

SIZE ASSORTMENT IN NEW WORLD BAT COMMUNITIES

RICHARD D. STEVENS AND MICHAEL R. WILLIG

Program in Ecology and Conservation Biology, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, TX 79409-3131

We evaluated ubiquity of morphological overdispersion, which is characteristic of competitive interactions, in feeding guilds from 15 bat communities from North, Central, and South America. Overdispersion was detected in 10 of 15 communities and 4 of 5 feeding guilds. Although overdispersed morphological patterns exist, they are not a consistent attribute of the structure of feeding guilds within bat communities. Because of factors ranging from environmental attributes such as heterogeneity to species-specific attributes such as high mobility, morphological overdispersion in bats may at best only be a transitory outcome of the effect of competitive interactions on community structure.

Key words: bats, community structure, competition, null model, feeding guild, morphometrics, ecomorphology, meta-analysis

For at least a quarter of a century, community ecologists have acrimoniously debated factors that are responsible for the structure of communities. Processes such as competition, disturbance, predation, and mutualism each are championed as the major factor responsible for community composition (Cody and Diamond, 1975; Diamond and Case, 1986; Gee and Giller, 1987; Kikkawa and Anderson, 1986; Polis, 1991; Ricklefs and Schluter, 1993; Strong et al., 1984). Nonetheless, most evidence is equivocal, preventing any one mechanistic view from assuming hegemony. Although the search for general patterns and mechanisms continues, studies addressing more than one community are rare.

Nature is characterized by substantial temporal and spatial heterogeneity (Brown, 1992), and environmental gradients likely mediate the degree to which at least some structuring mechanisms operate (Andrewartha and Birch, 1954, 1988; Chesson, 1988). For example, the richness of local species pools may be a consequence of strong latitudinal gradients in diversity for bats (Willig and Lyons, 1998; Willig and Sandlin, 1991; Willig and Selcer, 1989) and other mammals (Kaufman and Willig, 1998; Willig and Gannon, 1997). If composition of

species pools affect the efficacy of mechanisms structuring communities, then community structure itself may exhibit latitudinal gradients. Single-community studies offer few means of accounting for such heterogeneity and provide little insight toward distinguishing the most important structuring mechanism across sites from the various possibilities. Although the environmental context of a feeding guild, trophic level, or community, has bearing on the importance of particular phenomena that affect structure, community ecologists have been impulsive in discounting the importance of various phenomena based on data from a paucity of communities. Comprehensive, comparative studies at a number of geographic localities representing a variety of climatic and abiotic conditions must be conducted before the influence of any factor on community structure can be ascertained with confidence. Indeed, new philosophies of science (Greene, 1985) are predicated on recognizing levels of organization, spatial heterogeneity, and the importance of history in determining when, where, and why some processes are more important than others (Pickett et al., 1994).

A popular method of evaluating community structure has involved examination

of morphological patterns. Reasons abound. Morphological attributes are informative for inferring ecological relationships among species at the community level (Wainright and Reilly, 1994); they correlate well with ecological characteristics and are good predictors of resource utilization (Bonaccorso, 1975; Brown and Lieberman, 1973; Dayan and Simberloff, 1994; Findley and Black, 1983; Findley and Wilson, 1982; Freeman, 1981, 1984, 1988, 1992; Hespeneide, 1973; Smartt, 1978). Equally important, morphological measurements are highly repeatable and easily made compared to direct ecological characteristics (e.g., diet, behavior).

Morphological patterns have been described for many bat communities and faunas (Fenton, 1972; Findley, 1973, 1976, 1993; Findley and Black, 1983; McNab, 1971; Schum, 1984; Tamsitt, 1967; Willig, 1982, 1986; Willig and Moulton, 1989). Most species form a core of fairly similar species, with fewer species on the morphological periphery (Findley and Black, 1983; Fleming, 1986). Increases in species richness are facilitated by increases in size of the total morphological hypervolume rather than through increases in the degree of species packing (Willig, 1986). Nonetheless, the degree to which these morphological patterns are the product of biotic interactions, or any other mechanism is unclear.

Ultimately, competitive interactions should yield hyperdispersed morphological patterns within communities (Hutchinson, 1959; MacArthur and Levins, 1967). If species that are morphologically alike consume similar resources that are limiting, they should experience interspecific competition. These interactions should cause species to diverge by character displacement or be driven to extinction at the local level by competitive exclusion (Case and Sidell, 1983). Community equilibria occur when competitive interactions are minimized by hyperdispersed morphological patterns of constituent species. Although morphological hyperdispersion is commonplace under

a variety of environmental conditions (Simberloff and Boeklen, 1981), comprehensive accounts of the ubiquity of hyperdispersion rarely are conducted for the same taxon in different environments. We evaluated morphological patterns within bat communities throughout the New World and explored if hyperdispersion was ubiquitous. More formally, we addressed two questions. Does morphological structure, consistent with competition theory, exist within bat feeding guilds and communities, and are effects of competitive interactions pervasive within bat communities throughout the New World?

