranean climate with mild, wet winters and hot, dry summers (see Fig. 1b). There is an approximate complementarity of wet and dry seasons between Purica and Carmel.

METHODS

Vegetation sampling

Ten 0.05-ha circles were randomly established on each 10-ha plot following methods modified from James and Shugart (1970). Tree density was estimated by av-

eraging, over plots, the number of trees ($\text{dbh} > 8 \text{ cm}$) encountered in the circles on each plot multiplied by 2. Percent vegetation within 1.5-m height classes (collectively referred to as tree profile), tree height, and percent ground and canopy cover were sampled using line transects originating at the center of each circle. Transect direction was randomly selected from eight equally spaced azimuths. Two 50-m transects were established per circle yielding 1000 m of transect per plot, with sampling points two paces apart ($\approx 1.4 \text{ m}$) along each transect. An aluminum rod marked in 1.5-m intervals was placed vertically at each sampling point to ascertain the presence of foliage or wood within each height stratum, and for ground and canopy cover. Ground cover was sampled every 3 wk throughout the study period. Shrub density was sampled by recording the number of woody stems $\leq 8 \text{ cm}$ diameter occurring in a swath $\approx 2 \text{ m}$ wide along each transect to the perimeter of the circle (James and Shugart 1970). Total number of stems encountered on each plot was multiplied by 10, then averaged, yielding shrub density per hectare. Vegetation parameters were determined by averaging results from the three plots at each site.

Censusing and foraging behavior

Data collection was restricted to the arboreal component ($\approx 60\%$) of the oak woodland avian community at both sites, i.e., to those species using some part of a tree in the majority of their food-capturing activities.

A modified "spot-map" method (International Bird Census Committee 1969) was used to sample the breeding species and their densities. Ten censuses were conducted on the single plot at Purica from 28 March to 1 May 1977, and on the single Carmel plot from 25 May to 6 June 1977. Five censuses were conducted on each of the three plots at Purica from 28 March to 17 April 1978, and on the Carmel plots from 16 May to 7 June 1978. Censuses were initiated at approximately the beginning of the breeding season at both sites, despite the differences in dates. All censuses were conducted from 0600 to 0900 Mountain Daylight Time (MDT).

Foraging behavior was quantified in breeding species using the metronome technique of Wiens et al. (1970). Landres and MacMahon (1980) discuss some of the problems with this technique. Only actively foraging birds were monitored, with recordings on each bird taken at 15-s intervals and limited to 2 min to reduce sampling bias. During observation periods (0600 to 1800) the following components of foraging behavior were recorded: (1) foraging technique, defined as gleaning (taking food from a surface), probing (taking food from beneath a surface), or sallying (taking food after flying from a perch); (2) portion of the tree being used, defined as inner (a vertical axis extending from the tree's base to its top including, and 1 m away from, the trunk), outer (the outermost periphery of the tree and extending 1 m in towards the tree's center), or

middle (that region between inner and outer portions); (3) perch site, estimated as twig ($< 1.5 \text{ cm}$ diameter), branch ($\geq 1.5 \text{ cm}$ and $\leq 15.0 \text{ cm}$), trunk ($> 15.0 \text{ cm}$), or ground; (4) food site, defined as foliage (including both perennial and annual leaves, and flowers), twig, branch, trunk, ground, or air; and (5) vertical height of the perch site (1.5-m height classes). The metronome was not used for sallying individuals; instead, each sally was used as the signal to record the above data. The foraging techniques and substrates together constitute 23 foraging variables that were used in the foraging behavior analyses. In the discussion that follows we have assumed that the amount of time spent foraging on a substrate is proportional to the amount of food derived from that substrate.

Analysis

A *G* test (Sokal and Rohlf 1969), based on the number of foraging observations, was used to test for significant differences in foraging among species ($P < .01$ unless stated otherwise).

Cluster analysis, with the unweighted pair-group method on arithmetic averages (Sokal and Sneath 1963), was used to classify species into guilds. Resemblance coefficients were based on Euclidean distances. A discriminant function analysis, using the *a posteriori* guilds as the grouping variable, was used to verify results of the cluster analysis. That is, if species were "correctly" classified in the cluster analysis, the "predicted" group membership of the species (based on the discriminant function algorithm) would correspond closely to the "actual" group membership (based on the cluster analysis).

Reciprocal averaging ordination (RA) was used to examine foraging relationships among species (Hill 1973, Sabo and Whittaker 1979). Principal components analysis (PCA) with varimax rotation (Nie et al. 1975) was employed to elucidate those variables (among the 23 defined above), or combinations thereof, that accounted for the greatest amount of variation in species foraging behavior. Variables with high loadings are considered to be those most important in the organization of guilds and communities (Holmes et al. 1979). To assess similarity in the overall pattern of foraging behavior at Purica and Carmel a Spearman's rank correlation (SRC) was performed on the PCA loadings between sites in each principal component factor.

Numerous indices of resource use breadth and overlap are available in the literature. Linton et al. (1981) presented a statistical assessment of some of the more commonly used overlap indices, concluding that Schoener's (1970) index generally was the most accurate. Colwell and Futuyma (1971), however, noted several potential problems in the use of simple measures of overlap such as Schoener's, offering their own indices of breadth and overlap as an alternative. Although they have not been assessed statistically, Colwell and Futuyma's indices appear more accurate than

other indices, especially for intercommunity comparisons, and were therefore used in this study. Intracommunity comparisons of resource use breadth and overlap for each species and guild were calculated using the percent of foraging observations with "relative" metrics (i.e., maxima scaled to a value of 1) and the "noncircular" method (i.e., resource state weighting factors are recomputed for each calculation). Intercommunity comparisons of breadth and overlap were made using "absolute" metrics (i.e., maxima scaled by the total resource-state heterogeneity) to alleviate problems of differing resource levels in such comparisons (Colwell and Futuyma 1971, Inger and Colwell 1977). A Mann-Whitney *U* test ($P < .05$ unless stated otherwise) was used in comparing breadth and overlap values among species and guilds, unless sample sizes were ≥ 20 , in which case a *t* test was used.

In assessing avian energetic demands made on an ecosystem, consuming biomass is a better index than either population density, or total biomass alone (Salt 1957, Karr 1968). Species consuming biomass (CB) was estimated as

$$CB = NW^x,$$

where N is the number of individuals per 10 ha, W is the mean mass (g) of the species, and x is the exponent 0.5876 for passerines, and 0.6722 for nonpasserines, in temperate habitats at an average 19°C (Karr 1971).

Foraging data from both years were combined to form a single data set for each site (Appendices 1 and 2), upon which all subsequent analyses were performed. A preliminary test of the effects of combining data sets in this manner was made by comparing the combined data with data derived from a Monte Carlo simulation. Each datum in the Appendices represents a mean value calculated from the 1977 and 1978 data; a corresponding standard deviation was also calculated from these data. Simulated data were derived from computer generated random numbers that were within 1.65 standard deviations (i.e., 90%) of a normal distribution. These random numbers were then multiplied by the calculated standard deviation, and added to the value of each datum in the Appendices. Thus, each cell of the simulated data matrix represents a random number based on the mean and standard deviation of the original datum, within 90% confidence limits, and reflects the amount of variation obscured by combining the original 1977 and 1978 data. The simulated data matrix was then subjected to analyses performed on the original data, and the results qualitatively compared. In all cases no major differences between the two analyses resulted, corroborating use of the combined data at each site.

RESULTS AND DISCUSSION

Vegetation

The mean number of trees per hectare (271), mean tree height (7.7 m) and mean canopy cover (38.6%) at

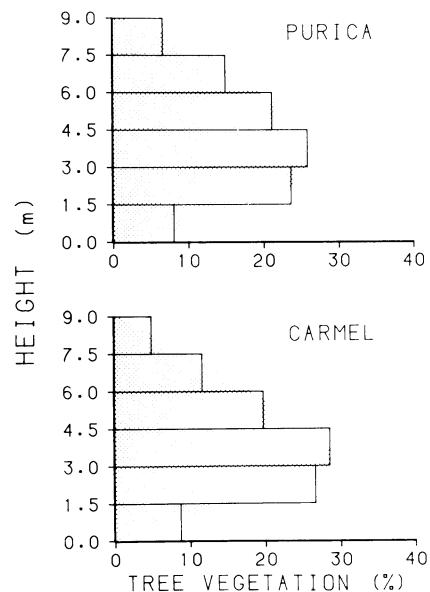


FIG. 2. Average percent tree vegetation per height class (tree profile) at Purica and Carmel. Shaded area represents the "typical" tree profile at each site.

Purica were not significantly different (*t* test) from these same parameters at Carmel (274 trees/ha, 7.4 m, 40.5%, respectively). There was no statistical difference (χ^2 test) in the tree profile among plots at either site, nor was a difference detected between Purica and Carmel when plots from each site were compared in a 6×6 χ^2 matrix (see Fig. 2). Mean ground cover differed between Purica (70%) and Carmel (100%), and did not change at either site during the study. A mean of 2280 shrubby stems/ha was encountered at Purica, mostly of *Mimosa* and *Chilopsis*. Carmel had a mean of 836 stems/ha, primarily of dead oak branches and a few *Rhamnus* and *Ribes* stems. These results indicate a strong similarity in structure of the trees at the two study sites. Bark rugosity, although not quantified, appeared similar at the two sites. Possible effects of the disparities in ground cover and shrub density on the comparison of the two avian communities are discussed below.

Species density and consuming biomass

Of the 15 species breeding at Purica, and the 10 at Carmel, only 4 (19%) occurred at both sites (Table 1): Acorn Woodpecker, White-breasted Nuthatch, Bush-tit, and Ash-throated Flycatcher. In addition, 6 congeneric dyads in 4 genera occurred between the two sites (Table 1). At Purica three woodpeckers (Gila, Ladder-backed, and Arizona) were not observed in 1977. The presence of Gila and Ladder-backed woodpeckers in 1978 appears somewhat anomalous, because these woodpeckers were not observed in pine-oak forests in northeastern Sonora (Marshall 1957), or

TABLE 1. Species densities (pairs/10 ha) for Purica and Carmel in both study years. Data for 1978 are mean densities from the three plots censused that year (see Landres 1981), with standard deviations in parentheses for comparison with densities in 1977.

