

DIETARY OVERLAP IN FRUGIVOROUS AND INSECTIVOROUS BATS FROM EDAPHIC CERRADO HABITATS OF BRAZIL

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Previous studies on size patterns within frugivorous and insectivorous bat guilds from northeastern Brazil suggest significant ecological separation of species. Nonetheless, recent simulation studies indicate that stochastic processes alone, rather than competition or coevolution, account for the morphological structure of these communities. To evaluate the dietary consequences of observed morphological structure, monthly samples of bats were collected (September 1976–May 1978) within edaphic Cerrado habitats on the Chapada do Araripe in northeastern Brazil. For each of the 11 most common species, stomach contents were identified, and the diets characterized for wet and dry seasons. Nonparametric statistical analyses of dietary constituents revealed two non-overlapping groups of frugivores based upon a posteriori contrasts: those that specialize on one food source, *Vismia* sp. (*Carollia perspicillata*, *Artibeus planirostris*, *A. lituratus*), and those that are more generalistic in their feeding habits (*Glossophaga soricina*, *Sturnira lilium*, *Vampyrops lineatus*). Statistical analyses of insectivorous species produced a homogeneous group (*Anoura geoffroyi*, *Phyllostomus discolor*, *P. hastatus*, *Molossus molossus*) based on classification of diet into hard-bodied versus soft-bodied insects. Like the ecomorphological assessments of community structure, our results failed to detect pervasive dietary differences among species that are related to size considerations.

Key words: dietary overlap, bats, Brazil, frugivory, insectivory

Although it has long been recognized that high mammalian diversity in Neotropical areas primarily is attributable to the Chiroptera (Willig and Sandlin, 1991; Willig and Selcer, 1989; Wilson, 1974; contrasted with Pagel et al., 1991), less is understood about the ecological mechanisms that facilitate local coexistence in bat communities (Fleming, 1973; Willig, 1986). Initial attempts to understand “rules” governing bat community assemblage focused on either ecomorphological approaches (Fenton, 1972; Findley, 1976) or simplified schemes in which feeding guild affiliation and size provided preliminary insights into mechanisms of coexistence (Fleming et al., 1972; McNab, 1971). Perhaps the greatest impediment to progress in further understanding the community ecology of bats is a product

of our incomplete or cursory knowledge of the autecology of component species. Data on diet selection (Gardner, 1977), roosting preferences (Kunz, 1982), and foraging strategies (Fleming, 1982) rarely are obtained for even the common species within a community during a complete annual cycle. Of course, important exceptions exist for communities in Panama and Costa Rica (Bonaccorso, 1979; Fleming, 1988, 1991; Fleming et al., 1972; Heithaus et al., 1975), or particular species in South America (Marinho-Filho, 1991). However, these studies alone do not provide a sufficient basis for reasonable extrapolation of species’ ecological attributes to other communities, much less assess the patterns or processes that characterize interspecific interactions within bat communities in general.

Many studies in community ecology consider the structure of present day communities to be the result of deterministic processes, especially competition (Connell, 1983; Miller, 1967; Schoener, 1983). Extensive sampling of two bat communities in northeastern Brazil (edaphic Cerrado and Caatinga) indicated the potential of morphological differentiation among species producing ecologically diversified niches (Willig, 1986). Although guild-size niche matrices, based upon Hutchinson's ratio (see Fleming et al., 1972; Roth, 1981), failed to corroborate the role of size in structuring communities, correlation analysis suggested that species packing may be based upon larger species requiring more ecological space than their smaller counterparts. Based upon simulation studies, Willig and Moulton (1989) more recently concluded that the ecomorphological pattern observed in these same two communities was not different from that generated by a stochastic model. The observed ecomorphological structure was attributed to an interaction of the heterogeneity of habitats within biomes, the unpredictable nature of climatic fluctuations, and the dispersal ability of bats. In concert, these did not allow deterministic processes (e.g., competition or coevolution) to be sufficiently intensive or extensive to influence the assembly of species in these communities.

Regardless of the factors producing observed morphological patterns, it is of interest to examine their ecological consequences in terms of diet composition and overlap. For the most part, knowledge of the food habits of bats is cursory (Arata et al., 1967; Gardner, 1977), especially in Neotropical ecosystems. Data rarely are obtained in a systematic fashion to characterize the diet of a particular population on an annual basis. Nonetheless, intraspecific as well as interspecific comparisons of the diets of sympatric populations are critical for understanding the ecology of bats at the population and community level (Fleming et al., 1972). A growing consensus (Willig,