MATERIALS AND METHODS

We evaluated 15 bat communities from North, South, and Central America (Table 1). Although studies that determine community composition from distribution maps or faunal surveys (Fenton, 1972; Findley, 1973, 1976; Schum, 1984; Voss and Emmons, 1996) provide general information regarding potential species that may occur in a particular community, we feel that such data characterize a higher level of organization (e.g., fauna) and consequently may not accurately reflect co-occurring groups of species at a particular place and time. We chose to focus only on those studies that fulfilled a number of criteria: 1) data must have been the product of regular sampling in all seasons when bats are active locally; 2) sampling must have occurred for at least 1 year; and 3) sampling area must have been well-delimited and represent an actual community of species that, because of spatial proximity, had the potential to interact. Even data that adhere to those three requirements suffer from limitations. For example, data were collected during different years and by different investigators. Although similar protocols were used, different amounts of effort probably were employed. Nonetheless, those limitations likely did not bias conclusions regarding the role of size assortment in community organization.

Feeding guilds.—Seven feeding guilds (sensu Root, 1967) were used to categorize each community: aerial insectivores, frugivores, gleaning animalivores, molossid insectivores, nectarivores, piscivores, and sanguinivores. Although feeding guilds have standard definitions, they of-

TABLE 1.—*Bat communities used to evaluate ecomorphological structure: aerial insectivore (A), frugivore (F), gleaning animalivore (G), nectarivore (N) and molossid insectivore (M) feeding guilds.*

Community	Country	Feeding guilds	Reference
California	United States	A	Supernant, 1977
Iowa	United States	A	Kunz, 1973
Chiapas	Mexico	A, F, G, M	Medellin, 1993
Guanacaste	Costa Rica	A, F, G	Fleming et al., 1972
Guanacaste	Costa Rica	A, F, G, M, N	Laval and Fitch, 1977
Heredia	Costa Rica	A, F, G, N	Laval and Fitch, 1977
Puntarenas	Costa Rica	A, F, N	Laval and Fitch, 1977
Sherman	Panama	A, F, G	Fleming et al., 1972
Rodman	Panama	A, F, G	Fleming et al., 1972
Barro Colorado Island	Panama	A, F, G	Bonaccorso, 1975
Zabelitas	Colombia	A, F, G, N	Thomas, 1972
Pance	Colombia	F	Thomas, 1972
Peru	Peru	A, G, M, N	C. F. Ascorra and D. L. Gorchov, in litt.
Caatinga	Brazil	A, F, G, M, N	Willig, 1982
Edaphic Cerrado	Brazil	A, F, G, M	Willig, 1982

ten are difficult to delineate for a diverse group of species. More generally defined guilds also may be required when the range of communities is broad and extensive. Species were assigned to feeding guilds based on food items that locally composed the majority of their diet (e.g., blood, fish, fruit, animal, nectar). Other trophic classifications have been suggested. For example, Bonaccorso (1975) and Fleming et al. (1972) categorized frugivores into upper and lower canopy guilds. This is problematic because some of our sites contained only short-stature vegetation that did not exhibit multistratal vertical structure. Upper canopy versus lower canopy distinctions would not apply consistently across sites. Similarly, it is commonplace to distinguish gleaning insectivores from gleaning carnivores. In this study, we considered both groups to be gleaning animalivores. Evidence is not sufficient to suggest that carnivores exhibit carnivory throughout most of the year, and in many places, bats that would be designated as carnivores actually exhibit omnivory (Willig et al., 1993). Thus, our operational definition of a gleaning animalivore was any species that consumed mainly animals (vertebrates or invertebrates) that were gleaned from surfaces. Remaining guild associations were based on designations published in either the account of the community or from related published information (Gardner, 1977; Wilson, 1975).

Sanguinivores and piscivores always were omitted from analyses. At most, real communi-

ties contained one piscivore, rendering detection of a hyperdispersion in morphology impossible. The pool of sanguinivores could at most include three species (all extant members of the Desmodontinae), and consequently no selection of species, no matter how deterministic, could be shown to be a rare occurrence (Willig and Moulton, 1989). If a feeding guild at a particular site did not contain at least three species, it was omitted from analyses at that site.

Morphological structure.—Seven attributes were used to ecomorphologically characterize each species. Those included forearm length, greatest length of skull, condylobasal length, width across postorbital constriction, breadth of braincase, length of maxillary toothrow, and breadth across upper molars. Measurements were obtained from Swanepoel and Genoways (1979) for most phyllostomids and from museum specimens for other taxa. In most cases, eight individuals, four males and four females, contributed to the mean of each character for each species.

Common logarithms of each character were used in analyses (Ricklefs and Travis, 1980). Log transformations enhance normality and equalize variances (Sokal and Rohlf, 1995). Moreover, if principal components are calculated by factoring the covariance matrix, the distortion of multivariable space is minimized (Ricklefs and Travis, 1980; Ricklefs and Miles, 1994). Morphological relationships of species were determined for each guild separately using

principal components analyses (PCA—SAS program PRINCOMP; Ray, 1982), as suggested by Moulton and Pimm (1986, 1987) and Willig and Moulton (1989). That technique maintained morphological distances among species, yet eliminated redundancy of highly correlated characters by constructing a linear combination of original variables. Consequently, the number of dimensions necessary to illustrate relationships was less than the original number of characters (Ricklefs and Miles, 1994; Ricklefs and Travis, 1980). By extraction from a covariance matrix, two principal components characterized relationships among species. Subsequently, minimum spanning trees (MST), based on principal component scores of the morphological variables, were calculated to determine the distance of species in two dimensions (principal components 1 and 2). Minimum spanning trees were the shortest sum of $N-1$ line segments needed to connect N species within a guild. Thus, length of the minimum spanning tree reflected the magnitude of interspecific morphological difference.

