

The structure of Neotropical bat communities: a preliminary analysis

La estructura de comunidades de murciélagos neotropicales:
un análisis preliminar

THEODORE H. FLEMING

Department of Biology, University of Miami, Coral Gables, FL 33124, USA

ABSTRACT

I review the taxonomic composition and ecology of the bat fauna of Venezuela and examine the structure of several mainland and Caribbean island phyllostomid bat communities in an effort to discern general rules in the assembly of Neotropical bat communities. The structure of species-rich phyllostomid communities appears to closely resemble the taxonomic, trophic, and morphological characteristics of the phyllostomid fauna. These communities contain clusters of morphologically similar species that tend to be less common and ecologically more specialized than a handful of abundant and broad-niched core species that are found in almost all faunas. As overall biological diversity decreases along rainfall and elevational gradients, specialist species drop out of communities whereas the generalists persist. Phyllostomid generalists come from each of the major trophic and size adaptive zones into which this family has radiated. Mutualistic interactions with plants appear to have had a more profound influence on community structure in this family than have competitive interactions.

Key words: Neotropical bats, community structure, competition, mutualism, zoogeography.

RESUMEN

En este trabajo reviso la composición taxonómica y la ecología de la fauna de murciélagos de Venezuela y examino la estructura de varias comunidades de murciélagos filostómidos en áreas continentales y de islas caribeñas, con el propósito de discernir reglas generales en el ensamblaje de comunidades neotropicales de murciélagos. La estructura de comunidades de filostómidos con alta riqueza de especies refleja claramente las características taxonómicas, tróficas y morfológicas de la fauna de filostómidos en general. Dichas comunidades contienen especies morfológicamente similares que tienden a ser menos comunes y ecológicamente más especializadas que un pequeño grupo de especies nucleares abundantes y generalistas que se encuentran en casi todas las faunas. En la medida que la diversidad biológica decrece a lo largo de gradientes crecientes de pluviosidad y elevación, las especies especialistas desaparecen de las comunidades, en tanto que las generalistas persisten. Los filostómidos generalistas provienen de cada una de las grandes zonas adaptativas tróficas y de tamaño dentro de las cuales la familia ha radiado. Las interacciones mutualistas con plantas parecen haber tenido una influencia más profunda que aquellas de tipo competitivas en la estructuración comunitaria de esta familia de murciélagos.

Palabras claves: Murciélagos neotropicales, estructura comunitaria, competencia, mutualismo, zoogeografía.

INTRODUCTION

Patterns of species diversity and the factors that influence the structure of communities (i.e., species richness and relative abundance of species) have been of long-standing interest to ecologists (Elton 1927, Hutchinson 1959, Cody & Diamond 1975). Recent studies of vertebrate community structure have focused on determining the degree to which communities differ from random assemblages of sympatric species that do not interact ecologically or evolu-

tionarily (e.g., papers in Strong *et al.* 1984). The role of competition in structuring communities has been a central focus in these studies. Both views (non-random vs. random assemblages; importance vs. unimportance of competition) have their strong advocates (e.g., Wiens 1983, Brown & Bowers 1984, Grant & Schluter 1984, Simberloff 1984). To reconcile different viewpoints, most investigators agree that detailed field observations and, whenever possible, controlled field experiments are needed.

A variety of approaches has been used to study the structure of bat communities. An ecological approach aimed at documenting the relative abundances of species and their food niche relationships has been used by Fleming *et al.* (1972), Black (1974), LaVal & Fitch (1977), and Bonaccorso (1979). A primarily morphological approach has been used by Tamsitt (1967), McNab (1971), Fenton (1972), Findley (1973, 1976), Findley & Black (1983), and Schum (1984). Both approaches have led to the conclusion that many bat communities contain species that are tightly packed in ecological and morphological space. The extent to which competitive interactions influence (or have influenced) interspecific relationships, however, is still unclear.

I have three goals in this paper. First, I will review our current knowledge of the structure of Neotropical bat communities with particular emphasis being placed on the family Phyllostomidae, the New World fruit bat family. Second, I will attempt to identify general trends in the "assembly" of phyllostomid communities that are indicative of general "assembly rules" in Neotropical bat communities. Third, I will compare the results of this study with previous studies of insectivorous bat communities and faunas conducted by Fenton (1972), Findley (1973, 1976), and Schum (1984), and with studies of bird communities and faunas conducted by Karr & James (1975) and Ricklefs & Travis (1980), in an attempt to identify general assembly rules in communities of volant vertebrates. An underlying theme in this analysis will be the degree to which interspecific interactions (e.g., competition and mutualism) influence bat community structure. I want to emphasize the preliminary nature of this inductive exercise. A complete analysis requires a much more extensive set of ecological, behavioral, and morphological data, and a more sophisticated statistical analysis. I strongly suspect, however, that the general patterns that I have found will hold up under more detailed scrutiny. Humphrey & Bonaccorso (1979) discussed this subject from a different viewpoint.

An Overview of the Neotropical Bat Fauna

The Neotropical bat fauna consists of approximately 282 species classified in nine families, six of which are endemic to the

New World (Table 1). Members of eight of the nine families are insectivorous (with the exception of *Noctilio leporinus*, which is primarily a fish-eater). As reviewed by Gardner (1977), members of the Phyllostomidae, in which six subfamilies are currently recognized (Jones & Carter 1976) and whose species make up one-half of the total fauna, consume a diverse array of foods, including insects, vertebrates, nectar and pollen, fruit, and blood.

The bat fauna of Venezuela has been extensively sampled by field crews directed by C. O. Handley, Jr. (see Handley 1976) and can be used to obtain an overview of general trends in the species richness, geographic distributions, and relative abundance of Neotropical bats. I will use the results of this faunal overview to predict the detailed structure of bat communities under the assumption that community structure merely reflects faunal structure (or vice versa). This assumption will serve as a null hypothesis in this study.

Distributions by Life Zones

As shown in Fig. 1, bat species are unevenly distributed among life zones (as designated by Holbridge 1947 in Venezuela). A strong diversity peak occurs in tropical dry and tropical moist life zones, and a secondary peak occurs in subtropical or lower montane moist life zones. The insectivorous families show this basic pattern (Fig. 1) except that species are equally represented in both the tropical dry and tropical moist life zones whereas they are better represented in the subtropical moist than in the subtropical wet life zone. Distributions of modal life zones differ among phyllostomid subfamilies (Fig. 1). Phyllostomines (which are insectivorous-omnivorous) peak strongly in tropical moist life zones; glossophagines (which are nectarivorous) peak in the tropical moist and subtropical moist zones; no strong dominance of one life zone occurs in the frugivorous carollines; and two peaks occur in the frugivorous stenodermines (tropical moist and subtropical wet-lower montane moist zones). These distributional data indicate that faunal and community diversity is highest in lowland moist forests in both insectivorous and plant-visiting bats and that a secondary radiation has occurred in certain groups at mid-elevations.

TABLE 1

Families of Neotropical bats and their general food habits.
 Data taken from Nowak & Paradiso (1983)
 Familias de murciélagos neotropicales y sus hábitos alimenticios generales.
 Datos obtenidos de Nowak & Paradiso (1983)

FAMILY	NUMBER OF SPECIES	GENERAL FOOD HABITS
Emballonuridae	21	Insectivorous
Noctilionidae ^a	2	Insectivorous/piscivorous
Mormoopidae ^a	8	Insectivorous
Phyllostomidae ^a	143	
Phyllostominae (Phyllos.) ^b	34	Many insectivorous, occasionally frugivorous; some carnivorous
Glossophaginae (Glosso.)	34	Nectarivorous, occasionally frugivorous & insectivorous
Carollinae (Caroll.)	7	Frugivorous, occasionally insectivorous & nectarivorous
Stenoderminae (Steno.)	57	Frugivorous, occasionally insectivorous & nectarivorous
Brachyphyllinae (Brachy.)	8	Nectarivorous & frugivorous
Desmodontinae (Desmo.)	3	Sanguinivorous
Natalidae ^a	4	Insectivorous
Furipteridae ^a	3	Insectivorous
Thyropteridae ^a	2	Insectivorous
Vespertilionidae	63	Insectivorous
Molossidae	36	Insectivorous

^a Neotropical endemics.

^b Abbreviations used in figures.

Distributions by Elevation

From the preceding analysis, we expect bat species richness to be inversely related to elevation. Except in two groups (the Vespertilionidae and Stenoderminae), lowland forms greatly outnumber highland forms in Venezuela (Fig. 2). Koopman (1978) and Graham (1983) have documented a similar trend in the Peruvian Andes. With the exception of the Vespertilionidae and a few molossids, insectivores, regardless of their evolutionary history, are more-or-less restricted to the lowlands. The highland vespertilionids are represented by two genera, *Eptesicus* (which is common in north temperate regions) and *Histiotus* (which is widespread in south temperate regions). The phyllostomid subfamilies display a variety of patterns: (1) like other insectivores, the phyllostomines are strongly lowland; (2) the glossophaginae are basically lowland, but two genera (*Anoura* and *Lonchophylla*) contain highland forms; (3) the carollinae have one mid-elevation re-

presentative (*Carollia brevicauda*); and (4) the stenoderminae are well-represented in the highlands with two genera (*Sturnira* and *Vampyrops*) containing several upland species. These results imply that at the community level, species diversity in all trophic groups will decrease with increasing elevation. Some taxonomic turnover will occur with increasing elevation. Lowland taxa will be replaced by highland taxa within insectivores, nectarivores, and stenodermine frugivores.