1986) is that guild classification for bats represents potential foraging behavior, rather than limitations on diet composition (e.g., glossophagines exhibit a variety of adaptations for nectarivory, but are not restricted to consume only pollen and nectar, and may be frugivorous or insectivorous depending upon season and habitat). Arata et al. (1967) reported on the diet of 13 species of bats from Colombia in which stomach contents were classified into broad categories (e.g., plants, insects). Bats previously believed to be obligate frugivores, like *Carollia*, were documented to consume insects as well. Szazima (1976) later reported on the diets of phyllostomids in southeastern Brazil; he suggested that most members of the family are nectarivorous to some extent. More detailed or comprehensive works on the diets of Neotropical bats are those of Fleming et al. (1972), Gardner (1977), and Heithaus et al. (1975); brief notes on diets of selected bats from northeastern Brazil are provided by Willig (1983). The purpose of our work was twofold: to define and compare the diets of bat populations during wet and dry seasons in edaphic Cerrado habitats of Brazil, and to evaluate the dietary consequences of size variation within frugivorous and insectivorous bat guilds.

MATERIALS AND METHODS

Study site.—The Caatinga of northeastern Brazil is a large (650,000 km²) semi-arid area characterized by climatic uncertainty and topographic heterogeneity (Mares et al., 1985; Willig, 1983). Thorn-scrub vegetation dominates in extensive low-lying areas. 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, that of the Cerrado biome of central Brazil. Edaphic Cerrado is a fairly homogeneous open woodland with a pervasive grass component. Small trees (3–5 m tall) and shrubs (0.5–3 m tall) compose one-half of the ground cover, with various grass species occupying the remaining area. The canopy is open, irregular, and undulatory in profile. Taller trees and shrubs have gnarled trunks and twisted branches; root

penetration into the sandstone bedrock is minimal, and as a result, treefalls are frequent.

Sampling regime.—Bats were collected monthly by netting (September 1976–May 1978) within a 315-km² area of edaphic Cerrado vegetation on the Chapada do Araripe in the Floresta Nacional Araripe-Apodí (07°14'S, 39°23'W) near Crato, Ceará, Brazil. Digestive tracts were removed, fixed in formaldehyde, and preserved in 70% ethanol. Dietary constituents later were examined using a dissecting microscope (Whitaker, 1988). Fruits were identified based upon comparison with a monthly reference collection from the same study site. In the absence of a local collection of arthropods, insects and arachnids were identified solely based upon key morphological characteristics. This, in combination with the highly efficient masticatory abilities of bats, restricted most prey identifications of arthropods to the ordinal or familial level. Similarly, estimates of prey numbers or volume would be misleading. Consequently, we only evaluated the presence or absence of prey items in the digestive tract of each individual bat and report the prevalence of each food type for a species as the percent of individuals (not including those with empty digestive tracts) whose diet included that food type. Assessment of nectarivory was not undertaken herein for methodological reasons. Although the digestive tracts of individual bats were stored in separate cheese-cloth sacks, all sacks were jointly stored in large plastic containers. Thus, pollen associated with a particular digestive tract could have originated from many different specimens or species. This limitation may be important when evaluating the dietary ecology of glossophagines, but is likely of less consequence for most other bat taxa.

Intraspecific comparisons.—For each bat species, data (number of specimens containing a particular prey taxon) were combined for both sexes from mid-May to mid-November to represent the dry-season diet, and from mid-November to mid-May to represent the wet-season diet. The high frequency of empty digestive tracts precluded analyses of diets on a monthly basis and prevented intersexual comparisons as well. Seasonal differences in diet composition (i.e., the proportional representation of prey taxa) were evaluated by separate *G*-tests (Sokal and Rohlf, 1981) for each bat species, with prey taxa pooled if required to meet the assumptions of the underlying statistical model.

Interspecific comparisons.—Dietary items were classified into five categories (*Vismia* sp., *Solanum* sp., other fruit material, soft-bodied insects, and hard-bodied insects) for each bat species to satisfy the requirements of *G*-test procedures as suggested by Sokal and Rohlf (1981). Combining data for males and females within each season because of small samples will result in conservative statistical tests of seasonal differences in diet if sex-based differences in diet composition characterize one or both seasons. Interspecific comparisons of the diet of predominantly frugivorous species (*Artibeus planirostris*, *A. lituratus*, *Vampyrops lineatus*, *Sturnira lilium*, *Carollia perspicillata*, *Glossophaga soricina*) were conducted separately from comparisons among predominantly insectivorous or omnivorous species (*Phyllostomus discolor*, *P. hastatus*, *Anoura geoffroyi*, *Molossus molossus*). In each case, *G*-tests followed by a posteriori comparisons (Sokal and Rohlf, 1981) were used to identify groups of bat taxa with statistically indistinguishable diets within each guild.