Two descriptive statistics (mean and variance) were calculated for segment lengths of minimum spanning trees. If competition prevented morphologically similar species from coexisting within communities, overdispersions in morphology should evince in one or both of two ways: mean segment lengths of actual minimum spanning trees should be greater than would be expected due to chance, or the variance of minimum spanning tree segment lengths should be smaller than expected due to chance (Moulton and Pimm, 1986; Willig and Moulton, 1989).

Species pools.—The demonstration of large means and small variances for segment lengths from minimum spanning trees requires an appropriate context. Many artifacts can give rise to seemingly large means and small variances. If some aspect of the history of a particular taxon created a particular pattern in morphology within a clade, the random assembly of species into a community likely will recapitulate that pattern. Thus, species pools representing faunal groups from which communities are assembled must be used in analyses; actual communities must be compared to those assembled at random from a faunal pool. Simulation provides the basis for an unbiased assessment of such characteristics of guilds.

Appropriate species pools often are difficult to construct (Gotelli and Graves, 1996; Graves

and Gotelli, 1983; Willig and Moulton, 1989). As suggested by Gotelli and Graves (1996), pools should include those species that have a reasonable probability of occurring in a particular community. Indeed, size of the species pool is possibly the most critical decision in designing such studies. Pool size is of importance because it determines the biogeographic scenario from which communities are assembled. Because no a priori pool size is preferred, we used seven pools, five of which were defined by concentric circles with diameters of 500, 1,000, 2,000, 4,000, and 8,000 km (Fig. 1). The first pool represented only those species whose distribution overlapped the actual community, and the last pool represented all bats in the New World. Distribution maps for bat species were prepared using Hall (1981) for North and Central America, and Koopman (1982), Eisenberg (1989), and Redford and Eisenberg (1992) for South America. Morphological patterns from each guild were compared to those randomly drawn from each of seven faunal pools. For each pool, randomly drawn guilds were assembled using the algorithm of Moulton (1985), Moulton and Pimm (1987), and Willig and Moulton (1989). If N species occurred in an actual guild and S was the number of species in a species pool, then the number of different guild combinations (C) was $S!/(N!(S-N)!)$. The number of possible combinations was often large. When C was >500 , we randomly selected 500 combinations to calculate random guild statistics. When C was ≤ 500 , we used each combination once to minimize redundancy. Each set of descriptive statistics from randomly assembled guilds formed distributions under the null hypothesis (random guild assembly) to which corresponding statistics from the actual feeding guild were compared. If the mean segment length from an actual guild was $>90\%$ of the simulated values, or if the variance of the segment lengths was $<90\%$ of the simulated values, we concluded that nonrandom morphological combinations existed in the actual guild.

RESULTS

Principal components analyses.—Ecological guilds are morphologically distinct (Fig. 2) based on PCA of log-transformed characters. The first and second principal component accounted for 80.1% and 9.4% of the variation among species, respectively. The consistent di-

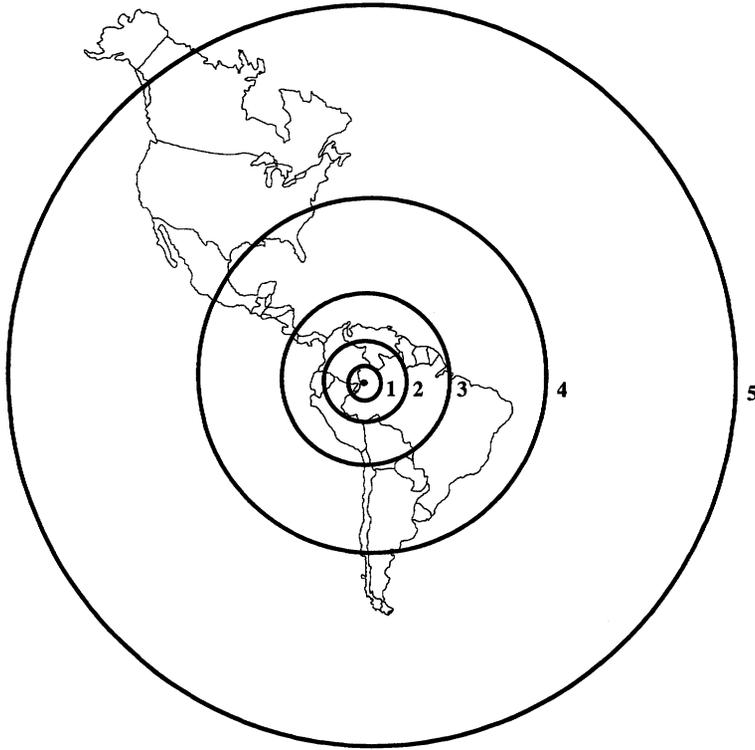


FIG. 1.—Graphical representation of faunal pools (after Willig and Moulton, 1989). The solid dot represents the location of a particular community. Faunal pool 0 corresponds to all species whose distributions overlap the community. Faunal pools 1, 2, 3, 4, and 5 correspond to the set of all species whose distributions occur within concentric rings of diameters 500, 1,000, 2,000, 4,000, and 8,000 kilometers, respectively. Faunal pool 6 corresponds to all species of bats from the mainland of the New World.

rection and large magnitude of the correlation between original characters and PC1 scores (from -0.82 to -0.96 ; Fig. 2, inset) suggested that size was an important characteristic that contributed to differentiation of species. In contrast, the correlation between original characters and PC2 was variable in magnitude and direction (-0.48 to 0.29), suggesting that bat species also differed in shape. The non-overlapping arrangement of guild centroids ($\pm 2 SE$) strongly suggested that morphology, including attributes of both size and shape, reflected important ecological attributes related to the foraging biology of bats. Although most of the variation among species was related to size (PC1), foraging guilds were differentiated by shape to a larger degree than by size, based upon the dispersion of centroids in morphological space.

