

19 Biogeography of West Indian Bats: An Ecological Perspective

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Abstract — The West Indies forms a zoogeographically distinct region within the Neotropics. Modern bat faunas in these islands are likely the consequence of overwater dispersal rather than random assemblages from tropical mainland source pools. Of the 56 extant species of bats known from the West Indies, 28 (50%) are endemic. The core community is represented by six species (*Monophyllus redmani*, *Brachyphylla cavernarum*, *Artibeus jamaicensis*, *Noctilio leporinus*, *Tadarida brasiliensis*, and *Molossus molossus*). Proximity to mainland sources, presence of caves, diversity of food resources, existence of “gatekeeper” islands, and island area all are important in defining species-packing patterns.

INTRODUCTION

A number of excellent reviews have been published on the biogeography of West Indian bats. However, we believe that the body of knowledge massed to date, although incomplete, warrants a reexamination of patterns, which may lead to a better understanding of the forces that have structured these insular communities. As with previous biogeographical accounts, we have made a number of taxonomic and geographical decisions. For decisions concerning named taxa, we follow Baker et al. (1984), but have incorporated some changes introduced by Silva-Taboada (1979), Jones (1989), and Koopman (1989). Disagreements were settled by following Koopman (1993) and Nowak (1994).

BIOGEOGRAPHY OF ANTILLEAN BATS

The West Indies forms a zoogeographically distinct region within the Neotropics. Although most islands within the archipelago are small and remote, thus faunistically depauperated, levels of endemism at the specific level (50%) are high (Table 1).

GEOGRAPHY AND SPECIES

Pending additional studies, we provisionally follow Genoways et al. (1998) in recognizing a boundary delineating the West Indies faunal subregion as “Koopman’s Line.” This faunal boundary excludes Grenada and the Grenadines, based on significant differences in genetic distances observed between populations of *Artibeus jamaicensis* in Grenada and other islands to the south (see Phillips et al., 1989; Pumo et al., 1996; Genoways et al., 1998). To the south, this region also excludes the islands of Trinidad, Tobago, Margarita, Aruba, Bonaire, and Curaçao. To the west, it excludes Isla Cozumel, Isla Mujeres, Halfmoon Cay, Roatan, Bonacca, and San Andreas. To the north, Koopman’s Line includes all of the Bahamas (Genoways et al., 1998).

Nine of the ten bat species found in the Bahamas are shared with Cuba, and 60% are West Indian endemics. Reports of extant populations of *A. jamaicensis* and *Molossus molossus* in south Florida and the Florida Keys suggest recent dispersal events from Cuba and/or Jamaica (reviewed in Genoways et al., 1998). Fossil taxa of the West Indies are mostly from the late Pleistocene or Holocene and therefore are essentially part of the modern fauna (Baker and Genoways, 1978). Because they are not part of extant communities we will consider the fossil record separately

TABLE 2
Species Extirpated from the West Indies and Islands
from Which Fossils Have Been Reported

Species	Location
<i>Pteronotus pristinus</i>	Cuba
<i>Mormoops megalophylla</i>	Cuba, Bahamas, Hispaniola
<i>M. magna</i>	Cuba
<i>Toniata bidens</i>	Jamaica
<i>Phyllonycteris major</i>	Puerto Rico, Antigua
<i>Artibeus anthonyi</i>	Cuba
<i>Phyllops vetus</i>	Cuba
<i>Desmodus rotundus</i>	Cuba

(Table 2). Recent fossil assemblages reported from south Florida and the Florida Keys include other taxa with West Indian affinities, including *Eumops glaucinus*, *Mormoops megalophylla*, and *Pteronotus* sp. (Genoways et al., 1998).