RESULTS AND DISCUSSION

The edaphic Cerrado bat community comprised 25 species (for a complete systematic listing, see Willig and Mares, 1989). Of these, 14 were rare or represented by specimens with empty digestive tracts. As a result, dietary analyses could not be performed on *Saccopteryx leptura*, *Noctilio leporinus*, *Pteronotus davyi*, *Micronycteris megalotis*, *M. minuta*, *Uroderma magnirostrum*, *Desmodus rotundus*, *Natalus stramineus*, *Myotis nigricans*, *Eptesicus furi-nalis*, *Lasiurus borealis*, *L. ega*, *Molossops temminckii*, and *Tadarida laticaudata*. Only two of the 12 examined specimens of *Koopmania concolor* (Owen, 1991, recently established the generic name *Koopmania* for *Artibeus concolor*) contained identifiable fruit pulp. No other published dietary record of *K. concolor* exists. Subsequent considerations are limited to the other 10 species (Table 1). A detailed systematic listing of arthropod prey (Table 2) revealed a considerable dietary diversity including >50 families in 11 orders of insects and two orders of arachnids. In contrast, fruits from

TABLE 1.—Abundance, size (mean length of forearm in mm), and dietary classification of 11 edaphic Cerrado bat species from the Floresta Nacional Araripe-Apodí, Crato, Ceará, Brazil (from Willig, 1983). Bat species that share the same superscript have statistically indistinguishable diets (numbers, frugivores; letters, insectivores).

Taxon	Abundance	Size	Guild
<i>Koopmania concolor</i>	common-rare	47.2	frugivore
<i>Artibeus planirostris</i> ^{1,2}	abundant	52.3	frugivore
<i>Artibeus lituratus</i> ²	abundant	70.4	frugivore
<i>Vampyrops lineatus</i> ⁴	abundant	46.6	frugivore
<i>Sturnira lilium</i> ^{3,4}	common-rare	42.1	frugivore
<i>Carollia perspicillata</i> ¹	abundant	42.5	frugivore
<i>Glossophaga soricina</i> ³	abundant	35.4	frugivore
<i>Anoura geoffroyi</i> ^a	common	42.9	insectivore
<i>Phyllostomus discolor</i> ^a	abundant	60.0	insectivore
<i>Phyllostomus hastatus</i> ^a	abundant	82.9	insectivore
<i>Molossus molossus</i> ^a	abundant	40.4	insectivore

two plant species dominated the diet of frugivores.

Frugivores.—Fruits of *Vismia* constituted an appreciable portion of all but one frugivore's (*V. lineatus*) diet. Insect consumption was variable: absent in *A. lituratus*, *S. lilium*, and *V. lineatus*; minimal for *C. perspicillata* and *A. planirostris*; and appreciable for *G. soricina*. Details of diet content and seasonal comparisons follow for each common frugivore.

Many specimens originally referred to as *A. jamaicensis* from northeastern South America (like those from northeastern Brazil; see Willig and Mares, 1989) are now recognized as representing *A. planirostris*, so in many cases some confusion persists concerning the biology of these congeners. Reported dietary constituents (Gardner, 1977) for that geographic subset of bats likely to represent *A. planirostris* included fruits from *Achras sapota*, *Psidium guajava*, and *Ficus* sp. Of the 156 examined specimens of *A. planirostris*, 72 contained identifiable food items. Although the diet is predominantly fruit ($\geq 90\%$ prevalence; Fig. 1), five individuals consumed mites (Acari), worker ants (Formicidae), or beetles (Coleoptera). The mites and the ants could have occurred on fruits and been ingested accidentally. Such exclusive reliance upon fruit is distinct from the situation in Panama and Costa

Rica (Fleming et al., 1972), where 25% of the diet of *A. jamaicensis*, a morphologically similar species, was insects. No significant dietary differences existed between wet and dry season ($G = 5.5$, $d.f. = 2$, $0.1 > P > 0.05$); *Vismia* consistently constituted the bulk (80% prevalence) of the diet.

Heithaus et al. (1975) considered *A. lituratus* to be mostly nectarivorous in Panama, with fruit and insects as secondary dietary constituents. Similarly, in the dry forests of Costa Rica and Panama, the diet of *A. lituratus* was mostly nectar, with insects of secondary importance (Fleming et al., 1972). Of the 280 examined specimens of *A. lituratus*, 151 contained identifiable food items. The diet was exclusively fruit (Fig. 1) and dominated by *Vismia* (85% prevalence), with *Solanum* (7% prevalence) as the second most-important food item. No significant dietary differences existed between wet and dry seasons ($G = 0.2$, $d.f. = 1$, $0.9 > P > 0.5$).