Because insectivores of different phylogenetic affinities and different thermoregulatory capabilities (McNab 1982) are concordant in their elevational distributions, I hypothesize that this distributional similarity has a trophic rather than a physiological basis. That is, reduced food availability, rather than reduced physiological capacity to tolerate low nocturnal temperatures or cool daytime roosts, has restricted insectivores to the lowlands. McNab (1982) similarly concluded that, except for the vampire *Desmodus rotundus*, food availa-

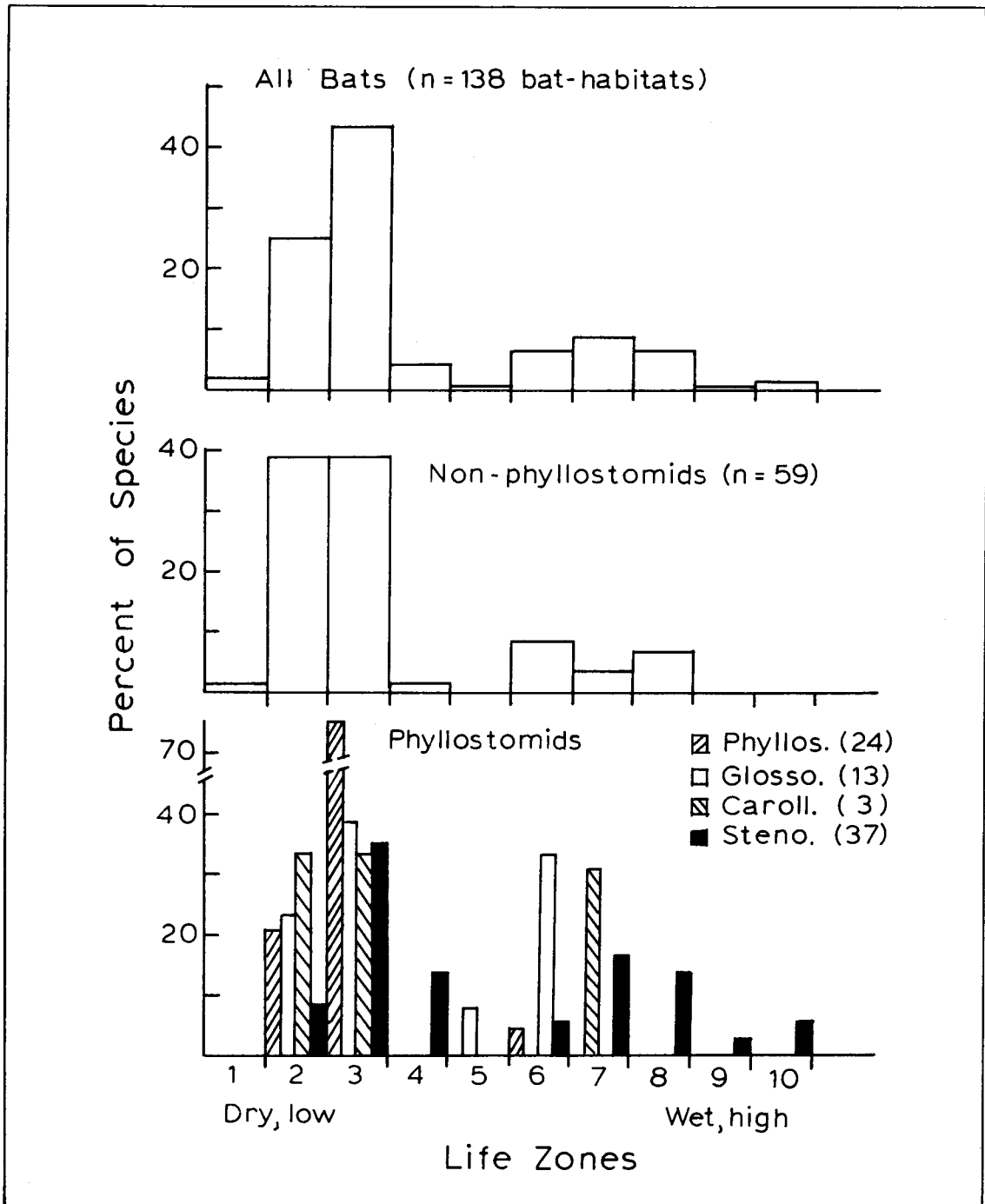


Fig. 1. Distribution of Venezuelan bats by life zone. Data are based on the modal life zone of each species as determined from capture data presented in Handley (1976). Abbreviations of phyllostomid subfamilies as in Table 1. Life zones are as follows: (1) Tropical thorn forest, (2) Tropical dry forest, (3) Tropical moist forest, (4) Tropical wet forest, (5) Subtropical dry forest, (6) Subtropical moist forest, (7) Subtropical wet forest, (8) Lower montane moist forest, (9) Lower montane wet forest, (10) Montane moist forest.

Distribución de los murciélagos venezolanos por zona de vida. Los datos están basados en la zona de vida modal de cada especie, determinada a través de datos de captura documentados por Handley (1976). Las zonas de vida son las siguientes: (1) Bosque espinoso tropical, (2) Bosque seco tropical, (3) Bosque húmedo tropical, (4) Bosque perhúmedo tropical, (5) Bosque seco subtropical, (6) Bosque húmedo subtropical, (7) Bosque perhúmedo subtropical, (8) Bosque húmedo de montaña baja, (9) Bosque perhúmedo de montaña baja, (10) Bosque húmedo de montaña alta.

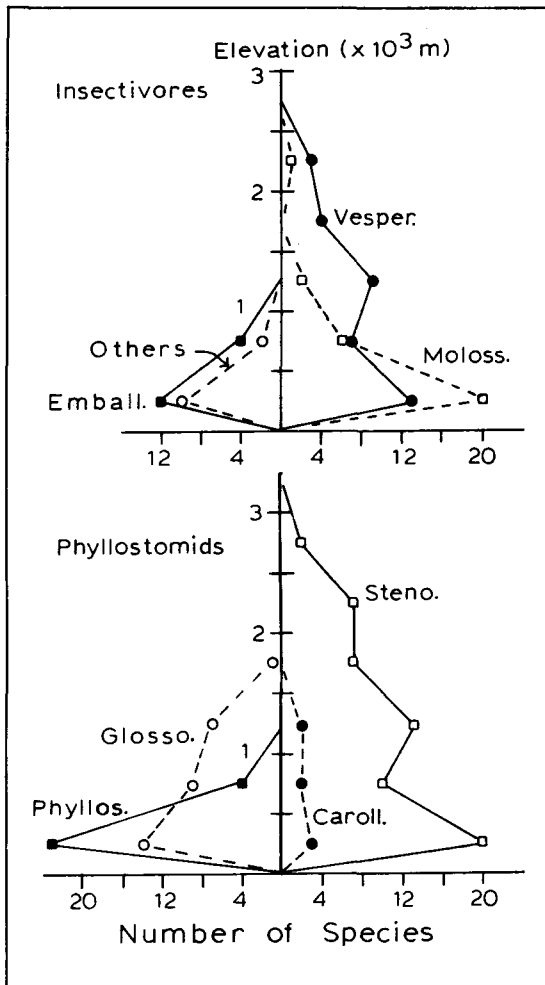


Fig. 2. Elevational distributions of Venezuelan bats. Number of species occurring in 500 m elevation blocks are shown for different families and subfamilies based on data in Handley (1976). Abbreviations for insectivores: Emball. = Emballonuridae, Moloss. = Molossidae, Vesper. = Vespertilionidae.

Distribución de los murciélagos venezolanos por altitud. Se documenta el número de especies de distintas familias y subfamilias que se encuentran en segmentos secuenciales de elevación de 500 m, de acuerdo a datos publicados por Handley (1976). Abreviaturas para murciélagos insectívoros: Emball. = Emballonuridae, Moloss. = Molossidae, Vesper. = Vespertilionidae.

bility rather than physiology limits the latitudinal and altitudinal distributions of Neotropical bats.