Taxonomic questions and presence/absence data raise another set of problems. Conclusions could be biased by choosing incorrect taxonomies, or because of incomplete data sets. For example, as recently as 1996, *P. parnelli*, *Micronycteris megalotis*, and *Tadarida brasiliensis* were recorded for the first time in St. Vincent (Vaughan and Hill, 1996), thus increasing the list of bats for this 345 km² island from 9 to 12 species. *Sturnira thomasi* was recently recorded for the first time in Montserrat (Pedersen et al., 1996; Genoways et al., 1998). Taxonomic questions, although important, present lesser problems for our analysis. Varona's (1974) conservative classification of the genera *Artibeus*, *Stenoderma*, *Phyllops*, and *Ardops* into a single genus *Stenoderma* (which we are not adopting) would raise the species-genus ratio, but would have little practical effect on the way a community is visualized without negating the fact that a community with ten species in ten genera is more diverse than one with ten species in one genus. On the other hand, Koopman's (1989) argument for the inclusion of all Greater Antillean *Eptesicus* into *E. serotinus* (not followed here) does have the effect of reducing the number of species, especially the endemic species. However, for all practical purposes the relevance of this decision is irrelevant to our discussion, since these almost indistinguishable sibling species on different islands would be considered ecologically equivalent.

ROUTES OF INVASION

Dispersal over water rather than vicariance events is likely to be the primary source of modern, West Indian bat faunas (Baker and Genoways, 1978; Jones, 1989; Koopman, 1989; Genoways et al., 1998). Although a limited vicariance model best explains the distribution of early Antillean colonizers (Griffiths and Klingener, 1988), three routes of overwater dispersal can be identified.

The Western Route

The western route from the Honduran bank to Jamaica and from Yucatan to Cuba is the main source of West Indian immigrants, with these two islands as major centers of endemism (Silva-Taboada, 1979).

The Northern Route

A northern route from Florida to Cuba directly, or through the Bahamas, has been postulated for species such as *Eptesicus fuscus*, *Tadarida brasiliensis*, and *Lasiurus borealis*. However, these

species could have invaded from the west as well. One reason for the relative unimportance of Florida as a source habitat is its depauperate bat fauna. Florida has 15 species of bats (Whitaker, 1998) as compared to the Yucatan Peninsula and south-central Mexico to the west with at least 67 (Arita and Ortega, 1998) and Trinidad to the south with more than 64 species (Goodwin and Greenhall, 1961; Carter et al., 1981).

The Southern Route

The southern route represents the invasion from South America through the Lesser Antilles. Some 14 species, including four endemics are derived from this route, although five reach only as far as Grenada. From a zoogeographical perspective, Grenada can be excluded from the West Indies (Koopman, 1989; Genoways et al., 1998), since it has a completely continental fauna, lacking any West Indian endemics. *Artibeus jamaicensis* and *Molossus molossus* are common throughout the Antilles and probably invaded from the south as well as the west (Jones, 1989; Phillips et al., 1989; Genoways et al., 1998). The same may be true for *Pteronotus parnelli* (Vaughan and Hill, 1996). A probable reason for the relative unimportance of this route is that the small, xeric Grenadines serve as a filter for the large pool of bats in South America (Phillips et al., 1989; Genoways et al., 1998).

PATTERNS IN BAT COMMUNITIES

Bat communities have been compared based on different guild structures. For example, Findley (1995) compared Central American bat communities based on eight guilds: forest and clearing aerial insectivores, open-air insectivores, water bats, gleaning insectivores–carnivores–omnivores, nectarivores, ground-story frugivores, canopy frugivores, and sanguivores. Willig and Gannon (1996) compared 14 Neotropical communities based on taxonomy and feeding guilds, namely, nectarivore, frugivore, aerial insectivore, gleaning carnivore, molossid insectivore, sanguivore, and piscivore. When this scheme is applied, aerial insectivores and frugivores are the dominant classes in the West Indies, as is the case in most of the 14 communities examined by Willig and Gannon (1996). The inclusion of all frugivores into a single guild in the latter scheme seems justified based on the observed overlap between canopy and understory frugivores. However, the same argument also could be made for aerial insectivores. Although the degree of overlap remains to be examined, it is possible to observe *Pteronotus quadridens*, *Eptesicus fuscus*, and *Molossus molossus* foraging sympatrically in large clearings along ravines, or to observe *Tadarida brasiliensis* foraging in the understory, immediately after nightly emergence (Whitaker and Rodríguez-Durán, 1999). Kalko (1997) and Schnitzler and Kalko (1998) proposed a standardization of guilds based on the dominant sensory and motor adaptations of bats. The resulting scheme consists of ten guilds, based on the recognition of four separate guilds of aerial insectivores. Some of the same difficulties mentioned above remain unsolved under this system, but Kalko (1997) points out that this suite of guilds should not be considered definitive.