Only 30 of the 151 digestive tracts from *V. lineatus* contained identifiable food items. The diet was exclusively frugivorous (Fig. 1), with *Solanum* (54% prevalence) and unidentified fruit pulp (40% prevalence) composing the bulk of the diet. No significant differences in diet were detected between wet and dry seasons ($G = 0.7$, $d.f. = 1$, $0.5 > P > 0.1$). In other areas, *V. lineatus* has

TABLE 2.—*Arthropod prey consumed by edaphic Cerrado bats from the Floresta Nacional Araripe-Apodí, Crato, Ceará, Brazil (September 1976–May 1978). Numbers in the body of the table represent the number of digestive tracts within which a prey item occurred.*

Prey taxon	<i>Artibeus planirostris</i>	<i>Anoura geoffroyi</i>	<i>Phyllostomus discolor</i>	<i>Phyllostomus hastatus</i>	<i>Molossus molossus</i>
Collembola			1		
Orthoptera				1	
Blattodea				11	
Isoptera			3	4	1
Homoptera					
Delphacidae			1		
Cicadellidae					1
Hemiptera					
Lygaeidae				1	
Miridae				1	
Coreidae				1	
Unknown				3	
Neuroptera			1		
Coleoptera					
Carabidae		1	2	9	2
Cicindelidae				1	
Rhipiceridae				1	
Scarabaeidae		8	5	15	3
Lucaenidae				3	
Histeridae		1		3	
Dermestidae				1	
Silphidae				1	
Chrysomelidae			1	3	3
Tenebrionidae				4	2
Buprestidae			1		3
Cantharidae				1	
Meloidae		1		1	
Oedemeridae			1		
Staphylinidae				4	
Cerambycidae			2	1	1
Cleridae		1		1	
Elateridae				2	
Nitidulidae				1	
Scolytidae				1	
Curculionidae				1	
Unknown	1	6	20	24	2
Lepidoptera					
Microlepidoptera			1	2	
Noctuidae					3
Sphingidae					1
Unknown				2	1
Diptera	1			2	
Hymenoptera					
Formicidae	2	3	4	18	7
Unknown	1	1	1	4	
Insecta (unknown)	1	1		2	2
Arachnida					
Araneae		1			
Acarina	2				

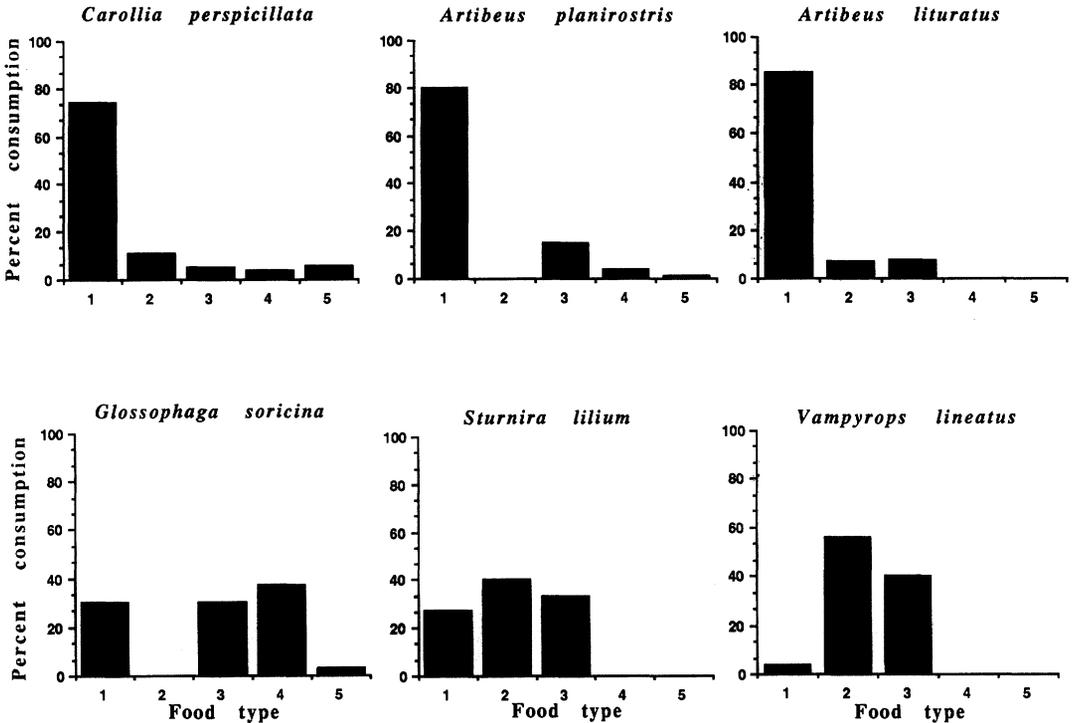


FIG. 1.—Diets of frugivorous bats from edaphic Cerrado habitats of Brazil after pooling prey items into five general categories (1 = *Vismia*; 2 = *Solanum*; 3 = other fruits or pulp; 4 = soft-bodied arthropods; 5 = hard-bodied arthropods). Species with identical numeric superscripts have statistically indistinguishable diets based upon a posteriori *G*-tests (Sokal and Rohlf, 1981). The ordinate indicates the frequency of all non-empty digestive tracts that contained a particular food type.

been reported to consume fruits and insects (Gardner, 1977); moreover, Sazima (1976) observed individuals that consumed nectar from flowers of *Musa* and *Lafeonsia*.