Species (abbreviation)	Scientific name	Purica		Carmel	
		1977	1978	1977	1978
Acorn Woodpecker (AW)	<i>Melanerpes formicivorus</i>	3.0	1.7 (± 0.6)	3.5	2.3 (± 0.6)
Gila Woodpecker (GW)	<i>Melanerpes uropygialis</i>		1.3 (± 0.6)		
Ladder-backed Woodpecker (LB)	<i>Picoides scalaris</i>		0.3 (± 0.6)		
Arizona Woodpecker (ZW)	<i>Picoides arizonae</i>		0.3 (± 0.6)		
Nuttall's Woodpecker (NW)	<i>Picoides nuttallii</i>			1.0	0.7 (± 0.6)
White-breasted Nuthatch (WN)	<i>Sitta carolinensis</i>	3.0	2.0 (± 0.0)	3.0	2.0 (± 0.0)
Scott's Oriole (SO)	<i>Icterus parisorum</i>	2.0	0.7 (± 0.6)		1.3 (± 1.2)
Northern Oriole (NO)	<i>Icterus galbula</i>			2.0	
Bewick's Wren (BW)	<i>Thryomanes bewickii</i>	6.0	5.7 (± 0.6)		
Bridled Titmouse (BT)	<i>Parus wollweberi</i>	5.0	3.3 (± 0.6)		
Plain Titmouse (PT)	<i>Parus inornatus</i>			6.0	3.3 (± 0.6)
Bushtit (BU)	<i>Psaltriparus minimus</i>	2.0	1.0 (± 1.0)		0.3 (± 0.6)
Blue-gray Gnatcatcher (BG)	<i>Polioptila caerulea</i>			2.0	2.0 (± 0.0)
Warbling Vireo (WV)	<i>Vireo gilvus</i>			1.0	1.0 (± 1.0)
Lucy's Warbler (LW)	<i>Vermivora luciae</i>	3.0	2.3 (± 0.6)		
Cassin's Kingbird (CK)	<i>Tyrannus vociferans</i>	4.0	2.0 (± 0.0)		
Ash-throated Flycatcher (AF)	<i>Myiarchus cinerascens</i>	4.0	2.0 (± 0.0)	2.0	0.3 (± 0.6)
Dusky Flycatcher (DF)*	<i>Empidonax oberholseri</i>	2.0	2.0 (± 0.0)		
Vermilion Flycatcher (VF)	<i>Pyrocephalus rubinus</i>	1.0	2.3 (± 0.6)		
Eastern Bluebird (EB)	<i>Sialia sialis</i>	2.0	2.0 (± 1.0)		
Western Bluebird (WB)	<i>Sialia mexicana</i>			2.0	2.0 (± 0.0)
Total richness (number of species)		12	15	9	10
Total density (pairs/10 ha)		37.0	28.9	22.5	15.2

* See MacMahon and Landres (1981) for commentary on the inclusion of this species.

in oak woodlands in southeastern Arizona (Balda 1970). The Purica study site, however, is well within both species' ranges (Phillips et al. 1964). At Carmel, Bush-tits were not seen in 1977, although they are generally considered residents of the local oak woodlands (Linsdale 1947). The absence of Bewick's Wren in the blue oak woodland at Carmel is probably a result of the reduced shrub density there: both Miller (1941) and Wagner (1981) indicate that a high density of low twigs is preferred by this wren.

Densities of breeding species for 1978 were derived by averaging the three plots censused that year; variability in species densities among plots was generally small at both sites (Table 1). The Purica avifauna exhibited 1.4 times the species richness, and 1.8 times the density of the Carmel avifauna over both years (Table 1). Roth (1977) also found large differences in density (males/40 ha) in bird communities inhabiting structurally similar brush-grasslands. Total CB at Purica averaged 1.6 times greater than that at Carmel both years (Table 2). Despite these differences between sites, the average number of pairs per species and CB per species at Purica (2.5 pairs and 31.4 g/species) was similar to Carmel (2.0 pairs and 30.2 g/species). Species and genera common to both sites exhibited roughly similar CB, except for the Ash-throated Flycatcher and the congeneric woodpeckers which have a greater CB at Purica.

Species' foraging behavior

Ordination of the 15 species at Purica, using the 23 foraging variables, indicated three distinct groups of

species discernible on RA axes I and II (Fig. 3). These groups may tentatively be labeled as bark probbers, salliers, and foliage gleaners. Bewick's Wren and Scott's Oriole are in a position between the bark prob-

TABLE 2. Species' mass and mean consuming biomass (g/10 ha) from both years at Purica and Carmel.

Species	Mass (g)	Consuming biomass	
		Purica	Carmel
Acorn Woodpecker	80.2*	89.5	110.5
Gila Woodpecker	65.0†	21.5	
Ladder-backed Woodpecker	36.0†	3.4	
Arizona Woodpecker	42.5‡	3.8	
Nuttall's Woodpecker	37.4‡		19.4
White-breasted Nuthatch	25.4*	33.5	33.5
Scott's Oriole	32.9†	22.2	
Northern Oriole	48.5*		32.3
Bewick's Wren	15.9*	59.5	
Bridled Titmouse	10.4*	32.9	
Plain Titmouse	16.6*		48.5
Bushtit	8.0*	10.2	1.0
Blue-gray Gnatcatcher	6.9*		12.4
Warbling Vireo	18.0*		10.9
Lucy's Warbler	7.3*	17.1	
Cassin's Kingbird	48.5*	58.7	
Ash-throated Flycatcher	35.0*	48.5	3.6
Dusky Flycatcher	17.5*	21.5	
Vermilion Flycatcher	13.9‡	15.5	
Eastern Bluebird	35.5*	32.6	
Western Bluebird	30.8*		30.0
Total		470.5	302.1

* From J. Weiner (personal communication).

† From Miller and Stebbins (1964).

‡ Estimated from linear interpolation of length-to-mass ratio of taxonomically similar species of known mass.

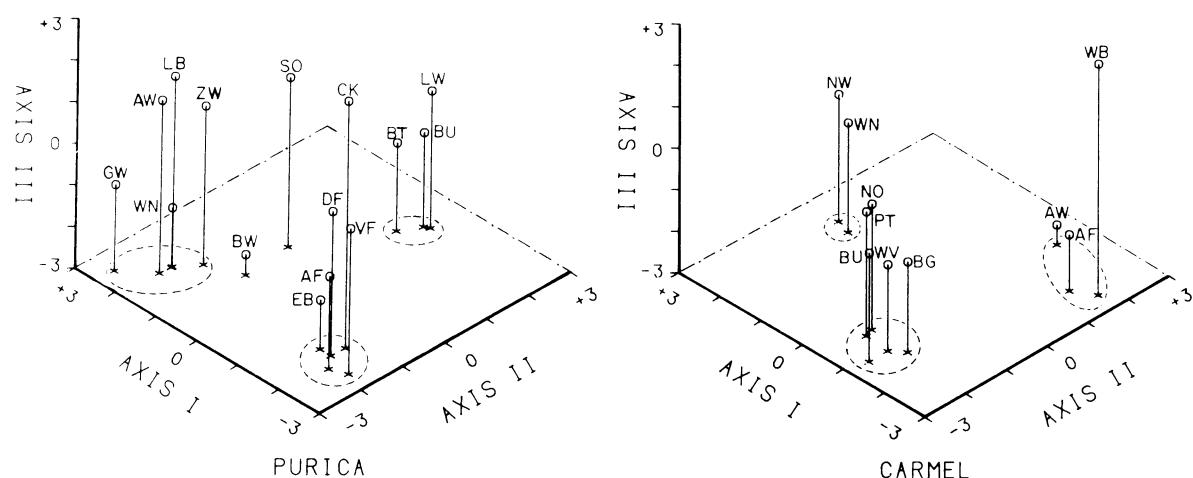


FIG. 3. Reciprocal averaging ordination of the 15 bird species at Purica, and the 10 species at Carmel, with the 23 foraging variables (see text). Species abbreviations as in Table 1. Ellipses drawn by eye. Axes have been rescaled for graphical purposes.

ers and foliage gleaners. RA ordination at Carmel (Fig. 3) yields the same three distinct groups. RA axis I appears to be associated with technique at Purica, and food site at Carmel, while RA axis II is associated with food site at Purica, and technique at Carmel. At both sites RA axis III effectively separates the species according to their foraging heights.

A varimax rotation of PCA factors was used to examine correlations of foraging variables associated with each principal component (Table 3), and to assess similarity in foraging of the two avifaunas. The first three PCA axes accounted for $\approx 75\%$ of the variance in foraging behavior at both sites. The avian communities at Purica and Carmel exhibited similar patterns of foraging as indicated by strong intersite correlations of the loadings on the foraging variables in all four PCA axes (Table 3). If interspecific competition was important in structuring the pattern of foraging in these communities, different competitive regimes at each site (as indicated by different species composition) would be expected to promote differences in those patterns. The data presented above do not support this expectation. The birds appear instead to be responding to the similarity in tree structure at both sites, and presumably a similar distribution of arthropod prey. Similarity in foraging of the two avifaunas can occur by species foraging similarly at both sites, or by a combination of species at one site foraging similarly to one or more species at the other site.

Foraging comparisons of species and genera common to both sites

Foraging behaviors of both conspecifics and congeners were compared (Table 4, *G* test) to determine if shifts in foraging behavior occurred between sites. Acorn Woodpeckers and White-breasted Nuthatches displayed significant differences between sites in all foraging categories. Ash-throated Flycatchers foraged

similarly only in technique, and Bushtits differed only in perching height between the two sites. Of the six congeneric comparisons, the Bridled Titmouse–Plain Titmouse; Scott's Oriole–Northern Oriole; Gila Woodpecker–Acorn Woodpecker; and Arizona Woodpecker–Nuttall's Woodpecker exhibited significant differences in all foraging categories. The Eastern Bluebird–Western Bluebird foraged similarly only in technique, and the Ladder-backed Woodpecker–Nuttall's Woodpecker foraged differently only in technique and perching height. In all comparisons the use of perch heights was different, indicating that this aspect of species foraging behavior is quite flexible.

If competition is the dominant factor influencing changes in foraging behavior, compensatory shifts in foraging of other species would be expected. The large number of species in each community, and the possibility of diffuse competition, however, may make compensatory shifts difficult to detect at this species level of resolution (see Compensatory Shifts in Foraging).

Species' foraging breadth and overlap

The concepts of species' breadth and overlap in resource use are important in community analyses, the former indicating the degree of ecological specialization and the latter the degree of potential interaction between species (McNaughton and Wolf 1979). Species' foraging breadths and overlaps for each of the foraging categories, and in total resource use (estimated by subjecting the entire matrix of all foraging categories combined to the breadth and overlap computations), are given in Landres (1981).³

³ For a complete list of species' foraging breadths and overlaps at both sites consult ESA Supplementary Publication Service Document No. 8310 for 16 pages of supplementary material. For a copy of this document, contact the first author or order from The Ecological Society of America, Cornell University, Ithaca, New York 14853 USA.

TABLE 3. Principal component factors I-IV for the Purica and Carmel avifaunas with varimax-rotated factor loadings for each foraging variable. Spearman's rank correlations are given for each factor comparing the loadings from the two sites. † = important loadings. *** = $P < .001$.

Foraging category	Factor I		Factor II		Factor III		Factor IV	
	Purica	Carmel	Purica	Carmel	Purica	Carmel	Purica	Carmel
Technique								
Glean	-0.223	-0.248	0.934†	0.940†	-0.034	-0.094	0.100	0.034
Probe	0.840†	0.962†	-0.001	0.037	0.495†	0.114	-0.047	-0.192
Sally	-0.494†	-0.271	-0.766†	-0.927†	-0.371	0.031	-0.044	0.070
Portion								
Outer	-0.891†	-0.775†	-0.256	-0.570†	-0.101	-0.046	-0.109	0.009
Middle	0.340	0.371	0.291	0.742†	0.175	0.035	-0.094	-0.047
Inner	0.923†	0.959†	0.114	0.170	0.014	0.021	0.029	-0.175
Ground	0.049	-0.146	-0.014	0.373	-0.094	0.098	0.963†	0.887†
Perch site								
Twig	-0.917†	-0.820†	0.022	0.186	-0.354	-0.509†	-0.125	-0.120
Branch	0.636†	0.702†	-0.025	-0.230	0.594†	0.637†	0.130	0.084
Trunk	0.910†	0.969†	-0.007	-0.131	-0.038	-0.027	-0.130	-0.112
Ground	0.059	-0.135	-0.019	0.353	-0.103	0.104	0.963†	0.891†
Food site								
Foliage	-0.483†	-0.699†	0.830†	0.643†	-0.035	-0.187	-0.151	-0.237
Twig	-0.126	-0.213	0.757†	0.875†	0.053	-0.121	0.529†	0.301
Branch	0.684†	0.949†	0.083	0.258	0.673†	0.158	0.095	0.008
Trunk	0.907†	0.968†	-0.006	0.062	-0.044	0.057	-0.129	-0.213
Ground	-0.243	-0.077	-0.539†	-0.575†	-0.582†	-0.413	0.140	0.560†
Air	-0.547†	-0.229	-0.702†	-0.688†	-0.054	0.410	-0.099	-0.200
Height (m)								
Grd-1.5	-0.332	0.026	-0.632†	-0.361	-0.280	-0.455†	0.436	0.764†
1.6-3.0	-0.137	-0.103	-0.280	0.003	-0.459†	-0.894†	0.002	0.237
3.1-4.5	0.300	-0.197	0.313	0.065	-0.620†	-0.933†	-0.056	-0.069
4.6-6.0	0.270	0.168	0.904†	0.389	0.058	0.341	-0.168	-0.612†
6.1-7.5	0.120	0.085	0.417	0.043	0.659†	0.947†	-0.377	-0.161
7.6-9.0	0.157	0.063	0.043	-0.223	0.871†	0.939†	-0.251	0.022
Spearman's r_s	.902***		.815***		.728***		.816***	
% variance	38.9	37.0	20.1	24.1	13.1	17.4	8.9	12.5
Cumulative %	38.9	37.0	59.0	61.1	72.1	78.5	81.0	91.0

TABLE 4. Comparison between sites of foraging behavior (G test) of species and genera occurring at both Purica and Carmel. *** = $P < .001$.

