CHAPTER 8

Macroecology of Caribbean Bats: Effects of Area, Elevation, Latitude, and Hurricane-Induced Disturbance

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Introduction

Understanding the geographic and environmental characteristics of islands that affect aspects of biodiversity is a major theme in ecology (Begon et al. 2006; Krebs 2001) and biogeography (Cox and Moore 2000; Drakare et al. 2006; Lomolino et al. 2006). Such understanding has become particularly relevant over the past century because human activities on continents have fragmented natural landscapes, often creating islands of isolated habitat dispersed within a sea of land uses that include agriculture, forestry, and various degrees of urban and suburban development. The increasingly fragmented or islandlike structure of mainland habitats has critical ramifications to conservation biology, as it provides insights regarding the mechanisms leading to species persistence and loss. Consequently, the study of patterns and mechanisms associated with island biodiversity is of interest in its own right (Whittaker 1998; Williamson 1981), and may provide critical insights into mainland phenomena that otherwise could not be studied because of ethical, financial, or logistical considerations involved with the execution of large-scale manipulative experiments.

Island Biogeography and Area's Signal

The study of patterns of species richness on islands as a quantitative science was promoted greatly by the foundational work of MacArthur and Wilson (1963, 1967), in which an equilibrium perspective suggested that the richness of an island was a consequence of a dynamic balance between rates of immigration and extinction, as affected by distance to source pools and island area, respectively. The theory has enjoyed broad success, at least from a heuristic perspective, despite considerable controversy about the dynamic or equilibrium nature of many island systems (Brown 1981; Coleman et al. 1982; Gilbert 1980; Mueller-Dombois 2001; Sismondo 2000; Whittaker 1998; Williamson 1981). As a simplifying assumption, much research in island biogeography focuses on a particular archipelago or group of islands, with each island presumed to have an equal likelihood of colonization from a shared species pool. In those simplified scenarios, the operational question reduces to a quantification of ecology's oldest law: von Humboldt's observation (1807) that larger areas support more species than do smaller areas. In short, research has focused on questions related to the form and parameterization of species richness–area relationships. Although a number of competing models (e.g., sigmoidal, semilogarithmic, and power functions) about the form of the species-area relationships exist (see Gray et al. 2004a, 2004b; Scheiner 2003, 2004), the most common incarnation (Arrhenius 1921, 1923a, 1923b) is

$$S = CA^z,$$

where S is species richness, A is island area, and the fitted constants, C and z, are determined by least-squares analysis of the linear relationship between log S and log A (or via nonlinear regression techniques). A comparison of parameters among island systems provides insight into the ecological and evolutionary forces that shape biodiversity in different geographic contexts (e.g., Losos 1996).

Caribbean Islands

The Caribbean is an area of high species richness and high species endemism (Woods 1989; Woods and Sergile 2001). Consequently, it is recognized as a hot spot of biodiversity for terrestrial biotas (Myers et al. 2000). Despite the relatively small extent of land represented by constituent islands (266,500 km^2), the Caribbean harbors 7,000 endemic vascular plants and 779 endemic vertebrates, making it one of the hottest of hot spots (Myers 2001), especially for bats (Baker and Genoways 1978; Griffiths and Klingener 1988; Jones 1989; Koopman 1989; Morgan 1989; Rodríguez-Durán and Kunz 2001). Both historical (e.g., geological and evolutionary) and ecological (e.g., island size and distance to mainland) factors contribute to complex patterns of endemism and richness (Hedges 1996; Rosen 1976; Woods and Sergile 2001). Moreover, changes in climate during the late Quaternary modified the distribution, size, and abiotic characteristics of caves, significantly altering the distribution of bats in the Caribbean (Morgan 2001). Widespread extinctions of cave-dwelling species on small islands (e.g., Bahamas and Cayman Islands) resulted from flooding that was associated with rising sea levels or erosional collapse. Additional extinctions of cavernicolous bats on large islands in the Greater Antilles during this period likely were induced by microclimatic changes in caves that paralleled global climate changes. Nonetheless, caves still represent an important island characteristic that molds assemblage composition and distinguishes it from mainland assemblages (Rodríguez-Durán, chapter 9, this volume).

The Caribbean Basin is a region characterized by high cyclonic activity (Landsea et al. 1999). As such, the composition and structure of biotas in the Caribbean have been molded by a disturbance regime dominated by hurricanes for a considerable time. Moreover, global warming likely will increase the number and intensity of tropical storms and hurricanes in the region (Goldenberg et al. 2001; Webster et al. 2005). In addition, the Caribbean is experiencing a drying trend (i.e., negative precipitation anomaly), which may be related to global warming or may represent normal long-term variation in rainfall (Neelin et al. 2006). Although considerable research has focused on the effects of hurricanes on the structure and function of biotas in the Caribbean (e.g., Walker et al. 1991; Walker et al. 1996), including bats (e.g., Gannon and Willig 1994, 1998, chapter 10, this volume; Jones et al. 2001), little work has examined how variation in hurricane-related disturbance characteristics might affect patterns of biodiversity on Caribbean islands in general.

The Caribbean also is an area of conservation concern because of the extent to which accelerating rates of anthropogenic activity threaten the persistence of species. Symptomatic of this concern, the primary vegetation of the Caribbean extends to slightly more than one-tenth (29,840 km^2 of 263,500 km^2) of its original cover (Myers 2001). Moreover, conservation action in the Caribbean is more complex than on the mainland of North or South America. The Caribbean is home to more than a score of small nations and territories. The human inhabitants of the Caribbean islands represent a diversity of social, political, and cultural heritages, with populations speaking a variety of languages, challenging the production or execution of comprehensive conservation planning. In addition, the nations of the Caribbean are among the most poor (U.S. Central Intelligence Agency 2006) and most densely populated areas in the hemisphere (24 of the 25 most densely populated countries in the Western Hemisphere are in the Caribbean; U.S. Census Bureau 2004), further exacerbating conservation efforts.

We assess the extent to which a suite of environmental characteristics affect variation in aspects of biodiversity on three groups of islands in the Caribbean, including the Bahamas, Greater Antilles, and Lesser Antilles. In addition, we evaluate the extent to which such relationships differ among island groups. Moreover, the database that forms the foundation for our analysis is updated compared to that used for previous investigations, and is consequently more comprehensive and accurate.

Materials and Methods

Based on biogeographic considerations (Baker and Genoways 1978; Koopman 1959), the oceanic islands of the Caribbean can be categorized into three broad groups: Greater Antilles (fig. 8.1A), Bahamas (fig. 8.1B), and Lesser Antilles

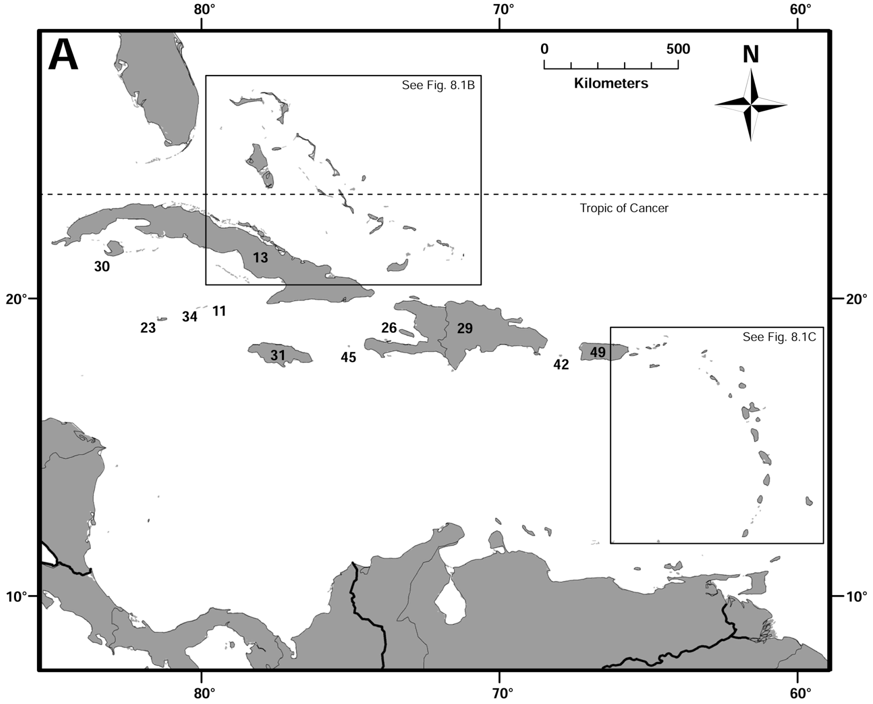

Figure 8.1. The islands of the Caribbean. *Numbers* indicate those islands that were included in analyses (see appendix 8.1 for island names and characteristics). *A*, Islands of the Greater Antilles (numbered) in relation to the Bahama Islands and the Lesser Antilles; *B*, the Bahama Islands in relation to Cuba (island 13); *C*, the Lesser Antilles in relation to Puerto Rico (island 49). Figure 8.1 continues on p. 220.

(fig. 8.1C). These islands differ greatly in area, elevational relief (maximum elevation), latitude, longitude, disturbance characteristics, and distance from sources of colonization (appendix 8.1). The three routes of dispersal by bats from the mainland of the New World to the islands of the Caribbean implicate the location of sources of colonization: subtropical North America, the Yucatán of Central America, and northern South America (Baker and Genoways 1978). The North American source, primarily subtropical Florida, is estimated by the location of Miami in Florida. The Central American source is estimated by the location of Puerto Juárez in Quintana Roo, Mexico. The tropical South American source is estimated by the location of Carúpano in Bermudez, Venezuela. Island areas and maximum elevation were obtained from an equal-area projection map (National Geographic Society 1985) and various geographic gazetteers. Interisland distances were calculated using the Great Circle Distances calculator (Earth.exe for Windows) by J. A. Byers (online at http://www.wcrl.ars.usda.gov/cec/moregen.htm).

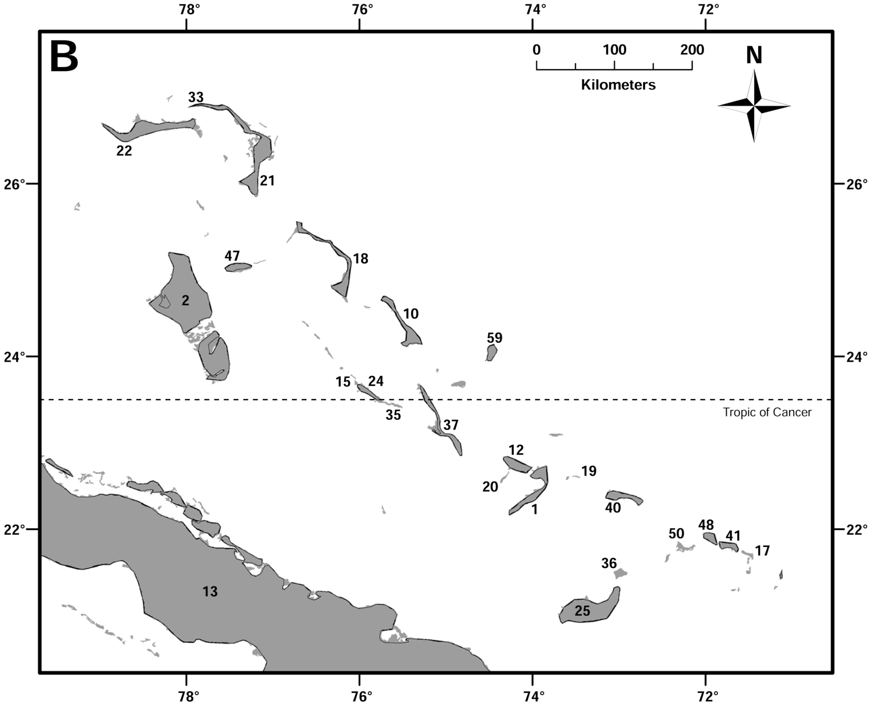

Figure 8.1. *(continued)*

Faunal Distributions

The distribution of bats on islands of the Caribbean, as defined by Baker and Genoways (1978), was augmented and updated by a number of subsequent distributional records and systematic revisions, to populate a species-occurrence matrix for the islands (appendix 8.2). Nomenclature followed the recommendations of Simmons (2005) except for recognizing *Eptesicus lynni* (Arnold et al. 1980; Genoways et al. 2005) as an endemic of Jamaica and distinct from *E. fuscus* elsewhere in the Caribbean. In addition, each species was categorized based on the literature (e.g., Gardner 1977; Patterson et al. 2003; Wilson 1973) into one of six feeding guilds: aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, piscivores, or nectarivores. Some species of bat (e.g., *Micronycteris* spp., *Phyllostomus* spp.) are not classified easily into guilds because they can forage on multiple resource bases. In lieu of creating a category of omnivores that would pool species that perform different trophic roles into a single group, we classified species based on their dominant dietary constituents. From this matrix, we estimated taxonomic or functional aspects of biodiversity for islands in the Caribbean. Taxonomic aspects included the