One way to test this hypothesis is to compare the elevational distributions of bats with those of trophically similar birds. Parallel elevational trends in both groups would suggest the operation of similar

underlying factors; concordance, however, does not eliminate the possibility that different factors affect the distributions of bats and birds. In Fig. 3 I have plotted the elevational distributions of Panamanian birds, as reported in Ridgely (1976), by trophic group. Trophically analogous chiropteran groups include: canopy frugivores — stenodermines (especially *Artibeus* and *Vampyrops*); understory frugivores — carollines and certain stenodermines (especially *Sturnira*); nectarivores — glossophagines; consumers of large insects — large phyllostomines; understory insectivores — small phyllostomines, certain emballonurids, and other small insectivores; aerial insectivores — certain vespertilionids and molossids.

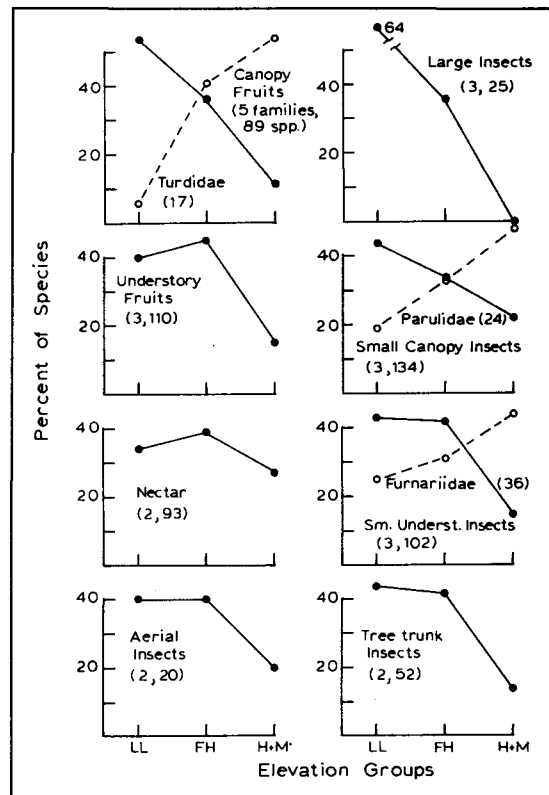


Fig. 3. Elevational distributions of Panamanian bird families grouped by food habits; migrants are excluded from this analysis. Data are from Ridgely (1976). Elevation groups include lowlands (LL, < 600 m), foothills (FH, 450-1200 m), highlands and mountains (H + M, > 900 m).

Distribuciones altitudinales de las familias de aves panameñas, agrupadas por hábitos alimenticios; los migrantes están excluidos de este análisis. Los datos provienen de Ridgely (1976). Las agrupaciones por elevación incluyen: tierra bajas (LL, < 600 m), laderas de montañas (FH, 450-1200 m), altiplanicies y montañas (H + M, > 900 m).

Comparison of Figs. 2 and 3 reveals that the elevational distributions of Neotropical bats basically resemble those of Neotropical birds. Except for the Trochilidae and three additional families with strong temperate zone representation (Turdidae, Parulidae, and Furnariidae), the species richness of each avian trophic group decreases with elevation. The decrease is particularly rapid in canopy frugivores (but is not as rapid in stenodermine bats) and in birds eating large insects (as is the case in large phyllostomines). Using more refined distributional data, Terborgh (1977) and Stiles (1983) reported similar trends in Peruvian and Costa Rican birds. Stiles further noted that highest bird diversity occurs where the humid lowlands meet the foothills (e.g. at Finca La Selva) and at the lower edge of cool wet "cloud" forest at an elevation of 1000-1200 m, where insect diversity and biomass tend to be high (Janzen 1973). Terborgh (1977) noted that the mid-elevation peak in Peru was caused by an increased density and diversity of insectivorous birds. As documented below, bat diversity is also very high at La Selva, but, unlike the avian situation, bat diversity is not particularly high at a mid-elevation site in Costa Rica (cf. sites LS and MV in Fig. 6). Therefore, precise one-to-one mapping of bat and bird diversity does not occur along elevational gradients in Costa Rica and probably elsewhere in Latin America.

Geographical Ranges in Venezuela

Some idea of the breadth of the ecological tolerances of each bat species in Venezuela can be obtained by examining the number of collecting stations at which it was found. Because collections were made at many (100) sites in a variety of different life zones, bats collected at many sites can be considered to have broader ecological tolerances than those collected at only a few sites. This analysis assumes, of course, that equal collecting efforts were made for all species at all sites. To judge from the great differences among sites in numbers of bats collected (approximate range = 10 - 3800), however, this assumption is unrealistic, but the extent to which collecting biases influence this analysis is unknown.

Distributions of the number of collection sites per species are summarized in Fig. 4. A majority (65%) of the non-phyllostomid bat species were caught at five or

fewer sites. Only the mormoopid *Pteronotus parnellii* was caught at more than 30 sites. Phyllostomids were generally more widespread than non-phyllostomids. Except in the glossophagines, most phyllostomids were captured at more than five collecting sites. Geographically (and ecologically) widespread phyllostomids included *Micronycteris megalotis*, *Trachops cirrhosus*, and *Phyllostomus discolor* (Phyllostominae); *Glossophaga soricina* (Glossophaginae); *Carollia perspicillata* (Carollinae); and *Sturnira lilium* and *Artibeus jamaicensis* (Stenodermatinae). The vampire *Desmodus rotundus* (Desmodontinae) was also collected at over 45 sites. Each of these widespread Venezuelan phyllostomids (plus others that were collected at somewhat fewer sites) ranges widely throughout the Neotropics from Mexico to southern Brazil or northern Argentina (Koopman 1982).

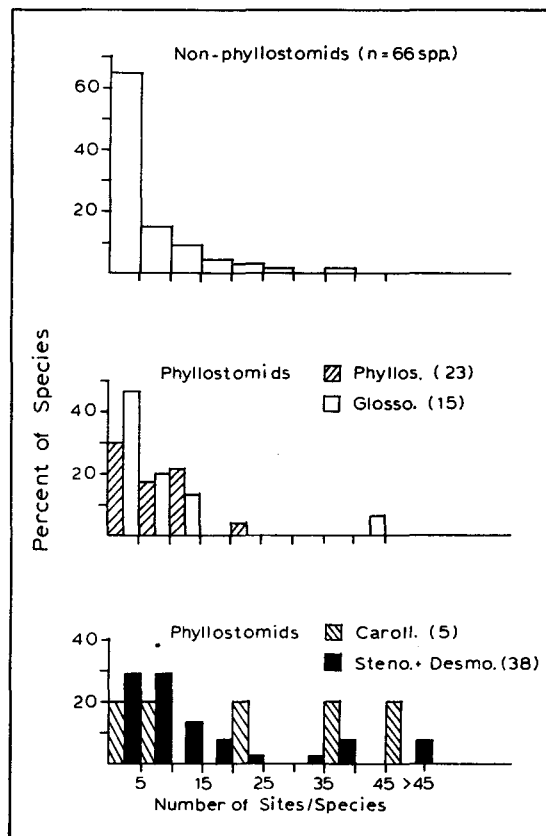


Fig. 4. Frequency distributions of the number of collection sites per species of Venezuelan bats. Data from Handley (1976).

Distribución de frecuencias del número de sitios de colecta para especies de murciélagos venezolanos. Los datos provienen de Handley (1976).

Taken at face value, these results suggest that non-phylostomids have narrower habitat breadths than do phyllostomid bats, and, because number of collection sites per species is positively correlated with the number of individuals collected ($r = 0.79$, $P < 0.001$), they are less common than phyllostomids (see Brown, 1984). However, because of the much greater ease of capturing phyllostomid bats than other kinds of bats in mist nets (LaVal & Fitch 1977), I believe these conclusions are open to serious question. Until unbiased sampling methods for all kinds of bats are devised, it will be impossible to compare the abundance and distribution of different families of bats solely from museum collections.

The fact that certain species of bats are abundant and geographically widespread has important implications for the struc-

ture of chiropteran communities. As we will see, these taxa represent "core" species that are common elements of many lowland Neotropical bat communities. They (or their close relatives) are the numerically dominant members of their feeding guilds in both low and high diversity communities.