Species	Foraging category				
	Technique	Portion	Perch	Food	Height
Conspecific					
Acorn Woodpecker	1772.25***	1079.89***	308.27***	1705.66***	80.27***
Ash-throated Flycatcher	1.94	191.84***	79.50***	504.09***	1121.80***
Bushtit	16.42***	3.38	0.30	5.94	86.32***
White-breasted Nuthatch	39.29***	228.55***	305.71***	33.59***	339.93***
Congeneric					
Bridled Titmouse —Plain Titmouse	25.74***	66.38***	67.20***	179.64***	163.16***
Eastern Bluebird —Western Bluebird	9.65	290.73***	155.14***	72.82***	169.99***
Ladder-backed Woodpecker —Nuttall's Woodpecker	39.15***	15.56	15.55	13.89	303.42***
Arizona Woodpecker —Nuttall's Woodpecker	21.22***	79.09***	18.46***	47.41***	223.61***
Scott's Oriole —Northern Oriole	424.25***	161.68***	198.39***	238.13***	284.23***
Gila Woodpecker —Acorn Woodpecker	1850.22***	1625.70***	1060.18***	1984.44***	254.00***

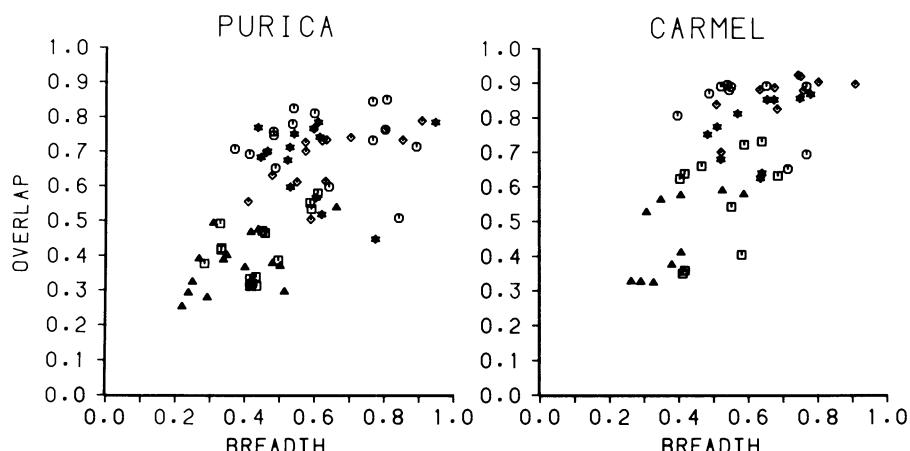


FIG. 4. Foraging overlap vs. breadth of each species in technique (squares), portion of the tree (circles), perch site (stars), food site (triangles), and height (diamonds) at Purica and Carmel.

At Purica, Bewick's Wrens generally exhibited the widest breadth in each foraging category, as well as in total resource use, and along with the White-breasted Nuthatch, overlapped other species the most. At Carmel, Northern Orioles exhibited widest breadth in most of the foraging categories. The White-breasted Nuthatch and Plain Titmouse had total resource use breadth values that were larger than the rest of the Carmel avifauna. There was no consistent pattern in species exhibiting the highest, or lowest, mean overlap at Carmel. In both avifaunas Bushtits appeared to be the specialists, with the narrowest total resource use breadth.

At both Purica and Carmel there generally was a positive relationship between species' breadth and overlap during foraging (Fig. 4). At both sites, however, species with low to intermediate breadth values (0.37–0.55 at Purica, 0.40–0.60 at Carmel) exhibited nearly the entire range of overlap values. Rotenberry and Wiens (1980) also found that among grassland birds, species with the narrowest breadth were not always those with the lowest overlap. These data indicate that at both Purica and Carmel, ecological specialization is not necessarily correlated with a decreased potential for species interaction, and that generalists have a greater potential for encountering other species while foraging.

Community breadth, an indicator of the range of

resources used by the arboreal avifauna, in each foraging category was estimated by averaging breadth values over all species (Table 5). Community breadth in technique and food site was narrower than the other foraging categories at both sites ($P < .001$ for both categories at Purica; $P = .13$ for technique and $P < .005$ for food site at Carmel). This indicates specialization along these two dimensions and suggests that technique and food site are of greater importance in community organization. These data corroborate results from the ordination on important foraging variables at both Purica and Carmel.

The average amount of overlap within the community in each foraging category (Table 5) was estimated by averaging all pairwise overlap values. This single value may be used to make comparisons within each community on the average degree of resource division among species within each of the foraging categories. Community overlap values for technique and food site were much lower (t test, $P < .001$) than for other foraging categories at both Purica and Carmel, again suggesting the greater importance of these two categories in resource allocation.

Guild classification

Three methods were used to develop the guild classification used throughout the remainder of this paper: reciprocal averaging ordination, cluster analysis, and

TABLE 5. Community breadth and community overlap in the use of each foraging category at Purica and Carmel (\pm standard error). See text for derivation of breadth and overlap values.

Foraging category	Purica		Carmel	
	Breadth	Overlap	Breadth	Overlap
Technique	0.439 (± 0.026)	0.416 (± 0.040)	0.518 (± 0.034)	0.568 (± 0.054)
Portion	0.629 (± 0.044)	0.734 (± 0.023)	0.597 (± 0.040)	0.838 (± 0.025)
Perch site	0.581 (± 0.035)	0.680 (± 0.028)	0.625 (± 0.032)	0.773 (± 0.033)
Food site	0.379 (± 0.032)	0.381 (± 0.033)	0.385 (± 0.033)	0.461 (± 0.043)
Height	0.626 (± 0.037)	0.676 (± 0.025)	0.703 (± 0.039)	0.867 (± 0.018)

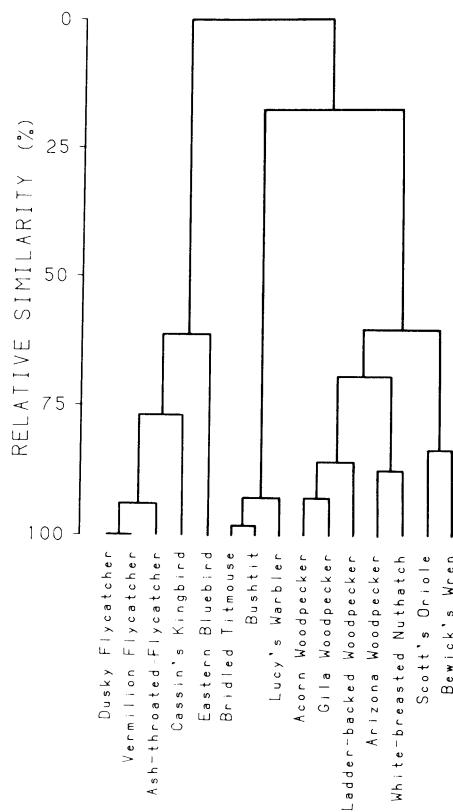


FIG. 5. Dendrogram of the Purica avifauna from cluster analysis of combined technique and food site foraging observations. Cophenetic correlation = 0.951.

discriminant function analysis. This approach was used to increase the objectivity in defining guilds, although it is recognized that guild boundaries are somewhat arbitrary (MacMahon et al. 1981). The ordination, and breadth and overlap analyses indicated that technique and food site were the most important foraging categories in avian community organization at both sites. Thus, these two categories were selected for use in a cluster analysis to determine the relative similarity of the foraging behavior of species, i.e., to define guilds. (To verify the use of only technique and food site categories in guild classification, all of the important variables on PCA axes I and II [see Table 3] were used in a separate cluster analysis; results of this analysis were identical to the former classification at both sites, except for changes of position within bark-using birds at Purica.) The 65% level of relative similarity was subjectively chosen to delineate guilds (cf. Landres and MacMahon 1980).

Five guilds were recognized in the cluster analysis at Purica (Fig. 5): foliage gleaners (Bridled Titmouse, Bushtit, Lucy's Warbler), bark gleaners (Scott's Oriole, Bewick's Wren), bark probers (Acorn, Arizona, Gila, and Ladder-backed woodpeckers, White-breasted Nuthatch), air salliers (Cassin's Kingbird, Dusky,

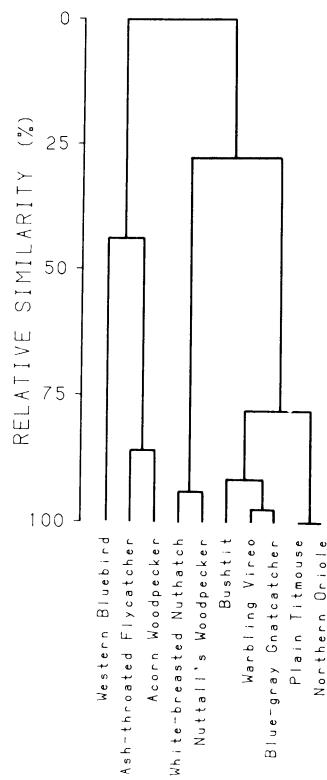


FIG. 6. Dendrogram of the Carmel avifauna from cluster analysis of combined technique and food site foraging observations. Cophenetic correlation = 0.983.

Vermilion, and Ash-throated flycatchers), and a ground sallier (Eastern Bluebird). Ordination (Fig. 3) similarly grouped each of the species, and a discriminant function analysis using the five a posteriori guilds as the grouping variable correctly classified 100% of the species. Individual technique and food site cluster analysis cophenetic matrices were strongly correlated to the combined cophenetic matrix ($r = .85$ and $.97$, respectively), indicating little information loss as a result of combining these foraging categories into a single matrix.

Four guilds were recognized in the cluster analysis at Carmel (Fig. 6): foliage gleaners (Northern Oriole, Plain Titmouse, Blue-gray Gnatcatcher, Warbling Vireo, Bushtit), bark probers and gleaners (Nuttall's Woodpecker, White-breasted Nuthatch; hereafter referred to as bark probers because probing is used nearly 20% more than gleaning, although the nuthatch does glean slightly more than it probes), air salliers (Acorn Woodpecker [see Appendix 2], Ash-throated Flycatcher), and a ground sallier (Western Bluebird). Ordination (Fig. 3) similarly grouped each of the species, and discriminant function analysis using the four a posteriori guilds as the grouping variable correctly classified 100% of the species. Individual technique and food site cluster analysis cophenetic matrices were

TABLE 6. Guild density and consuming biomass averaged from both study years at Purica and Carmel.