The assignment of nectarivores to a single feeding guild poses another problem (Willig et al., 1993). Individual *Monophyllus redmani* have been captured with their stomachs full of nectar (Silva-Taboada, 1979), but upon examination of the feces it is often difficult to distinguish the contents from that of an aerial insectivore (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987). Moreover, large frugivores such as *Brachyphylla* show large amounts of pollen and insects in their stomachs (Silva-Taboada, 1979), and *Artibeus jamaicensis*, another large frugivore, has been observed displacing *M. redmani* from banana (*Musa*) flowers to drink the dripping nectar (A. Rodríguez-Durán, personal observation).

The high level of insect consumption by low-intensity echolocating phyllostomids raises another important question. How do these “whispering” bats capture insects? Although perhaps it is not technically possible for *M. redmani* to detect and capture flying insects, this bat may be able to employ aerial hawking (R. Houston, personal communication). Another possibility is that this

bat obtains insects from flowers, or it gleans them from foliage. *Monophyllus redmani* has been observed hovering in the foliage surrounding flowers (A. Rodríguez-Durán, personal observation). If aerial hawking does indeed occur, another guild would need to be added to those represented in the West Indies.

The gleaning carnivore and the sanguivore guilds have no reported representatives in the West Indies, although *Desmodus rotundus* is known from the fossil record in Cuba. The absence of sanguivores is easily understood based on the historical lack of large mammals or birds in sufficient numbers to sustain populations of these bats. On the other hand, anoline lizards (Reagan, 1996) and leptodactylid frogs (Stewart and Woolbright, 1996), which could serve as a resource for gleaning carnivores, are very abundant. Densities of small frogs of the genus *Eleutherodactylus* in Puerto Rico and Jamaica are the highest recorded for frogs anywhere in the world (Stewart and Woolbright, 1996), and theoretically could support populations of carnivorous bats.

BODY SIZE AND DIET

Albeit with some overlap, body size and diet are categories used to separate most faunas into clearly distinguishable classes (e.g., Case et al., 1983; Fleming, 1991). In comparing the bat faunas among different islands within the West Indies, we have classified each species of bat as small (forearm [FA] < 45 mm), medium (45 mm > FA < 50 mm) or large (FA > 50 mm), zoophagous or phytophagous bats (Table 3). As with guild classes discussed above, there are some blurry boundaries to this scheme. Some bats are omnivores, or the range of forearm length of a species may cross boundaries, especially in species with wide distributions. In any event, a species will always lean more heavily toward one category. Similar problems were confronted in the examination of other Neotropical bat faunas (Willig et al., 1993). Despite its limitations (Willig, 1986), comparison of bat faunas on the basis of feeding guilds provide valuable insights into the species-packing patterns of different communities.

Graphical representation of the faunas of the Greater Antilles and of the Lesser Antilles, with species richness similar to that of Puerto Rico (Figure 1), reveals a packing pattern consisting of a central cluster of similar values and lesser numbers of off-centered ones. This familiar packing pattern often rises from products of random variables (May, 1981), and has been documented for organisms as disparate as birds and diatoms (May, 1981) and for equivalent guilds from distant localities (Pianka, 1988).

As with most bat faunas compared to date (Findley, 1995), the dominant taxa on most islands are small and zoophagous, although small phytophagous species are common in St. Vincent and especially in Grenada. The two latter islands are the southernmost of the West Indies, and are closer to South America than are the rest of the Lesser Antilles. Grenada hosts no endemic Antillean species, a fact that compelled Koopman (1989) to omit this island from his analysis of the West Indies. This same argument led Genoways et al. (1998) to exclude Grenada and the Grenadines from the West Indian faunal region, a decision that was strengthened by significant genetic distances observed between populations of *Artibeus jamaicensis* on Grenada and islands to the north. The faunal differences among islands (Figure 1) are not statistically significant (G-Test of Independence; $p > 0.05$), although total G is suspiciously higher when St. Vincent and Grenada are considered.