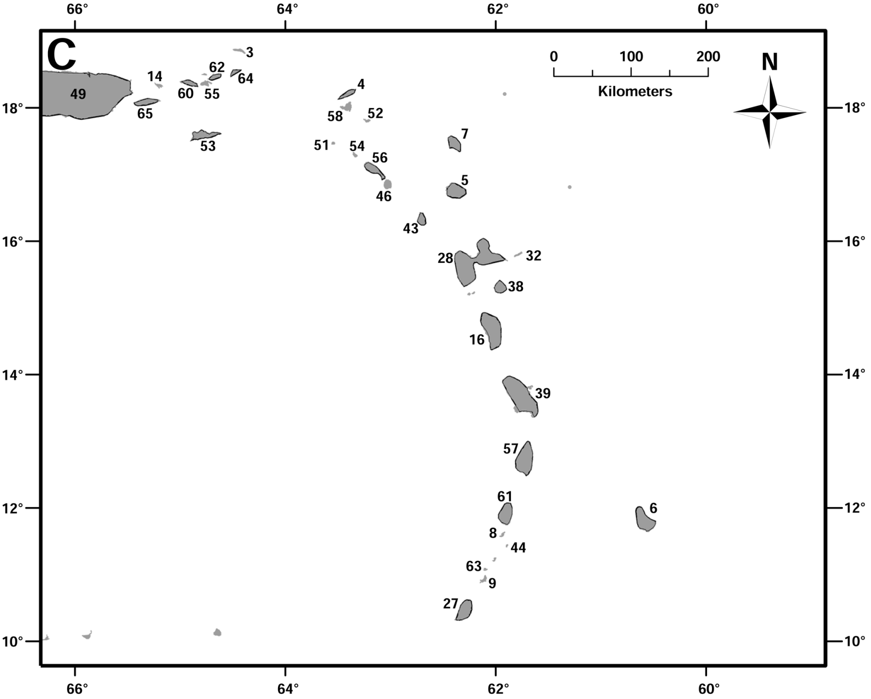

Figure 8.1. *(continued)*

species richness (the number of species per island) and generic richness (the number of genera per island) of bats on each island. Guild richness (the number of feeding guilds per island) was the only aspect of functional biodiversity to characterize each island.

To facilitate the identification of core constituents of assemblages for each of the three island groups separately, we determined the frequency of occurrence (the proportion of islands on which a species occurs) of each species; this is equivalent to occupancy in the recent macroecological literature (e.g., Gaston 2003). We considered a species to be an infrequent constituent if its frequency of occurrence (f_i) was less than the average frequency of occurrence ($\overline{f}$) of species in the island group, where

$$\overline{f} = \sum_{i}^{S} f_i/S,$$

and S is species richness of the island group. This is equivalent to the abundance-based metric of rarity advocated in a number of ecological scenarios (e.g., Camargo 1992, 1993; Chalcraft et al. 2004; Stevens and Willig 2000; Willig et al. 2003b).

Hurricane Disturbance

For islands in the Caribbean, we characterized the history of disturbance by major hurricanes (category 3 and above on the Saffir-Simpson scale; Saffir 1973; Simpson 1974) using historical storm track data collected by the NOAA Coastal Services Center (http://hurricane.csc.noaa.gov/hurricanes/). Because monitoring of storms by aircraft and satellites did not begin until 1944 and the mid-1960s, respectively, and storm tracks from before these innovations are uncertain, we used only data from 1944 to 2004. For each island we counted the number of times it experienced a hurricane of each category of intensity, assuming that hurricane-force winds extend, on average, approximately 100 km from the center of a storm (Kimball and Mulekar 2004). We considered a hurricane to directly strike an island if >50% of the area of that island was within this radius. In some cases, islands were sufficiently large that the intensity of a storm might vary as the storm passed over different parts of the island. In such a situation we estimated an average intensity of wind speed for the island. For example, if a hurricane of category 4 struck Hispaniola, but then decreased in intensity to category 3, such that half of the island experienced category 4 winds and half of the island experienced category 3 winds, we assigned the storm an intensity of 3.5. We then quantified disturbance for each island using the following six measures:

1. Number of times the island was struck by hurricanes with an intensity of category 3 or greater (TH).
2. Cumulative intensity of major hurricanes to strike the island (CI). For example, Crooked Island was struck by one category 3 hurricane and two category 4 hurricanes, resulting in a cumulative intensity of 11 (3 + [2 × 4]).
3. Mean intensity of major hurricanes in the Caribbean as experienced by the island (MI). Hurricanes that did not strike the island are included in calculations, each represented by an intensity of 0 (e.g., because 30 hurricanes struck the Caribbean during the time period of interest, MI for Crooked Island was 0.367 (11/30 = {{[27 ×0] + [1 × 3] + [2 × 4]}/30}).
4. Average intensity of major hurricanes experienced by the island (AI), excluding hurricanes that did not strike the island (e.g., AI for Crooked Island was 3.67 = 11/3).
5. Mean return time of major hurricanes striking the island (RT).
6. Standard error of return time of major hurricanes striking the island (SE).

Taken together, these hurricane metrics reflect important attributes of disturbance such as frequency, intensity, and extent. For only one island (Jamaica), major hurricanes made landfall in both of the years representing the endpoints of the time series (i.e., 1944 and 2004). As such, estimates of return time for most islands are based on empirical data that encompass only a portion of the study period. Because these incomplete time series bias estimates of return

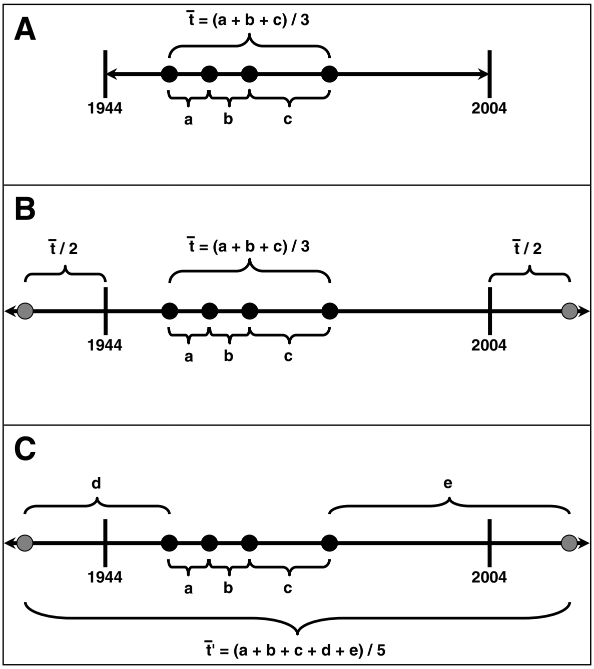

Figure 8.2. Graphic representation of metrics for estimation of return time for hurricanes. The *horizontal line* represents the time line of hurricane disturbance for a particular island. The four *black circles* represent a hypothetical series of hurricanes striking that island between 1944 and 2004, and the *brackets* labeled *a*, *b*, and *c* encompass the time interval between each pair of storms. Return time within the time period encompassing the four hurricanes is estimated as the mean number of years between storms (panel *A*). The best estimate of the year of the nearest storm prior to the observed time series (represented by the leftmost *gray circle* in panel *B*) is found by adding one-half of the mean number of years between observed storms to the endpoint of the observed time series, yielding an estimate of the number of years that passed between the last hurricane prior to 1944 and the first observed hurricane (represented by bracket *d* in panel *C*). The timing of the nearest future storm is estimated likewise (represented by bracket *e* in panel *C*). Overall return time is then estimated as the mean number of years between storms, including both observed and estimated values (panel *C*).

time, we assumed that additional hurricanes struck each island before 1944 and that additional hurricanes will strike each island after 2004, and estimated the time of arrival of these storms by adding one-half of the mean number of years separating each observed hurricane to each end of the time series (fig. 8.2 illustrates details of this calculation). For islands that did not experience any major hurricanes from 1944 to 2004, we similarly assumed that hurricanes had struck the island in the past and would do so again in the future, and we estimated return time as 121 years (the entire time series plus 30.5 years on either side). It is important to note that these metrics are incomplete measures of the potential effects of hurricanes on island ecosystems. Metrics are not based on the observable effects of hurricanes (e.g., habitat destruction and resulting habitat heterogeneity or changes in resource availability) on the particular islands. As such, these metrics are imperfect estimates of hurricane-related disturbance on Caribbean island ecosystems, a necessary weakness when estimating effects of many large, complex disturbance events.

We characterized variation in disturbance history among islands of the Caribbean using principal components analysis (PCA) as implemented by program FACTOR (SPSS 1990b) based on the correlation matrix with a varimax rotation of factors. This approach reduces the six disturbance metrics to a smaller number of composite variables that encapsulate variation among islands. The Kaiser-Meyer-Olkin (Kaiser 1970, 1974) measure of sampling adequacy (KMO) determines how well each variable is characterized by PCA. KMO-values approaching 1 indicate small partial correlations, and KMO values ≥ 0.60 are recommended for optimum functionality of PCA (Tabachnick and Fidell 1989). The KMO for AI was 0.35, considerably below the 0.60 threshold. Therefore, AI was removed from the analysis, and PCA was conducted with only the remaining five measures of hurricane-induced disturbance.

Latitude and Faunal Pools

In general, the geographic distribution of the islands of the Caribbean corresponds to a northwestern to southeastern band (fig. 8.1) that has a strong latitudinal component. In addition, the sources of colonization occur on the periphery of the basin on the mainland of North, Central, or South America. Consequently, latitude and distances to the three sources of colonization are confounded from a statistical perspective. For the 64 islands, latitude is correlated highly and significantly with distance to Miami ($r = 0.930$, $p < 0.001$), Juárez ($r = 0.775$, $p < 0.001$), and Carúpano ($r = 0.916$, $p < 0.001$), each a potential source of colonists. Indeed, 92% of latitudinal variation among islands is accounted for by variation with respect to distances to the three sources of colonization. As a result, we used only latitude in subsequent statistical analyses, recognizing that this variable is a surrogate for geographic position with respect to the three sources of colonization, as well as with respect to the equator.

Statistical Analyses

For each island group (i.e., Bahamas, Greater Antilles, and Lesser Antilles), we evaluated whether the ratio of the number of species of phytophage (i.e., frugivores and nectarivores as a group) to number of species of zoophage (i.e., aerial insectivores, foliage-gleaning insectivores, high-flying insectivores, and piscivores as a group) depended on the classification of taxa as infrequent versus frequent. To do so, we constructed two-by-two contingency tables, and determined significance based on a G-test (Sokal and Rohlf 1995).

As executed in program PROXIMITIES (SPSS 1990b), pairwise similarities in species composition between islands was estimated based on a geometric mean using Ochiai's index (S_3),

$$S_3 = c\,[(c + b)\,(c + a)]^{-0.5},$$

where a is the number of bat species on island A, b is the number of bat species on island B, and c is the number of species common to both islands A and B (Orloci 1966). The resultant island by-island matrix of compositional similarity was transformed to a dissimilarity matrix and subjected to analysis by classical nonmetric multidimensional scaling (MDS) for ordinal data (Schiffman et al. 1981; Young 1981) using program ALSCAL (SPSS 1990a). This method, a nonparametric analog of PCA, facilitates visualization of interisland similarity and delineation of groups of islands with similar species composition.

For each of the island groups separately, least-squares linear regression assessed the extent to which variation in each of a suite of environmental characteristics (i.e., area, maximum elevation, latitude, and hurricane-induced disturbance) influenced variation in either species richness or guild richness. For data combined from all three island groups, an analysis of covariance (ANCOVA, island group as factor, environmental characteristic as covariate, and the factor by covariate interaction) quantified the extent to which each aspect of biodiversity changed with environmental characteristics in an indistinguishable manner for the three island groups. Both ANOVAs and ANCOVAs were executed via the linear model option (R Development Core Team 2005) in R (http://www.R-project.org).