Guild	Density (pairs/10 ha)		Consuming biomass (g/10 ha)	
	Purica	Carmel	Purica	Carmel
Foliage glean	8.4	9.6	60.2	105.1
Bark glean	7.2	...	81.7	...
Bark probe	4.6	3.4	151.8	52.9
Air sally	9.7	4.1	144.2	114.1
Ground sally	2.0	2.0	32.6	30.0

strongly correlated to the combined matrix ($r = .95$ for both matrices).

Guild density and consuming biomass

The pattern of species densities within guilds (pairs/10 ha) was similar at both sites in three of five guilds (Table 6): a distinct bark gleaning guild was absent at Carmel, and air salliers were 2.4 times more numerous at Purica than at Carmel. Guild consuming biomass (grams per 10 ha) differed between sites, except for ground salliers (Table 6).

Analysis of relative guild density (guild density/community density) averaged over both years (Fig. 7) shows: (1) foliage gleaners and bark gleaners together constitute 49% of the community's relative density at Purica, (2) in contrast, at Carmel foliage gleaners alone constitute 50% of the relative density, and (3) relative densities of other guilds were similar between sites, as were relative densities of species using the three foraging techniques: gleaners constituted $\approx 50\%$, probers $\approx 15\%$, and salliers $\approx 34\%$ of both avifaunas. Considering the intersite differences in species composition, these results are striking.

Analysis of relative guild CB (guild CB/community CB) averaged over both years (Fig. 7) shows: (1) that foliage gleaners and bark gleaners at Purica together contributed 34% to the relative community CB, (2) in Carmel foliage gleaners alone constitute 32% of the community CB, suggesting a similar limit to which either site can support gleaning activities, possibly related to a similar total gleaning surface at both sites, and (3) the proportion of community CB contributed by the other guilds was significantly different between sites: gleaners contributed roughly one-third of the avifauna's CB at both sites, prober CB was 80% greater at Purica, and sallier CB was 30% greater at Carmel. Thus, CB data, in contrast to density data, indicate that these different oak woodland avifaunas exhibit different guild structures. The differences between density and CB data indicate that interpretations based on density alone should be made with caution, and that when available the CB data be used (Roth 1977).

Although gleaners dominate their respective communities in terms of average relative density, salliers generally dominate in terms of average relative CB, probably due to the larger average size of salliers ($\bar{x} =$

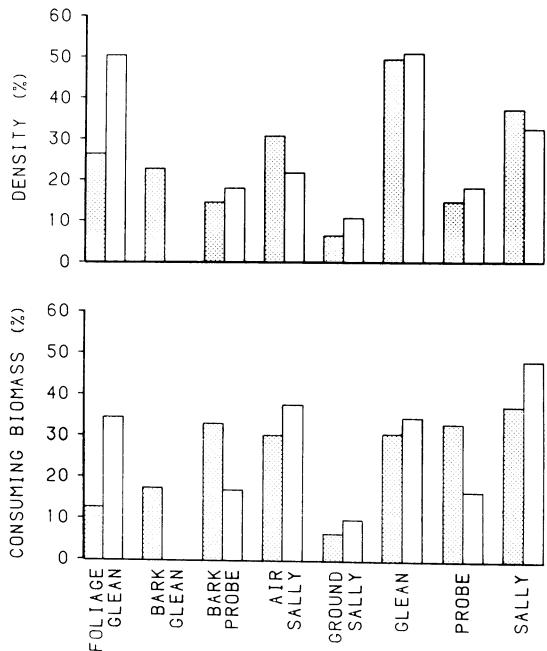


FIG. 7. Relative density and relative consuming biomass for each guild at Purica (stippling) and Carmel (open). Density and consuming biomass of species using each of the three foraging techniques derived from summation of appropriate guilds.

30.1 and 48.7 g at Purica and Carmel, respectively) vs. gleaners ($\bar{x} = 8.6$ and 19.6 g at Purica and Carmel, respectively). Tangentially, these data also suggest that there may be an upper limit to the size of insect gleaners, possibly related to a greater quantity of prey occurring in the periphery of the tree where (1) small twigs would not support heavy birds for perching, (2) a greater density of twigs would reduce accessibility and freedom of movement of large birds, and (3) there is an energetic constraint for a large bird in deriving adequate food by active searching for insects in trees.

Comparison of guild structure

Guild structure at the two sites was compared using (1) Jaccard's coefficient of similarity (see Janson and Vegelius 1981), and (2) a G test of the distribution of guild CB within each avifauna. A Jaccard coefficient (0 denotes no similarity, 100 complete similarity) of 89 indicates marked similarity in the kinds of guilds within the two avian communities. The distribution of guild CB, however, was significantly different between sites ($G = 142$, $df = 4$). Thus, although these two arboreal avifaunas exhibit different guild structures, the functional roles performed within the communities are similar.

Separation in the foraging of species within guilds

Ecological differences among species within guilds at both sites were estimated by averaging G values

TABLE 7. Intraguild comparisons of species' foraging behavior at Purica and Carmel. Data are mean *G* values from pairwise species comparisons within each guild. Ground salliers excluded from analysis. *** = $P < .001$.

Guild	Technique	Foraging category			
		Portion	Perch	Food	Height
Purica					
Foliage glean	9.85	222.31***	161.46***†	125.28***	262.78***‡
Bark glean	1.56	417.13***	372.32***	531.45***	931.31***
Bark probe	209.78***	157.07***	137.71***	175.28***	182.53***
Air sally	4.00	499.03***	170.83***	252.60***	970.67***
Carmel					
Foliage glean	101.08***‡	118.08***§	187.14***	267.01***	130.30***
Bark probe	81.64***	18.22***	4.95	33.08***	146.88***
Air sally	142.16***	120.54***	771.44***	329.85***	786.06***

† 1 of 3 pairwise comparisons not significant.

‡ 3 of 10 pairwise comparisons not significant.

§ 1 of 10 pairwise comparisons not significant.

derived from intraguild comparisons of species foraging behavior (Table 7). In Purica, members of each guild showed differences in each foraging category except technique, with bark probers foraging differently in technique as well. In Carmel, guild members showed differences in each foraging category, except for bark probers in their use of perch sites. These data indicate that marked segregation in the foraging of species within each guild exists at both sites. Statistical difference in foraging substrates used by guild members is necessary but insufficient evidence to invoke interspecific competition as the principal process structuring avian communities, either in the present or past (Connell 1980).

Despite the overall differences in foraging of species within guilds, foliage gleaners exhibited high overlap values among themselves at both sites when all foraging categories were combined (Landres 1981). In Purica, overlap values between the Bushtit and both the Lucy's Warbler and Bridled Titmouse were .907 and .974, respectively. Overlap between the Ash-throated Flycatcher and Vermilion Flycatcher in the air sallying guild was also very high (.971). In Carmel, overlap values between Bush tits and both Warbling Vireos and Blue-gray Gnatcatchers were .985 and .961, respectively. Overlap between Northern Orioles and Plain Titmouses was also high (.983). Working in similar oak woodlands near Carmel, Root (1967) found that foliage gleaners overlapped extensively in "... foraging repertoires, foraging beats, and diets." In the bark probing guild the overlap value between Nuttall's Woodpecker and White-breasted Nuthatch was .963. As pointed out by Colwell and Futuyma (1971), Sale (1974), and Feinsinger (1976), high overlap may be indicative of abundant resources and reduced competition, rather than intense competition.

If species interactions occur primarily within guilds (Willson 1974, Landres and MacMahon 1980), overlap among species within guilds would be expected to be higher than the overlap among species between guilds.

Since guilds were defined in this study on the basis of technique and food site, higher overlap of guild members in these foraging categories would be expected. Overlap of guild members in each foraging category was higher than the overlap of species from different guilds at both sites (*t* test, $P < .01$), except for foraging height at Carmel. These data generally support the idea that there is a greater potential for species interactions within rather than among guilds. This does not imply more, or less, competition within guilds, but merely that guild members are more likely to encounter one another while foraging because of their greater spatial overlap in the tree.

Guild foraging space

The foraging space used by the various guilds was estimated as

$$\sum pFO_i CB_i,$$

where pFO_i is the proportion of foraging observations of species i on each foraging variable and CB_i is the species' consuming biomass, summed over the species in the guild (Table 8). The resulting values may then be considered as the weighted proportion (in grams per 10 ha) of species within a guild that use a particular foraging technique and substrate. Emlen (1981) used a similar index to determine the "foraging pressure" of birds on bark and tree foliage. Community use of each foraging category ("All species" in Table 8) was estimated by summing the weighted proportions over all the species in each community. Breadth and overlap of guilds (Tables 9 and 10) in each foraging category were calculated using the data from Table 8 to estimate the degree of specialization and the potential interaction among the guilds at both sites. In addition, a diagrammatic representation of the foraging space used by each community (Fig. 8) was obtained by summing, over the appropriate species, the CB_i -weighted proportion of foraging observations of the technique used at each food site.

TABLE 8. Percent weighted foraging activities (see text) of guilds and the community ("All species") at Purica and Carmel. Number of foraging observations given in parentheses. + denotes 0.1–0.9%. Columns total 500%.

Foraging category	Purica						Carmel					
	All species (15126)	Foliage glean (3335)	Bark glean (2052)	Bark probe (4042)	Air sally (4682)	Ground sally (1015)	All species (10014)	Foliage glean (4744)	Bark probe (2069)	Air sally (1853)	Ground sally (1348)	
Technique												
Glean	28	97	59	15	+	1	40	91	45	+	0	
Probe	34	2	41	81	+	0	16	3	53	16	0	
Sally	38	1	0	4	99	99	44	6	2	84	100	
Portion												
Outer	40	51	17	9	76	54	52	41	12	72	82	
Middle	37	41	41	48	21	46	36	48	51	23	15	
Inner	20	8	30	43	0	+	10	6	37	5	0	
Ground	3	+	12	+	3	+	2	5	0	0	3	
Perch site												
Twig	47	88	27	3	83	66	37	69	7	13	67	
Branch	35	12	48	58	15	33	54	26	69	82	22	
Trunk	15	+	13	39	0	+	7	0	24	5	8	
Ground	3	+	12	+	2	+	2	5	0	0	3	
Food site												
Foliage	14	78	14	1	3	1	20	55	+	+	3	
Twig	6	15	18	1	2	+	8	19	6	0	0	
Branch	26	6	43	56	+	0	23	18	67	14	0	
Trunk	15	+	13	38	+	0	6	0	25	3	0	
Ground	18	+	12	+	31	94	10	6	0	+	82	
Air	21	+	0	3	64	5	33	2	2	82	15	
Height (m)												
0.0–1.5	21	2	22	5	46	18	6	9	4	+	22	
1.6–3.0	13	9	14	6	19	13	9	15	9	1	20	
3.1–4.5	15	21	16	15	3	58	18	24	21	6	34	
4.6–6.0	16	29	19	21	6	10	29	29	36	29	17	
6.1–7.5	24	32	20	35	17	+	25	18	23	38	6	
7.6–9.0	11	7	9	18	9	+	13	5	7	25	+	

The avian community at Purica used every substrate for foraging, by gleaning on foliage, probing on branches and trunks, and sallying to the ground and air (Fig. 8). Each foraging technique was used about equally, as were five of six food sites. In Carmel a

somewhat different pattern was evident, with foraging by gleaning on foliage and branches, probing on branches, and sallying to the air (Fig. 8). Probing was used less than the other foraging techniques at Carmel, while twigs and trunks were used less, and branches

TABLE 9. Intracommunity comparisons of guild breadth and mean overlap in each foraging category at Purica and Carmel, derived from weighted proportion of foraging observations summed over each species in the guild (see text). "All" refers to breadth and overlap of total resource use computed from all foraging categories combined.

