

THE ROLE OF STOCHASTIC AND DETERMINISTIC PROCESSES IN STRUCTURING NEOTROPICAL BAT COMMUNITIES

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ABSTRACT.—The extent to which deterministic or stochastic processes affect the composition and morphological structure of communities is an intense debate in evolutionary ecology. For many years, competition was considered to be the dominant deterministic factor that affected structure of animal communities. More specifically, interspecific competition can affect morphological patterns within communities by either size assortment or size adjustment. We investigated the extent to which size assortment could have structured bat assemblages from two well-defined bat communities from northeast Brazil by comparing real ecomorphological characteristics (mean and variance of segment lengths of minimum-spanning trees from principal component scores) to the distribution of like statistics obtained from simulations derived from nested-species pools. Regardless of species pool, the ecomorphological patterns of bat assemblages were no more structured than expected by random selection of taxa from the available species pool. This was true for frugivorous, nectarivorous, and foliage-gleaning insectivorous guilds, and for the phyllostomid community in general, from both Caatinga and edaphic Cerrado biomes. The alternative hypothesis, that coevolutionary processes determine ecomorphological patterns in these neotropical communities, similarly is not supported by our results. The characteristic spatial and temporal heterogeneity of northeast Brazil, combined with the mobile nature of bats, could decrease the intensity, pervasiveness, or predominance of deterministic interactions, thereby leading to an ecomorphological structure indistinguishable from that produced by stochastic processes.

The exact role of competition in producing morphological patterns in natural communities has been the subject of intense debate (Diamond and Case, 1986; Strong et al., 1984). This is a result, in part, of the existence of different competitive mechanisms and their resultant patterns. As suggested by Case and Sidell (1983), competition might affect morphological patterns by either size assortment or size adjustment. Size assortment is the situation in which the probability of persistence of a species is diminished by presence of morphologically similar species. Size adjustment refers to evolutionary shifts in some morphological characteristic that species undergo to minimize competition. In either instance, an exact understanding of the role of competition has been hampered by a variety of methodological problems. In particular, determination of guild membership and formation of appropriate species pools for constructing null communities have been sources of continuing consternation (Connor and Simberloff, 1983; Moulton and Pimm, 1987). Recently, Moulton and Pimm (1986a) suggested that to structure communities (i.e., produce morphological patterns) competition must be intensive enough to force extinctions, extensive enough to involve most species, and finally, these effects must predominate at the community level.

Several authors found morphological patterns within lower taxonomic categories such as genera (Abbot et al., 1977) or families (Bowers and Brown, 1982; Schoener, 1984), or within ecologically defined units, such as guilds (Case et al., 1983). These patterns are typically nonexistent at the community level (Bowers and Brown, 1982; Strong et al., 1979; Wiens and Rotenberry, 1980), although there are some exceptions (Brown and Bowers, 1985; Moulton and Pimm, 1983, 1987). The emerging view from these studies is that competitive effects operate principally at some intermediate organizational level. When competitive effects appear at one level, but disappear at the community level, it is unclear whether these effects simply are not sufficiently extensive or if other forces predominate. Moreover, many of these studies involve island communities; it is uncertain that similar results will obtain for mainland communities. Furthermore, those studies involving mainland communities (Bowers and Brown, 1982; Brown and Bowers, 1985; Schoener,

1984) are restricted to the Temperate Zone; it is possible that tropical communities are not structured by the same forces.

Herein, we present an analysis of three well-defined foraging guilds (*sensu* Root, 1967) of tropical bats from each of two different mainland communities in northeast Brazil. Our methodological approach does not include the possibility that competitively mediated size adjustment affected nonrandom morphological patterns in northeast Brazilian bat communities because the subspecific status of many South American phyllostomids is unclear and complete mensural data frequently are unavailable for geographically widespread taxa (Honacki et al., 1982; Jones and Carter, 1976). In our study, one of the methodological difficulties inherent in island studies (*i.e.*, determination of the species pool) does not exist.

MATERIALS AND METHODS

The composition of local phyllostomid communities was obtained from Willig (1983) for Caatinga and edaphic Cerrado biomes of northeast Brazil. Details of sampling regime and habitat characteristics are presented by Mares et al. (1981) and Willig (1983, 1986), and are noted only briefly herein.