Separate principal components analyses were conducted on each of the five feeding guilds.

Percent variation accounted for by the first and second principal components ranged from 76.8 to 89.2 and 5.9 to 16.4, respectively (Table 2). Nonetheless, contributions of particular characters to principal components were different, depending on feeding guild. All characters, regardless of feeding guild, were correlated positively with the first principal component describing overall size (Table 3). No pattern existed among guilds regarding contribution of morphological characters to the second principal component. Shape differed among species in a guild-specific fashion and was likely a consequence of modification of structure to enhance ecological efficiency. Clearly, feeding guild distinctions often corresponded to morphological and phylogenetic differences. Thus, it is not surprising that differences exist in the relative contribution of variables to the second principal component

Minimum spanning trees.—Simulation analy-

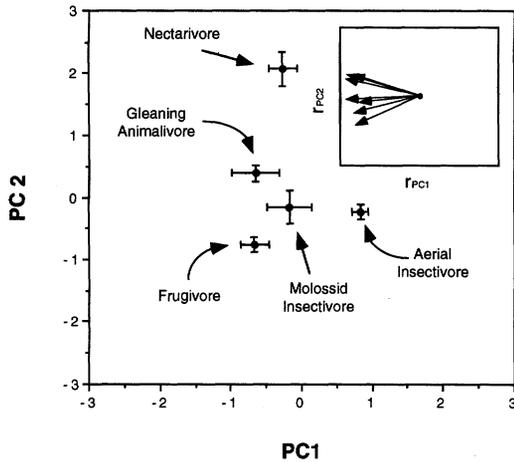


FIG. 2.—Morphological characterization of New World bats (mainland only) based on the first two principal components derived from a suite of 7 morphological characters. Bars represent dispersion ($\pm 2 SE$) whereas dots represent centroids for each of 5 feeding guilds. Morphological characters are strongly, and uniformly, correlated with the first principal component, whereas characters are more weakly and variably correlated with the second principal component (inset). From top to bottom, arrows in the insert represent the correlation of breadth of braincase, greatest length of skull, condylobasal length, length of maxillary toothrow, width across postorbital constriction, and breadth across upper molars, with the first two principal components.

ses indicated that nonrandom morphological patterns, consistent with competition theory, existed within bat communities. Twelve of 15 locations, and 3 of 5 feeding guilds exhibited mean

segment lengths that were significantly greater than those derived from random assembly (Appendix I). Furthermore, segment-length variances were nonrandom at eight locations and in three feeding guilds (Appendix I). When feeding guilds represented nonrandom faunal subsets, morphological patterns most often manifest as greater distances between species in morphological space.

No conspicuous pattern existed as to which communities or feeding guilds exhibited nonrandom morphological structure. Consequently, we used Fisher's test (Sokal and Rohlf, 1995) to combine probabilities from all feeding guilds within a community as well as to combine locations within feeding guilds to determine if each community or feeding guilds exhibited nonrandom morphological patterns. Three communities exhibited unusually high mean segment lengths for most species pools, and three communities exhibited atypically small variances across most species pools (Table 4). From the perspective of guilds, aerial insectivores exhibited unusually higher mean segment lengths for most pools; frugivores exhibited significantly smaller variances of segment lengths for most species pools (Table 5).

DISCUSSION

Although seemingly hyperdispersed morphological patterns are not uncommon within communities, evaluations using null models have determined that statistically nonrandom hyperdispersions represent a minority (Simberloff and Boeklen, 1981). Research concerning size assortment in South American bat communities did not

TABLE 2.—Eigenvalues and percent variation accounted for by the first two principal components (PC) in analyses conducted on a suite of log-transformed ecomorphological characters for species in each guild.

Feeding guild	Species richness	PC1		PC2	
		Eigenvalue	Percent variation	Eigenvalue	Percent variation
Aerial insectivore	94	0.028	76.9	0.004	10.7
Frugivore	63	0.047	88.9	0.003	5.9
Gleaning animalivore ^a	35	0.073	89.2	0.005	6.0
Molossid insectivore	29	0.055	87.7	0.005	7.4
Nectarivore	29	0.022	78.0	0.005	16.4

^a Any species that consumed mainly animals that were gleaned from surfaces.

TABLE 3.—Pearson product-moment correlations of each of seven ecomorphological characters with the first and second (in parentheses) principal components derived for each of five feeding guilds.