Guild	Foraging category									
	Technique		Portion		Perch site		Food site		Height	
	Breadth	Overlap	Breadth	Overlap	Breadth	Overlap	Breadth	Overlap	Breadth	Overlap
Purica										
Foliage glean	0.275	0.298	0.664	0.834	0.534	0.770	0.253	0.432	0.791	0.834
Bark glean	0.628	0.381	0.956	0.723	0.893	0.851	0.703	0.570	0.976	0.904
Bark probe	0.508	0.593	0.696	0.590	0.583	0.539	0.318	0.323	0.832	0.867
Air sally	0.438	0.326	0.382	0.657	0.557	0.786	0.471	0.425	0.696	0.837
Ground sally	0.444	0.334	0.504	0.760	0.688	0.855	0.195	0.348	0.751	0.827
Carmel										
Foliage glean	0.473	0.458	0.763	0.885	0.777	0.703	0.652	0.532	0.862	0.909
Bark probe	0.724	0.352	0.742	0.719	0.644	0.736	0.181	0.545	0.823	0.913
Air sally	0.572	0.257	0.634	0.874	0.558	0.792	0.256	0.434	0.606	0.746
Ground sally	0.435	0.218	0.513	0.837	0.750	0.701	0.455	0.355	0.671	0.759

TABLE 10. Intercommunity comparisons of guild breadth and mean overlap in each foraging category at Purica and Carmel, derived from weighted proportion of foraging observations summed over each species in the guild (see text). "All" refers to breadth and overlap of total resource use computed from all foraging categories combined.

Guild	Foraging category										
	Technique		Portion		Perch site		Food site		Height		All
	Breadth Overlap		Breadth Overlap		Breadth Overlap		Breadth Overlap		Breadth Overlap		Breadth Overlap
Foliage glean											
Purica	0.185	0.207	0.156	0.181	0.131	0.184	0.113	0.196	0.110	0.107	0.052
Carmel	0.263	0.154	0.197	0.173	0.178	0.114	0.345	0.234	0.115	0.094	0.073
Bark glean											
Purica	0.506	0.312	0.205	0.129	0.290	0.235	0.407	0.304	0.165	0.138	0.127
Bark probe											
Purica	0.387	0.354	0.113	0.078	0.091	0.068	0.152	0.148	0.116	0.112	0.069
Carmel	0.490	0.108	0.074	0.055	0.134	0.120	0.088	0.216	0.106	0.092	0.062
Air sally											
Purica	0.291	0.149	0.063	0.099	0.148	0.201	0.222	0.177	0.076	0.082	0.060
Carmel	0.366	0.124	0.145	0.106	0.127	0.132	0.177	0.178	0.029	0.030	0.059
Ground sally											
Purica	0.298	0.155	0.102	0.139	0.225	0.266	0.082	0.123	0.067	0.067	0.059
Carmel	0.220	0.076	0.086	0.110	0.204	0.136	0.192	0.125	0.043	0.042	0.051
											0.040

and the air were used more as food sites. Community breadth in foraging technique, food site, and all foraging categories combined at Purica was 0.720, 0.481, and 0.148 respectively; the corresponding breadth values at Carmel were 0.589, 0.450, and 0.125. Thus, the range of resources used by the birds within each of these oak woods is similar, except for the greater use of probing at Purica.

Foliage gleaners at Purica obtained most of their food from foliage, and 1% from the air by sallying; in

contrast, foliage gleaners at Carmel relied more on woody substrates, obtaining 37% of their food from twigs and branches, and 6% by sallying (Table 8). Foliage gleaners at Carmel occupied part of that foraging space used by the bark gleaners at Purica (see below), and exhibited significantly wider foraging breadth than at Purica in foraging technique and food site (Table 10). Individual species breadths of foliage gleaners at Carmel were also wider ($P < .05$) than those at Purica (Landres 1981; foraging technique $\bar{x} = 0.323$ vs. 0.236; food site $\bar{x} = 0.229$ vs. 0.147, respectively). Hertz et al. (1976) discussed the importance of foraging shifts in foliage gleaners in a California oak woodland. Although the tree structure in these oak woodlands is similar, the abundance of arthropod prey available to the foliage gleaners may be dissimilar (see below), accounting for the differences in foraging behavior between the two communities.

Bark gleaners at Purica used a combination of gleaning and probing to acquire food from every substrate but air (Table 8); branches were used most often. Of all the guilds at Purica, bark gleaners exhibited significantly wider breadth in each foraging category (Table 9). Bark gleaners were the generalists at Purica, yet exhibited significantly higher overlap values than the other guilds only in food site (Table 9). A distinct bark gleaner guild was absent at Carmel (cf. Salt 1953), possibly due to the low shrub density.

Bark probbers at Purica obtained 82% of their food probing on branches and trunks, and 15% by gleaning on these same substrates; in contrast, bark probbers at Carmel both probed and gleaned about equally (Table 8). Bark probbers at Purica exhibited narrower breadths than at Carmel in foraging technique and perch site (Table 10). The mean breadths of individual bark prob-

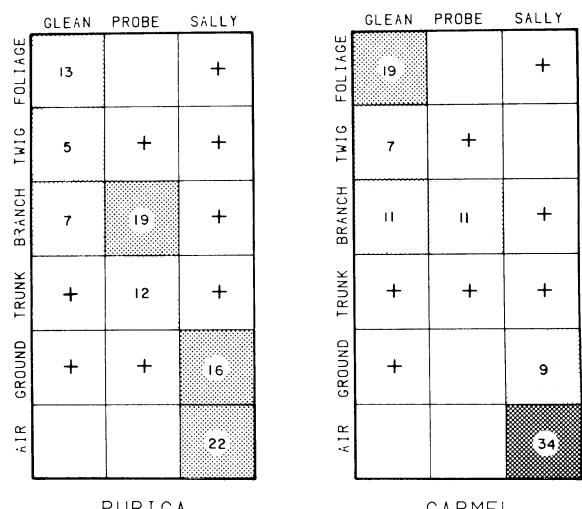


FIG. 8. Diagrammatic summary of the foraging technique used at each food site for the avian communities at Purica and Carmel. Numbers are the summed weighted proportion (expressed as percentage) of foraging observations (see text), with percent values represented graphically by + denoting 0.1–4.9%, and shadings thereafter being progressively darker (in 10% intervals) with greater values.

ers at Purica were also wider in each foraging category ($.01 < P < .05$), while mean overlaps of these species did not differ significantly between sites.

The wider guild breadth in foraging technique and perch site, and examination of Table 8, indicates that bark probers at Carmel occupied a foraging space similar to bark gleaners and bark probers, combined, at Purica. Although consistent with an hypothesis of competitive release (Pianka 1978; i.e., species would exploit a wider range of resources where potential competitors are absent), the wider foraging breadth of bark probers at Carmel also results from inclusion of the White-breasted Nuthatch, which gleans 51% of the time (Appendix 2).

Air salliers at Purica obtained 31% of their food from the ground. In contrast, air salliers at Carmel took almost no food from the ground, and probed branches and trunks 17% of the time (Table 8). Air salliers at Purica exhibited narrower breadths than at Carmel only in technique and portion of the tree foraging categories (Table 10). Wider breadth in foraging technique at Carmel, associated with probing, is due to inclusion of the Acorn Woodpecker in the air sallying guild; although sallying most of the time (Appendix 2), this species occasionally probed in branches for stored acorns and insects. Acorn Woodpeckers were also responsible for the high frequency of branches used as a perch site by air salliers at Carmel.

Differences between sites in ground cover may also have had an important impact on these comparisons of air sallier foraging behavior. The complete ground cover at Carmel may have obscured crawling arthropods and prevented their easy capture (see Cody et al. 1977). For example, tall, dense grass apparently caused a shift in the foraging of Mockingbirds (*Mimus polyglottos*) from gleaning ground-herb substrates to sallying on above-ground substrates (Roth 1979). Consistent with this idea is the greater use of ground as a food site by air salliers at Purica (31%) compared to Carmel (<1%). In addition, despite a 21% greater CB of air salliers at Purica, air salliers at Carmel still took 19% more food from the air (Table 8). Thus, differences in ground cover, by altering the availability of prey resources, may have been a significant contributor to the foraging patterns of air salliers observed in this study.

The ground sallier at Purica obtained nearly all of its food from the ground, whereas at Carmel this guild took 14% of its food from the air (Table 8). This difference between sites in the proportion of ground to air use is most likely due to differences in ground cover at the two sites (see above). The ground sallier at Carmel exhibited wider breadth than at Purica only in food site (Table 10). If diffuse competition had been a factor in the intersite differences in ground sallier foraging, a greater use of ground and/or less use of air as a food site by the Carmel avifauna would be expected. However, at Carmel ground-use was 8% less, and air-

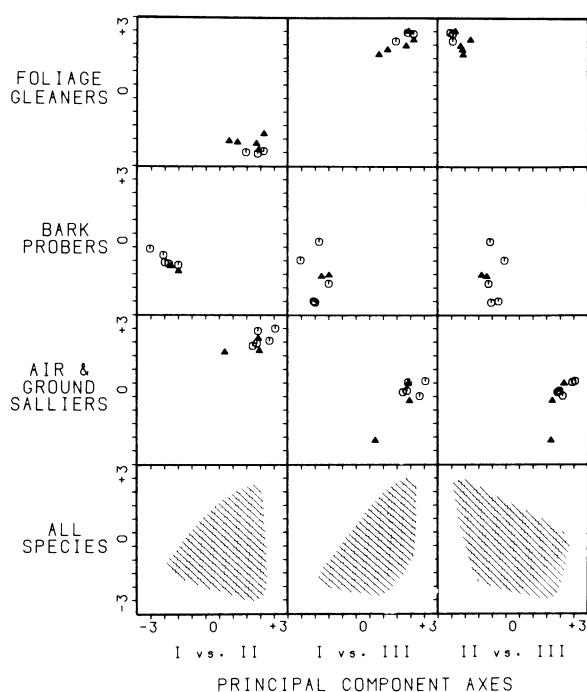


FIG. 9. Principal components analysis of species in guilds common to both Purica (circles) and Carmel (triangles) with the 23 foraging variables, plotted on the first three PCA axes. Shadings for "All species" derived from outlining individual species from Purica (stippling) and Carmel (diagonal lines).

use 13% more than at Purica ("All species" in Table 8), in contrast to the above expectation.

Similarity between sites in the overall pattern of guild foraging was also examined with a PCA of all the species from both sites with all 23 foraging variables. Species were organized according to guilds that occurred at both sites, and plotted on PCA axes I, II, and III, allowing visual comparison of the PCA-space occupied by the avian community at each site ("All species" in Fig. 9) was derived from outlining the total space occupied by the species at that site. Similarity between sites in the foraging of each guild and the community is apparent, especially along PCA axes I and II. The Acorn Woodpecker stands apart from the other salliers at Carmel, as might be expected, although it still lies within that general region of PCA-space occupied by salliers.