Habitat descriptions.—The Caatinga (*sensu lato*) is a large (650,000 km²) semiarid region occupying nine states of northeastern Brazil. The region is subjected to an unpredictable climate, in part affected by the interaction of orographic barriers, three mobile, moisture-laden air masses, and the southeast trade winds. The Caatinga biome (*sensu stricto*) comprises four recognizable habitats: Caatinga Baixa (lowland thorn-scrub), Caatinga Alta (drought-adapted, semideciduous thorn forest), Lajeiros (granitic outcrops and rock piles), and Serrotes (mesic, granitic mountains). In areas unaffected by post-Cretaceous erosion, the original sandstone substrate remains as extensive plateaus or chapadas that support edaphic Cerrado vegetation reminiscent of, but distinct from, the Cerrado biome of Central Brazil. Edaphic Cerrado contains a flora distinct from that of the Caatinga in terms of species composition and physiognomy. The habitat is a fairly homogeneous shrub and tree woodland savannah with a pervasive grass component. The Caatinga site was located in Exu, Pernambuco (07°35'S, 39°40'W) whereas the edaphic Cerrado site was located approximately 40 km to the northeast on the Chapada do Araripe in the Floresta Nacional Araripe-Apodí in Crato, Ceará (07°14'S, 39°23'W).

Guilds and species pools.—We followed Willig (1983, 1986) and categorized phyllostomids into feeding guilds based upon the qualitative analysis of the contents of fecal samples obtained from specimens in the field; qualitative analysis of stomach contents determined in the laboratory from recently sacrificed specimens; and reference to the work of Wilson (1973) and Gardner (1977). Phyllostomids occupied five feeding guilds, including foliage-gleaning insectivores, nectarivores, frugivores, sanguinivores, and omnivores. Moreover, no taxa other than phyllostomids were represented in these feeding guilds. Subsequent analyses excluded sanguinivorous and omnivorous guilds. The former guild was not considered for methodological reasons; the species pool at most could include three species (all extant taxa of the phyllostomid subfamily, Desmodontinae). This precludes meaningful statistical analyses because no species selection, even if entirely deterministic, could be shown to be a rare occurrence under any null hypothesis. The omnivorous guild was excluded for ecological reasons; this guild comprises an eclectic group of species, not easily categorized into other guilds because of their polyphagous diets, and is most likely a "waste basket" category.

A series of concentric circles, centered at the midpoint between Exu and Crato, defined the boundaries of species pools. Circle radii formed a geometric progression (1, 2, 4, 8, all of South America) in which the smallest to largest diameter (in km) was 500 (half the distance from the center to coastal Brazil at Recife, Pernambuco), 1,000, 2,000, 4,000, and 8,000 (all of South America). The identity of constituent species within pools was determined from range maps of Koopman (1982).

Structure.—Morphometric data for most taxa were obtained from Swanepoel and Genoways (1979); additional mensural data were obtained from Genoways and Williams (1980) for *Tonatia schultzei*; Hernandez-Camacho and Cadena-G (1978) for *Lonchophylla marinkellei*; Hill (1980) for *Lonchophylla handleyi*; Sazima et al. (1978) for *Lonchophylla bokermanni*; and Shamel (1927) for *Sturnira bogotensis*. We used forearm length, greatest length of skull, condylobasal length, postorbital constriction, breadth of braincase, length of maxillary toothrow, and breadth across upper molars to characterize each specimen, but represented each species by the mean from eight individuals if possible, including both males and females. We calculated the common logarithms of each character following Ricklefs and Travis (1980) and depicted morphological space for all species by using principal-component analysis of the log-transformed mean morphometric characters by SAS procedure PRINCOMP (Ray, 1982). Principal components were extracted from the

covariance matrix of log-transformed variables as recommended by Ricklefs and Travis (1980) for each guild.