Character	Feeding guild									
	Aerial insectivore		Frugivore		Gleaning animalivore ^a		Molossid insectivore		Nectarivore	
Length of forearm	0.925	(0.102)	0.949	(0.245)	0.952	(-0.094)	0.958	(-0.175)	0.914	(0.207)
Greatest length of skull	0.855	(0.230)	0.978	(0.106)	0.982	(-0.119)	0.994	(-0.008)	0.956	(-0.253)
Condylbasal length	0.931	(0.111)	0.966	(0.056)	0.991	(-0.054)	0.986	(-0.088)	0.949	(-0.299)
Postorbital constriction	0.769	(-0.625)	0.839	(0.439)	0.843	(0.536)	0.838	(0.246)	0.677	(0.630)
Breadth of braincase	0.927	(-0.016)	0.951	(0.243)	0.968	(0.008)	0.963	(0.145)	0.912	(0.298)
Length of maxillary toothrow	0.843	(0.367)	0.950	(-0.273)	0.947	(-0.087)	0.973	(-0.153)	0.935	(-0.307)
Breadth across upper molars	0.924	(0.008)	0.928	(-0.230)	0.954	(-0.202)	0.655	(0.732)	0.703	(0.674)

^a Any species that consumed mainly animals that were gleaned from surfaces.

detect morphological hyperdispersion in Caatinga or edaphic Cerrado habitats of northeastern Brazil (Willig and Moulton, 1989). Although these two locations are the only evaluation of size assortment in bat communities, they may not characterize size assortment for bats in general. In contrast, our findings, based on communities spanning ca. 50° latitude in the New World, demonstrate that nonrandom morphological hyperdispersion exists in feeding guilds from a number of localities. In fact, hyperdispersion even characterized some communities in general. Nonetheless, hyperdispersion is an inconsistent attribute of community structure of bats, and this may be the consequence of variability in the strength of competitive interactions. Competitive interactions can be sufficiently strong to produce deterministic structure but only under certain circumstances.

Considerable variation exists regarding the degree to which feeding guilds at particular sites, feeding guilds in general, or even overall communities are deterministically structured. Communities exhibit deterministic structure overall only in a minority of cases. This could be a consequence of a dilution effect similar to that described by Diamond and Gilpin (1982). Dilution occurs when ecologically heterogeneous groups of species are combined in

evaluations of effects of biotic interactions on community structure (i.e., species with no potential to interact are included in analyses). Thus, when communities include more than one ecological group, species must be assigned appropriately to each group and separate analyses should be conducted on each group. Similarly, different trophic guilds within communities may not respond in the same fashion to environmental gradients. As such, it would be naive to expect overall structure to be deterministic because effects of environmental gradients on the ability of competitive interactions to manifest are different and independent among trophic guilds. Accordingly, combining results from ecologically heterogeneous group and using them to evaluate "community" structure may not be advisable when communities span one or more environmental gradient. Guild-specific responses may serve to dilute the appearance of the operation of biotic interactions. This suggests that like "communities" compiled from distribution maps and faunas, real bat communities may represent a level of organization that is also an inappropriate focus for studies evaluating certain kinds of biotic interactions.

Two of the five analyzed feeding guilds exhibited a significant tendency toward overall deterministic structure based on

TABLE 4.—Results of Fisher's test of combined probability for overall significance (boldface print indicates $P \leq 0.10$) regarding the mean and variance of minimum spanning tree segment lengths from each of 15 bat communities. Pools 0–6 correspond to the seven faunal pools represented in Fig. 1.

Community	Statistic	Pool						
		0	1	2	3	4	5	6
Iowa	Mean	0.341	0.058	0.082	0.222	0.494	0.436	0.486
	Variance	0.568	0.480	0.414	0.444	0.262	0.264	0.232
California	Mean	0.010	0.006	0.002	0.018	0.094	0.118	0.098
	Variance	0.454	0.458	0.494	0.384	0.240	0.250	0.236
Chiapas	Mean	0.151	0.182	0.158	0.137	0.120	0.137	0.137
	Variance	0.441	0.299	0.525	0.296	0.263	0.270	0.270
Guanacaste ^a	Mean	0.297	0.344	0.245	0.190	0.160	0.134	0.134
	Variance	0.802	0.742	0.745	0.750	0.665	0.682	0.682
Guanacaste ^b	Mean	0.054	0.044	0.040	0.026	0.028	0.029	0.029
	Variance	0.603	0.572	0.530	0.414	0.431	0.438	0.438
Puntarenas	Mean	0.917	0.909	0.915	0.835	0.837	0.790	0.790
	Variance	0.933	0.849	0.902	0.913	0.883	0.901	0.901
Heredia	Mean	0.078	0.048	0.028	0.008	0.009	0.019	0.019
	Variance	0.429	0.415	0.506	0.468	0.525	0.493	0.493
Sherman	Mean	0.845	0.755	0.773	0.484	0.425	0.423	0.423
	Variance	0.056	0.049	0.017	0.019	0.018	0.008	0.008
Rodman	Mean	0.709	0.690	0.627	0.532	0.407	0.377	0.377
	Variance	0.157	0.119	0.079	0.072	0.092	0.088	0.088
Barro Colorado Island	Mean	0.181	0.174	0.156	0.072	0.063	0.055	0.055
	Variance	0.029	0.027	0.016	0.017	0.012	0.018	0.018
Zabelitas	Mean	0.093	0.207	0.278	0.257	0.252	0.255	0.255
	Variance	0.159	0.225	0.216	0.236	0.266	0.259	0.259
Pance	Mean	0.218	0.370	0.422	0.398	0.416	0.416	0.416
	Variance	0.528	0.388	0.422	0.408	0.440	0.440	0.440
Peru	Mean	0.635	0.467	0.278	0.277	0.142	0.158	0.158
	Variance	0.929	0.913	0.936	0.934	0.917	0.916	0.916
Edaphic Cerrado	Mean	0.838	0.824	0.840	0.764	0.723	0.446	0.472
	Variance	0.234	0.194	0.149	0.132	0.131	0.125	0.154
Caatinga	Mean	0.761	0.638	0.755	0.760	0.705	0.553	0.514
	Variance	0.209	0.127	0.169	0.152	0.079	0.058	0.061

^a Community at Guanacaste sampled by LaVal and Fitch (1977).