In summary, the foraging space occupied by each guild at both Purica and Carmel was distinct, with only partial overlap (Table 9) along technique and food site foraging dimensions. Overlap values in the other foraging categories, especially foraging height, were quite high. These data suggest that at the guild level of resolution, as at the species level discussed above, foraging technique and food site are important in the organization of these oak woodland avian communities. It appears that differences in the foraging space used

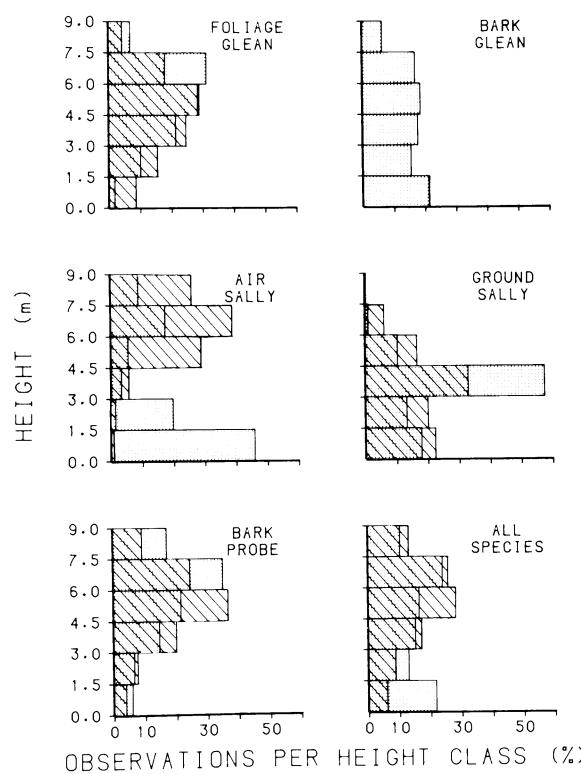


FIG. 10. Foraging height profiles for guilds and the community ("All species") at Purica (stippling) and Carmel (diagonal lines).

by the guilds at each site may be largely influenced by the availability of resources.

Guild use of foraging height

Avian foraging height is generally considered to be an important component in apportionment of resources within avian communities (e.g., Mac Arthur 1972, Roth 1980), and is correlated with the height distribution of tree foliage in *Quercus* spp. in southeastern Arizona (Balda 1969). We therefore examined the correspondence of foraging height with the relative amount of vegetation per height class, and the degree of overlap among species within guilds in their height use at Purica and Carmel.

The CB-weighted proportion of foraging observations per height class (hereafter referred to as foraging height profile) for each guild and the community was different from the average tree profile (G test, $P < .001$) at both Purica and Carmel (Fig. 10). Furthermore, at Purica the foraging height profile of only the ground sallier was positively correlated (SRC, $P = .07$) with tree profile. In Carmel, foraging height profiles of only foliage gleaners and the ground sallier were positively correlated (SRC, $P = .05$ and $.07$, respectively) with tree profile. These data indicate that avian height use is not generally related to the tree profile, per se, in either community.

TABLE 11. Mean overlap in foraging height within each guild at Purica and Carmel.

Guild	Purica	Carmel
Foliage glean	.904	.907
Bark glean	.456	...
Bark probe	.875	.908
Air sally	.747	.594

Differences in the distribution of prey used preferentially by the various guilds might account for the general lack of correlation between foraging height profiles and the tree profile. Other factors that may contribute to the foraging height profiles observed in this study are (1) competitive interactions with other birds in the community, and (2) important structural features of the trees not accounted for in this study.

If competitive interactions are important in influencing the pattern of height use during foraging, we would hypothesize that under differing competitive regimes the pattern of height use would be different by species in guilds inhabiting oak woodlands with similar tree structure. To test the null hypothesis of no difference in the pattern of height use, foraging height profiles of each guild (Fig. 10) were examined. Foliage gleaners foraged at heights from 3.1 to 7.5 m 82% of the time at Purica and 72% of the time at Carmel. Bark probers at Purica, and bark probers and air salliers at Carmel, foraged predominantly at upper heights. In contrast, bark gleaners at Purica used all heights about equally, and air salliers foraged below 3.0 m 66% of the time. The ground sallier at both sites used the 3.1 to 4.5 m height class a greater proportion of the time (58% at Purica and 34% at Carmel) than other heights. Thus, bark probers derive most of their food from upper heights, foliage gleaners mostly from intermediate to upper heights, and ground salliers perch mostly at intermediate heights. These data fail to reject the null hypothesis of no difference in the pattern of height use. In contrast, air salliers at Purica perch predominantly at lower heights, while at Carmel upper heights are used most frequently. Although refuting the above null hypothesis, intersite differences in foraging heights of air salliers may be more parsimoniously explained by intersite differences in ground cover, as suggested above.

Overlap in foraging height of species within each guild (Table 11) is high except in bark probers at Purica, and air salliers at Carmel. Thus, foraging height, per se, does not appear to be an important aspect of resource allocation in most of these avian guilds.

Complementarity

Interspecific complementarity of resource use is often considered as evidence that competition is an important factor influencing community structure (e.g., Schoener 1974, Pianka 1978). Complementary use of

resource axes would be indicated by a negative relationship, i.e., high interspecific overlap on one axis would be associated with low overlap on another, independent axis. We tested the null hypothesis of no complementarity in the use of different resource axes, indicative that interspecific competition has not influenced species' foraging. Complementarity within both avifaunas, and in each guild at both sites with three or more constituent species (i.e., foliage gleaners, bark probbers, and air salliers at Purica, and foliage gleaners at Carmel), was examined by comparing species' overlap values in all combinations of foraging substrates. Hutto (1981) demonstrated the considerable independence among foraging variables similar to those used in this study.

Within the entire community no significant negative association was found (Kendall's coefficient of association τ , $P > .1$) at either site. Of the within-guild overlap comparisons, only air salliers exhibited a trend with negative associations in five of six foraging substrate overlap comparisons. These data fail to reject the null hypothesis, suggesting that interspecific competition is not a major determinant of the pattern of resource use within either community, except possibly for air salliers at Purica.

Compensatory shifts in foraging

Change in a species' foraging due to the presence of potential competitors, i.e., a compensatory "niche" shift, has been used as evidence for the importance of interspecific competition in organizing communities (Schoener 1977, Diamond 1978, Pianka 1978). We therefore examined the foraging of species and genera common to both sites in relation to the foraging of potential competitors, i.e., other guild members. The importance of interspecific competition in influencing these shifts is supported if a difference in foraging between sites is associated with a complementary pattern of foraging by probable competitors at that site.

Intersite differences in foraging of the Acorn Woodpecker are related to a shift to air sallying at Carmel. Acorn Woodpeckers commonly flycatch throughout their entire range, particularly in spring, probably in response to the presence of flying Coleoptera and Hymenoptera (MacRoberts and MacRoberts 1976). The use of flying insects at Carmel is therefore reasonable. The use of air as a food site by the other air salliers (in terms of the proportion of CB-weighted foraging activities) at Carmel was 80%, and at Purica 64%. These data suggest that the lack of a sallying response by the Acorn Woodpecker at Purica is not a function of a reduced resource availability via diffuse competition. The reasons for the restriction to bark probing at Purica remain obscure.

The White-breasted Nuthatch at Purica foraged mostly in inner portions of the tree, on trunks and branches, from lower to upper heights. At Carmel, the nuthatch foraged in the middle portion of the tree, on

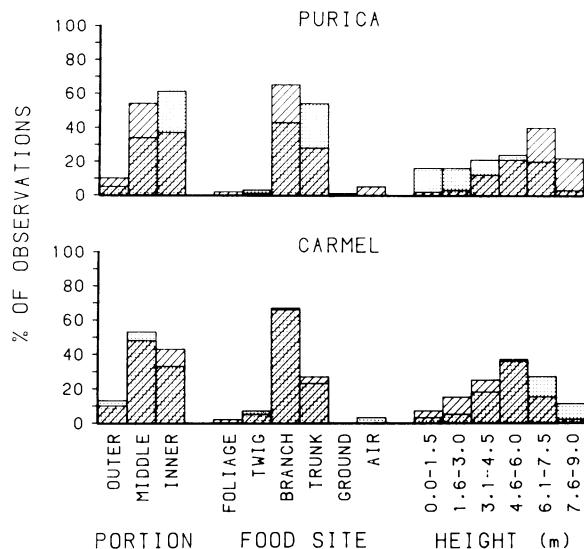


FIG. 11. Weighted proportion of foraging observations (see text) of the White-breasted Nuthatch (stippling) and the summed, weighted proportion of other guild members (diagonal lines) at Purica (Acorn, Arizona, Ladder-backed, and Gila woodpeckers) and at Carmel (Nuttall's Woodpecker).

branches, at intermediate to upper heights. The pattern of foraging at Carmel does not appear to be a result of interspecific competition because the nuthatch's greatest potential competitor, Nuttall's Woodpecker, foraged in a similar manner (Fig. 11; see also Miller and Bock 1972). The shift in foraging behavior from Purica to Carmel appears to be an opportunistic response, perhaps due to a change in resource availability. In Purica, however, the nuthatch's foraging is complementary to that of the other species in the bark probing guild, particularly in regard to food site (Fig. 11).

Intersite differences in the foraging of the Bushtit occurred only in foraging height. Intermediate to upper heights were used at Purica, whereas at Carmel, low to intermediate heights were used most often. Other members of the foliage gleaning guild used a range of foraging heights similar to the Bushtit at both sites (Fig. 12). This result suggests opportunism in the use of foraging heights by Bushtits.

The Ash-throated Flycatcher foraged differently between sites in portion of the tree, food site, and height. In Purica, foraging was initiated predominantly from the outer portion of the tree at low height, with sallies to both ground and air. In contrast, foraging at Carmel was initiated from both outer and middle portions of the tree at intermediate height, with sallies predominantly to the air and occasionally to foliage. The flycatcher's most likely potential competitor at Carmel, the Acorn Woodpecker, foraged similarly (Fig. 13), except for greater use of the outer portion of the tree at upper heights. These data, and a decrease in open ground on which to forage at Carmel, suggest that the

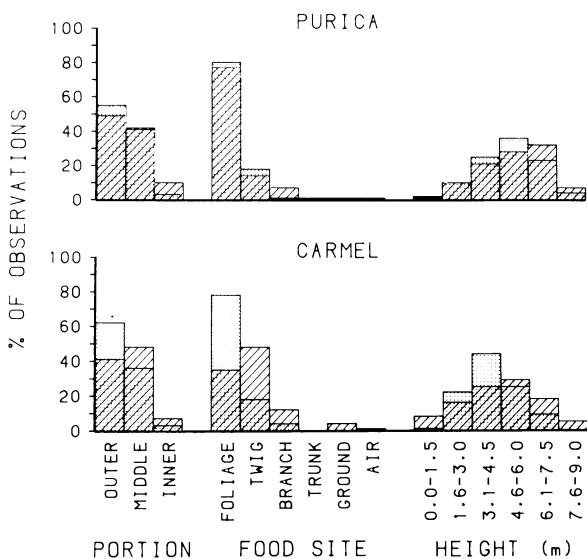


FIG. 12. Weighted proportion of foraging observations (see text) of the Bushtit (stippling) and the summed, weighted proportion of other foliage gleaners (diagonal lines) at Purica (Bridled Titmouse, Lucy's Warbler) and at Carmel (Northern Oriole, Plain Titmouse, Blue-gray Gnatcatcher, Warbling Vireo).

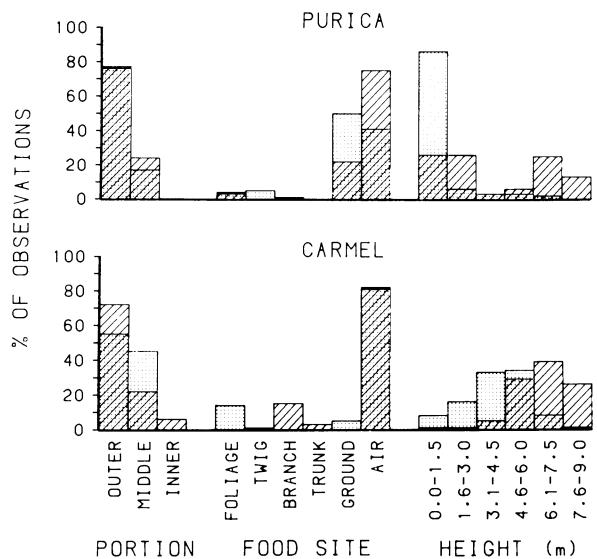


FIG. 13. Weighted proportion of foraging observations (see text) of the Ash-throated Flycatcher (stippling) and the summed, weighted proportion of other air salliers (diagonal lines) at Purica (Cassin's Kingbird, Dusky, and Vermilion flycatchers) and at Carmel (Acorn Woodpecker).

shift in the Ash-throated Flycatcher's foraging at Carmel is in response to differing resource availabilities and not interspecific competition. In Purica, greater use of the ground as a food site by the flycatcher, relative to its use at Carmel, could be a response to the greater use of the air as a food site by the other air salliers (Fig. 13).