Of course, variation in biodiversity among islands likely is a consequence of simultaneous variation among islands in area, elevation, latitude, and hurricane-induced disturbance. Moreover, such relationships may depend on the identity of the island group (i.e., interactions between each of the covariates and a factor representing island group). A multivariate analysis of covariance quantified the extent to which variation in biodiversity was a function of island group (categorical factor), each of four environmental characteristics (covariates), or a pairwise interaction between each of the four environmental characteristics and island group. These analyses were executed using the linear model option (R Development Core Team 2005) in R (http://www.R-project.org) separately for species richness and for guild richness.

Interisland distances also can affect aspects of biodiversity (MacArthur and Wilson 1967; Morand 2000; Ricklefs and Lovette 1999). Strings of islands can act as stepping stones for colonization from the mainland, or can act as sources of recolonization after local extinction events (i.e., rescue effects, sensu Brown and Kodric-Brown 1977; metapopulation dynamics, sensu Gotelli 1991). This is particularly important in disturbance-mediated systems, such as the Caribbean, where many islands are relatively small and harbor small, extinction-prone populations. Use of interisland distances is a severe violation of assumptions of independence associated with least-squares techniques; consequently, a permutation approach is much preferred over classical regression models in this situation (Manly 1991; Morand et al. 1996). To evaluate the effect of interisland distances in the context of the effects of other environmental characteristics (e.g., area, elevation, and hurricane-induced disturbance), we conducted a multivariate analysis based on distance matrices (Legendre et al. 1995) using program Permute 3.4 (Morand 2000). Analyses were conducted for each of the three island groups separately. Latitude was removed from analyses because it measures the latitudinal aspect of interisland distances and would reduce the amount of unique variation explained by pairwise interisland distances, the variable of primary interest in these analyses. In essence, for each environmental characteristic as well as for species richness and guild richness, we produced an island-by-island matrix of differences in character values, and for distance we produced an island-by-island matrix of interisland geographic distances. In addition, we produced a similar matrix for each of two dependent variables, log species richness and log guild richness. Based on these matrices, multiple regressions were performed to assess the extent to which each matrix for a dependent variable (species richness or guild richness) was a function of a suite of environmental matrices (i.e., island-by-island differences in area, maximum elevation, and hurricane-induced disturbance) as well as interisland distances. Multiple regressions were based on step-up procedures, and were performed for the empirical data, as well as for 999 simulations in which the arrangement of cells in the dependent variable matrix were randomized. Partial regression coefficients from the empirical data were compared to the distribution of equivalent partial regression coefficients obtained from regressions involving the randomizations. Significance was estimated as the proportion of randomized coefficients that were greater than or equal to the empirical coefficient.

Results

We identified 65 islands (19 in the Greater Antilles, 23 in the Bahamas, and 23 in the Lesser Antilles) in the Caribbean for which reliable data were available concerning bat species composition and selected environmental characteristics (appendix 8.1). Aspects of biodiversity as well as environmental characteristics were quite variable among islands. For example, island area spanned ~5 orders of magnitude (5.0 km^2 on East Plana Cay to 114,524.0 km^2 on Cuba) and elevation spanned ~3 orders of magnitude (3,175.0 m on Hispaniola to 5 m on Grand Bahama). Bat species richness attained a maximum of 26 on Cuba; generic richness attained a maximum of 22 on Cuba; and guild richness attained a maximum of 6 on Cuba, Grenada, Hispaniola, Isle of Pines, Jamaica, and St. Vincent. A number of islands in each of the three groups harbored 1 species, and thus only 1 genus and 1 guild (appendix 8.1). Because of the high correla-

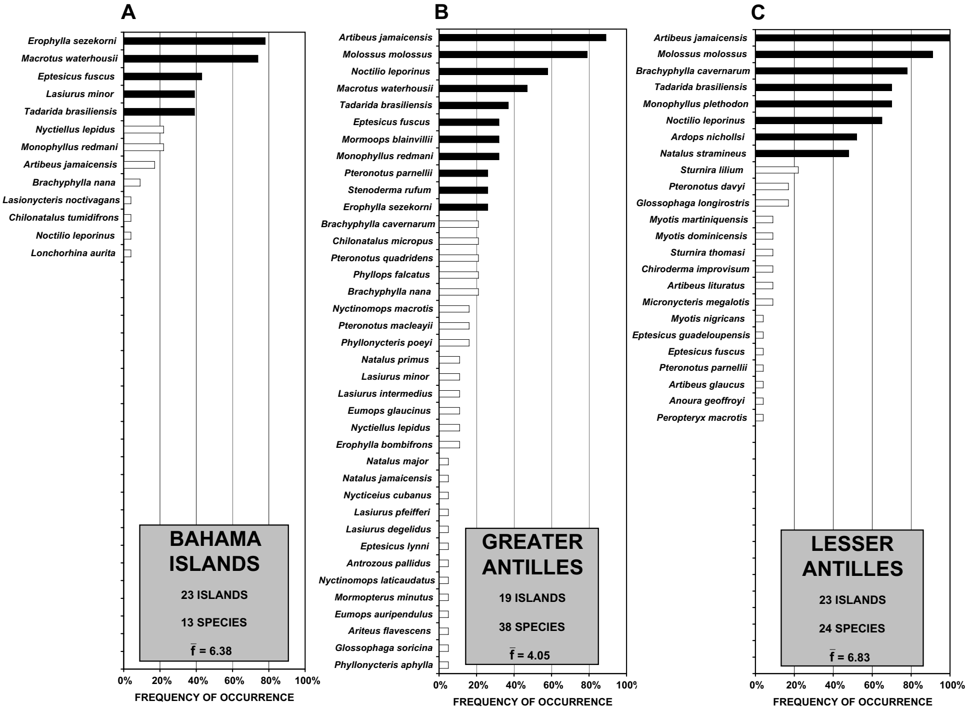

Figure 8.3. Frequency of occurrence of bat species on islands in the Bahamas (*A*), Greater Antilles (*B*), and Lesser Antilles (*C*). Frequent constituents of island assemblages are those whose occurrence exceeds the average frequency of occurrence ($\bar{f}$) of all species in the island group (*black bars*).

tion of species richness to generic richness on each island group (Bahamas, r = 1.000; Greater Antilles, r = 0.996; Lesser Antilles, r = 0.990), we do not present results for statistical analysis of generic richness.

Five species (1 phytophage and 4 zoophages) were frequent members ($f_i > \bar{f}$) of island assemblages in the Bahamas (fig. 8.3A), including 1 nectarivore (*Erophylla sezekorni*), 1 gleaning animalivore (*Macrotus waterhousii*), 2 aerial insectivores (*Eptesicus fuscus*, *Lasiurus minor*), and 1 high-flying insectivore (*Tadarida brasiliensis*). Eleven species (4 phytophages and 7 zoophages) were frequent members of island assemblages in the Greater Antilles (fig. 8.3B), including 2 frugivores (*Artibeus jamaicensis*, *Stenoderma rufum*), 2 nectarivores (*Er. sezekorni*, *Monophyllus redmani*), 1 gleaning animalivore (*Ma. waterhousii*), 2 high-flying insectivores (*Molossus molossus*, *T. brasiliensis*), 3 aerial insectivores (*Ep. fuscus*, *Mormoops blainvillei*, *Pteronotus parnellii*), and 1 piscivore (*Noctilio leporinus*). Eight species (4 phytophages and 4 zoophages) were frequent members of island assemblages in the Lesser Antilles (fig. 8.3C), including 3 frugivores (*Ardops nichollsi*, *Art. jamaicensis*, *Brachyphylla cavernarum*), 1 nectarivore (*Mon.

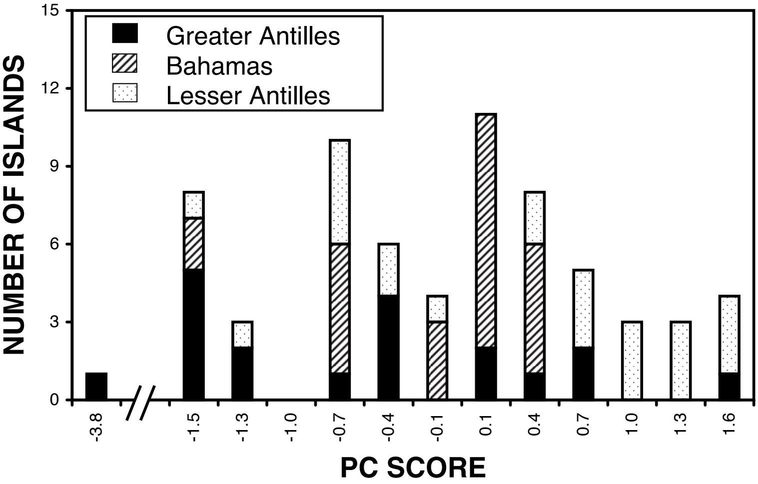

Figure 8.4. Graphical representation of the number of islands from each island group that experienced a particular level of hurricane-induced disturbance, as estimated by the first axis of a principal components analysis of disturbance metrics (see text for details).

plethodon), 1 aerial insectivore (*Natalus stramineus*), 2 high-flying insectivores (*Mol. molossus*, *T. brasiliensis*), and 1 piscivore (*No. leporinus*). The ratio of phytophages to zoophages was independent of whether species were frequent or infrequent members of island assemblages for each of the three island groups: the Bahamas ($G = 1.25$, df = 1, $p = 0.268$), the Lesser Antilles ($G = 0.08$, df = 1, $p = 0.772$), and the Greater Antilles ($G = 0.06$, df = 1, $p = 0.799$). Thus, feeding guild affiliations do not predispose species to successfully colonize or persist on islands.

Variation among 64 islands in hurricane-induced disturbance characteristics can be visualized by a single principal component (PC score) axis that accounts for 87.5% of the interisland variation in the original characteristics (fig. 8.4). Measures of hurricane frequency (TH) and intensity (CI and MI) were correlated positively to PC score, whereas measures of return time (RT and SE) were correlated negatively to PC score. Islands from each of the three groups were represented throughout the range of the PC axis. However, Cuba occurred to the far left of the axis (low frequency, low intensity, and high return time), and mean PC scores were higher (high frequency, high intensity, and low return time) for Lesser Antilles than for other island groups.

Simple Patterns of Species Richness

In general, variation in area or, to a lesser extent, elevation had significant effects on variation in bat species richness, whereas variation in latitude had a significant effect only in the Greater Antilles and hurricane disturbance had no significant effects (table 8.1). More specifically, the relationship between species richness and area was positive and significant for each of the three island groups (fig. 8.5A), although it was somewhat weaker in the Bahamas than in either the Greater or Lesser Antilles (table 8.1). The rate of increase in species richness with area depended on island group (significant interaction, table 8.2), being greater on the Lesser Antilles and Greater Antilles, and smaller on the Bahamas (fig. 8.5A).

The relationship between species richness and elevation was positive and significant for the Greater and Lesser Antilles, but not significant for the Bahamas (table 8.1). Because the standard errors of the slopes were generally high for each of the three island groups and range of elevations in the Bahamas was small (fig. 8.5B), no significant differences were detected among island groups with respect to elevational rates of increase in richness (table 8.2).

Simple Patterns of Guild Richness

Guild richness increased with area for each of the three island groups (table 8.1), and did so in a parallel fashion (nonsignificant interaction, table 8.2). The impression of differences in slope among the island groups (fig. 8.5C) is no greater than expected by chance alone, given the variability in the estimates of slope.

For the Greater and Lesser Antilles, guild richness significantly increased with elevational relief (table 8.1). Because the standard errors of the slopes generally were high for each of the three island groups and range of elevations

Table 8.1. Regression results of the effects of island area, elevation, latitude, and hurricane–induced disturbance on bat species and guild richness in the Bahamas, Greater Antilles, and Lesser Antilles

	Species richness				Guild richness			
	Slope	Standard error	r^2	p–value	Slope	Standard error	r^2	p–value
Area								
Bahamas	**0.115**	**0.053**	**0.181**	**0.043**	**0.095**	**0.045**	**0.173**	**0.049**
Greater Antilles	**0.255**	**0.029**	**0.823**	**<0.001**	**0.117**	**0.020**	**0.672**	**<0.001**
Lesser Antilles	**0.262**	**0.045**	**0.622**	**<0.001**	**0.168**	**0.034**	**0.546**	**<0.001**
Elevation								
Bahamas	3.616	3.140	0.077	0.267	3.860	2.591	0.122	0.156
Greater Antilles	**0.293**	**0.064**	**0.550**	**<0.001**	**0.126**	**0.038**	**0.390**	**0.004**
Lesser Antilles	**0.321**	**0.079**	**0.441**	**<0.001**	**0.148**	**0.065**	**0.199**	**0.033**
Latitude								
Bahamas	0.003	0.025	0.001	0.905	−0.001	0.021	0.000	0.982
Greater Antilles	**0.141**	**0.065**	**0.216**	**0.045**	0.066	0.034	0.182	0.069
Lesser Antilles	0.030	0.022	0.079	0.195	0.012	0.016	0.027	0.451
Hurricane								
Bahamas	0.033	0.061	0.013	0.600	0.014	0.052	0.003	0.793
Greater Antilles	−0.078	0.069	0.069	0.278	−0.033	0.036	0.048	0.368
Lesser Antilles	0.010	0.058	0.001	0.866	−0.018	0.040	0.009	0.662

Note: Slope and standard error represent changes in log(richness) per log(km^2), km, and degree for analyses of area, elevation, and latitude, respectively. Bold numbers represent significant regressions.