Randomly assembled guilds were constructed by use of the algorithm of Moulton (1985) and Moulton and Pimm (1987). If N species occur in a "real" guild, and S is the total number of potential species of the guild available from the pool, then the number of different guild compositions possible (C) is given by $S!/(N!(S-N)!)$. The number of possible combinations often was large. When C was >200 , we randomly selected 200 combinations to calculate random guild statistics. When C was ≤ 200 , we used each possible combination only once to avoid redundancy. We calculated the minimum-spanning tree for each "real" guild and for each randomly assembled guild. The minimum-spanning tree minimizes the sum of the $N-1$ line segments that connect the N species in a guild (Moulton and Pimm, 1986a). These segments represent interspecific morphological differences within guilds. We calculated the mean and variance of segment lengths of minimum-spanning trees for each guild, "real" and randomly assembled. If competition was an important force affecting species composition of guilds, then "real" minimum-spanning trees should be distinct from most randomly generated minimum-spanning trees for a particular guild. We predicted that minimum-spanning trees from "real" guilds should contain larger mean segment lengths and smaller segment-length variance than those obtained from guilds assembled at random. The set of statistics from randomly generated minimum-spanning trees forms a distribution under the null hypothesis (random guild membership) to which we can compare observed-guild minimum-spanning trees. A similar protocol was used by Case and Sidell (1983) to evaluate size assortment in the Galapagos finch (*Geospizinae*) fauna.

RESULTS

Over 6,000 specimens representing 38 species, 28 genera, and 8 families were obtained from Caatinga and edaphic Cerrado habitats. In addition to the components of the phyllostomid guilds listed in Table 1, a variety of nonphyllostomid species were obtained in each area (Willig and Mares [in press] provided an updated checklist of Caatinga mammals). The Caatinga harbored four aerial insectivores (*Peropteryx macrotis*, *Furipterus horrens*, *Myotis riparius*, and *Lasiurus ega*), one piscivore (*Noctilio leporinus*), and seven molossid aerial insectivores (*Molossops planirostris*, *Molossops temminckii*, *Tadarida laticaudata*, *Neoplatymops mattogrossensis*, *Molossus ater*, *Molossus molossus*, and *Eumops* sp.). Similarly, edaphic Cerrado habitats contained seven aerial insectivores (*Saccopteryx leptura*, *Pteronotus gymnonotus*, *Natalus stramineus*, *Myotis riparius*, *Eptesicus furinalis*, *Lasiurus borealis*, and *L. ega*) and three molossid aerial insectivores (*Molossops temminckii*, *Tadarida laticaudata*, and *M. molossus*).

Principal-component analyses.—Results of the three principal-component analyses were similar. The first and second eigenvalues (each followed by the proportion of total variance accounted for by the corresponding principal component in parentheses) from the principal-component analysis on each of the three guilds were: nectarivore, 0.025 (0.84); 0.003 (0.11); foliage-gleaning insectivore, 0.044 (0.84); 0.005 (0.09); and frugivore, 0.043 (0.87); 0.003 (0.07). In each analysis, the first two principal components accounted for 93 (foliage-gleaners)–95% (nectarivores) of the total variance. Although these analyses were based on the same morphological characteristics for all species, the relative contributions of each original variable to the principal component could vary among guilds. Nevertheless, in all analyses the Pearson product-moment correlation coefficients between the original variables and first principal component were significant ($P < 0.0001$) for the three guilds, respectively: forearm length, 0.932, 0.960, 0.928; greatest length of skull, 0.959, 0.968, 0.976; condylobasal length, 0.958, 0.984, 0.965; postorbital constriction, 0.810, 0.809, 0.783; breadth of braincase, 0.964, 0.959, 0.931; length of maxillary toothrow, 0.953, 0.831, 0.951; and breadth across upper molars, 0.839, 0.941, 0.909. The second principal component was correlated with postorbital constriction in the three guilds, respectively (0.503 [$P = 0.0239$], -0.573 [$P = 0.0034$], 0.492 [$P = 0.0003$]). However, in the nectarivore guild, the second principal component also was correlated with breadth across upper molars (0.499 [$P = 0.0251$]). In the frugivore analysis, the second principal component also was correlated with forearm length (0.296 [$P = 0.039$]) and breadth of braincase (0.299 [$P = 0.0368$]). Factor loadings (i.e., eigenvectors of the covariance matrix) for the first and second (in parentheses) principal components for the three guilds, respectively, were: forearm length, 0.365, 0.445, 0.379 (0.065, 0.009, 0.436);

TABLE 1.—Feeding guild association, and relative abundance of phyllostomid bats from Caatinga (Exu, Pernambuco) and Cerrado (Crato, Ceará) biomes of northeast Brazil.