The Relative Abundances of Phyllostomid Bats

To minimize biases caused by sampling problems, I will restrict my analysis of the relative abundance of Venezuelan bats to the Phyllostomidae. As is the case in many groups of organisms, each phyllostomid subfamily contains one to three common species and a few to many uncommon species (Fig. 5). Because degree of dominance of the one or two top-ranking

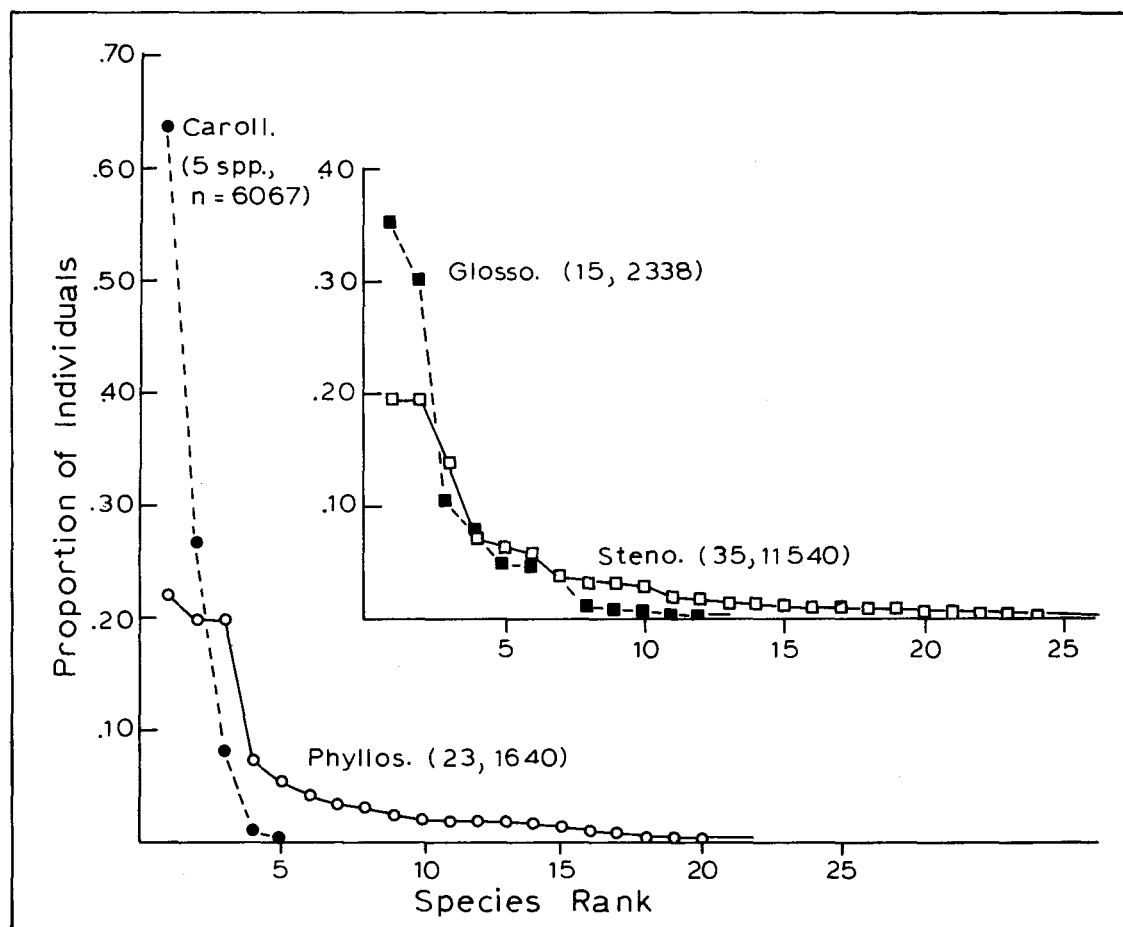


Fig. 5. The relative abundances of species of Venezuelan phyllostomid bats by subfamilies based on mist net capture data in Handley (1976).

Abundancias relativas de especies por subfamilia de los murciélagos filostómidos venezolanos, basadas en datos de captura con redes de niebla documentados por Handley (1976).

(most common) species is inversely related to each subfamily's species richness, differences between subfamilies in this regard are statistical artifacts. Numerically dominant species include many of the same species mentioned above (*P. discolor*, *T. cirrhosus*, *G. soricina*, *C. perspicillata*, *S. lilium*, and *A. jamaicensis*) plus *Phyllostomus hastatus* and *Glossophaga longirostris*. These species are the core elements of lowland phyllostomid communities.

Trends in the Community Structure of Phyllostomid Bats

Although species of insectivorous bats comprise at least one-half of the Neotropical chiropteran fauna, their population and community ecology is poorly known because, relative to phyllostomid bats, they are difficult to capture in mist nets set at ground level. Differences in ease of capture undoubtedly also exist among phyllostomids, but these have not been studied systematically. In the absence of data on differential catchability, I will assume that capture data accurately reflect the relative abundance of phyllostomid bats, at least at ground level. Because of their relatively high catchability, I will focus my attention in the rest of this paper on phyllostomid bats.

Mainland Communities

Trends in species richness at six well-studied sites in Costa Rica, Panama, and Brazil are summarized in Fig. 6. As expected, species richness increases along a rainfall/vegetational gradient in the lowlands. The mid-elevation site contains fewer species and lacks members of the Phyllostominae. Despite a three-fold difference in species richness among the lowland sites, the proportional representation of each subfamily does not differ significantly among sites ($X^2(6) = 3.98$, $p = 0.86$, Glossophaginae and Carolliinae combined into one group). Therefore, no differential enrichment by subfamily occurs with an increase in phyllostomid diversity.

Trends in the distribution of species by subfamily in two-dimensional morphological space at the five lowland sites are shown in Fig. 7. To ordinate species in 2-space I chose one measure of overall size (forearm length) and one measure of skull size (breadth across the upper molars which

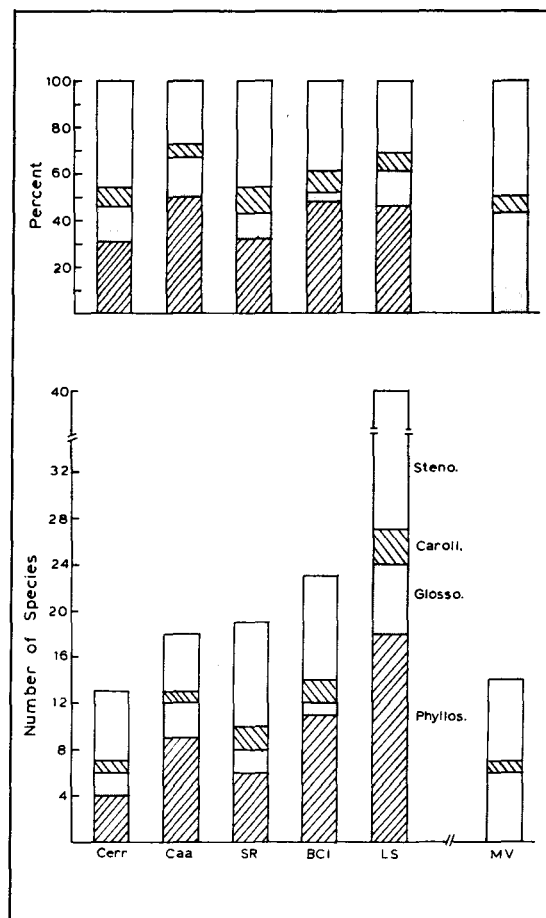


Fig. 6. Proportional representation and species richness of four phyllostomid subfamilies in six Neotropical communities as follows: Cerr = Brazilian "edaphic" Cerrados (elevation < 1000 m, annual rainfall < 1600 mm), Caa = Brazilian Caatingas (< 1000 m, < 1600 mm), SR = Parque Nacional Santa Rosa, Costa Rica, tropical dry forest (300 m, 1660 mm), BCI = Barro Colorado Island, Panama, tropical moist forest (50 m, 2600 mm), LS = Finca La Selva, Costa Rica, tropical wet forest (100 m, 4000 mm), MV = Monteverde, Costa Rica premontane moist forest (1200 m, 2500 mm). Data are from LaVal & Fitch (1977), Bonaccorso (1979), Willig (1983), and Fleming (unpubl. data).

Representación proporcional y riqueza de especies de cuatro subfamilias de filostómidos en seis comunidades neotropicales: Cerr = cerrados "edáficos" brasileños (elevación < 1000 m, precipitación anual 1600 mm), Caa = caatingas brasileñas < 1000 m, 1600 mm), SR = Parque Nacional Santa Rosa, Costa Rica, bosque seco tropical (300 m, 1660 mm), BCI = Isla Barro Colorado, Panamá, bosque húmedo tropical (50 m, 2600 mm), LS = Finca La Selva, Costa Rica, bosque perhúmedo tropical (100 m, 4000 mm), MV = Monteverde, Costa Rica, bosque húmedo premontano (1200 m, 2500 mm). Los datos fueron extraídos de LaVal & Fitch (1977), Bonaccorso (1979), Willig (1983) y Fleming (no publicado).

should correlate with largest potential food particle size) using data in Swanepoel & Genoways (1979). Future analyses should include a greater number of morphological

variables so that multivariate statistical procedures can be used to yield more refined estimates of morphological relationships (Findley & Wilson 1982).