Table 8.2. Analysis of covariance showing the effects of island area, elevation, latitude, and hurricane-induced disturbance on bat species and guild richness

	Species richness					Guild richness				
	p-value					*p*-value				
	Island group	Independent variable	Interaction	Overall model	r^2	Island group	Independent variable	Interaction	Overall model	r^2
Area	<**0.001**	**<0.001**	**0.037**	**<0.001**	0.664	**0.012**	**<0.001**	0.379	**<0.001**	0.458
Elevation	**0.005**	**<0.001**	0.607	**<0.001**	0.461	0.156	**<0.001**	0.319	**0.002**	0.222
Latitude	**0.006**	0.058	0.072	**0.003**	0.195	0.071	0.226	0.244	0.094	0.071
Hurricane	**0.009**	0.442	0.409	**0.040**	0.105	0.081	0.428	0.752	0.280	0.022

Note: Bold numbers correspond to significant results for particular independent variables or overall models.

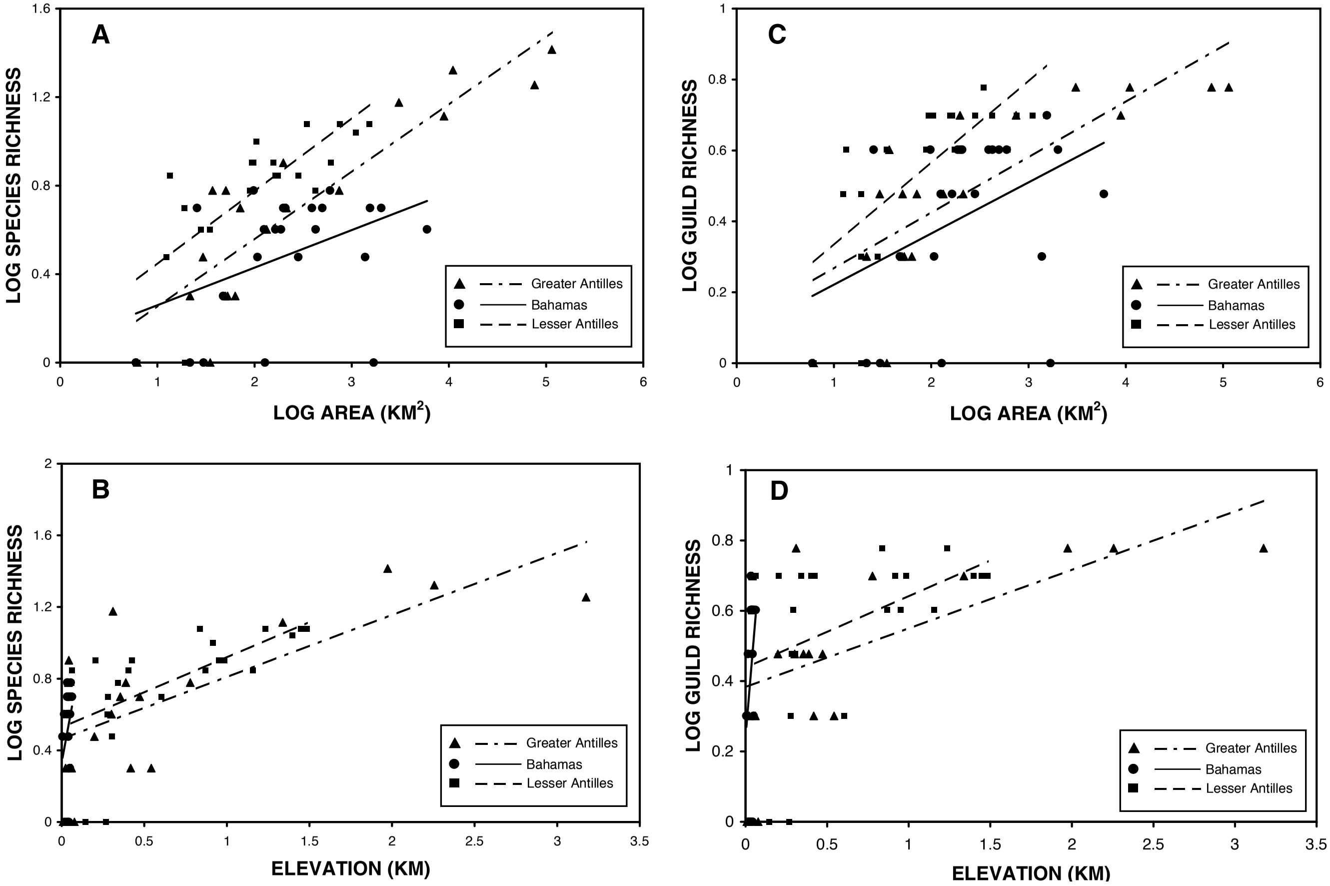

Figure 8.5. Scatter plots of log species richness (left column, *A*, *B*) and log guild richness (right column, *C*, *D*) as a function of log island area (top row, *A*, *C*) and elevation (bottom row, *B*, *D*).

in the Bahamas was small (fig. 8.5D), no significant differences were detected among island groups with respect to elevational rates of increase in guild richness (nonsignificant interaction, table 8.2).

Based on simple regressions, variation in latitude or hurricane-induced disturbance had no effect on variation in guild richness for any of the three island groups (table 8.1). This was reaffirmed by the nonsignificant effects of latitude and hurricane-induced disturbance on guild richness, whether assessed as a main effect or as an interaction with island group (table 8.2).

Complex Patterns

Bat species richness ($R^2 = 0.72$, $p << 0.001$) as well as guild richness ($R^2 = 0.49$, $p << 0.001$) responded in similar fashions to variation in environmental characteristics among islands based on multivariate analysis of covariance. Area ($R^2 = 0.55$), island group ($R^2 = 0.11$), and the interaction between island group and area ($R^2 = 0.03$) contributed significantly to variation in species richness, whereas effects of elevation ($R^2 = 0.02$) and the interaction between island group and elevation ($R^2 = 0.03$) on variation of species richness approached significance (table 8.3). Only area ($R^2 = 0.42$) contributed significantly to variation in guild richness, although effects of island group ($R^2 = 0.05$) on variation of guild richness approached significance (table 8.3).

Regardless of island group, multiple regression analyses based on matrix permutations were consistent for species richness. Only differences in area between islands statistically accounted for differences between islands in species richness (regression coefficients [*b*] for Bahamas, $b = 0.231$, $p = 0.019$; Greater Antilles, $b = 0.779$, $p = 0.001$; Lesser Antilles, $b = 0.533$, $p = 0.001$). Similarly, only differences in area between islands accounted for differences in guild richness between islands of the Bahamas ($b = 0.238$, $p = 0.015$). However, differences in area and elevation between islands statistically accounted for variation in

Table 8.3. Multivariate analysis of covariance showing the effects of island group, area, elevation, latitude, and hurricane-induced disturbance, as well as interactions between island group and each covariate, on bat species richness and guild richness, separately

		Species richness				Guild richness			
	df	SS	MS	F-value	Significance	SS	MS	F-value	Significance
Island group (IG)	2	0.464	0.232	10.987	***	0.081	0.041	2.904	@
Area (A)	1	2.419	2.419	114.685	***	0.678	0.678	48.498	***
Elevation (E)	1	0.067	0.067	3.175	@	0.001	0.001	0.097	
Latitude (L)	1	0.029	0.029	1.351		0.001	0.001	0.036	
Hurricane (H)	1	0.041	0.041	1.951		0.018	0.018	1.293	
IG × A	2	0.143	0.072	3.396	*	0.051	0.025	1.815	
IG × E	2	0.128	0.064	3.028	@	0.068	0.034	2.416	
IG × L	2	0.092	0.046	2.186		0.043	0.022	1.550	
IG × H	2	0.055	0.027	1.292		0.032	0.016	1.153	
Residuals	45	0.949	0.021			0.629	0.014		

Note: df = degrees of freedom; SS = sums of squares; MS = mean squares.

$^{@}0.050 < p \leq 0.100$ *$0.010 < p \leq 0.050$ *** $p < 0.001$

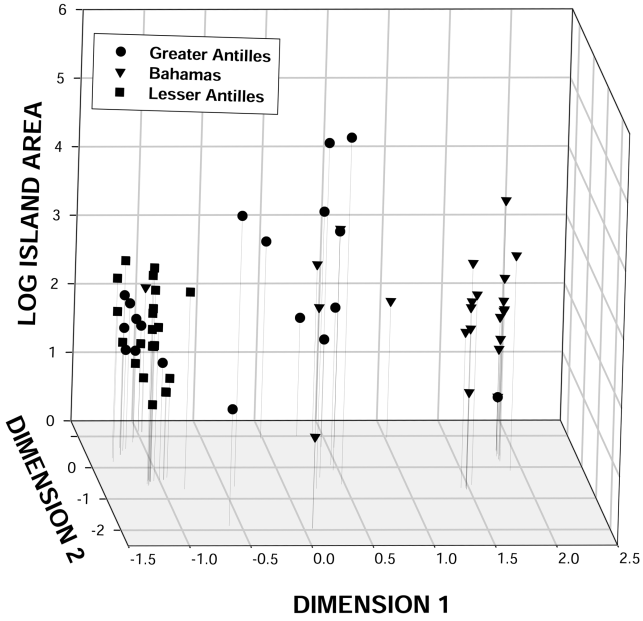

Figure 8.6. Three-dimensional representation of the relationships among islands of the Caribbean based on species composition (dimensions 1 and 2 from nonmetric multidimensional scaling) and island size (log area).

guild richness between islands of the Greater Antilles (area, $b = 0.821$, $p = 0.001$; elevation, $b = -0.356$, $p = 0.004$) or between islands of the Lesser Antilles (area, $b = 0.521$, $p = 0.002$; elevation, $b = -0.174$, $p = 0.007$). Importantly, interisland distance was not a strong candidate for entry into multiple regression solutions for species richness (Bahamas, $b = 0.012$, $p = 0.066$; Greater Antilles, $b = 0.062$, $p = 0.124$; Lesser Antilles, $b = 0.131$, $p = 0.030$) or guild richness (Bahamas, $b = -0.060$, $p = 0.234$; Greater Antilles, $b = 0.120$, $p = 0.075$; Lesser Antilles, $b = 0.024$, $p = 0.305$), compared to equivalent values for area.

Patterns of Compositional Similarity

The two-dimensional representation of islands based on similarities in species composition was quite faithful to the empirical interrelationships of islands in multidimensional space (MDS) based on presence and absence of species (stress was low, 0.187, and the squared correlation was high, 0.855). Three distinct clusters of islands can be recognized from the ordination of Ochiai's index using multidimensional scaling (fig. 8.6). For the most part, the three clusters correspond to the Bahamas (high positive scores [>1] on dimension 1), Greater Antilles (low positive scores [between 0 and 1] on dimension 1), and the Lesser Antilles (negative scores on dimension 1). A number of islands in the Bahamas (i.e., Fortuna, Great Inagua, Little Abaco, and Mayaguana), mostly larger and southern islands, were associated with the Greater Antilles cluster. Similarly, a number of islands in the Greater Antilles (i.e., Anegada, Culebra, St. Croix, St. Thomas, St. John, Tortola, Vieques, and Virgin Gorda), all small and near the Windward Islands, as well as a single island from the Bahamas (Little Inagua), were associated with the Lesser Antilles cluster.