ROOSTS

Roosts may limit the geographical occurrence of bats (Kunz, 1982; Arita, 1993). When Antillean bats are examined with respect to roosting preferences, few major differences stand out among islands (Table 4), and again the largest deviation occurs in Grenada with its continental fauna (Genoways et al., 1998). Although two islands host less than 30% of cave-dwelling bats, cave-dwellers comprise over 40% of the fauna on most islands. Interestingly, *Peropteryx macrotus* is the only cave-dwelling member of the family Emballonuridae known to have reached the Antilles

TABLE 3
Size/Diet Guilds for the West Indies

Size/Diet Category	Island																	
	CUB	JAM	HIS	PRB	SCX	SMB	SAB	SKB	ANB	MON	GUA	DOM	MAR	SLU	SVI	BAR	GRE	GRA
Large phytophagous	2	1	2	2	2	2	2	2	2	3	3	2	2	2	3	2	1	2
Medium phytophagous	2	2	2	2	0	0	0	1	0	2	2	1	1	1	1	0	0	0
Small phytophagous	2	3	2	1	0	1	0	0	1	1	1	2	2	2	4	1	1	6
Small zoophagous	11	8	7	5	1	3	1	2	3	3	3	4	3	2	2	2	1	3
Medium zoophagous	6	4	4	2	0	0	0	0	0	1	1	2	1	0	1	1	0	1
Large zoophagous	3	3	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1

Note: See Table 1 and text for details. Islands: CUB = Cuba; JAM = Jamaica; HIS = Hispaniola; PRB = Puerto Rico Bank; SCX = St. Croix; SMB = St. Martin Bank; SAB = Saba; SKB = St. Kitts Bank; ANB = Antigua Bank; MON = Montserrat; GUA = Guadeloupe; DOM = Dominica; MAR = Martinique; SLU = St. Lucia; SVI = St. Vincent; BAR = Barbados; GRE = Grenadines; GRA = Grenada.

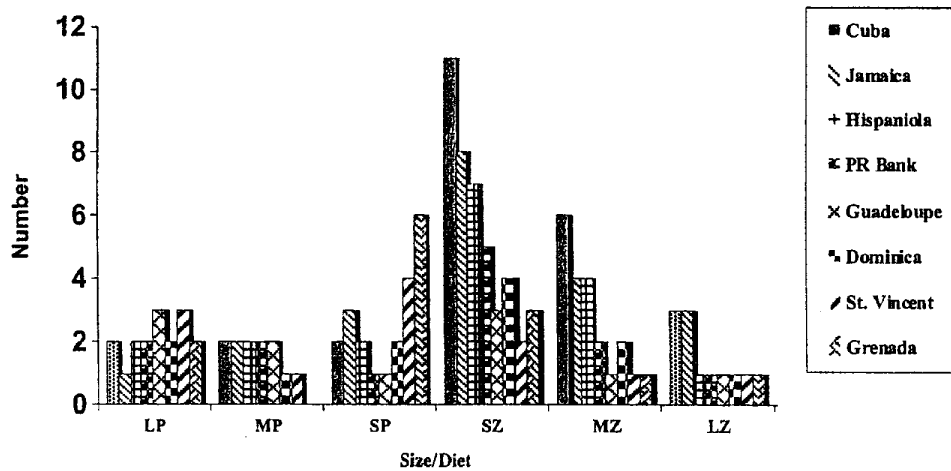


FIGURE 1 Number of species of bats in Cuba, Jamaica, Hispaniola, Puerto Rican bank, Guadeloupe, Dominica, St. Vincent, and Grenada categorized as large phytophagous (LP); medium phytophagous (MP); small phytophagous (SP); small zoophagous (SZ); medium zoophagous (MZ); and large zoophagous (LZ). See text for details.