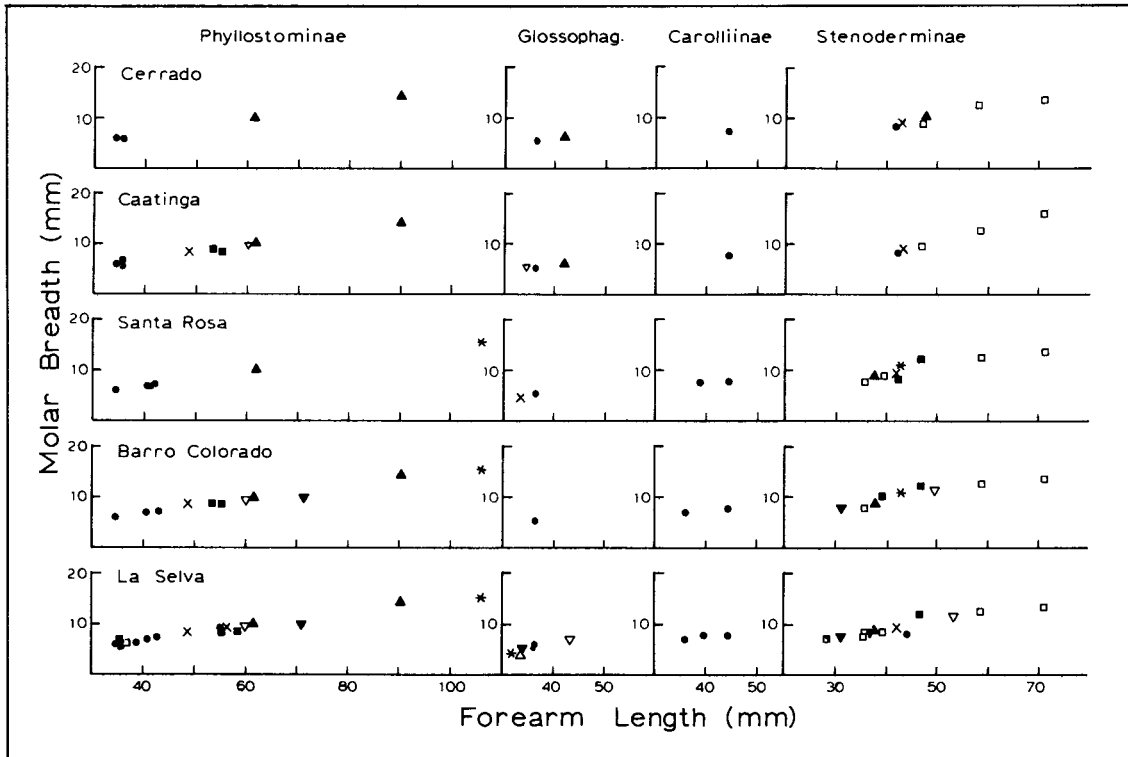


Fig. 7. Distribution of species of phyllostomid bats in two-dimensional morphological space in five mainland lowland communities. Within each subfamily, different symbols represent different genera.

Distribución de especies de murciélagos filostómidos en un espacio morfológico bidimensional en cinco comunidades de tierras bajas continentales. Dentro de cada subfamilia, símbolos diferentes representan géneros distintos.

Points that emerge from Fig. 7 include the following. (1) The range of sizes within subfamilies tends to increase with increased diversity (species richness) in the Glossophaginae, Carolliinae, and Stenoderminae but not in the Phyllostominae. (2) Small species (i.e., those with forearms smaller than the mid-point of a subfamily's size range) are added to a community faster than large species. (3) As a result, nearest neighbor distances in 2-space, measured as the Euclidean distance between pairs of species, decrease with increased diversity (Fig. 8). That is, mean crowding in morphological space increases with increased diversity, but it does so differentially by size in three of the four subfamilies. Small species are more crowded than large species irrespective of trophic adaptation.

To document trends in relative abundances with increasing diversity, I examined the capture data from two well-sampled Costa Rican sites, Santa Rosa (tropical dry forest) and La Selva (tropical wet forest). These data (Table 2) indicate that members of the two frugivorous subfamilies (Carolliinae and Stenoderminae) are more common than members of the other two subfamilies. Insectivorous (or omnivorous) and nectarivorous phyllostomids are only one-third to one-tenth as common as frugivores. An expanded analysis encompassing more sites yielded the same results (Fleming unpublished data).

Trends within subfamilies are summarized in Fig. 9. At both sites, one or two species dominated captures in three of the four subfamilies; strong numerical domi-

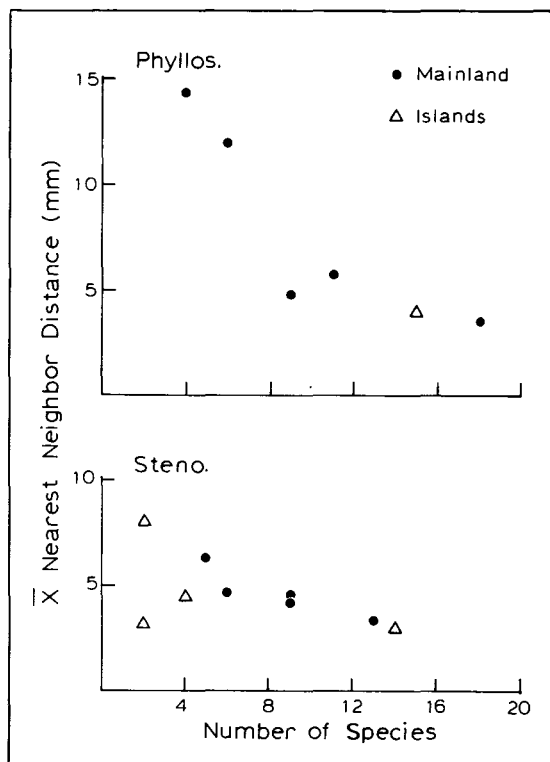


Fig. 8. Relationship between mean nearest neighbor distance in 2-space and species richness in two phyllostomid subfamilies in mainland and island communities.

Relación entre la distancia media al vecino más cercano en un espacio bidimensional y la riqueza de especies en dos subfamilias de filostómidos en comunidades continentales e insulares.

nance by a single species was absent in the Phyllostominae. In the dry forest, three species (*Glossophaga soricina*, *Carollia perspicillata*, and *Artibeus jamaicensis*) each in a different subfamily were numerically dominant. In the wet forest, five species

(*Glossophaga commissarisi*, *Carollia brevicauda*, *C. castanea*, *Artibeus jamaicensis* and *A. phaeotis*) were numerically dominant. Except in the Phyllostominae, the most common species were in the larger half of each subfamily's size range; *A. phaeotis* is also an exception to this pattern. In the Phyllostominae, the most common species were in the smaller half of the size range. This pattern reflects the trophic position of different phyllostomines; small species are primarily insectivorous whereas large species tend to be secondary carnivores (Freeman 1984).

Caribbean Island Communities

To see if diversity trends on islands are similar to those in mainland communities, I examined the bat faunas of four representative Caribbean islands plus Trinidad using species lists published in Baker & Genoways (1978) and Carter *et al.* (1981). The Caribbean bat fauna is taxonomically depauperate compared with the mainland fauna. Missing mainland families include Emballonuridae (except for *Peropteryx macrotis* on Grenada), Furipteridae, and Thyropteridae. In the Phyllostomidae, the Phyllostominae is represented only by *Macrotus waterhousii* in the Greater Antilles and *Micronycteris megalotis* on Grenada, and the Carollinae is represented only by *Carollia perspicillata* on Grenada. An endemic phyllostomid subfamily, Brachyphyllinae, with three genera, has radiated in the Greater Antilles, and one species (*Brachyphylla cavernarum*) is widespread in the Lesser Antilles. Elsewhere (Fleming 1982) I have examined diversity trends in West Indian bats and birds in greater detail.

TABLE 2

Relative abundance of four phyllostomid subfamilies in mist net samples at two Costa Rican sites. Data taken from LaVal & Fitch (1977) and Fleming (unpublished).

Abundancia relativa de cuatro subfamilias de filostómidos en capturas efectuadas con redes de niebla en dos localidades de Costa Rica. Los datos provienen de LaVal & Fitch (1977) y Fleming (no publicado)

SITE	SAMPLE SIZE	PROPORTION			
		PHYLLOSTOMINAE	GLOSSOPHAGINAE	CAROLLINAE	STENODERMINAE
Santa Rosa (dry forest)	6026	0.009	0.123	0.521	0.347
La Selva (wet forest)	1500	0.088	0.091	0.576	0.245