^b Community at Guanacaste sampled by Fleming et al. (1972).

more than two faunal pools. Aerial insectivores consistently exhibited high mean interspecific distances, and frugivores consistently exhibited low variances. Despite those significant tendencies, deterministic structure was not ubiquitous. Bats are highly mobile organisms (Hill and Smith, 1984; Rayner and Norberg, 1987, Thomas, 1987). Their vagility may minimize temporal persistence of morphological hyperdispersion. If vagility increases the likelihood of rescue effects (Brown and Kodric-Brown, 1977), morphological hyperdispersion may persist only during times when strong competitive

interactions transpire. As soon as relative resource levels increase, locally extinct bat species may quickly return to previously occupied communities, or new species may be able to enter and exploit the relatively less used portions of the resource spectrum. To this end, vagility may serve to obscure the "ghost of competition past" (Connell, 1980).

Environmental variability also may contribute to the lack of ubiquity of deterministic structure. Competitive interactions are density-dependent phenomena. Moreover, morphological hyperdispersion results from

TABLE 5.—Results of Fisher's test of combined probability determining overall significance of mean and variance of minimum spanning tree lengths for each of five feeding guilds. Boldface print indicates statistical significance ($P \leq 0.10$). Pools 0–6 correspond to the seven faunal pools represented in Fig. 1.

Feeding guild	Statistic	Pool						
		0	1	2	3	4	5	6
Aerial insectivore	Mean	0.005	0.002	< 0.001				
	Variance	0.454	0.360	0.411	0.504	0.460	0.458	0.483
Frugivore	Mean	0.993	0.992	0.995	0.999	0.999	0.999	0.999
	Variance	0.027	0.008	0.002	< 0.001	< 0.001	< 0.001	< 0.001
Gleaning animalivore ^a	Mean	0.925	0.566	0.306	0.108	0.102	0.088	0.088
	Variance	0.515	0.645	0.654	0.777	0.696	0.727	0.727
Molossid insectivore	Mean	0.495	0.583	0.573	0.777	0.752	0.795	0.795
	Variance	0.833	0.808	0.796	0.697	0.692	0.635	0.635
Nectarivore	Mean	0.081	0.422	0.555	0.641	0.755	0.762	0.762
	Variance	0.269	0.139	0.314	0.335	0.275	0.283	0.283

^a Any species that consumed mainly animals that were gleaned from surfaces.

intense, persistent competitive interaction (Moulton and Pimm, 1986). If communities are not allowed time to achieve equilibria or do not sustain equilibria, hyperdispersions likely will not persist. Communities in our study came from a spectrum of environmental conditions, and it was unlikely that they shared identical histories regarding variability and stability. Hence, it is not surprising that hyperdispersion is not a consistent indicator of structure. In fact, hyperdispersion may be an unrealistic prediction regarding the operation of competitive interactions across broad geographic areas.

Structure of many communities was no different from random expectations and in those communities morphologies were not hyperdispersed. Unfortunately, however, we can conclude much less regarding the operation of competitive interactions. It would be inappropriate to conclude that competitive interactions were not operating in situations where we obtained nonsignificance or that they did not structure those communities. Size assortment is only one of two ways that competitive interactions can cause morphological hyperdispersion (Case and Sidell, 1983) and only one of a plethora of ways that they may structure communities. Competitive interactions can give rise to morphological patterns, behavioral pat-

terns, and abundance patterns, to name only a few, and it would be hasty to refute the influence of competitive interactions on community organization by obtaining nonsignificance of size assortment alone.

Nonetheless, null hypotheses evaluating size assortment are a valuable and necessary step toward understanding the role of competition in the structure of bat communities. Hyperdispersion within feeding guilds represents the ultimate manifestation of competition at the community level. In fact, a more exhaustive suite of hypotheses (Krebs, 1985) would likely yield maximal resolution toward understanding the role of competition in community organization. For example, one might first evaluate morphological hyperdispersions within communities. Upon failure to reject the null hypothesis of random morphological dispersion, one might evaluate a null hypothesis of no association between morphological distance and abundance. Upon rejection of this null hypothesis, one might evaluate another putative manifestation of competitive interaction such as mutually exclusive behavioral patterns of competitors. Failure to reject single null hypotheses should not be an end but rather a beginning.

In summary, we evaluated the morphological structure of five feeding guilds from

15 New World bat communities based on predictions of competition theory. Deterministic structure was detected in many situations. Entire communities did not consistently exhibit deterministic structure overall, and we believe that this is due to the differential response of trophic guilds to environmental gradients. Two feeding guilds, aerial insectivores and frugivores, exhibited a general tendency toward deterministic structure. Nonetheless, a considerable amount of variation exists regarding the degree to which feeding guilds at particular sites exhibit deterministic structure. We believe that the particular nuances of the biology of bats (e.g., high vagility), combined with the particular circumstances necessary for the induction of morphological patterns (i.e., community equilibrium), affect deterministic structure in transitory circumstances and not in general. Approaches such as the one employed here, in which many communities from a spectrum of environmental conditions are evaluated, should examine other putative manifestations of biotic interactions in feeding guilds to better determine the impact of competition on bat community organization.