(Baker and Genoways, 1978), and it is considered a relatively recent invader either from Trinidad or the South American mainland (Genoways et al., 1998).

In a region where over 100 hurricanes have affected some islands since 1508 (Colón, 1977), cave-roosting habits should be an asset. Marked reductions in bat populations have been reported following severe cyclones (Rainey, 1998). Hurricane Hugo in 1989 caused marked declines in populations of *Artibeus jamaicensis*, *Stenoderma rufum*, and *Monophyllus redmani* in Puerto Rico (Gannon and Willig, 1994). The cave-dwelling *A. jamaicensis* and *M. redmani* returned to pre-disturbance levels within 2 years, although tree-roosting *S. rufum* declined to about 30% of prehurricane levels, and had not recovered after 3 years (Gannon and Willig, 1994). In Montserrat, Pedersen et al. (1996) reported a 20-fold decrease in bat populations compared to levels observed before Hurricane Hugo.

Caves provide critical habitat for bats during a hurricane, but the widespread devastation caused by this natural phenomenon still may take its toll on bats, especially on phytophagous species. Waide (1992a, 1992b) found that frugivorous and nectarivorous birds faced food shortages after Hurricane Hugo, but omnivorous and insectivorous species were not affected, or exhibited relative increases in abundance. Similar results were obtained for the bat fauna of Montserrat (Pedersen et al., 1996). Gannon and Willig (1994) found that the home range size of frugivorous bats increased fivefold following Hurricane Hugo. After Hurricane Georges in 1998, higher than usual mortality was observed in caves that hosted large populations of bats in Puerto Rico, and aggressive interactions increased at flowering banana (*Musa*) plants with flowers (A. Rodríguez-Durán, personal observation). Larger islands may also offer buffer zones that are not seriously affected by hurricanes and later can serve as habitats for areas that have been devastated.

ACTIVITY

Time is a resource that may be partitioned by bats (Kunz, 1973; Swift and Racey, 1983). In the West Indies, large assemblages of bats in caves have been documented for Jamaica (Goodwin, 1970), Cuba (Silva-Taboada, 1977, 1979), and Puerto Rico (Rodríguez-Durán, 1998). Nonrandom patterns of association among these cave-dwelling bats may be promoted by differences in patterns of activity of coexisting species (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987; Rodríguez-Durán, 1998). These differences in times of nightly emergence may also influence rates

TABLE 4
Roosting Behavior of the Bats of the West Indies

Roosting Behavior	Island																	
	CUB	JAM	HIS	PRB	SCX	SMB	SAB	SKB	ANB	MON	GUA	DOM	MAR	SLU	SVI	BAR	GRE	GRA
Cave-dwellers	11	12	10	7	1	4	2	2	4	4	5	5	4	3	5	2	1	3
Tree-dwellers	3	2	2	2	0	0	0	1	0	3	3	2	2	2	2	0	0	2
Generalists	12	7	6	4	3	3	1	3	3	3	3	5	4	3	5	5	3	8
Total	26	21	18	13	4	7	3	6	7	10	11	12	10	8	12	7	4	13

* Tree-dwellers include bats that roost in both foliage and tree-holes.

• Generalists are bats that use more than one kind of roost, most often anthropogenic structures.

TABLE 5
Characterization of Bats from Cuba and Puerto Rico
Based on Time of Departure from Roosts