Of the 12 intersite congeneric comparisons, only the Ladder-backed Woodpecker, Scott's Oriole, and Bridled Titmouse exhibited a shift in foraging consistent with the predictions of diffuse competition and/or competitive release hypotheses. The 9 remaining shifts in species' foraging could result from an opportunistic response to a change in resources between sites.

In summary, shifts in species' foraging at Purica are consistent with predictions of competition-based hypotheses in 5 of 10 pair-wise comparisons, whereas at Carmel none of the comparisons verify the predictions. Thus, although foraging shifts did occur at Carmel, they may be an opportunistic response to resource availability, rather than a result of interspecific competition. At Purica, however, interspecific competition may be influencing the foraging behavior of certain species within each of the guilds, resulting in the observed foraging shifts.

Other factors affecting community structure

Because this study represents a "natural experiment," no control over factors related to the different geographic locations of the study areas, which could also have affected community patterns, was possible.

Karr (1980) offered a conceptual model summarizing such factors and their interactions which might affect avian community structure. Each of these factors is therefore examined below for possible influences on the communities in this study.

Climate.—The local climate (temperature, available moisture, and their seasonality) can directly affect the quality, quantity, and spatial and temporal distribution of the arthropod food-resource base (see Kajak 1980), and thereby affect avian community patterns and processes (Grant and Grant 1980, Karr 1980). Climate may also directly influence the physiological status of a bird by inducing thermal or water stress. In addition, vegetation physiognomy is largely dependent on the local climate (Whittaker and Woodwell 1972), and may influence avian communities by controlling the availability of (1) over-wintering, egg-laying, and foraging sites of arthropod prey (Jackson 1979), and (2) nesting, roosting, and foraging sites of birds, i.e., structural features required by birds' "niche-gestalt" (James 1971).

The amount and variation of annual precipitation may be used as an indicator of the food-resource base available to birds (Wiens 1974, Grant and Boag 1980). Mean annual precipitation at Carmel (516 mm, based on recordings at Hastings Natural History Reservation, Carmel Valley, California, from 1939 to 1963 [White 1966]) is 72% greater than at Purica (300 mm, based on recordings at Douglas, Arizona, from 1941 to 1970 [National Climatic Center 1973]). Furthermore, total precipitation during, and 1 mo prior to the

study period at Carmel (16 April through 7 June, 1977 and 1978) was 82 mm, 114% greater than the 38 mm at Purica (1 March through 1 May, 1977 and 1978). The greater amount of precipitation at Carmel, both prior to and during the study period, is likely to be associated with a greater prey abundance (see also Orians and Solbrig 1977), perhaps explaining the preponderance of opportunistic foraging at Carmel compared to Purica.

Similarity in vegetation structure of trees, however, does not imply similarity in production at both sites. Brown (1973) found higher seed production at sand-dune sites receiving more rainfall than other sites with similar vegetation structure. At sites with structurally similar brush-grassland vegetation, Roth (1977) noted that differences among sites in avian composition probably resulted from differences in rainfall. Karr (1976b) suggested a similar reason for differences in avian breeding densities in coniferous forests of eastern and western North America. In addition, the greater ground cover at Carmel is likely to result in higher rates of leafy tissue production, and therefore greater arthropod abundance.

Greater precipitation, and an hypothesized abundance of prey, would be expected to allow a greater avian CB at Carmel. However, the avian community at Carmel exhibited 168 g/10 ha (36%) less CB than at Purica (see Table 6). The smaller CB at Carmel is a result of fewer birds using bark as a foraging substrate (see Fig. 8). One prominent reason for this smaller CB is the absence of Bewick's Wren, which accounts for ≈35% of the difference in CB between sites. Bewick's Wren, as discussed above, probably does not breed at the Carmel sites because of the absence of a suitable "shrub-gestalt." The smaller CB of bark-foraging birds at Carmel may be a result of (1) historical and zoogeographical factors affecting the number of species in that region, although Linsdale (1947) noted the occurrence of Hairy and Downy woodpeckers (*Picoides villosus* and *P. pubescens*) and the Brown Creeper (*Certhia familiaris*) on sites adjacent to those of this study; and/or (2) the prey population on the bark at Carmel was, for some unknown reason, depauperate compared to the bark population at Purica. Another factor possibly affecting this comparison is the small sampling period which, as demonstrated by Wiens (1981), can yield spurious results.

Biogeographical and evolutionary histories.—The biogeographical and evolutionary history of a species is important in affecting community composition and structure. Lawlor (1980), however, in discussing past vs. present competition, suggests that "Present competitive forces determine which species are found together in a community," a view also held by Diamond (1978). Thus, the question "To what extent are current community patterns a result of historical, or ecological factors?" needs to be critically examined in studies of community organization. In an analysis designed to

investigate this question in South American tropical montane avifaunas, Vuilleumier and Simberloff (1980) concluded that historical and ecological factors "... have played roles *together at all times*: they are indissolubly tied up, and there is probably no way to separate them . . ." (italics theirs) in their effect on avian community composition.

An oak woodland flora, derived from the Madro-Tertiary geoflora of the Mexican plateau in the middle and late Eocene, first appeared in the Oligocene with associations similar in floristic composition to present-day woodlands (Axelrod 1973). During Pleistocene glaciations, changing temperature and precipitation regimes caused fluctuations in the distribution of oak woodlands, with their present distribution occurring since the Holocene Xerothermic in both northern Mexico (Van Devender and Spaulding 1979) and California (Raven and Axelrod 1978).

The Purica avifauna probably originated from an ancestral oak woodland avifauna in the southwestern United States and northern Mexico in the mid-Pliocene, with subsequent differentiation during Pleistocene glaciations (see Hubbard 1973). The Carmel avifauna is probably derived from ancestors of Sonoran and Mexican plateau avifaunas that spread into California with the Madro-Tertiary geoflora, subsequently developing in the oak woodlands there during the Pliocene (Miller 1951). The two avifaunas are therefore taxonomically similar with 6 of 10 families (60%), and 8 of 15 genera (53%) shared between sites. The similarity between sites in taxonomic composition, and time of probable avifaunal development, has two important consequences for this study. First, similarity of community structure may result from parallel evolution, and not convergence. Second, intersite differences in community structure represent ecological "solutions" to prevailing conditions.

One conspicuous difference in taxonomic composition between sites is the number and density of tyrannid flycatchers. Four tyrannids occur at Purica, with a total density of 9.7 pairs/10 ha (29% of the community density), whereas at Carmel, only one tyrannid occurs, with 1.2 pairs/10 ha (6% of the community density). A similar pattern is also evident on a regional scale. In South America, tyrannids employ a variety of foraging modes, including gleaning, as far south as temperate Argentina (Keast 1972, Fitzpatrick 1980), whereas only sallying (including hover gleaning) species appear north of the neotropics, occurring as far north as Alaska. In comparing the avifaunas from Africa, Australia, and South America, Keast (1972) concluded that "The most potential individual force [determining how far and in what direction any particular family will evolve] is undoubtedly the associated fauna inhabiting that continent." Perhaps the paucity of tyrannids at Carmel (and in north temperate climates in general), and their restriction to sallying, is similarly a result of competitive pressures from North American

flycatchers and species that predominantly glean foliage or wood, but also flycatch (e.g., species in the families Parulidae, Vireonidae, Sylviidae, Paridae, and some Picidae, Sittidae, and Thraupidae). This speculation may warrant further investigation.

Biotic interactions.—Predation may influence population size and dispersion in invertebrates (Connell 1975), and is generally considered an important factor in community organization (see McNaughton and Wolf 1979). Predation may have an adverse effect on avian populations in the tropics (Skutch 1960, Pearson 1977a), but is of doubtful significance in temperate habitats (Lack 1966). Connell (1975) argued that predators have little effect on the community structure of birds or mammals. In the present study no instances of predation on birds were observed, although many avian, reptilian, and mammalian predators, especially of eggs and nestlings, potentially occur at both study sites. The effect of predators on the comparison of foraging patterns in this study is uncertain, but may be examined with manipulative field experiments (see Suggestions for Future Research, below).

Interspecific competition has long been considered a major factor affecting avian community structure (e.g., Elton 1946), although its exact role is now debatable (e.g., see Wiens 1977, Strong et al. 1979, Grant and Abbott 1980, Rotenberry 1980). Interestingly, interspecific competition may actually promote coexistence of species via indirect interactions (Levine 1976), as was demonstrated in ants (Davidson 1980). Competition between birds and distantly related taxa (e.g., as demonstrated for resources such as conifer seeds [Smith and Balda 1979], insects [Wright 1979], and nectar [Carpenter 1979]), may affect avian foraging behavior and community structure. For example, Karr (1976a) reasoned that squirrels in the African tropics exert selection pressures on trees to produce more nut-like fruits, reducing the availability of fleshy fruits, thereby influencing the birds' foraging behavior.

In this study only one nonbird tree-using insectivore inhabits either site: Yarrow's spiny lizard (*Sceloporus jarrovi*) at Purica, and the western fence lizard (*S. occidentalis*) at Carmel (Stebbins 1954, J. A. MacMahon, personal observation). Bats and predatory arthropods, especially spiders, are also possible competitors, but information regarding their distribution, biomass, and habits in trees, on these sites, is not available. We suggest that competition with distantly related taxa is inconsequential in causing different avian foraging patterns between Purica and Carmel (see also Cody et al. 1977).

Chance events.—Chance events may also have an important influence on community structure. For example, climatic or geologic anomalies may directly affect the species mix in the community by death or dispersal (e.g., see Thurber 1980), and may also influence the food-resource base and vegetation physiognomy. Any chance event in the past which influenced

TABLE 12. Summary of climatic, vegetation, and avifaunal parameters at Purica and Carmel. Values, where given, denote significant differences, while "Similar" denotes no difference between sites. (Also see Table 13.)

Characteristic	Purica	Carmel
Precipitation (mean annual; mm)	300	516
Vegetation structure		
Tree density	Similar	
Height	Similar	
Canopy cover	Similar	
Profile	Similar	
Shrub density (stems/ha)	2280	836
Ground cover (%)	70	100
Avifauna		
Number of species	15	10
Density (pairs/10 ha)	33	19
Consuming biomass (g/10 ha)	471	302
Number of pairs/species	Similar	
Consuming biomass/species	Similar	
Ordination of foraging	Similar	
Foraging breadth	Similar	
Foraging overlap	Similar	
Guild types	Similar	
Separation in foraging among guilds	Similar	
Separation in foraging within guilds	Similar	

the species mix, or their attributes, is likely to be expressed in the present community (see Vuilleumier and Simberloff 1980, Fowler and MacMahon 1982).

CONCLUSIONS

For convenience, a summary of climatic, vegetation, and avifaunal parameters contrasting Purica and Carmel are given in Table 12. Study sites were selected for their similarity of tree structure; differences in shrub density, ground cover, and precipitation, however, may have had an important influence in this avifaunal comparison. A lower shrub density at Carmel appears to be responsible for the absence of Bewick's Wren, and possibly contributed to the lack of a distinct bark gleaning guild. The complete ground cover at Carmel is associated with differences between sites in foraging of air and ground salliers. Differences in precipitation may have influenced arthropod availability, and thereby the use of foraging substrates. Despite these differences, the avifaunas at both sites exhibited many similarities in foraging, probably related to the similarity of tree structure at both sites, and also to the taxonomic similarity of the birds.