Discussion

Given the location of the West Indies within the Caribbean—a primary center of global evolution (Croizat 1952)—it is unsurprising that research in the Caribbean Basin has provided rich contributions to the disciplines of biogeography, systematics, and ecology (e.g., Liebherr 1988; Schwartz and Henderson 1991; Woods 1989; Woods and Sergile 2001). For example, the excellent fit of data for the West Indian herpetofauna to the log-log relationship predicted between richness and area provided compelling evidence of the power of quantitative models in biogeography (MacArthur 1972; MacArthur and Wilson 1967). The fit of data for West Indian bats was no less compelling, whether considering only Greater Antilles or only Lesser Antilles (Griffiths and Klingener 1988). Indeed, research in the Caribbean has provided critical contributions to the understanding of island biogeographic principles, especially as they apply to mammals (e.g., Baker and Genoways 1978; Dávalos 2004; Fleming 1982). Moreover, confidence in species-area models as predictive tools was so great that displacement of particular islands from best-fit lines (i.e., residual variation) became and remains fodder for discussion about the effects of extinction or colonization routes on the species composition of particular islands (e.g., Gannon et al. 2005; Griffiths and Klingener 1988; Willig and Gannon 1996).

Variation in Species Composition

In general, each of the three island groups harbors distinctive combinations of species. This is reflected in the clustering of islands based on dimension 1 in MDS (fig. 8.6). In situations where islands from one group were associated with a cluster of islands that represents another island group, they do so because of geographic proximity to that group. In terms of frequency of occurrence in island assemblages (fig. 8.3), our results reaffirm the designation of *Art. jamaicensis*, *Mol. molossus*, *No. leporinus*, *T. brasiliensis*, *Mon. redmani*, or *Mon. plethodon*, and *B. cavernarum* as core constituents of Antillean assemblages (Rodríguez-Durán and Kunz 2001). In addition, we identify the frequent appearance of *Ard. nichollsi* or *Na. stramineus* in an island assemblage as indicative of the Lesser Antilles, and the frequent appearance of *Mor. blainvillei*, *B. nana*, *Pt. parnelli*, or *S. rufum* in an island assemblage as indicative of the Greater Antilles. Only one species, *T. brasiliensis*, is a frequent member of assemblages in the Bahamas and a core species in Antillean assemblages. Otherwise, the infrequent appearance of *Art. jamaicensis*, and especially *Mol. molossus* and *No. leporinus*, distinguishes assemblages in the Bahamas from those on the Antilles.

Gradients of Biodiversity

Comparative island biogeographic analyses have documented that birds and bats in the Greater and Lesser Antilles evince parallel trends with respect to species-area relationships, trophic diversity-area relationships, and interisland faunal similarity (Fleming 1982). In contrast, the species richness of bats, birds, butterflies, and herptiles responded to a suite of island characteristics (i.e., area, elevation, habitat diversity) in a taxon-specific manner in the Lesser Antilles (Ricklefs and Lovette 1999). In particular, bat richness responded only to island area, whereas each of the other three groups responded to area as well as to elevation or habitat diversity. A reanalysis of Ricklefs and Lovette's data (1999) by Morand (2000) that included interisland distances arrived at similar general conclusions about taxon-specific responses to environmental variation among islands. However, the outcome for bats was quite remarkable in that island area, as well as maximum elevation and habitat diversity, had no effect on variation in species richness, whereas interisland distance was the only environmental characteristic to affect variation in species richness. This suggested that movement of individuals among islands in the Lesser Antilles buffered species populations and facilitated recolonization after local extinction events, thereby representing the dominant factor affecting richness.

Because environmental attributes of islands may be correlated highly, it is quite challenging, if not impossible, to disentangle their separate effects on species richness or guild richness. Moreover, the extent of correlation depends on the particular island system under study (table 8.4). In the Bahamas, none of the environmental characteristics exhibit significant correlations. In contrast, area and elevation are statistically and positively correlated in the Greater Antilles and in the Lesser Antilles. Hurricane-related disturbance is associated significantly and negatively with latitude in the Greater Antilles, but not in a linear fashion. In the Lesser Antilles, hurricane-related disturbance and latitude are related positively and significantly. These differences in aspects of correlation between environmental characteristics could give rise to different results in the context of multiple regression analysis even if the underlying mechanistic bases for variation in biodiversity are equivalent. Similarly, ANCOVA, which controls for differences among island groups, can lead to controvertible interpretations if island groups (the categorical factor in the ANCOVA), on average, differ with regard to environmental attributes.

The preponderance of evidence from our analyses (simple regression, table 8.1; ANCOVA, table 8.2; and multivariate ANCOVA, table 8.3), in contrast to those of Morand (2000), suggests that area or elevation have the dominant effect on taxonomic and functional aspects of bat biodiversity on islands in the Caribbean, and the magnitude and direction of the effects are consistent

Table 8.4. Correlations for log species richness, log generic richness, log guild richness, and environmental characteristics of islands for the Bahamas, Greater Antilles, and Lesser Antilles, separately

			Correlations						
	Min	Max	Species	Genera	Guilds	Area	Elevation	Latitude	Hurricane
Bahamas									
Species	0.00	0.78	—	**0.991**	**0.968**	**0.425**	0.277	0.026	0.115
Genera	0.00	0.78	**0.998**	—	**0.972**	0.388	0.361	−0.028	0.103
Guilds	0.00	0.70	**0.919**	**0.920**	—	**0.416**	0.349	−0.005	0.058
Area	0.78	3.78	0.346	0.330	0.396	—	−0.081	**0.481**	0.039
Elevation	5.00	62.50	0.320	0.344	0.276	−0.009	—	−0.103	0.090
Latitude	21.05	26.89	0.025	0.000	0.029	**0.456**	0.079	—	0.259
Hurricane	−1.48	1.72	0.086	0.079	0.004	0.146	0.091	0.249	—
Greater Antilles									
Species	0.00	1.41	—	**0.999**	**0.947**	**0.907**	**0.742**	**0.465**	−0.262
Genera	0.00	0.78	**1.000**	—	**0.955**	**0.897**	**0.725**	**0.466**	−0.259
Guilds	0.00	0.78	**0.978**	**0.978**	—	**0.820**	**0.625**	0.426	−0.219
Area	0.79	5.06	**0.849**	**0.849**	**0.844**	—	**0.866**	0.444	−0.383
Elevation	8.00	3175.00	**0.616**	**0.616**	**0.588**	**0.679**	—	0.131	−0.185
Latitude	17.73	21.96	0.259	0.259	0.285	0.131	−0.104	—	**−0.607**
Hurricane	−3.78	1.62	−0.200	−0.200	−0.257	−0.322	−0.106	−0.322	—
Lesser Antilles									
Species	0.00	1.08	—	**0.996**	**0.907**	**0.789**	**0.664**	0.280	0.037
Genera	0.00	0.78	**0.988**	—	**0.900**	**0.780**	**0.672**	0.306	0.044
Guilds	0.00	0.78	**0.860**	**0.824**	—	**0.739**	**0.446**	0.165	−0.096
Area	0.79	3.18	**0.787**	**0.792**	**0.741**	—	**0.625**	−0.026	−0.213
Elevation	59.00	1484.10	**0.727**	**0.768**	**0.470**	**0.608**	—	−0.020	−0.056
Latitude	12.11	18.22	0.046	0.065	−0.035	−0.140	−0.075	—	**0.642**
Hurricane	−1.23	1.70	0.041	0.055	−0.072	−0.229	−0.041	**0.520**	—

Note: **Values above dashes are** Pearson-product moment **correlations. Values below dashes are** Spearman rank correlations. Significant results (i.e., p–value ≤ 0.05) are bold. Range of values for biodiversity and island characteristics are reported as minima (Min) and maxima (Max). Species = log species richness; Genera = log generic richness; Guilds = log guild richness; Area = area in log of square kilometers; Elevation = maximum elevation in meters; Latitude = latitude in decimal degrees; Hurricane = hurricane-induced disturbance as PC1 score.

for each island groups (i.e., lack of significant interactions for most analyses; table 8.2, fig. 8.5). Considering the exceptional dispersal abilities of bats and the strong relationship between island area and bat species richness, interisland distances may not be sufficiently great to influence bat species richness (i.e., interisland dispersal may be accomplished equivalently regardless of interisland distance). The effects of hurricane-related disturbance on species richness are not sufficiently strong to appear in simple regressions for each island group (table 8.1). In addition, effects of latitude evinced a significant response only for species richness in the Greater Antilles. Moreover, when data for the three island groups are combined, the effects of hurricane-related disturbance and latitude fail to account for a significant portion of variation in species or guild richness (table 8.2). Clearly, latitude and hurricane-related disturbance play minor roles at best in affecting variation in aspects of biodiversity in these Caribbean islands.

Effects of area per se may be confounded by the positive association between habitat diversity and area, as has been suggested by many others (e.g., MacArthur 1972; MacArthur and Wilson 1963; Ricklefs and Lovette 1999). Habitat diversity on islands often arises as a consequence of variation in elevation and the underlying environmental gradients of temperature and precipitation. Moreover, the maximum elevation of islands is correlated with island area, at least for island groups with appreciable variation in area and elevation (e.g., the Greater and Lesser Antilles, but not the Bahamas; table 8.4); thus the effects of area per se and elevation per se are confounded by the positive association between them with respect to two of the three island groups (table 8.4). Importantly, the "unique" variation from a statistical analysis that is attributable to area, or to any particular environmental characteristic, does not equal the effects of area, per se (or any particular environmental character, per se). The confounded nature of variation in environmental characteristics in nature (e.g., correlation between area and maximum elevation in the Caribbean) prevents identification of the ultimate mechanism responsible for variation in an associated dependent variable, such as an aspect of biodiversity.

Development of the concepts of area per se and habitat heterogeneity relate clearly to parallel developments that consider species richness to have spatial components termed alpha, beta, and gamma diversity (Whittaker 1960). We recognize that a variety of definitions and quantifications exist for each type of diversity (e.g., Koleff and Gaston 2002; Whittaker 1972), but follow the convention (Schneider 2001; Willig et al. 2003a) of defining alpha diversity as species richness within a community or habitat type, beta diversity as the turnover in species composition among communities or habitat types, and gamma diversity as the richness of a landscape (in this context, an island). Using these conventions, we explore how parameters of species-area relationships (gamma diversity as a function of island area) relate to area per se and habitat heterogeneity, a controversy of some vehemence (Gray et al. 2004a, 2004b; Scheiner 2003, 2004). Little variation in elevation (and habitat diversity) characterizes the Bahamas (table 8.4). Consequently, the relationship between aspects of biodiversity and area (species richness, slope = 0.166, $r^2 = 0.190$; guild richness, slope = 0.145, $r^2 = 0.231$) in the Bahamas may essentially represent the effects of area per se, at least from the perspective of mobile vertebrates such as bats, rather than reflect the turnover of species that arises as a consequence of habitat heterogeneity. For the other two island groups, the effects of area on aspects of biodiversity likely reflect area per se as well as area's correlates (e.g., habitat diversity), and these manifest as greater slopes and higher values of r^2 for both species richness (Greater Antilles, slope = 0.303, $r^2 = 0.760$; Lesser Antilles, slope = 0.388, $r^2 = 0.588$) and guild richness (Greater Antilles, slope = 0.135, $r^2 = 0.535$; Lesser Antilles, slope = 0.243, $r^2 = 0.473$), compared to the situation in the Bahamas. If the average alpha diversity on islands in the Greater and Lesser Antilles is comparable to that in the Bahamas, then the effect of beta diversity in the Antilles is to double the rate of increase in richness with area on a log-log scale, and to do so while accounting for two to three times as much of the variation among island in richness. This spatial context for understanding variation in bat diversity is similar to that for anoline lizards in the Greater Antilles (Losos 1996), where the species-area relationship arose because larger islands had more occupied habitat niches and a greater number of closely related species that were ecologically similar and distributed allopatrically, compared to the situation on smaller islands. Additional evolutionary and ecological exploration from theoretical and empirical perspectives is necessary to fully understand the relative contributions of alpha and beta diversity to species-area curves concerning gamma diversity on islands.

In addition to significant associations between island area, elevation, and habitat diversity, elevational relief and area enhance the likelihood that caves exist on islands (Rodríguez-Durán, chapter 9, this volume). Caves augment species richness by providing suitable roosts for a number of Caribbean taxa (e.g., *Brachyphylla* spp., *Monophyllus* spp., *Erophylla* spp., *S. rufum*, *No. leporinus*, *T. brasiliensis*, *Mor. blainvillei*, *Pteronotus* spp., *Eptesicus* spp.; Gannon et. al. 2005; Rodríguez-Durán, chapter 9, this volume) and by buffering such species from the negative effects of intense disturbances such as hurricanes. Thus, islands with greater elevational relief (e.g., Greater and Lesser Antilles) likely provide a larger number of cave-roosting opportunities than do islands with less elevational relief (e.g., Bahamas), thereby enhancing bat species richness, especially that of cavernicolous taxa.