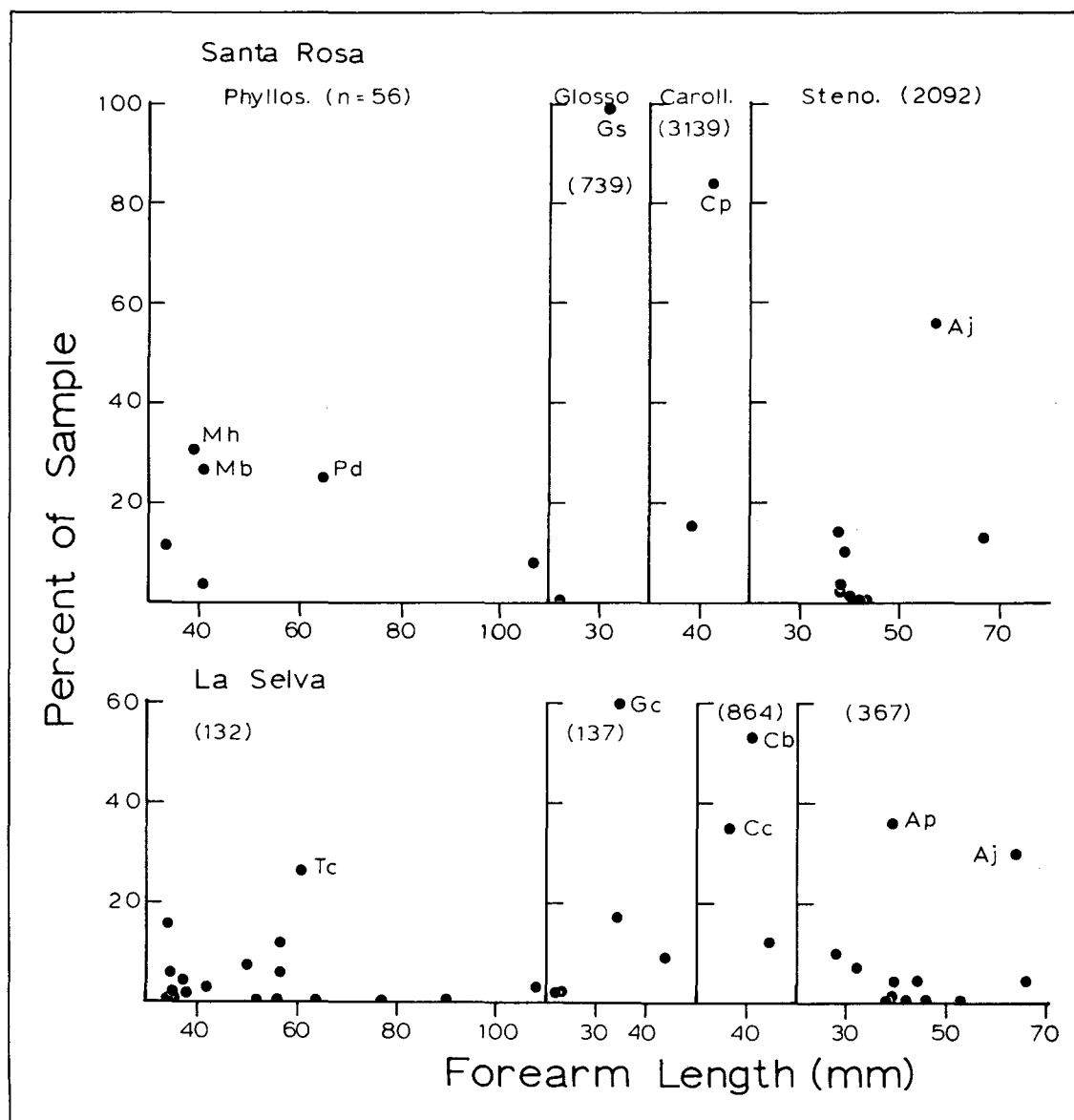


Fig. 9. The relationship between size and relative abundance of phyllostomid bats by subfamily at two Costa Rican sites. Within each subfamily, different symbols represent different genera. Abbreviations of common species are: Aj = *Artibeus jamaicensis*, Ap = *A. phaeotis*, Cb = *Carollia brevicauda*, Cc = *C. castanea*, Cp = *C. perspicillata*, Gc = *Glossophaga commarissarisi*, Gs = *G. soricina*, Mb = *Micronycteris brachyotis*, Mh = *M. hirsuta*, Pd = *Phyllostomus discolor*, Tc = *Trachops cirrhosus*.

Relación entre tamaño y abundancia relativa por subfamilia de murciélagos filostómidos en dos sitios de Costa Rica. Dentro de cada subfamilia, símbolos diferentes representan géneros distintos. Abreviaturas de especies comunes son: Aj = *Artibeus jamaicensis*, Ap = *A. phaeotis*, Cb = *Carollia brevicauda*, Cc = *C. castanea*, Cp = *C. perspicillata*, Gc = *Glossophaga commarissarisi*, Gs = *G. soricina*, Mb = *Micronycteris brachyotis*, Mh = *M. hirsuta*, Pd = *Phyllostomus discolor*, Tc = *Trachops cirrhosus*.

Trends in species richness and size are shown in Fig. 10. Points to note include the following. (1) In the least diverse fauna (Anguilla), the single species present in each subfamily is relatively large. If diet breadth is positively correlated with body

size in these bats (this is not always the case in mainland phyllostomids, Fleming in press), then generalists are more likely to occur in low diversity situations than specialists. (2) As in mainland communities, more small species are added to island

faunas than large species as diversity increases. (3) The Trinidad fauna is as crowded in 2-space as is a diverse mainland community (cf. Figs. 7 and 11; also see Fig. 8). (4) On Cuba (and elsewhere in the Greater Antilles), phyllostomid diversity is concentrated in the Brachyphyllinae and not in the Stenoderminae as it is in the Lesser

Antilles. The reason for this taxonomic shift is not clear because except for *Brachyphylla*, the brachyphyllines are ecologically more similar to glossophagines than they are to stenodermines. (5) As shown in Fig. 8, no clear relationship between nearest neighbor distance and species richness occurs in the Caribbean stenodermines.

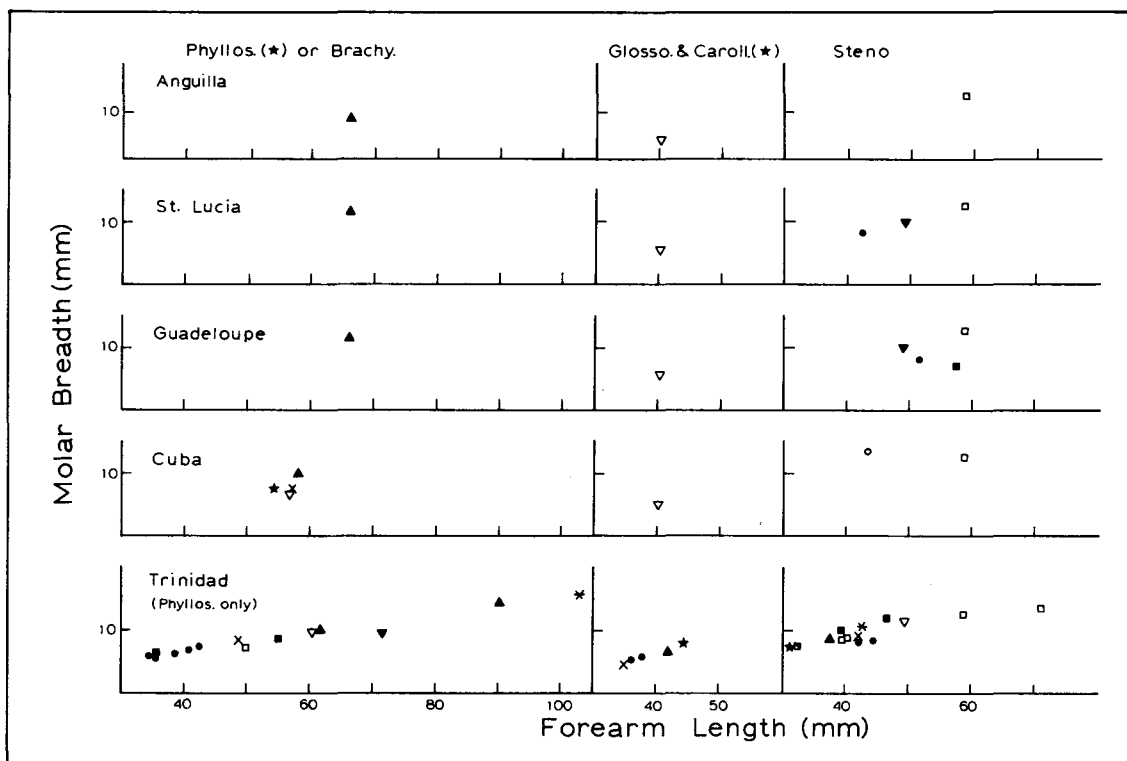


Fig. 10. Distribution of species of phyllostomid bats in two-dimensional morphological space in five Caribbean island faunas. Within each subfamily, different symbols represent different genera.

Distribución de especies de murciélagos filostómidos en un espacio morfológico bidimensional en cinco faunas insulares del Caribe. Dentro de cada subfamilia, símbolos diferentes representan géneros distintos.