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APPENDIX I

Simulation analyses evaluating if the mean or variance of segment lengths of minimum spanning trees from an actual feeding guild were indistinguishable from those under the null hypothesis of stochastic guild assembly. If the actual mean segment length was greater, or the actual variance smaller than 90% of the randomly generated statistics, the actual guild exhibited deterministic structure (boldface print). A dagger (†) indicates that the actual feeding guild comprises all species in the faunal pool. Pool sizes are defined in Fig. 1.

Community and feeding guild	Metric	Actual MST segment	Pool						
			0	1	2	3	4	5	6
Iowa									
Aerial insectivore	Mean	0.910	0.341	0.058	0.082	0.222	0.492	0.436	0.486
	Variance	0.129	0.568	0.480	0.414	0.444	0.262	0.264	0.232
California									
Aerial insectivore	Mean	1.177	0.010	0.006	0.002	0.018	0.094	0.118	0.098
	Variance	0.126	0.454	0.458	0.494	0.384	0.240	0.250	0.236
Chiapas									
Aerial insectivore	Mean	0.934	0.144	0.072	0.064	0.018	0.026	0.028	0.028
	Variance	0.128	0.232	0.164	0.288	0.334	0.318	0.262	0.262
Frugivore	Mean	0.583	0.118	0.494	0.640	0.836	0.894	0.896	0.896
	Variance	0.039	0.032	0.018	0.040	0.010	0.008	0.010	0.010
Gleaning animalivore ^a	Mean	0.765	0.582	0.458	0.386	0.380	0.230	0.230	0.230
	Variance	0.425	0.960	0.970	0.958	0.928	0.922	0.922	0.922
Molossid insectivore	Mean	1.686	0.250	0.210	0.168	0.368	0.314	0.366	0.366
	Variance	0.978	0.945	0.959	0.968	0.868	0.890	0.882	0.882
Guanacaste ^b									
Aerial insectivore	Mean	1.183	0.112	0.072	0.032	0.012	0.008	0.006	0.006
	Variance	0.365	0.836	0.872	0.902	0.872	0.830	0.868	0.868
Frugivore	Mean	0.999	0.268	0.286	0.372	0.560	0.556	0.570	0.570
	Variance	0.068	0.240	0.148	0.128	0.126	0.088	0.086	0.086
Gleaning animalivore ^a	Mean	0.884	0.740	0.556	0.500	0.422	0.396	0.396	0.396
	Variance	0.404	0.634	0.666	0.654	0.730	0.740	0.740	0.740
Molossid insectivore	Mean	1.114	0.138	0.378	0.376	0.474	0.552	0.552	0.552
	Variance	0.922	1.000	0.970	0.978	0.946	0.914	0.914	0.914
Nectarivore	Mean	0.940	0.884	0.868	0.804	0.810	0.810	0.756	0.756
	Variance	0.223	0.362	0.397	0.454	0.446	0.446	0.478	0.478
Guanacaste ^c									
Aerial insectivore	Mean	1.620	0.012	0.006	0.004	0.002	0.002	0.002	0.002
	Variance	0.647	0.970	0.956	0.968	0.952	0.966	0.954	0.954
Frugivore	Mean	0.847	0.190	0.322	0.450	0.558	0.606	0.656	0.656
	Variance	0.090	0.294	0.242	0.186	0.122	0.128	0.134	0.134
Gleaning animalivore ^a	Mean	0.835	0.910	0.798	0.764	0.674	0.684	0.684	0.684
	Variance	0.196	0.360	0.396	0.432	0.412	0.416	0.416	0.416
Puntarenas									
Aerial insectivore	Mean	0.934	0.740	0.684	0.642	0.396	0.370	0.332	0.332
	Variance	0.284	0.644	0.656	0.696	0.718	0.632	0.652	0.652
Frugivore	Mean	0.739	0.550	0.594	0.722	0.792	0.856	0.852	0.852
	Variance	0.345	0.978	0.932	0.888	0.888	0.868	0.826	0.826
Nectarivore	Mean	0.856	0.889	0.858	0.774	0.790	0.790	0.732	0.732
	Variance	0.290	0.630	0.431	0.544	0.558	0.558	0.620	0.620

APPENDIX I.—Continued.