Taxon	Abundance		Guild
	Caatinga	Cerrado	
Phyllostominae			
<i>Microncycteris megalotis</i>	rare-common	rare	foliage-gleaners
<i>Microncycteris minuta</i>	rare-common	rare	foliage-gleaners
<i>Tonatia bidens</i>	rare	absent	foliage-gleaners
<i>Tonatia brasiliense</i>	rare-common	absent	foliage-gleaners
<i>Tonatia silvicola</i>	common	absent	foliage-gleaners
<i>Mimon crenulatum</i>	rare-common	absent	foliage-gleaners
<i>Phyllostomus discolor</i>	rare-common	absent	omnivore
<i>Phyllostomus hastatus</i>	rare	abundant	omnivore
<i>Trachops cirrhosus</i>	common	absent	omnivore
Glossophaginae			
<i>Glossophaga soricina</i>	abundant	abundant	nectarivore
<i>Lonchophylla mordax</i>	common	absent	nectarivore
<i>Anoura geoffroyi</i>	rare	common	nectarivore
Carollinae			
<i>Carollia perspicillata</i>	abundant	abundant	frugivore
Stenoderminae			
<i>Sturnira lilium</i>	rare	common-rare	frugivore
<i>Uroderma magnirostrum</i>	rare	rare	frugivore
<i>Vampyrops lineatus</i>	abundant	abundant	frugivore
<i>Artibeus concolor</i>	absent	common-rare	frugivore
<i>Artibeus jamaicensis</i>	common	abundant	frugivore
<i>Artibeus lituratus</i>	common-rare	abundant	frugivore
Desmodontinae			
<i>Desmodus rotundus</i>	abundant	rare	sanguinivore
<i>Diphylla ecaudata</i>	rare	absent	sanguinivore

greatest length of skull, 0.405, 0.361, 0.357 (−0.279, 0.189, 0.147); condylobasal length, 0.432, 0.367, 0.384 (−0.327, 0.062, 0.070); postorbital constriction, 0.318, 0.400, 0.223 (0.563, −0.853, 0.505); breadth of braincase, 0.229, 0.315, 0.271 (0.078, −0.002, 0.315); length of maxillary toothrow, 0.488, 0.338, 0.529 (−0.362, 0.385, −0.531); and breadth across upper molars, 0.352, 0.404, 0.421 (0.597, 0.290, −0.383).

Minimum spanning trees.—The taxonomic composition of each guild in Caatinga and edaphic Cerrado sites allowed us to calculate mean and variance of segment length for minimum-spanning trees for comparison with distributions of these statistics derived from the simulations. The distribution of simulation statistics for a particular guild may vary for different species pools because ecomorphometric characteristics of the pool change if the pool contains different species. No trend in *P* values with increasing size of species pool was discernable, and none of the *P* values was even significant at the 0.10 level. More specifically, the smallest *P* value for mean comparisons in Caatinga, mean comparisons in edaphic Cerrado, variance comparisons in the Caatinga, and variance comparisons in edaphic Cerrado were 0.25, 0.14, 0.19, and 0.23, respectively. Regardless of site, guild, or pool, the observed guild statistics (both mean and variance) did not differ from those expected by the random selection of taxa from the species pool for that guild. Even if we consider “community” structure within a pool by combining probabilities for the guilds by use of Fisher’s test (Sokal and Rohlf, 1981), no evidence (*P* > 0.05 for all pools) suggests that deterministic processes affect species membership in the community. Similarly, we obtained structures indistinguishable from those produced by stochastic processes for each species pool when all phyllostomids (including sanguinivores and omnivores) were combined into a single assemblage.

DISCUSSION

Although there seems to be little disagreement among ecologists that competition occurs in nature, it is not obvious that competition can produce morphological patterns at the community level (Moulton and Pimm, 1986a). Schoener (1983) summarized the efforts of many authors who have detected evidence for competition among species, and emphasized that these results cannot be extrapolated uncritically to the level of communities. Nonetheless, particular predictions concerning community structure can be made if competition (by size assortment) has played a pivotal role in determining community composition. If these predictions are not realized, then the primacy of competition in structuring communities is diminished severely. We must caution, however, that in our analyses we did not evaluate the possibility that size adjustment by character displacement could result in competitively structured communities.