DISCUSSION

The Assembly of Phyllostomid Communities

Communities of phyllostomid bats (and other bat families) are composed of relatively few (one to three per subfamily) common and geographically widespread species, and a variable number of uncommon (but often widespread) species. Core species (sensu Hanski 1982) are rather evenly distributed among body sizes and trophic niches as follows: small insectivore (*Micronycteris megalotis*), medium-large

omnivores (*Trachops cirrhosus*, *Phyllostomus discolor*), small nectarivore-omnivore (*Glossophaga soricina*), medium understory frugivore (*Carollia perspicillata*), small canopy frugivore (*Artibeus phaeotis*), and medium-large canopy frugivore (*A. jamaicensis*). These species share several characteristics as follows: (1) they tend to be primitive members of their subfamilies (this is certainly true of *Micronycteris*, *Phyllostomus*, *Glossophaga*, *Carollia*, and *Artibeus*; Phillips 1971, Honeycutt 1981, Griffiths 1982, Hood & Smith 1982); (2) they tend to be intermediate-to-large members of their subfamilies (except for *M. megalotis* and *A. phaeotis*); and (3) they

tend to have generalized diets (Gardner 1977, Fleming in press) and are tolerant of a variety of ecological conditions.

As the diversity of phyllostomid communities increases along habitat gradients, less abundant (more specialized?) species are added to this core of generalists so that total morphological space, which probably reflects total niche space (Findley & Wilson 1982), increases. During this process, small species are added at a faster rate than large species, and species (especially the small ones) become more tightly packed in morphological space. Because we know relatively little about the ecology and behavior of uncommon phyllostomids, trends in actual (rather than hypothesized) niche relationships between species in diverse communities are currently poorly known (e.g., Humphrey *et al.* 1983). Behaviorally oriented field studies rather than morphological studies are needed to resolve questions about niche relationships and the degree to which species compete for limited resources. Especially desirable would be studies of microhabitat selection and roost use.

Because of the absence of members of the Phyllostominae and Carolliinae from most Caribbean Islands, the assembly of West Indian phyllostomid communities is somewhat different from that on the mainland. Conspicuously missing are folia-gleaning insectivores and medium-sized understory frugivores. Core members of island communities include one small nectarivore (*Glossophaga longirostris* or *Monophyllus* spp.) and two medium-large frugivores (*Brachyphylla* spp. and *Artibeus jamaicensis*). As island size increases in the Greater Antilles, up to three additional brachyphyllines are added; up to three stenodermines are added in the Lesser Antilles.

To what extent does the community structure of phyllostomid bats differ from random expectations as reflected in the structure of the phyllostomid fauna as a whole? To answer this question, I will compare the taxonomic composition (which actually reflects trophic structure) and size distributions of the five lowland mainland communities with those of the entire phyllostomid fauna. Taxonomically, the five communities (whose data I combined because they were not significantly heterogeneous) differ significantly from the fauna as a whole. Phyllostomines were over-

presented (42.5% of the species cf. an expected 25.8%) and glossophagines were under-represented (12.4% cf. 25.8%) in the communities ($X^2(3) = 11.84$, $P = 0.0079$). Carolliines (8.0%) and stenodermines (37.2%) closely resembled chance expectations. These taxonomic deviations result, in part, from the geographic ranges of phyllostomines being broader than those of glossophagines (Koopman 1982). Because more phyllostomine than glossophagine ranges overlap at any point in the lowland Neotropics, local communities should contain a higher proportion of the phyllostomine fauna than the glossophagine fauna.

Significant taxonomic deviations also occur up mountains and on Caribbean islands, primarily as a result of the absence of phyllostomine species. Reduced food availability seems to explain the absence of phyllostomines in both of these situations. Why the abundant and widespread *Carollia perspicillata* is not present on Caribbean islands when two of its principal food taxa, shrubs of the genus *Piper* and *Cecropia* trees, are widespread in the West Indies is currently unknown.

In summary, at least two factors interact to determine the taxonomic composition of phyllostomid communities: (1) the relative abundance of different classes of food (which affects the Phyllostominae more strongly than other subfamilies) and (2) differences in the geographic ranges of members of different subfamilies (which affects the Glossophaginae more strongly than other subfamilies).

I searched for significant departures from random expectations in size (forearm) distributions by comparing the size distributions of portions of two communities (the low diversity Caatinga and the high diversity La Selva sites) with those in the appropriate subfamilies in the entire mainland fauna using data in Swanepoel & Genoways (1979). The results of Kolmogorov-Smirnov one sample tests indicated that forearm distributions did not differ from random expectations in the Phyllostominae and Stenoderminae at the Caatinga site (P 's $\gg 0.05$) nor did they differ significantly in the Phyllostominae, Glossophaginae, and Stenoderminae at La Selva (P 's $\gg 0.05$). From these results I conclude that in these two communities (and by inspection of Fig. 7, in at least two others, Santa Rosa and Barro Colorado

Island) forearm distributions do not differ from those expected from a random draw from the appropriate subfamilies. Contrary to Humphrey *et al.* (1983), I see no evidence of "character displacement" by overall size among members of the Phyllostominae or any other subfamily. Fleming *et al.* (1972) reached a similar conclusion from an analysis of size (and food habit) distributions in two Panamanian and one Costa Rican bat community.

It should be noted that this one-dimensional analysis does not eliminate the possibility that species within subfamilies (guilds) are non-randomly arrayed in n-dimensional morphological space. For example, McKenzie & Rolfe (in press) have found that guilds of insectivorous bats foraging in mangrove stands in northwestern Australia are non-random regarding two morphological features that influence foraging behavior, aspect ratio and wing loading. Syntopic species show less overlap in these parameters than expected by chance.

Despite this caveat, I reach two tentative conclusions regarding the evolution of community structure in phyllostomid bats. First, where appropriate resources are available (particularly in the moist mainland lowlands) community structure basically reflects the taxonomic, trophic, and size structure of the fauna as a whole. To the extent that competitive interactions (which occur mostly within subfamilies) and mutualistic interactions have molded the evolution of this bat family, they have had a similar influence on ecological relationships within communities. Of the two ecological interactions, evidence for the importance of mutualism, (i.e., plant-pollinator interactions and fruit-frugivore interactions) is much more compelling than is evidence for the importance of competition. Plant-animal interactions have profoundly influenced the evolution of the Phyllostomidae as it has their Old World counterpart, the Pteropodidae (Heithaus 1982). The importance of competition is more problematical. Many authors (e.g., Heithaus *et al.* 1975, Humphrey & Bonaccorso 1979, Humphrey *et al.* 1983) have speculated that the potential for competition for food or roosts exists among phyllostomids, but clear-cut demographic, behavioral, or morphological evidence of competition is thus far lacking.

My second conclusion is that food availability, both in amounts and in kind, strongly influences the structure of phyllostomid communities. Insect availability appears to play a crucial role in the presence or absence of members of the Phyllostominae as does the availability of appropriate flowers for the Glossophaginae. Among mainland frugivores, the geographic and altitudinal ranges of many genera (e.g., *Carollia*, *Sturnira*, *Artibeus*, and *Vampyrops*) correspond to the ranges of their most preferred kinds of fruit (Fleming in press). Degree of food specialization appears to determine the presence and abundance of particular bats within phyllostomid communities. Generalist feeders form the core elements of these communities over a wide range of ecological conditions, and they are joined by more specialized taxa where high rainfall and high plant productivity promote high biological diversity.

Comparisons with other Bat and Bird Communities

How similar is the structure of communities of phyllostomid and non-phyllostomid microchiropteran bats? Do the same general assembly rules apply to bats regardless of their taxonomic and trophic affiliations? Definitive answers to these questions are not yet available because different techniques have been used to study different groups of bats. Current data, however, seem to point to the existence of general morphological rules. The studies of Fenton (1972), Findley (1976), Findley & Black (1983), and Schum (1984) indicate that most species in temperate and tropical insectivorous bat faunas are clustered together in 2- to n-dimensional morphological space. Communities or faunas consist of a central group of morphologically (and ecologically) similar species and a few morphological outliers. As expected given the log-normal size distributions found in many groups (Hutchinson & MacArthur 1959, Van Valen 1973), central species tend to be small in size whereas outliers are large. The distance between nearest neighbors, and hence how tightly species are packed together in morpho-space, tends to decrease but total morphological space tends to increase as species richness increases.

Similar morphological trends probably are widespread in other vertebrate communities (Findley & Black 1983). For example, Ricklefs & Travis (1980) documented similar trends in temperate communities of grassland birds as did Karr & James (1975) in forest bird communities. In mainland phyllostomid communities, clusters of similar-sized species occur in the Phyllostominae, Glossophaginae, and Stenoderminae (Fig. 7). These clusters, however, do not necessarily contain what I have called the "core" members of phyllostomid communities. My definition of "core" species is based on abundance and broad ecological tolerances, and, as I have previously noted, these species tend to be larger in size than species in the morphological core. This difference suggests that modal morphology does not always result in greatest ecological success, at least in phyllostomid bats.