The diet of *S. lilium* was exclusively frugivorous, with *Solanum* (40% prevalence) and *Vismia* (27% prevalence) comprising the bulk of the diet (Fig. 1). Statistical tests comparing diets in wet and dry seasons were not performed because only 15 of the 20 specimens examined in this study contained identifiable food items.

Throughout its range, *S. lilium* has been reported to be exclusively a frugivore, including a wide range of fruit types in its diet as well as pollen (Gardner, 1977). Among the fruits reported to be consumed are *Musa*, *Ficus*, *Piper*, *Cecropia*, and *Solanum* (Gardner, 1977; Heithaus et al., 1975). Recently, Marinho-Filho (1991) reported that the diet

of *Sturnira* in southeastern Brazil was dominated by fruits of *Solanum*.

The biology and ecology of *C. perspicillata* are known better than those of other Neotropical bats (Fleming, 1988). It is a frugivore, with a wide range of species in its diet. Dietary components differ from locality to locality, but some of the most-common forage taxa are *Piper*, *Solanum*, *Cecropia*, *Ficus*, *Muntingia*, *Vismia*, and *Chlorophora*. Insects were infrequent in the diet, with an occurrence of ca. 2%. Sazima (1976) observed *Carollia* consuming nectar from passion fruit (*Passiflora*) and banana (*Musa*). Fleming (1988) considered the diet of *Carollia* to be broader in the dry than in the wet season, although no statistically significant dietary differences were found in the proportional representation of prey species between the seasons. More recently,

Fleming (1991) examined the relation among body size, diet, and habitat use in all species of *Carollia* from Costa Rica. He found that reliance on *Piper*, and consumption of large fruits, are related to bat size in a fashion consistent with physiological constraints. Of the 283 examined digestive tracts of *C. perspicillata*, 242 contained identifiable food items. Fruits constitute the bulk of the diet (89% prevalence), with *Vismia* (74% prevalence) and *Solanum* (11% prevalence) as the most-important food items (Fig. 1). Nonetheless, a variety of arthropods was consumed and included beetles (6% prevalence) as well as alates of ants and termites (4% prevalence). Statistically significant differences between wet and dry seasons ($G = 8.3$, $d.f. = 3$, $0.05 > P > 0.03$) existed, primarily because of increased utilization of *Solanum* during the wet season.

Of the 146 digestive tracts examined from *G. soricina*, 68 contained identifiable food items. Most individuals (60%) consumed fruits, although many individuals (40%) consumed insects (Fig. 1). The most-important fruit was *Vismia* (29% prevalence), with the remainder (28% prevalence) consisting of unidentified fruit pulp. Ants (16%) and termites (13%) were the dominant insect taxa in the diet based upon prevalence (Table 2). Statistically significant dietary differences between wet and dry seasons ($G = 16.8$, $d.f. = 3$, $P < 0.001$) were affected by increased consumption of *Vismia* and decreased consumption of all insects in the dry season. As in other nectarivores, this shift to insect consumption may represent a response to physiological requirements associated with reproductive activity or a change in resource availability. Similarly, data compiled by Gardner (1977) suggests that this bat is a frugivore with significant insectivorous tendencies (i.e., they are not just opportunistic or infrequent consumers of insects). Research in Central America by Fleming et al. (1972) and Heithaus et al. (1975) produced similar results, in that *G. soricina* consumed a wide array of prey

types, ranging from pollen and nectar to insects.

Insectivores.—Considerable intraspecific and interspecific variation in diet characterized insectivorous bat species (Table 2). Indeed, this variability required the allocation of arthropod taxa into the hard-bodied and soft-bodied dichotomy for intraspecific evaluation of seasonality or determination of interspecific differences in diets. Hence, the failure to detect differences does not necessarily imply similar diets with respect to prey taxa; rather, it suggests that the proportional consumption of hard- and soft-bodied prey are indistinguishable.