Species	Category	Diet
<i>Mormopterus minutus</i>	Vespertine	Insects
<i>Noctilio lepidus</i>	Vespertine	Insects
<i>Pteronotus quadridens</i>	Vespertine	Insects
<i>Molossus molossus</i>	Vespertine	Insects
<i>Eptesicus fuscus</i>	Vespertine	Insects
<i>Tadarida brasiliensis</i>	Vespertine	Insects
<i>Eumops glaucinus</i>	Crepuscular	Insects
<i>Pteronotus macleayi</i>	Crepuscular	Insects
<i>P. parnellii</i>	Crepuscular	Insects
<i>Noctilio leporinus</i>	Crepuscular	Fish/insects
<i>Artibeus jamaicensis</i>	Crepuscular	Fish/leaves
<i>Mormoops blainvillii</i>	Nocturnal	Insects
<i>Macrotus waterhousi</i>	Nocturnal	Insects
<i>Monophyllus redmani</i>	Nocturnal	Nectar/fruits/insects
<i>Phyllonycteris poeyi</i>	Nocturnal	Nectar/pollen
<i>Brachyphylla nana</i>	Nocturnal	Nectar/pollen
<i>Erophylla bombifrons</i>	Nocturnal	Fruit/nectar

Note: See text for details.

of predation on bats (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1985; Rodríguez-Durán and Kunz, 1992; Rodríguez-Durán, 1996). When compared to the mainland Neotropics, nocturnal predators are few in the West Indies, and this may be one reason lunar phobia has not been observed in populations of *S. rufum* (Gannon and Willig, 1997).

Silva-Taboada (1979) arranged 16 species of Cuban bats based on their times of departure and return to roosts (Table 5). Bats were classified as vespertine when departing near sunset (light intensity at 500 to 900 Lux), crepuscular when departing slightly after sunset (38 to 187 Lux), and nocturnal when departing over 30 min after sunset (0 Lux). These patterns of activity correspond to those observed for four species of bats in Puerto Rico (Rodríguez-Durán and Lewis, 1987; Rodríguez-Durán, 1996). It is evident from Table 5 that most insectivorous bats are active around dusk, a behavior that corresponds with the peak of insect activity at this time. Two insectivorous species are nocturnal, and examination of their diet reveals a preponderance of moths (Silva-Taboada, 1979; Rodríguez-Durán and Lewis, 1987), which are known to be proportionately more abundant after the peak of insect abundance at dusk (Silva-Taboada, 1979; Rodríguez-Durán, 1984).

COMMUNITY STRUCTURING

West Indian bat faunas are not random assemblages from tropical mainland source pools (Fleming, 1982; McFarlane, 1989, 1991; Genoways et al., 1998). The absence from the West Indies of many species potentially capable of crossing wide water gaps suggests that differences in dispersal abilities alone cannot explain the observed distribution and diversity patterns (Fleming, 1982). Based on the relationship between island area and the species-genus ratio, and on the structured pattern of species co-occurrence, interspecific competition may be one factor that produces these faunas (McFarlane, 1989, 1991). Fleming (1982), however, suggested that noncompetitive deterministic factors, such as area, distance from biogeographical source, and habitat diversity, may account for 66% of the faunal similarity between bats and birds in the West Indies. He proposed that major

differences in resource availability between mainland and island habitats (e.g., Janzen, 1973) could better account for the absence of certain groups. The fact that Cuba and Jamaica are above their predicted equilibrium number of species, and Hispaniola and Puerto Rico are below, demonstrates, as Griffiths and Klingener (1988) postulated, that the relatively recent decreases in sea level during the Pleistocene may not have allowed enough time for eastward dispersal of some species.

In reviewing several studies on the structure of bat communities, Findley (1993) concluded that bats do not provide support for competition as a dominant factor in structuring these communities. He argued that diversity of bat communities could largely be explained by historical and geographical factors, without denying some importance to resources in differentiating bats in ways that allow the allocation of those resources (Findley, 1993). However, community structures indistinguishable from those produced by stochastic processes must be interpreted within the context of the continental systems where they were described, and where local extinctions resulting from competitive interactions might be blurred by immigration from source habitats (Willig and Moulton, 1989).

In this context, archipelagos provide better models than continents for examining the relative importance of deterministic (i.e., area, habitat diversity, distance from source habitats, and competition) and stochastic (i.e., dispersal and persistence independent of interaction) factors in structuring bat communities. Among the potential patterns that could be produced by competition, size assortment (i.e., the effect of the presence of one species on the probability of persistence of a morphologically similar species) is easier to detect with limited data than is size adjustment (i.e., shift in morphological characteristics to minimize competition). Inter-island morphological differences are known to occur among West Indian bats (Genoways et al., 1981, 1998; Genoways, 1998). However, the importance of these shifts in morphological characteristics, in the context of community structure, remains to be determined. Morphological shifts also occur with respect to mainland populations, and could be associated with differences in diet (Whitaker and Rodríguez-Durán, 1999).