In conclusion, the structure of species-rich Neotropical bat communities appears to closely resemble the taxonomic, trophic, and morphological characteristics of the Neotropical bat fauna as a whole. This is to be expected because diverse communities contain a substantial fraction of the total fauna. Such communities contain clusters of morphologically similar species that tend to be less common and ecologically more specialized than a handful of abundant and broad-niched core species. As overall biological diversity decreases along rainfall and elevational gradients, specialist species drop out of communities whereas the generalists persist. In the Phyllostomidae, generalists come from each of the major trophic-size adaptive zones into which these bats have radiated. Mutualistic interactions with plants appear to have had a more profound influence on community structure in this family than have competitive interactions.

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LITERATURE CITED

- BAKER RJ & HH GENOWAYS (1978) Zoogeography of Antillean bats. In: Gill F (ed) Zoogeography in the Caribbean. Academy of Natural Sciences, Philadelphia, Special Publication 13: 53-97.
- BLACK HL (1974) A north temperate bat community: structure and prey populations. *Journal of Mammalogy* 55: 138-157.
- BONACCORSO FJ (1979) Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum, Biological Sciences* 24: 359-408.
- BROWN JH (1984) On the relationship between abundance and distribution of species. *American Naturalist* 124: 255-279.
- BROWN JH & MA BOWERS (1984) Patterns and processes in three guilds of terrestrial vertebrates. In: Strong DR Jr *et al.* (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey: 282-296.
- CARTER CH, HH GENOWAYS, RS LOREGNARD, & RJ BAKER (1981) Observations on bats from Trinidad, with a checklist of species occurring on the island. *Occasional Papers, Museum of Texas Tech University* 72: 1-27.
- CODY ML & JM DIAMOND, eds (1975) *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts.
- ELTON CS (1927) *Animal Ecology*. Sedgwick & Jackson, London.
- FENTON MB (1972) The structure of aerial-feeding bat faunas as indicated by ears and wing elements. *Canadian Journal of Zoology* 50: 287-296.
- FINDLEY JS (1973) Phenetic packing as a measure of faunal diversity. *American Naturalist* 107: 580-584.
- FINDLEY JS (1976) The structure of bat communities. *American Naturalist* 110: 129-139.
- FINDLEY JS & HL BLACK (1983) Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* 64: 625-630.
- FINDLEY JS & DE WILSON (1982) Ecological significance of chiropteran morphology. In: TH Kunz (ed) *Ecology of bats*. Plenum Press, New York: 243-260.
- FLEMING TH (1982) Parallel trends in the species diversity of West Indies birds and bats. *Oecologia* 53: 56-60.
- FLEMING TH (1986) Opportunism vs. specialization: the evolution of feeding strategies in frugivorous bats. In: A Estrada & TH Fleming (eds) *Frugivores and seed dispersal*. W. Junk, the Netherlands: 105-118.
- FLEMING TH, ET HOOPER & DE WILSON (1972) Three Central American bat communities: structure, reproductive cycles, and movement patterns. *Ecology* 53: 655-670.
- FREEMAN PW (1984) Functional cranial analysis of large animalivorous bats (Microchiroptera). *Biological Journal of the Linnean Society* 21: 387-408.
- GARDNER AL (1977) Feeding habits. In: Baker RJ, JK Jones Jr, & DC Carter (eds) *Biology of bats of the New World family Phyllostomatidae*. Part II. Special Publication Museum Texas Tech University Number 13: 293-350.
- GRAHAM GL (1983) Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *Journal of Mammalogy* 64: 559-571.

- GRANT P & D SCHLUTER (1984) Interspecific competition inferred from patterns of guild structure. In: Strong DR Jr *et al.* (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey: 201-233.
- GRIFFITHS TA (1982) Systematics of the New World nectar feeding bats (Mammalia, Phyllostomidae), based on the morphology of the hyoid and lingual regions. *American Museum of Natural History Novitates* 2742: 1-45.
- HANDLEY CO JR (1976) Mammals of the Smithsonian Venezuelan project. *Brigham Young University Science Bulletin, Biological Series* 20: 1-91.
- HANSKI I (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210-221.
- HEITHAUS ER (1982) Coevolution between bats and plants. In: Kunz TH (ed) *Ecology of bats*. Plenum Press, New York: 327-367.
- HEITHAUS ER, TH FLEMING, & PA OPLER (1975) Patterns of foraging and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56: 841-854.
- HOLDRIDGE LR (1947) Determination of world plant formations from simple climatic data. *Science* 105: 367-368.
- HONEYCUTT RL (1981) Molecular evolution in New World leaf-nosed bats of the family Phyllostomidae with comments on the superfamily Noctilionoidea. PhD. Thesis, Texas Tech University, Lubbock, Texas.
- HOOD CS & JD SMITH (1982) Cladistical analysis of female reproductive histomorphology in phyllostomid bats. *Systematic Zoology* 31: 241-251.
- HUMPHREY SR & FJ BONACCORSO (1979) Population and community ecology. In: Baker RJ, JK Jones Jr, & DC Carter (eds) *Biology of bats of the New World family Phyllostomatidae. Part III. Special Publication Museum Texas Tech University* 16: 409-441.
- HUMPHREY SR, FJ BONACCORSO & TL ZINN (1983) Guild structure of surface-gleaning bats in Panama. *Ecology* 64: 284-294.
- HUTCHINSON GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93: 145-159.
- HUTCHINSON GE & RH MACARTHUR (1959) A theoretical ecological model of size distributions among species of animals. *American Naturalist* 93: 117-125.
- JANZEN DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54: 687-708.
- JONES JK JR & DC CARTER (1976) Annotated checklist, with keys to subfamilies and genera. In: RJ Baker, JK Jones Jr, & DC Carter (eds) *Biology of bats of the New World family Phyllostomatidae. Part I. Special Publication Museum Texas Tech University* 10: 7-38.
- KARR JR & FC JAMES (1975) Eco-morphological configurations and convergent evolution in species and communities. In: Cody ML & JM Diamond (eds) *Ecology and evolution of communities*. Belknap Press, Cambridge, Massachusetts: 258-291.
- KOOPMAN KF (1978) Zoogeography of Peruvian bats with special emphasis on the role of the Andes. *American Museum of Natural History Novitates* 2651: 1-33.
- KOOPMAN KF (1982) Biogeography of bats of South America. In: Mares MA & HH Genoways (eds) *Mammalian biology in South America. Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh* 6: 273-302.
- LAVAL RK & HS FITCH (1977) Structure, movements and reproduction in three Costa Rican bat communities. *Occasional Papers Museum of Natural History, University of Kansas* 69: 1-27.
- MCKENZIE NL & JK ROLFE (in press) Structure of insectivorous bat guilds in mangroves. *Journal of Animal Ecology*.
- MCNAB BK (1971) The structure of tropical bat faunas. *Ecology* 52: 352-358.
- MCNAB BK (1982) Evolutionary alternatives in the physiological ecology of bats. In: Kunz TH (ed) *Ecology of bats*. Plenum Press, New York: 151-200.
- NOWAK RM & JL PARADISO (1983) *Walker's Mammals of the world*. Volume 1, 4th edition. Johns Hopkins University Press, Baltimore, Maryland.
- PHILLIPS CJ (1971) The dentition of glossophagine bats: development, morphological characteristics, variation, pathology, and evolution. *Miscellaneous Publications University of Kansas Museum of Natural History* 54: 1-138.
- RICKLEFS RE & J TRAVIS (1980) A morphological approach to the study of avian community organization. *Auk* 97: 321-338.
- RIDGELY RS (1976) *Birds of Panama*. Princeton University Press, Princeton, New Jersey.
- SCHUM M (1984) Phenetic structure and species richness in North and Central American bat faunas. *Ecology* 65: 1315-1324.
- SIMBERLOFF D (1984) Properties of coexisting bird species in two archipelagoes. In: Strong DR Jr *et al.* (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey.
- STRONG DR JR, D SIMBERLOFF, LG ABELE & AB THISTLE, eds (1984) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey.
- SWANEPOEL P & HH GENOWAYS (1979) Morphometrics. In: RJ Baker, JK Jones Jr, & DC Carter (eds) *Biology of bats of the New World family Phyllostomatidae. Part III. Special Publication Museum Texas Tech University* 16: 13-106.
- STILES FG (1983) *Birds*. In: Janzen DH (ed) *Costa Rican natural history*. University of Chicago Press, Chicago: 502-530.
- TAMSITT JR (1967) Niche and species diversity in Neotropical bats. *Nature* 213: 784-786.
- TERBORGH J (1977) Bird species diversity along an Andean elevational gradient. *Ecology* 58: 1007-1019.
- VAN VALEN L (1973) Body size and number of plants and animals. *Evolution* 27: 27-35.
- WIENS JA (1983) Avian community ecology: an iconoclastic view. In: Brush AH & GA Clark (eds) *Perspectives in ornithology*. Cambridge University Press, Cambridge: 355-403.
- WILLIG MR (1983) Composition, microgeographic variation, and sexual dimorphism in Caatingas and Cerrado bat communities from northeastern Brazil. *Bulletin of the Carnegie Museum of Natural History* 23: 1-131.