Throughout its range, *A. geoffroyi* is considered an insectivore and a facultative nectarivore (Gardner, 1977). Similarly, Sazima (1976) observed *A. geoffroyi* visiting *Bauhinia* flowers with subsequent stomach analysis revealing insect remains as well. Only 23 of the 44 examined digestive tracts of *A. geoffroyi* contained identifiable food items; all were arthropods (Fig. 2) representing at least three orders and seven families. Scarabaeid beetles (36% prevalence) and other coleopterans (45% prevalence) in four other families (Histeridae, Meloidae, Cleridae, Carabidae) composed the largest part of the diet. Soft-bodied insect prey were mostly alates of ants and termites. Statistically significant dietary differences between wet and dry seasons ($G = 6.7$, $d.f. = 2$, $0.05 > P > 0.02$) primarily were caused by increased reliance on scarabaeid beetles in the dry season.

The diet of *P. discolor* from Costa Rican dry forest consisted of nectar (Heithaus et al., 1975), whereas in Costa Rican and Panamanian lowland wet forest, it was almost exclusively insectivorous (Fleming et al., 1972). Gardner (1977) cited that this bat also consumed fruits of *Piper*, *Musa*, and *Acnistus*. Of the 47 digestive tracts of *P. discolor*, 43 contained food items; the diet included exclusively insect prey (Fig. 2). Unfortunately, the majority of bat specimens (78%) were males from the wet season;

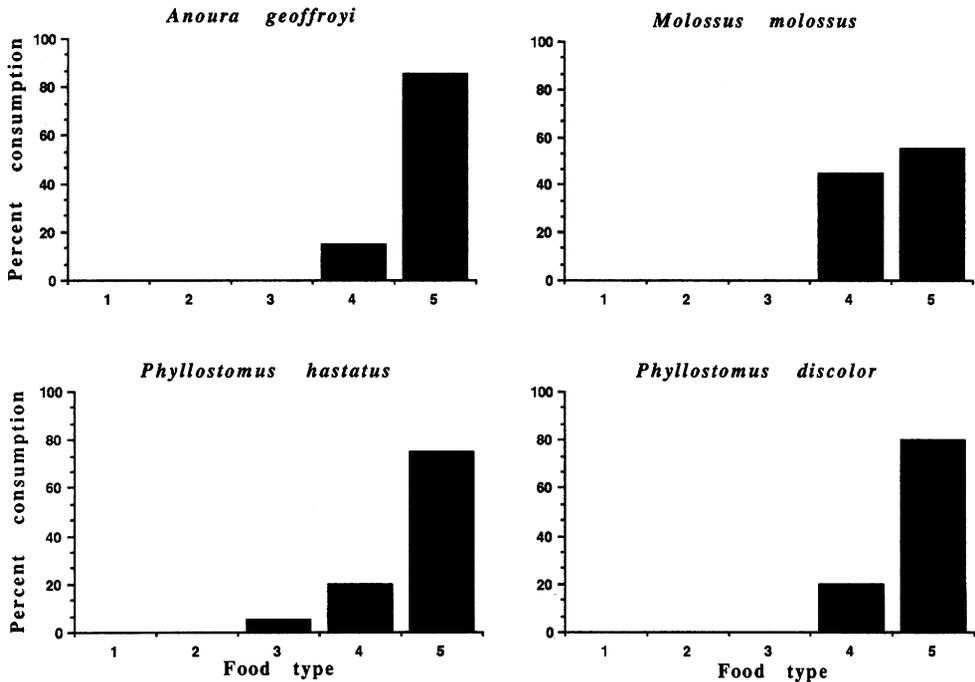


FIG. 2.—Diets of insectivorous bats from edaphic Cerrado habitats of Brazil after pooling prey items into five general categories (1 = *Vismia*; 2 = *Solanum*; 3 = other fruits or pulp; 4 = soft-bodied arthropods; 5 = hard-bodied arthropods). Species with identical numeric superscripts have statistically indistinguishable diets based upon a posteriori *G*-tests (Sokal and Rohlf, 1981). The ordinate indicates the frequency of all non-empty digestive tracts which contained a particular food type.

as a result, questions addressing dietary differences between sexes or seasons cannot be answered with the available data. In general, the diet was diverse, comprising at least seven orders and 12 families. Based upon prevalence, coleopterans clearly constituted the dominant dietary item (70%) with ants (9%) and termites (7%) of secondary importance. In addition, many individuals were foraging at flowering pequi trees (*Caryocar brasiliensis*), and contained appreciable pollen loads on their muzzles at the time of capture. No other bat species appeared to forage on this plant at any time.

Phyllostomus hastatus is classified as an omnivore (Gardner, 1977), consuming a wide variety of prey, from insects and small vertebrates, to nectar and flowers. Stomach content analysis of Costa Rican and Panamanian specimens (Fleming et al., 1972) showed that 96% of the diet (by volume)

was insects. Of the 189 digestive tracts from *P. hastatus*, 131 contained identifiable food items. The diet included at least eight orders and 28 families of insects, consequently this bat had the most diverse diet of any species from the edaphic Cerrado. Over 95% of all digestive tracts contained insects (Fig. 2); based upon prevalence, coleopterans were dominant (60%) [especially scarab beetles, 11%; wood and bark borers (Cerambycidae, Lucaenidae, Tenebrionidae, Dermestidae, Scolytidae, Elateridae, 10%); ground and carabid beetles, 7%], followed by ants (15%) and roaches (9%). Unidentified fruit pulp composed ca. 4% of the diet. No statistically significant dietary differences between wet and dry seasons were detected ($G = 4.5$, $d.f. = 11$, $0.95 > P > 0.90$).