West Indian phyllostomid communities differ somewhat from mainland communities. Core phyllostomid species of island communities, defined on the basis of abundance and broad ecological tolerance, include one small nectarivore (omnivore) and two frugivores (Fleming, 1986). When all bats are considered, a fish-eating species and two small insectivores are added to this core community (Table 1). Thus, although small insectivores are the main component of the West Indian bat faunas (Figure 1), the core community consists of one species of *Monophyllus*, one species of *Brachyphylla*, *A. jamaicensis*, *Noctilio leporinus*, *Tadarida brasiliensis*, and *Molossus molossus*. Insectivorous bats have lower mass-specific metabolic rates than other species (McNab, 1982), a relationship that has been used to explain the higher proportion of nonpasserine land birds on Caribbean islands compared with the tropical mainland (Faaborg, 1977).

As island size and habitat complexity increase in the Greater Antilles, three mormoopids, one species of *Erophylla*, and one species of *Macrotus* are added to the core community of bats. Cave-dwelling, endemic mormoopids, and especially *Monophyllus* and *Erophylla*, show marked reductions in mass-specific metabolic rates relative to expected values (Rodríguez-Durán, 1995), and several other species of endemic phyllostomids and natalids seem especially adapted to roosting in warm caves (Silva-Taboada, 1977, 1979; Sampedro-Marín et al., 1977) that could promote reduced metabolic rates (Rodríguez-Durán, 1995). Similarly, some species of flying foxes (*Pteropus*) on small islands show a general trend toward small body size and low mass-specific metabolic rates (McNab, 1994).

The nonrandomness of bat assemblages in caves (Rodríguez-Durán, 1998) and differences in activity (above) and packing patterns in morphospace (Silva-Taboada, 1979; Rodríguez-Durán et al., 1993) suggest that bats have differentiated in ways that contribute to resource partitioning. Based upon the consumption of hard-bodied vs. soft-bodied arthropods and skull robustness, the statistical analysis of insectivorous species in Puerto Rico produced two groups, one containing *E. fuscus* and *Molossus molossus* and the other containing all the mormoopids plus *T. brasiliensis* (Rodríguez-Durán et al., 1993).

Density compensation is another phenomenon commonly exhibited by island populations. A variety of factors can produce densities on islands higher than, comparable to, or lower than

densities in similar mainland habitats (MacArthur et al., 1972). Bat densities are poorly known in most habitats. However, populations of bats in caves of the more diverse islands of Cuba and Jamaica may have lower densities (Goodwin, 1970; Silva-Taboada, 1979) than similar caves in Puerto Rico (Rodríguez-Durán and Lewis, 1987; Rodríguez-Durán, 1996). However, these differences cannot immediately be ascribed to ecological release due to reduced species diversity, since densities in Puerto Rican caves are similar to those in more speciose regions of Mexico (Bateman and Vaughan, 1974; Aguilar-Morales and Ruiz-Castillo, 1995).

In summary, both deterministic and stochastic factors appear to influence the structure of bat communities in the West Indies, supporting the hypothesis that most patterns and processes in ecology and biogeography are influenced by several key, hierarchical variables, rather than by single-factor explanations (Ruggiero et al., 1998). Proximity to mainland sources, presence of caves, diversity of food resources, existence of "gatekeeper" islands, and island area, all play a part in defining packing patterns. However, clear nonrandom patterns of activity, roosting, and distribution in ecomorphological space, as well as shifts in the way some species may fit into insular as compared to mainland communities (Whitaker and Rodríguez-Durán, 1999), point toward resources as an important player in defining these packing patterns. The role of competition remains unclear because of lack of information on geographical variation in body size and population responses to competition.

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