Interisland Distance

Our analyses included all 18 islands for which Ricklefs and Lovette (1999) and Morand (2000) analyzed bat species richness in the Lesser Antilles. A comparison of the data used by those authors (table 1 in Ricklefs and Lovette 1999) to those derived from our literature search (appendix 8.2) reveals that distributional data for bats have improved for 11 of 18 islands in the Lesser Antilles, with new records representing additions of as many as eight species to a single island (i.e., Marie-Galante). Moreover, we obtained data for 5 additional islands. Analyses based on permutation methods that incorporate new and more accurate data for the Lesser Antilles support the conclusions of Ricklefs and Lovette (1999) rather than those of Morand (2000), at least with respect to bats. That is, interisland distance had no effect on species richness or guild richness, whereas area had a strong positive effect on both aspects of biodiversity in the Lesser Antilles, as well as in the Greater Antilles and the Bahamas (table 8.4).

Latitude

It was unexpected that variation in latitude would have such little effect on variation in aspects of biodiversity, especially given the rapid rate of increase in both bat species richness (Willig and Sandlin 1991; Willig and Selcer 1989) and trophic richness (Stevens et al. 2003) over a comparable range of latitudes on the continental New World (see Willig et al. 2003a). A variety of explanations may account for such nonsignificance. Analyses within island groups may comprise too small an extent to detect a latitudinal effect. Moreover, considerable variation in characteristics of island size and elevation at similar latitudes enhances dispersion, thereby diminishing power to detect latitudinal effects. When island groups are combined in an ANCOVA setting, the significance associated with island group may, in fact, reflect mean differences in the latitudinal distribution of islands, reducing the likelihood of detecting the effects of latitudinal covariates.

Disturbance

Surprisingly, variation in hurricane-related disturbance had little effect on variation in aspects of biodiversity for islands in the Caribbean. A number of explanations may account for this, in addition to the obvious conclusion that disturbance, or the multivariate surrogate for it, has no lasting effect on biodiversity. First, the likelihood of a particular island occurring in the path of a major hurricane is small, and when such disturbance does cause local extinctions, rescue effects from nearby islands countermand the reduction in richness. This explanation accounts for the absence of an effect for hurricane-related disturbance and for interisland distance, which may counterbalance each other, so that their separate effects are undetectable. Alternatively, the long-term effects of hurricane-related disturbance may be area-dependent. That is, aspects of biodiversity on large islands may be enhanced by hurricanes, as these disturbances effectively maintain or increase habitat heterogeneity, prevent dominant species from outcompeting less dominant species, and have relatively low likelihood of causing islandwide extirpation of a species. In contrast, on small islands, the effects of hurricanes may be devastating, enhancing species extinction rates, or effectively negligible, as interisland recolonization may countermand hurricane effects.

Conclusions

Our results strongly support the contention that area and its correlates (e.g., habitat diversity or elevation) are the primary factors determining variation in aspects of biodiversity among islands within the Bahamas, Greater Antilles, and Lesser Antilles. Moreover, spatial attributes such as latitude or interisland distance contributed little to no variation in aspects of biodiversity within island groups. Nonetheless, island group was a significant factor affecting aspects of biodiversity, including species composition. Island group reflects spatial position (e.g., latitude) as well as proximity to mainland sources of colonization. As such, the relevance of latitude and proximity to sources of colonization may not be discounted, even though they clearly play a smaller role than does area and its correlates in determining patterns of species richness or guild richness. Finally, local extinctions associated with hurricane-related disturbance may be countermanded by interisland rescue effects, such that neither characteristic assumes pervasive importance in determining patterns of biodiversity on Caribbean islands.

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APPENDIX 8.1

Table A8.1. Geographic characters and bat richness estimates for 64 Caribbean islands

Island code	Island name	Island group	Area (km^2)	Maximum elevation (m)	North latitude	West longitude	Distance (km)			Previous records[a]	Bat richness		
							Miami	Juárez	Carúpano		Species	Genus	Guild
1	Acklins	BA	497.0	43.3	22.42	73.96	708	1,280	1,715		5	5	4
2	Andros	BA	5,957.0	15.0	24.39	77.92	209	926	2,078		4	4	3
3	Anegada	GA	34.0	8.0	18.74	64.34	1,805	2,349	900		1	1	1
4	Anguilla	LA	88.0	59.0	18.22	63.06	1,932	2,468	817	5	6	6	4
5	Antigua	LA	279.7	402.0	17.07	61.79	2,105	2,632	708	7	7	7	5
6	Barbados	LA	422.0	340.0	13.17	59.57	2,531	2,986	472	6	6	6	5
7	Barbuda	LA	161.9	62.5	17.64	61.81	2,078	2,614	771	6	7	6	5
8	Bequia	LA	18.1	268.2	13.01	61.23	2,413	2,841	336		1	1	1
9	Carriacou	LA	33.7	291.0	12.47	61.45	2,434	2,831	272		4	4	4
10	Cat Island	BA	388.0	62.5	24.40	75.52	463	1,189	1,942		5	5	4
11	Cayman Brac	GA	36.0	40.0	19.72	79.80	689	779	2,038		6	6	4
12	Crooked Island	BA	196.8	47.2	22.74	74.20	672	1,289	1,742		5	5	4
13	Cuba	GA	114,524.0	1,974.0	21.96	78.92	290	200	1,561	26	26	22	6
14	Culebra	GA	28.5	198.0	18.32	65.29	1,745	2,261	874		3	3	3
15	Darby Island	BA	28.9		23.69	76.05	456	1,203	2,014		1	1	1
16	Dominica	LA	750.0	1,447.0	15.43	61.34	2,223	2,713	535	12	12	12	5
17	East Caicos	BA	46.6	49.7	21.71	71.51	981	1,782	1,499		2	2	2
18	Eleuthera	BA	424.8	51.2	25.24	76.28	345	1,125	2,042		4	4	4
19	East Plana Cay	BA	5.0	19.2	22.62	73.51	763	1,431	1,733		1	1	1
20	Fortune Island	BA	20.7		22.59	74.35	684	1,348	1,791		1	1	1
21	Great Abaco	BA	2,009.8	41.0	26.41	77.20	281	1,080	2,214		5	5	4
22	Grand Bahama	BA	1,373.0	5.0	26.65	78.45	163	989	2,314		3	3	2
23	Grand Cayman	GA	196.8	43.0	19.30	81.25	699	590	2,133		8	8	5
24	Great Exuma	BA	186.0	32.0	23.57	75.88	445	1,125	1,924		4	4	4
25	Great Inagua	BA	1,544.0	33.2	21.05	73.36	835	1,343	1,543		5	5	5
26	Gonâve	GA	743.3	778.0	18.84	73.05	1,036	1,430	1,363		6	6	5
27	Grenada	LA	344.0	838.0	12.11	61.67	2,432	2,831	218	12	12	10	6
28	Guadeloupe	LA	1,510.0	1,484.1	16.26	61.56	2,160	2,659	608	10	12	11	5
29	Hispaniola	GA	76,070.8	3,175.0	18.93	71.09	944	1,307	1,007	17	18	17	6
30	Isle of Pines	GA	3,059.2	310.0	21.70	82.82	512	384	2,388		15	15	6
31	Jamaica	GA	10,991.0	2,256.0	18.16	77.33	753	935	1,606	21	21	18	6
32	La Désirade	LA	27.0	276.0	16.32	61.03	2,231	2,750	684		4	4	2
33	Little Abaco	BA	1,681.0	431.3	26.89	77.71	279	1,124	2,340		1	1	1

Table A8.1. (*continued*)

Island code	Island name	Island group	Area (km^2)	Maximum elevation (m)	North latitude	West longitude	Distance (km)			Previous records[a]	Bat richness		
							Miami	Juárez	Carúpano		Species	Genus	Guild
35	Little Exuma	BA	24.6		23.43	75.58	529	1,180	1,923		5	5	4
36	Little Inagua	BA	127.0	33.5	21.49	73.01	890	1,466	1,607		1	1	1
37	Long Island	BA	596.0	54.2	23.39	75.10	472	1,207	1,815		6	6	4
38	Marie-Galante	LA	155.4	204.0	15.93	61.26	2,214	2,713	608	1	8	8	5
39	Martinique	LA	1,100.7	1,397.0	14.65	61.02	2,296	2,768	472	9	11	11	5
40	Mayaguana	BA	280.9	40.0	22.38	72.93	811	1,413	1,638		3	3	3
41	Middle Caicos	BA	124.3		21.81	71.73	954	1,544	1,518		4	4	3
42	Mona Island	GA	49.2	60.0	18.08	67.89	1,521	2,001	960		2	2	2
43	Montserrat	LA	103.6	915.0	16.73	62.19	2,087	2,605	672	7	10	10	5
44	Mustique	LA	5.2	145.0	12.87	61.18	2,423	2,859	327		1	1	1
45	Navassa	GA	5.2	77.0	18.42	75.03	983	1,264	1,508		1	1	1
46	Nevis	LA	93.0	985.0	17.15	62.58	2,033	2,549	708	1	8	8	5
47	New Providence	BA	207.0	37.5	25.04	77.41	272	1,026	2,151		5	5	4
48	North Caicos	BA	106.2		21.90	71.96	936	1,528	1,535		3	3	2
49	Puerto Rico	GA	8,897.0	1,338.0	18.24	66.46	1,552	2,051	853	13	13	12	5
50	Providenciales	BA	97.0	34.0	21.78	72.25	917	1,547	1,582		6	6	4
51	Saba	LA	12.4	869.0	17.64	63.23	1,951	2,478	762	3	7	7	4
52	Saint Barthélemy	LA	18.0	281.0	17.90	62.83	1,969	2,505	790	1	5	5	3
53	Saint Croix	GA	212.2	354.8	17.73	64.73	1,797	2,296	799		5	5	3
54	Saint Eustatius	LA	18.0	603.0	17.49	62.98	1,978	2,496	744	5	5	5	2
55	Saint John	GA	49.7	388.0	18.35	64.74	1,770	2,305	853		6	6	3
56	Saint Kitts	LA	173.5	1,156.0	17.33	62.76	1,997	2,523	726	4	7	7	4
57	Saint Lucia	LA	609.0	950.0	13.90	60.97	2,369	2,822	417	8	8	8	4
58	Saint Martin	LA	95.8	424.0	18.06	63.06	1,942	4,278	799	5	8	8	5
59	San Salvador	BA	163.0	43.0	24.05	74.48	599	1,280	1,869		4	4	3
60	Saint Thomas	GA	70.2	472.4	18.35	64.93	1,752	2,278	853		5	5	3
61	Saint Vincent	LA	344.5	1,234.0	13.25	61.19	2,396	2,822	345	9	12	11	6
62	Tortola	GA	62.2	542.5	18.42	64.63	1,779	2,314	862		2	2	2
63	Union Island	LA	11.4	304.8	12.60	61.43	2,423	2,831	290		3	3	3
64	Virgin Gorda	GA	20.7	417.6	18.48	64.39	1,797	2,332	871		2	2	2
65	Vieques	GA	132.1	301.0	18.12	65.44	1,729	2,245	859		4	4	3

Note: BA = Bahamas, GA = Greater Antilles, and LA = Lesser Antilles.

[a] Species richness reported by Baker and Genoways (1978); species records for the Bahamas (9), Virgin Islands (6), and Grenadines (1) not reported for individual islands.