Molossus molossus is the only non-*Phyllostomus* bat in our study. Freeman (1979) suggested that molossids, which primarily

consume hard-bodied insects, can be distinguished from bats that eat soft-bodied insects based on jaw and dental morphology. These structures are adapted to puncture and fragment the hard exoskeleton of most beetles. Our findings support these predictions. Insects were the exclusive prey in all 31 of the 80 examined digestive tracts from *M. molossus* that contained food (Fig. 2). At least five orders and 12 families were represented in the diet. Although ants (21%) and moths (15%) were important prey, beetles (59%) dominated the diet based upon prevalence. Statistically significant dietary differences between wet and dry seasons ($G = 8.3$, $d.f. = 3$, $0.05 > P > 0.02$) were attributable to an appreciable shift toward ants and moths (64% of specimens) in the wet season versus beetles (100% of specimens) in the dry season.

Community implications.—Differences in body size have been considered to be the product of evolutionary adjustments to facilitate coexistence of species by minimizing the extent of niche overlap (Brown, 1981; Hutchinson, 1959; Lack, 1971; Schoener, 1984). Nonetheless, it remains unclear how often morphological differences correlate with ecological niche differentiation, whether any limiting similarity in morphology applies across either distantly or closely related taxa, or what limiting resources are most closely associated with morphology. In vertebrates in general (Demment and von Soest, 1985; Gaulin, 1979; Jarman, 1974), and in bats in particular (Fleming, 1991), it has been suggested that body size affects diet and habitat selection through physiological constraints. Size-based differences in diet may be directly influenced by physical limitations related to transporting and processing prey, or indirectly affected by the higher energy and protein demands of smaller species. In either case, larger species should have different diets than those of smaller species. Fleming's (1991) work in Costa Rica demonstrated that *Carollia* adheres to some size-based tenets concerning foraging (habitat use and diet selection), but

that a significant relation between dietary overlap and size differences did not obtain.

Frugivores.—The size and taxonomic differences among the bats considered herein exceed those of Fleming's study (at most three congeners in one area); as a result, greater dietary differences might be expected in the edaphic Cerrado, especially between more distantly related species or between species with greater size differences. Patterns of dietary differentiation among edaphic Cerrado frugivores are complex and involve variation in the proportion of food types as well as the presence or absence of particular taxa in the diet. The ecological distinction between the two significantly different groups of frugivores (Fig. 1) centers upon the degree to which diets are stenophagic. *C. perspicillata*, *A. planirostris*, and *A. lituratus* differ from the other frugivores by specializing on *Vismia* ($\geq 70\%$ of the diet); differences within the group are derived from the degree to which arthropods do (*C. perspicillata*) or do not (*A. lituratus*) supplement the diet. *G. soricina*, *S. lilium*, and *V. lineatus* are less stenophagic and consume less *Vismia* ($\leq 30\%$ prevalence in the diet) than the other frugivores (Fig. 1). Differences within this group are affected by the seasonal reliance of *G. soricina* on arthropod prey and the minimal consumption of *Vismia* by *V. lineatus*. Moreover, the dietary distinctiveness of *G. soricina* likely was underestimated by failing to evaluate nectarivory.

Size differences among consumers do not appear to play a consistent role in producing dietary differences in frugivores. The size differences between congeneric and adjacent-sized competitors (*A. lituratus*, *A. planirostris*) in this study (large-to-small ratio = 1.35) exceeds that of the most divergent pair of sympatric *Carollia* studied by Fleming (1991). His prediction that the smaller species would include more energy- or protein-rich food types in the diet does not obtain for *Artibeus* from the edaphic Cerrado, as the diets of *A. jamaicensis* and *A. lituratus* are statistically indistinguish-

able. In contrast, *S. liliium* and *C. perspicillata* are similar in size (large-to-small ratio = 1.01), but have statistically different diets. Similarly, *C. perspicillata* and *V. lineatus* are adjacent-sized competitors with statistically indistinguishable mean sizes (based upon length of forearm) and with overlap between ranges of individual size (Willig, 1986); nevertheless, they have statistically distinct diets. Morphological distinction between pairs of frugivores does not necessarily give rise to dietary differences.