Species presence or absence in a community, although primarily a product of biogeographic or ecological processes, may be reflected in the morphologies of the constituent species of the community (Lack, 1947). In competitively structured (size assorted) communities, species should be more different morphologically than expected by chance, resulting in overdispersion in morphological space, and species should be more evenly distributed in morphological space (Ricklefs and Travis, 1980). In either situation, the importance of competition is assessed by comparing real community statistics to a distribution of those from a number of randomly generated communities, each with the same number of species as the real community. These communities are formed by randomly drawing species from some larger set of species called the species pool. Because the content of the species pool ultimately determines if a community has nonrandom structure (Colwell and Winkler, 1984; Moulton and Pimm, 1986a), it is not surprising that much controversy surrounds decisions regarding which species should be included in the species pool (Diamond and Case, 1986; Strong et al., 1984). Moulton and Pimm (1986a, 1986b, 1987) circumvented such problems by examining the success or failure of birds introduced to the Hawaiian Islands. They have shown clearly that within forests, morphological structure was significantly nonrandom. Conversely, our results clearly demonstrate that the morphological structure of guilds or "communities" of phyllostomids from northeastern Brazil does not differ from chance expectation. It is important to reiterate that the species composition of Caatinga and edaphic Cerrado bat guilds or "communities" is based upon intensively censused local areas, so it is unlikely that any species were omitted from real communities. Moreover, equivalent results were obtained using each of the five different nested species pools defined by the geometric sequence of circle diameters. Hence, it is unlikely that our results are an artifact of examining incompletely censused assemblages rather than guilds, or of including or excluding appropriate taxa from species pools.

The results of Case et al. (1983) and Moulton and Pimm (1987), although demonstrating nonrandom morphological patterns, must be interpreted within the context of island systems. On islands, colonization events likely are infrequent and propagules frequently are small. Local extinctions or failed invasions resulting from competitive effects would be expected to have lasting effects. When considering continental systems, local extinctions that result from competitive interactions might be inapparent because immigration of conspecifics from surrounding areas provides new colonists on a continual basis (the rescue effect—Brown and Kodric-Brown, 1977). More specifically, biogeographic and ecological factors other than competition may interact to produce nonsignificance in our results. The numerous granitic mountains (Serrotes) that punctuate the otherwise flat landscape of the Caatinga act as mesic refugia during stressful periods of drought in ecological time and may have been microrefugia for bats during more xeric periods of evolutionary time (de Andrade-Lima, 1957; de Andrade and Caldas Lins, 1964; Mares et al., 1985; Willig, 1986). Hence, even if competition were to cause local extinctions, these effects could be countermanded by immigration from nearby refugia within or adjacent to the Caatinga. Morphologically mediated biotic interactions other than competition could affect community membership as well. Brown and Bowers (1985) interpreted morphological underdispersion within hummingbird (Trochilidae) guilds as a product of coevolutionary processes.

Although our analyses were designed specifically to evaluate competition-based processes (one-tailed tests), the data can shed light on coevolutionary hypotheses as they apply to bat communities in northeast Brazil. If coevolution between consumers and their food sources is the predominant and pervasive force structuring communities, then species within a guild might be expected to be underdispersed, with smaller mean segment lengths of minimum-spanning trees than those obtained by chance alone. Neither nectarivore nor foliage-gleaning-insectivore guilds from Caatinga or Cerrado communities exhibited significant deviations from random structure in the direction suggested by the coevolutionary hypotheses (the additive inverse of the P values from the competition hypothesis provide an estimate of the probability of chance affecting structure in the direction of underdispersion). Analyses for frugivores approach significance for some intermediate-size species pools (using one-tailed tests), but only attain significance at the 5% level for the Cerrado frugivores when compared to the third largest pool (2,000 km in diameter). Hence, even if our initial hypothesis were based upon coevolutionary processes determining morphological structure within communities, we would have arrived at the conclusion that random selection of species from a species pool frequently gives rise to patterns at least as structured as that obtained in northeast Brazilian communities by chance alone. The characteristic spatial and temporal heterogeneity of the Caatinga, combined with the mobile nature of bats, could decrease the intensity, pervasiveness, or predominance of deterministic interactions in bat communities in northeastern Brazil, thereby leading to a morphological structure indistinguishable from that produced by stochastic processes.

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