APPENDIX 8.2

Table A8.2. Island-bat matrix showing islands from which each species of bat was documented, the guild designation for each species of bat, and the number of islands from which each species was recorded

		Bahamas											
Family/Subfamily/Species	Feeding guild	Acklins	Andros	Cat	Crooked	Darby	East Caicos	Eleuthera	East Plana Cay	Fortune	Great Abaco	Grand Bahama	Great Exuma
Emballonuridae													
Peropteryx macrotis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Phyllostomidae													
Brachyphyllinae													
Brachyphylla cavernarum	F	0	0	0	0	0	0	0	0	0	0	0	0
Brachyphylla nana	F	0	0	1	0	0	0	0	0	0	0	0	0
Phyllonycterinae													
Erophylla bombifrons	N	0	0	0	0	0	0	0	0	0	0	0	0
Erophylla sezekorni	N	1	1	1	1	0	1	1	0	0	1	1	1
Phyllonycteris aphylla	N	0	0	0	0	0	0	0	0	0	0	0	0
Phyllonycteris poeyi	N	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaginae													
Anoura geoffroyi	N	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaga longirostris	N	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaga soricina	N	0	0	0	0	0	0	0	0	0	0	0	0
Monophyllus plethodon	N	0	0	0	0	0	0	0	0	0	0	0	0
Monophyllus redmani	N	1	0	0	1	0	0	0	0	0	0	0	0
Phyllostominae													
Lonchorhina aurita	F	0	0	0	0	0	0	0	0	0	0	0	0
Macrotus waterhousii	GA	1	1	1	1	1	1	1	1	0	1	0	1
Micronycteris megalotis	GA	0	0	0	0	0	0	0	0	0	0	0	0
Stenodermatinae													
Ardops nichollsi	F	0	0	0	0	0	0	0	0	0	0	0	0
Ariteus flavescens	GA	0	0	0	0	0	0	0	0	0	0	0	0
Artibeus glaucus	F	0	0	0	0	0	0	0	0	0	0	0	0
Artibeus jamaicensis	F	0	0	0	0	0	0	0	0	0	0	0	0
Artibeus lituratus	F	0	0	0	0	0	0	0	0	0	0	0	0
Chiroderma improvisum	F	0	0	0	0	0	0	0	0	0	0	0	0
Phyllops falcatus	F	0	0	0	0	0	0	0	0	0	0	0	0
Stenoderma rufum	F	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	F	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira thomasi	F	0	0	0	0	0	0	0	0	0	0	0	0
Noctilionidae													
Noctilio leporinus	P	0	0	0	0	0	0	0	0	0	0	0	0

Table A8.2. (*continued*)

		Bahamas											
Family/Subfamily/Species	Feeding guild	Acklins	Andros	Cat	Crooked	Darby	East Caicos	Eleuthera	East Plana Cay	Fortune	Great Abaco	Grand Bahama	Great Exuma
Mormoopidae													
Mormoops blainvillei	AI	0	0	0	0	0	0	0	0	0	0	0	0
Pteronotus davyi	AI	0	0	0	0	0	0	0	0	0	0	0	0
Pteronotus macleayii	AI	0	0	0	0	0	0	0	0	0	0	0	0
Pteronotus parnellii	AI	0	0	0	0	0	0	0	0	0	0	0	0
Pteronotus quadridens	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalidae													
Chilonatalus micropus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Chilonatalus tumidifrons	AI	0	0	0	0	0	0	0	0	0	1	0	0
Natalus jamaicensis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalus major	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalus primus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalus stramineus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Nyctiellus lepidus	AI	0	0	1	0	0	0	1	0	0	0	0	0
Molossidae													
Eumops auripendulus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Eumops glaucinus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Molossus molossus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Mormopterus minutus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Nyctinomops laticaudatus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Nyctinomops macrotis	HF	0	0	0	0	0	0	0	0	0	0	0	0
Tadarida brasiliensis	HF	1	0	0	1	0	0	1	0	1	1	0	1
Vespertilionidae													
Antrozous pallidus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	AI	1	1	0	1	0	0	0	0	0	1	1	1
Eptesicus guadeloupensis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus lynni	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus degelidus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus intermedius	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus minor	AI	0	1	1	0	0	0	0	0	0	0	1	0
Lasiurus pfeifferi	AI	0	0	0	0	0	0	0	0	0	0	0	0
Myotis dominicensis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Myotis martiniquensis	AI	0	0	0	0	0	0	0	0	0	0	0	0

Myotis nigricans	AI	0	0	0	0	0	0	0	0	0	0	0	0
Nycticeius cubanus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Island bat species richness		5	4	5	5	1	2	4	1	1	5	3	4

		Bahamas										
Family/Subfamily/Species	Feeding guild	Great Inagua	Little Abaco	Little Exuma	Little Inagua	Long	Mayaguana	Middle Caicos	North Caicos	New Providence	Providenciales	San Salvador
Emballonuridae												
Peropteryx macrotis	AI	0	0	0	0	0	0	0	0	0	0	0
Phyllostomidae												
Brachyphyllinae												
Brachyphylla cavernarum	F	0	0	0	0	0	0	0	0	0	0	0
Brachyphylla nana	F	0	0	0	0	0	0	1	0	0	0	0
Phyllonycterinae												
Erophylla bombifrons	N	0	0	0	0	0	0	0	0	0	0	0
Erophylla sezekorni	N	1	0	1	0	1	1	1	1	1	1	1
Phyllonycteris aphylla	N	0	0	0	0	0	0	0	0	0	0	0
Phyllonycteris poeyi	N	0	0	0	0	0	0	0	0	0	0	0
Glossophaginae												
Anoura geoffroyi	N	0	0	0	0	0	0	0	0	0	0	0
Glossophaga longirostris	N	0	0	0	0	0	0	0	0	0	0	0
Glossophaga soricina	N	0	0	0	0	0	0	0	0	0	0	0
Monophyllus plethodon	N	0	0	0	0	0	0	0	0	0	0	0
Monophyllus redmani	N	0	0	0	0	0	0	1	1	0	1	0
Phyllostominae												
Lonchorhina aurita	F	0	0	0	0	0	0	0	0	1	0	0
Macrotus waterhousii	GA	1	0	1	0	1	0	0	1	1	1	1
Micronycteris megalotis	GA	0	0	0	0	0	0	0	0	0	0	0
Stenodermatinae												
Ardops nichollsi	F	0	0	0	0	0	0	0	0	0	0	0
Ariteus flavescens	GA	0	0	0	0	0	0	0	0	0	0	0
Artbeus glaucus	F	0	0	0	0	0	0	0	0	0	0	0
Artibeus jamaicensis	F	1	0	0	1	0	1	0	0	0	1	0
Artibeus lituratus	F	0	0	0	0	0	0	0	0	0	0	0
Chiroderma improvisum	F	0	0	0	0	0	0	0	0	0	0	0
Phyllops falcatus	F	0	0	0	0	0	0	0	0	0	0	0
Stenoderma rufum	F	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	F	0	0	0	0	0	0	0	0	0	0	0
Sturnira thomasi	F	0	0	0	0	0	0	0	0	0	0	0

Table A8.2. (*continued*)

Family/Subfamily/Species	Feeding guild	Bahamas										
		Great Inagua	Little Abaco	Little Exuma	Little Inagua	Long	Mayaguana	Middle Caicos	North Caicos	New Providence	Providenciales	San Salvador
Noctilionidae												
Noctilio leporinus	P	1	0	0	0	0	0	0	0	0	0	0
Mormoopidae												
Mormoops blainvillei	AI	0	0	0	0	0	0	0	0	0	0	0
Pteronotus davyi	AI	0	0	0	0	0	0	0	0	0	0	0
Pteronotus macleayii	AI	0	0	0	0	0	0	0	0	0	0	0
Pteronotus parnellii	AI	0	0	0	0	0	0	0	0	0	0	0
Pteronotus quadridens	AI	0	0	0	0	0	0	0	0	0	0	0
Natalidae												
Chilonatalus micropus	AI	0	0	0	0	0	0	0	0	0	0	0
Chilonatalus tumidifrons	AI	0	0	0	0	0	0	0	0	0	0	0
Natalus jamaicensis	AI	0	0	0	0	0	0	0	0	0	0	0
Natalus major	AI	0	0	0	0	0	0	0	0	0	0	0
Natalus primus	AI	0	0	0	0	0	0	0	0	0	0	0
Natalus stramineus	AI	0	0	0	0	0	0	0	0	0	0	0
Nyctiellus lepidus	AI	0	0	1	0	1	0	0	0	0	0	1
Molossidae												
Eumops auripendulus	HF	0	0	0	0	0	0	0	0	0	0	0
Eumops glaucinus	HF	0	0	0	0	0	0	0	0	0	0	0
Molossus molossus	HF	0	0	0	0	0	0	0	0	0	0	0
Mormopterus minutus	HF	0	0	0	0	0	0	0	0	0	0	0
Nyctinomops laticaudatus	HF	0	0	0	0	0	0	0	0	0	0	0
Nyctinomops macrotis	HF	0	0	0	0	0	0	0	0	0	0	0
Tadarida brasiliensis	HF	0	1	1	0	1	0	0	0	0	0	0
Vespertilionidae												
Antrozous pallidus	AI	0	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	AI	0	0	1	0	1	0	0	0	1	0	1
Eptesicus guadeloupensis	AI	0	0	0	0	0	0	0	0	0	0	0
Eptesicus lynni	AI	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	AI	0	0	0	0	0	0	0	0	0	1	0
Lasiurus degelidus	AI	0	0	0	0	0	0	0	0	0	0	0
Lasiurus intermedius	AI	0	0	0	0	0	0	0	0	0	0	0
Lasiurus minor	AI	1	0	0	0	1	1	1	0	1	1	0
Lasiurus pfeifferi	AI	0	0	0	0	0	0	0	0	0	0	0

Myotis dominicensis	AI	0	0	0	0	0	0	0	0	0	0	0
Myotis martiniquensis	AI	0	0	0	0	0	0	0	0	0	0	0
Myotis nigricans	AI	0	0	0	0	0	0	0	0	0	0	0
Nycticeius cubanus	AI	0	0	0	0	0	0	0	0	0	0	0
Island bat species richness		5	1	5	1	6	3	4	3	5	6	4

		Greater Antilles										
Family/Subfamily/Species	Feeding guild	Anegada	Cayman Brac	Cuba	Culebra	Grand Cayman	Gonâve	Grass*	Guana*	Hispaniola	Isle of Pines	Jamaica
Emballonuridae												
Peropteryx macrotis	AI	0	0	0	0	0	0	0	0	0	0	0
Phyllostomidae												
Brachyphyllinae												
Brachyphylla cavernarum	F	0	0	0	0	0	0	1	1	0	0	0
Brachyphylla nana	F	0	0	1	0	1	0	0	0	1	1	0
Phyllonycterinae												
Erophylla bombifrons	N	0	0	0	0	0	0	0	0	1	0	0
Erophylla sezekorni	N	0	1	1	0	1	0	0	0	0	1	1
Phyllonycteris aphylla	N	0	0	0	0	0	0	0	0	0	0	1
Phyllonycteris poeyi	N	0	0	1	0	0	0	0	0	1	1	0
Glossophaginae												
Anoura geoffroyi	N	0	0	0	0	0	0	0	0	0	0	0
Glossophaga longirostris	N	0	0	0	0	0	0	0	0	0	0	0
Glossophaga soricina	N	0	0	0	0	0	0	0	0	0	0	1
Monophyllus plethodon	N	0	0	0	0	0	0	0	0	0	0	0
Monophyllus redmani	N	0	0	1	0	0	1	0	0	1	1	1
Phyllostominae												
Lonchorhina aurita	F	0	0	0	0	0	0	0	0	0	0	0
Macrotus waterhousii	GA	0	1	1	0	1	1	0	0	1	1	1
Micronycteris megalotis	GA	0	0	0	0	0	0	0	0	0	0	0
Stenodermatinae												
Ardops nichollsi	F	0	0	0	0	0	0	0	0	0	0	0
Ariteus flavescens	GA	0	0	0	0	0	0	0	0	0	0	1
Artibeus glaucus	F	0	0	0	0	0	0	0	0	0	0	0
Artibeus jamaicensis	F	1	1	1	1	1	1	0	1	1	1	1
Artibeus lituratus	F	0	0	0	0	0	0	0	0	0	0	0
Chiroderma improvisum	F	0	0	0	0	0	0	0	0	0	0	0
Phyllops falcatus	F	0	1	1	0	1	0	0	0	1	0	0
Stenoderma rufum	F	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	F	0	0	0	0	0	0	0	0	0	0	0
Sturnira thomasi	F	0	0	0	0	0	0	0	0	0	0	0