Although the size of fruits of *Solanum* is somewhat greater than those of *Vismia* (difference $<0.7\text{cm}^3$), the data do not suggest that larger bats eat a larger proportion of the larger fruit. The only recognizable pattern obtained from examination of dietary patterns based upon size is that no frugivorous species exhibits a diet that is indistinguishable from both its larger and smaller adjacent-sized competitors. Examination of dietary comparisons in frugivorous bats from other communities will provide a means of evaluating the generality of this pattern.

Insectivores.—Based upon the consumption of hard-bodied versus soft-bodied arthropods, the statistical analysis of insectivores produced a homogeneous group that comprises *A. geoffroyi*, *P. discolor*, *P. hastatus*, and *M. molossus*. Unfortunately, the statistical analysis failed to distinguish between small soft-bodied alates of ants and termites from larger hard-bodied beetles. The former requires an aerial foraging strategy, whereas the latter involves a gleaning strategy. Moreover, the observed nectarivory in *P. discolor* and the potential nectarivory in *A. geoffroyi* may ecologically segregate these taxa from the other insectivores.

Detection of dietary differences among these bats also may be predicated on finer resolution of the taxonomic identity of their prey (Table 2). Even with a resolution of arthropod prey limited to the familial level, *P. hastatus* has a much more diverse diet (29 insect families from 131 samples) than its smaller congener *P. discolor* (12 arthro-

pod families from 23 samples) or any other insectivorous bat from the edaphic Cerrado. However, caution must be used in interpreting this trend as it may reflect effective sample sizes. For any species, the smaller the number of digestive tracts with contents, the smaller the number of prey taxa in the diet; rare or occasional forage items likely would be undetected in the diet by chance alone, resulting in reduced diversity. Finally, morphological and behavioral considerations suggest that *M. molossus* is a fast, high-flying, aerial insectivore, that *P. discolor* and *P. hastatus* are foliage gleaners, and that *A. geoffroyi* is potentially nectarivorous and able to hover. These differences likely lead to significant vertical segregation in the activity of these taxa, which might be reflected in dietary differences if a finer taxonomic resolution of prey was possible. As a consequence of these biological and statistical (low power associated with pooling prey taxa into dichotomous categories) constraints, the absence of significant dietary differences primarily may obtain from the conservative nature of the analyses.

Overview.—The year-round abundance of *Vismia* and *Solanum* may represent a seasonally reliable and sufficient food base that does not constitute a limiting resource for frugivorous bats in this study. Factors other than dietary content, such as foraging mode (solitary compared to group) or roost-site attributes may constitute the resource axes along which community assemblage is ordered in edaphic Cerrado habitats. Alternatively, the absence of pervasive dietary differences may reflect the same phenomena considered by Willig and Moulton (1989) to mitigate or reduce the impact of deterministic processes in structuring communities. This is not to claim that competition, for example, is unimportant; it simply may not affect most species in a guild, may only act occasionally, or may not be intensive enough to cause local extinction (Wiens, 1977). Population density, roost or feeding sites, and behavior may be modified by deterministic factors; however, these effects

may not be translated into community-level patterns of assembly or into size-mediated dietary differences among taxa within feeding guilds.

RESUMEN

Trabajos previos sugieren que existen patrones de tamaños en los gremios de murciélagos insectívoros y frugívoros del noreste de Brasil. Por lo contrario, estudios recientes de simulación indican que procesos estocásticos son responsables de la estructura morfológica observada en estas comunidades, y no procesos determinísticos como competencia o coevolución. Para evaluar las consecuencias dietéticas en las estructuras morfológicas observadas, muestras mensuales de murciélagos fueron colectadas (septiembre 1976–mayo 1978), en los hábitculos del Cerrado edáfico en el noreste de Brasil. Llevamos a cabo análisis de contenidos estomacales en 11 de las especies más comunes para caracterizar las dietas de las temporadas de lluvia y sequía. Dos grupos de frugívoros se detectaron basandonos en pruebas de comparaciones a posteriori: especies que se especializan en el consumo de *Vismia* sp. (*Carollia perspicillata*, *Artibeus planirostris*, *A. lituratus*); y aquellas que son más generalistas en sus hábitos alimentarios (*Glossophaga soricina*, *Sturnira lilium*, *Vampyrops lineatus*). Los análisis estadísticos de las especies insectívoras no detectaron diferencias significativas entre especies, produciendo un solo grupo (*Anoura geoffroyi*, *Phyllostomus discolor*, *P. hastatus*, *Molossus molossus*) cuando las presas son clasificadas como insectos de cuerpos duros versus insectos de cuerpos blandos. Al igual que en los estudios ecomorfológicos de la estructura de comunidades, nuestros resultados fallaron en detectar diferencias alimentarias entre especies las cuales están relacionadas a consideraciones de tamaño.

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