A summary of the questions examined in this study and results from testing the null hypotheses (Table 13) illustrates the differences in community organization between the two sites. At Carmel, every prediction and hypothesis based on the assumed importance of competition was rejected. This suggests that interspecific competition does not currently influence the foraging behavior of the arboreal birds. Instead, it ap-

TABLE 13. Summary of questions and null hypotheses examined in this study comparing the arboreal birds inhabiting oak woodlands at Purica and Carmel.

Question	Observation	
1) Variables important in explaining variation in foraging behavior.	Technique and food site the most important at both sites as indicated by ordination and breadth and overlap analyses.	
2) Overall foraging behavior of the two avifaunas.	No significant differences between sites as indicated by rank correlation of PCA loadings.	
3) Partitioning of resources within each avifauna.	Foliage gleaning and air sallying used more frequently at Carmel; probing on trunks and ground sallying used more at Purica.	
4) Guild structure.	Foliage gleaning, bark probing, air and ground sallying guilds at both sites; distinct bark gleaners only at Purica. Distribution of relative guild CB significantly different at each site.	
5) Changes in foraging behavior between sites.	At Purica 50% of the changes are consistent with predictions of competition theory. At Carmel all of the changes appear to be an opportunistic response.	
Hypothesis	Expected (null)	Observed
6) Foraging heights in a different competitive milieu.	Similar between sites.	Similar between sites except in air salliers.
7) Complementarity in resource use during foraging.	Does not occur.	Occurs only in air salliers at Purica. Does not occur at Carmel.

pears that the birds at Carmel forage opportunistically, exploiting a seasonal pulse of arthropod prey promoted by spring precipitation. Hypotheses based on opportunistic foraging certainly warrant further investigation in community studies (e.g., see Wiens and Rotenberry 1979, Rotenberry 1980). In contrast, at Purica where some of the competition-based predictions were supported (Table 13), interspecific competition appears important in determining avian foraging behaviors of some species, especially air salliers. A lack of complementarity in foraging, and generally high overlap values, however, suggest that the competitive forces are rather weak (see also Lister 1980). A lack of spring precipitation, and consequent delay in arthropod development, may be the single greatest factor contributing to the competitive pressures at Purica during the spring breeding season.

Additional conclusions gained from this study are:

1) Other factors, especially ground cover, shrub density, and the local climate, have influenced the foraging behavior and structure of the arboreal avifaunas at both sites.

2) As a whole, the avian communities at Purica and Carmel foraged quite similarly, despite a significant difference in guild structure. Similarities in community structure are most likely long-term evolutionary responses to similarity in tree structure, influencing the adaptive strategies of the birds. Differences in community structure probably result from short-term behavioral flexibility in microhabitat use in response to differences in prey distribution and abundance.

3) Interspecific competition is not a prerequisite for resource partitioning. Most studies of resource partitioning dogmatically assume that interspecific competition is the driving force responsible for observed differences in resource use among sympatric species.

Partitioning of the trees in each foraging category was clearly evident in this study, both within and among guilds, yet competitive pressures appeared marginal at Purica, and unimportant at Carmel. Competitive interactions during an "ecological crunch" in the past may have influenced present-day patterns of resource use, although Wiens (1977) argued forcefully that "... competitive processes are not the only possible explanation of the observed patterns." We suggest that the use of different resources by sympatric species in these oak woodlands is largely a result of morphological and behavioral specializations developed during allopatric speciation (see Grant 1975, Connell 1980, Bloom 1981).

SUGGESTIONS FOR FUTURE RESEARCH

A significant shortcoming of this study is the lack of data on the arthropod food-resource base used by the birds. Although Hespenheide (1975) states that "... foraging behavior determined both prey size and prey type . . .," arthropod data would certainly improve the ability to reach meaningful conclusions. Two types of arthropod data need to be collected concurrently with observations on the foraging behavior of birds: (1) the potential avian food-resource base, and (2) prey actually consumed by the birds. Quantification of bark rugosity (see Jackson 1979) may also aid understanding of those factors affecting arthropod distribution.

In addition, observations conducted in a wider range of study sites (e.g., oak woodlands that occur in the Pacific Northwest, southern California, and Texas), over a greater number of years, would greatly increase understanding of resource use. Marking individuals would allow discernment of within- and between-phenotype components of community patterns in foraging

(see Roughgarden 1972). Furthermore, studies on resource use need to be conducted throughout the year.

Mutually exclusive hypotheses leading to predictions that can be tested in field experiments are rare in community studies. Results from this study suggest three such experiments. First, at Purica, Vermilion and Dusky flycatchers perch $\approx 80\%$ of the time on low dead twigs protruding beneath the canopy of the trees (Appendix 1). Removal of these twigs on experimental plots would allow tests of competition-based hypotheses when compared to unmanipulated control plots. For example, the hypothesis that these flycatchers are competing for the use of twigs predicts that, upon partial removal of these twigs, only one species will continue to use them. An alternative hypothesis, based on opportunism, would predict that both species would use these twigs less, in proportion to the amount removed, than on control plots.

A second manipulation could involve the addition of shrub-like material to experimental plots at Carmel, creating suitable habitat for Bewick's Wren. The wren is a regular inhabitant near the Carmel sites (Linsdale 1947), and would be a potential competitor of the White-breasted Nuthatch and Nuttall's Woodpecker if induced to breed on experimental plots. Predictions similar to those above may be offered, and tested.

Third, the effect of predation on the foraging of birds at both study sites may be tested by placing metal collars around the trunks of trees on experimental plots, reducing access of most predators.

Manipulations of this type allow alteration of only one variable, assuring that other parameters of the experimental system are similar to those of the control. Investigations employing such manipulations offer great promise to increase the understanding of resource use and community organization.

ACKNOWLEDGMENTS

We thank Keith Dixon, James Gessaman, John Kadlec, and Ivan Palmlad for their help in developing this study. We are extremely grateful for the critical reading and comments from Douglas Andersen, John T. Emlen, James Karr, Kimberly Smith, Stephen Vander Wall, and an anonymous reviewer, which vastly clarified the organization, ideas, and writing of the manuscript. Robert Bayn, Jr. and Eric Zurcher gave invaluable assistance in many ways. Thomas and Maria Lopez Matresa gave consent to use their land in the Sierra la Purica foothills, and Paul Foxman helped collect vegetation data there. At Carmel, John Davis offered housing and friendship, and Jimmy Bell provided character and the use of his land for a study site. Linda Finchum and Bette Peitersen offered editorial assistance throughout the preparation of the manuscript, and Mac Brandon helped in data preparation. Special thanks to Paul Foxman, Helyne Landres, and Mary Ruth Martin for emotional support, and to Patrick Stallcup for pointing the way.

Financial assistance was provided by the Department of Biology and the Ecology Center of Utah State University, the Frank M. Chapman Fund of the American Museum of Natural History, and Sigma Xi, the Scientific Research Society of North America. Computing funds were generously

supplied by the College of Science, Utah State University, and National Science Foundation grants DEB 78-05328 and DEB 79-04534 to James A. MacMahon.

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APPENDIX 1.

Combined 1977 and 1978 foraging data (%) of species at Purica for each foraging variable. Species abbreviations as in Table I. Number of observations given in parentheses. + denotes 0.1-0.9%. Columns total 500%.

Foraging category	Species															
	AW (1252)	ZW (295)	LB (252)	GW (897)	WN (1346)	SO (713)	BW (1339)	BT (1356)	BU (825)	LW (1154)	CK (1168)	DF (1199)	AF (1140)	EB (1015)	VF (1175)	
Technique																
Glean	3	21	15	3	52	60	58	97	99	97	0	0	0	1	1	0
Probe	91	79	85	97	48	40	42	2	+	+	+	0	0	0	0	0
Sally	6	0	0	0	+	0	0	1	0	2	100	100	99	99	100	
Portion																
Outer	11	29	15	1	5	32	11	37	55	77	87	33	76	54	96	
Middle	58	52	56	28	34	56	36	49	42	23	13	67	17	46	4	
Inner	31	19	29	71	61	12	36	14	3	+	0	0	0	+	0	
Ground	0	0	0	0	+	0	17	+	0	0	0	0	0	7	+	0
Perch site																
Twig	4	14	5	+	3	32	25	82	93	95	93	83	66	66	97	
Branch	68	62	80	33	43	67	41	17	7	5	7	17	26	33	3	
Trunk	28	24	15	67	54	+	18	+	0	0	0	0	0	+	0	
Ground	0	0	0	0	+	0	16	+	0	0	0	0	0	8	+	0
Food site																
Foliage	1	11	0	+	0	33	7	71	80	91	2	7	4	2	+	
Twig	+	9	5	+	3	14	20	19	18	4	0	1	5	+	+	
Branch	66	56	80	33	43	52	39	9	2	3	0	+	+	+	0	
Trunk	27	24	15	67	54	+	17	+	0	0	0	+	0	+	0	
Ground	+	0	0	0	+	0	17	1	0	0	11	38	50	93	42	
Air	5	0	0	0	0	0	0	0	0	2	87	54	41	5	58	
Height (m)																
0.0-1.5	2	3	+	3	16	0	30	2	+	2	10	32	86	18	81	
1.6-3.0	3	5	4	6	16	+	18	13	10	4	19	57	6	13	10	
3.1-4.5	11	14	9	21	21	7	20	27	25	6	3	4	3	58	2	
4.6-6.0	20	13	18	26	24	25	17	30	36	24	9	4	3	10	2	
6.1-7.5	41	51	25	32	20	39	13	25	24	48	38	2	2	+	5	
7.6-9.0	23	14	43	12	3	28	2	3	4	16	21	+	+	+	+	

APPENDIX 2.

Combined 1977 and 1978 foraging data (%) of species at Carmel for each foraging variable. Species abbreviations as in Table 1. Number of observations given in parentheses. + denotes 0.1–0.9%. Columns total 500%.

Foraging category	Species									
	AW (1257)	NW (666)	WN (1403)	NO (996)	PT (1291)	BG (1285)	BU (270)	WV (902)	WB (1348)	AF (596)
Technique										
Glean	+	35	51	97	92	79	96	83	0	0
Probe	17	65	46	2	5	0	2	+	0	0
Sally	83	+	3	+	3	21	2	16	100	100
Portion										
Outer	72	10	13	36	35	67	61	51	82	55
Middle	22	48	54	51	51	28	36	48	15	44
Inner	6	42	33	3	9	4	3	1	0	0
Ground	0	0	0	10	5	+	0	0	3	+
Perch site										
Twig	11	6	7	49	71	95	92	86	67	75
Branch	84	67	70	40	25	5	8	14	22	23
Trunk	5	27	23	0	0	0	0	0	8	1
Ground	0	0	0	11	4	0	0	0	3	+
Food site										
Foliage	0	2	0	46	50	77	78	81	4	14
Twig	0	5	7	20	23	8	18	11	0	+
Branch	15	66	67	23	22	+	4	3	0	+
Trunk	3	27	23	+	0	0	0	0	0	0
Ground	0	0	0	10	5	+	0	0	82	4
Air	82	+	3	0	+	14	+	5	14	81
Height (m)										
0.0–1.5	+	7	3	11	10	5	+	+	22	8
1.6–3.0	+	15	5	10	21	12	22	5	20	16
3.1–4.5	5	25	18	19	28	23	44	23	34	33
4.6–6.0	29	36	36	31	23	36	25	43	17	34
6.1–7.5	39	15	27	20	15	21	9	23	6	8
7.6–9.0	26	2	11	9	3	3	+	5	+	1