Community and feeding guild	Metric	Actual MST segment	Pool						
			0	1	2	3	4	5	6
Heredia									
Aerial insectivore	Mean	0.967	0.100	0.052	0.018	0.012	0.004	0.012	0.012
	Variance	0.268	0.834	0.884	0.888	0.828	0.856	0.826	0.826
Frugivore	Mean	0.611	0.328	0.210	0.386	0.656	0.648	0.648	0.648
	Variance	0.071	0.232	0.242	0.218	0.110	0.152	0.126	0.126
Gleaning animalivore ^a	Mean	0.762	0.234	0.068	0.058	0.008	0.028	0.028	0.028
	Variance	0.280	0.416	0.478	0.456	0.686	0.628	0.628	0.628
Nectarivore	Mean	1.058	0.111	0.542	0.458	0.504	0.504	0.476	0.476
	Variance	0.193	0.222	0.163	0.296	0.350	0.350	0.376	0.376
Sherman									
Aerial insectivore	Mean	1.425	0.338	0.246	0.270	0.098	0.082	0.082	0.082
	Variance	0.074	0.100	0.088	0.060	0.122	0.118	0.122	0.122
Frugivore	Mean	0.491	0.936	0.934	0.982	0.988	0.988	0.988	0.988
	Variance	0.038	0.034	0.032	0.012	0.006	0.006	0.002	0.002
Gleaning animalivore ^a	Mean	0.811	0.818	0.788	0.732	0.666	0.614	0.614	0.614
	Variance	0.380	0.638	0.638	0.632	0.676	0.692	0.692	0.692
Rodman									
Aerial insectivore	Mean	1.669	0.384	0.362	0.368	0.226	0.166	0.144	0.144
	Variance	0.018	0.066	0.050	0.054	0.050	0.072	0.070	0.070
Frugivore	Mean	0.544	0.848	0.900	0.968	0.968	0.960	0.962	0.962
	Variance	0.090	0.438	0.342	0.158	0.166	0.166	0.160	0.160
Gleaning animalivore ^a	Mean	1.005	0.468	0.436	0.316	0.358	0.290	0.290	0.290
	Variance	0.176	0.330	0.368	0.410	0.364	0.364	0.364	0.364
Barro Colorado Island									
Aerial insectivore	Mean	1.342	0.052	0.040	0.028	0.012	0.012	0.010	0.010
	Variance	0.098	0.110	0.102	0.126	0.138	0.172	0.178	0.178
Frugivore	Mean	0.622	0.448	0.596	0.844	0.846	0.866	0.850	0.850
	Variance	0.053	0.128	0.096	0.038	0.036	0.028	0.046	0.046
Gleaning animalivore ^a	Mean	0.903	0.508	0.468	0.400	0.300	0.246	0.246	0.246
	Variance	0.076	0.064	0.082	0.084	0.090	0.058	0.058	0.058
Zabelitas									
Aerial insectivore	Mean	1.466	0.548	0.570	0.552	0.434	0.284	0.292	0.292
	Variance	0.351	0.566	0.610	0.600	0.586	0.694	0.660	0.660
Frugivore	Mean	0.472	0.790	0.922	0.956	0.918	0.952	0.952	0.952
	Variance	0.069	0.230	0.176	0.184	0.188	0.226	0.226	0.226
Gleaning animalivore ^a	Mean	1.301	0.649	0.226	0.212	0.182	0.174	0.174	0.174
	Variance	0.164	0.192	0.328	0.286	0.318	0.344	0.344	0.344
Nectarivore	Mean	1.489	0.004	0.036	0.066	0.088	0.130	0.130	0.130
	Variance	0.073	0.108	0.142	0.146	0.148	0.126	0.126	0.126
Pance									
Frugivore	Mean	0.747	0.218	0.370	0.422	0.398	0.416	0.416	0.416
	Variance	0.134	0.528	0.388	0.422	0.408	0.440	0.440	0.440

APPENDIX I.—Continued.

Community and feeding guild	Metric	Actual MST segment	Pool						
			0	1	2	3	4	5	6
Peru									
Aerial insectivore	Mean	0.933	0.720	0.558	0.488	0.392	0.140	0.164	0.164
	Variance	0.338	0.768	0.782	0.798	0.814	0.840	0.832	0.832
Gleaning animalivore ^a	Mean	0.887	0.212	0.148	0.046	0.058	0.044	0.044	0.044
	Variance	0.396	0.864	0.752	0.810	0.840	0.810	0.810	0.810
Molossid insectivore	Mean	1.292	0.460	0.398	0.476	0.492	0.514	0.514	0.514
	Variance	0.302	0.804	0.806	0.740	0.724	0.674	0.674	0.674
Nectarivore	Mean	1.020	0.672	0.660	0.694	0.656	0.704	0.704	0.704
	Variance	0.177	0.400	0.402	0.472	0.448	0.428	0.428	0.428
Cerrado									
Aerial insectivore	Mean	1.311	0.312	0.324	0.324	0.240	0.212	0.072	0.082
	Variance	0.140	0.192	0.158	0.158	0.212	0.220	0.222	0.316
Frugivore	Mean	0.630	0.834	0.834	0.904	0.968	0.970	0.962	0.962
	Variance	0.072	0.266	0.266	0.170	0.110	0.088	0.090	0.090
Gleaning animalivore ^a	Mean	1.169	0.672	0.672	0.672	0.582	0.602	0.482	0.482
	Variance	0.506	0.692	0.692	0.692	0.722	0.736	0.790	0.790
Molossid insectivore	Mean	1.130	0.698	0.626	0.626	0.625	0.564	0.586	0.586
	Variance	0.004	0.151	0.131	0.131	0.117	0.136	0.114	0.114
Caatinga									
Aerial insectivore	Mean	1.657	0.200	0.232	0.232	0.202	0.140	0.054	0.044
	Variance	0.286	0.476	0.504	0.504	0.500	0.490	0.546	0.588
Frugivore	Mean	0.682	0.698	0.698	0.792	0.908	0.942	0.966	0.966
	Variance	0.102	0.102	0.102	0.096	0.066	0.040	0.024	0.024
Gleaning animalivore ^a	Mean	0.872	0.790	0.790	0.790	0.646	0.606	0.532	0.532
	Variance	0.137	0.186	0.186	0.186	0.282	0.212	0.258	0.258
Molossid insectivore	Mean	0.800	0.820	0.732	0.732	0.746	0.692	0.726	0.726
	Variance	0.149	0.482	0.484	0.484	0.374	0.340	0.304	0.304
Nectarivore	Mean	1.232	†	0.222	0.364	0.416	0.514	0.656	0.656
	Variance	0.010	†	0.111	0.200	0.205	0.158	0.132	0.132

^a Any species that consumed mainly animals that were gleaned from surfaces.

^b The community at Guanacaste sampled by LaVal and Fitch (1977).

^c The same community as sampled by Fleming et al. (1972).