Table A8.2. *(continued)*

		Greater Antilles										
Family/Subfamily/Species	Feeding guild	Anegada	Cayman Brac	Cuba	Culebra	Grand Cayman	Gonâve	Grass*	Guana*	Hispaniola	Isle of Pines	Jamaica
Noctilionidae												
Noctilio leporinus	P	0	0	1	1	0	0	0	0	1	1	1
Mormoopidae												
Mormoops blainvillei	AI	0	0	1	0	0	1	0	0	1	0	1
Pteronotus davyi	AI	0	0	0	0	0	0	0	0	0	0	0
Pteronotus macleayii	AI	0	0	1	0	0	0	0	0	0	1	1
Pteronotus parnellii	AI	0	0	1	0	0	1	0	0	1	0	1
Pteronotus quadridens	AI	0	0	1	0	0	0	0	0	1	0	1
Natalidae												
Chilonatalus micropus	AI	0	0	1	0	0	0	0	0	1	1	1
Chilonatalus tumidifrons	AI	0	0	0	0	0	0	0	0	0	0	0
Natalus jamaicensis	AI	0	0	0	0	0	0	0	0	0	0	1
Natalus major	AI	0	0	0	0	0	0	0	0	1	0	0
Natalus primus	AI	0	0	1	0	0	0	0	0	0	1	0
Natalus stramineus	AI	0	0	0	0	0	0	0	0	0	0	0
Nyctiellus lepidus	AI	0	0	1	0	0	0	0	0	0	1	0
Molossidae												
Eumops auripendulus	HF	0	0	0	0	0	0	0	0	0	0	1
Eumops glaucinus	HF	0	0	1	0	0	0	0	0	0	0	1
Molossus molossus	HF	0	1	1	1	1	1	0	1	1	1	1
Mormopterus minutus	HF	0	0	1	0	0	0	0	0	0	0	0
Nyctinomops laticaudatus	HF	0	0	1	0	0	0	0	0	0	0	0
Nyctinomops macrotis	HF	0	0	1	0	0	0	0	0	1	0	1
Tadarida brasiliensis	HF	0	0	1	0	1	0	0	0	1	1	1
Vespertilionidae												
Antrozous pallidus	AI	0	0	1	0	0	0	0	0	0	0	0
Eptesicus fuscus	AI	0	1	1	0	1	0	0	0	1	1	0
Eptesicus guadeloupensis	AI	0	0	0	0	0	0	0	0	0	0	0
Eptesicus lynni	AI	0	0	0	0	0	0	0	0	0	0	1
Lasionycteris noctivagans	AI	0	0	0	0	0	0	0	0	0	0	0
Lasiurus degelidus	AI	0	0	0	0	0	0	0	0	0	0	1
Lasiurus intermedius	AI	0	0	1	0	0	0	0	0	0	1	0
Lasiurus minor	AI	0	0	0	0	0	0	0	0	1	0	0
Lasiurus pfeifferi	AI	0	0	1	0	0	0	0	0	0	0	0

Myotis dominicensis	AI	0	0	0	0	0	0	0	0	0	0	0
Myotis martiniquensis	AI	0	0	0	0	0	0	0	0	0	0	0
Myotis nigricans	AI	0	0	0	0	0	0	0	0	0	0	0
Nycticeius cubanus	AI	0	0	1	0	0	0	0	0	0	0	0
Island bat species richness		1	6	26	3	8	6	1	3	18	15	21

		Greater Antilles											
Family/Subfamily/Species	Feeding guild	Little Cayman	Little Tatch*	Lovango*	Mona	Navassa	Norman*	Puerto Rico	St. Croix	St. John	St. Thomas	Tortola	Virgin Gorda
Emballonuridae													
Peropteryx macrotis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Phyllostomidae													
Brachyphyllinae													
Brachyphylla cavernarum	F	0	1	0	0	0	1	1	1	1	1	0	0
Brachyphylla nana	F	0	0	0	0	0	0	0	0	0	0	0	0
Phyllonycterinae													
Erophylla bombifrons	N	0	0	0	0	0	0	1	0	0	0	0	0
Erophylla sezekorni	N	0	0	0	0	0	0	0	0	0	0	0	0
Phyllonycteris aphylla	N	0	0	0	0	0	0	0	0	0	0	0	0
Phyllonycteris poeyi	N	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaginae													
Anoura geoffroyi	N	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaga longirostris	N	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaga soricina	N	0	0	0	0	0	0	0	0	0	0	0	0
Monophyllus plethodon	N	0	0	0	0	0	0	0	0	0	0	0	0
Monophyllus redmani	N	0	0	0	0	0	0	1	0	0	0	0	0
Phyllostominae													
Lonchorhina aurita	F	0	0	0	0	0	0	0	0	0	0	0	0
Macrotus waterhousii	GA	1	0	0	0	1	0	0	0	0	0	0	0
Micronycteris megalotis	GA	0	0	0	0	0	0	0	0	0	0	0	0
Stenodermatinae													
Ardops nichollsi	F	0	0	0	0	0	0	0	0	0	0	0	0
Ariteus flavescens	GA	0	0	0	0	0	0	0	0	0	0	0	0
Artibeus glaucus	F	0	0	0	0	0	0	0	0	0	0	0	0
Artibeus jamaicensis	F	1	0	1	0	0	0	1	1	1	1	1	1
Artibeus lituratus	F	0	0	0	0	0	0	0	0	0	0	0	0
Chiroderma improvisum	F	0	0	0	0	0	0	0	0	0	0	0	0
Phyllops falcatus	F	0	0	0	0	0	0	0	0	0	0	0	0
Stenoderma rufum	F	0	0	0	0	0	0	1	1	1	1	0	0
Sturnira lilium	F	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira thomasi	F	0	0	0	0	0	0	0	0	0	0	0	0

Table A8.2. *(continued)*

		Greater Antilles											
Family/Subfamily/Species	Feeding guild	Little Cayman	Little Tatch*	Lovango*	Mona	Navassa	Norman*	Puerto Rico	St. Croix	St. John	St. Thomas	Tortola	Virgin Gorda
Noctilionidae													
Noctilio leporinus	P	0	0	0	1	0	1	1	1	1	1	0	0
Mormoopidae													
Mormoops blainvillei	AI	0	0	0	1	0	0	1	0	0	0	0	0
Pteronotus davyi	AI	0	0	0	0	0	0	0	0	0	0	0	0
Pteronotus macleayii	AI	0	0	0	0	0	0	0	0	0	0	0	0
Pteronotus parnellii	AI	0	0	0	0	0	0	1	0	0	0	0	0
Pteronotus quadridens	AI	0	0	0	0	0	0	1	0	0	0	0	0
Natalidae													
Chilonatalus micropus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Chilonatalus tumidifrons	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalus jamaicensis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalus major	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalus primus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Natalus stramineus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Nyctiellus lepidus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Molossidae													
Eumops auripendulus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Eumops glaucinus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Molossus molossus	HF	0	0	0	0	0	0	1	1	1	1	1	1
Mormopterus minutus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Nyctinomops laticaudatus	HF	0	0	0	0	0	0	0	0	0	0	0	0
Nyctinomops macrotis	HF	0	0	0	0	0	0	0	0	0	0	0	0
Tadarida brasiliensis	HF	0	0	0	0	0	0	1	0	1	0	0	0
Vespertilionidae													
Antrozous pallidus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	AI	0	0	0	0	0	0	1	0	0	0	0	0
Eptesicus guadeloupensis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus lynni	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus degelidus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus intermedius	AI	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus minor	AI	0	0	0	0	0	0	1	0	0	0	0	0
Lasiurus pfeifferi	AI	0	0	0	0	0	0	0	0	0	0	0	0
Myotis dominicensis	AI	0	0	0	0	0	0	0	0	0	0	0	0

Myotis martiniquencis	AI	0	0	0	0	0	0	0	0	0	0	0	0
Myotis nigricans	AI	0	0	0	0	0	0	0	0	0	0	0	0
Nycticeius cubanus	AI	0	0	0	0	0	0	0	0	0	0	0	0
Island bat species richness		2	1	1	2	1	2	13	5	6	5	2	2

Family/Subfamily/Species	Feeding guild	Greater Antilles	Lesser Antilles								
		Vieques	Anguilla	Antigua	Barbados	Barbuda	Bequia	Carriacou	Dominica	Grenada	Guadeloupe
Emballonuridae											
Peropteryx macrotis	AI	0	0	0	0	0	0	0	0	1	0
Phyllostomidae											
Brachyphyllinae											
Brachyphylla cavernarum	F	0	1	1	1	1	0	0	1	0	1
Brachyphylla nana	F	0	0	0	0	0	0	0	0	0	0
Phyllonycterinae											
Erophylla bombifrons	N	0	0	0	0	0	0	0	0	0	0
Erophylla sezekorni	N	0	0	0	0	0	0	0	0	0	0
Phyllonycteris aphylla	N	0	0	0	0	0	0	0	0	0	0
Phyllonycteris poeyi	N	0	0	0	0	0	0	0	0	0	0
Glossophaginae											
Anoura geoffroyi	N	0	0	0	0	0	0	0	0	1	0
Glossophaga longirostris	N	0	0	0	0	0	0	1	0	1	0
Glossophaga soricina	N	0	0	0	0	0	0	0	0	0	0
Monophyllus plethodon	N	0	1	1	1	1	0	0	1	0	1
Monophyllus redmani	N	0	0	0	0	0	0	0	0	0	0
Phyllostominae											
Lonchorhina aurita	F	0	0	0	0	0	0	0	0	0	0
Macrotus waterhousii	GA	0	0	0	0	0	0	0	0	0	0
Micronycteris megalotis	GA	0	0	0	0	0	0	0	0	1	0
Stenodermatinae											
Ardops nichollsi	F	0	0	0	0	0	0	0	1	0	1
Ariteus flavescens	GA	0	0	0	0	0	0	0	0	0	0
Artibeus glaucus	F	0	0	0	0	0	0	0	0	1	0
Artibeus jamaicensis	F	1	1	1	1	1	1	1	1	1	1
Artibeus lituratus	F	0	0	0	0	0	0	0	0	1	0
Chiroderma improvisum	F	0	0	0	0	0	0	0	0	0	1
Phyllops falcatus	F	0	0	0	0	0	0	0	0	0	0
Stenoderma rufum	F	1	0	0	0	0	0	0	0	0	0
Sturnira lilium	F	0	0	0	0	0	0	0	1	1	0
Sturnira thomasi	F	0	0	0	0	0	0	0	0	0	1

Table A8.2. *(continued)*

Family/Subfamily/Species	Feeding guild	Greater Antilles	Lesser Antilles								
		Vieques	Anguilla	Antigua	Barbados	Barbuda	Bequia	Carriacou	Dominica	Grenada	Guadeloupe
Noctilionidae											
Noctilio leporinus	P	1	0	1	1	1	0	1	1	1	1
Mormoopidae											
Mormoops blainvillei	AI	0	0	0	0	0	0	0	0	0	0
Pteronotus davyi	AI	0	0	0	0	0	0	0	1	1	0
Pteronotus macleayii	AI	0	0	0	0	0	0	0	0	0	0
Pteronotus parnellii	AI	0	0	0	0	0	0	0	0	0	0
Pteronotus quadridens	AI	0	0	0	0	0	0	0	0	0	0
Natalidae											
Chilonatalus micropus	AI	0	0	0	0	0	0	0	0	0	0
Chilonatalus tumidifrons	AI	0	0	0	0	0	0	0	0	0	0
Natalus jamaicensis	AI	0	0	0	0	0	0	0	0	0	0
Natalus major	AI	0	0	0	0	0	0	0	0	0	0
Natalus primus	AI	0	0	0	0	0	0	0	0	0	0
Natalus stramineus	Ai	0	1	1	0	1	0	0	1	0	1
Nyctiellus lepidus	AI	0	0	0	0	0	0	0	0	0	0
Molossidae											
Eumops auripendulus	HF	0	0	0	0	0	0	0	0	0	0
Eumops glaucinus	HF	0	0	0	0	0	0	0	0	0	0
Molossus molossus	HF	1	1	1	1	1	0	1	1	1	1
Mormopterus minutus	HF	0	0	0	0	0	0	0	0	0	0
Nyctinomops laticaudatus	HF	0	0	0	0	0	0	0	0	0	0
Nyctinomops macrotis	HF	0	0	0	0	0	0	0	0	0	0
Tadarida brasiliensis	HF	0	1	1	0	1	0	0	1	0	1
Vespertilionidae											
Antrozous pallidus	AI	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	AI	0	0	0	0	0	0	0	1	0	0
Eptesicus guadeloupensis	AI	0	0	0	0	0	0	0	0	0	1
Eptesicus lynni	AI	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	AI	0	0	0	0	0	0	0	0	0	0
Lasiurus degelidus	AI	0	0	0	0	0	0	0	0	0	0
Lasiurus intermedius	AI	0	0	0	0	0	0	0	0	0	0
Lasiurus minor	AI	0	0	0	0	0	0	0	0	0	0
Lasiurus pfeifferi	AI	0	0	0	0	0	0	0	0	0	0
Myotis dominicensis	AI	0	0	0	0	0	0	0	1	0	1

Myotis martiniquensis	AI	0	0	0	1	0	0	0	0	0	0
Myotis nigricans	AI	0	0	0	0	0	0	0	0	1	0
Nycticeius cubanus	AI	0	0	0	0	0	0	0	0	0	0
Island bat species richness		4	6	7	6	7	1	4	12	12	12

		Lesser Antilles									
Family/Subfamily/Species	Feeding guild	La Désirade	Marie-Galante	Martinique	Montserrat	Mustique	Nevis	Saba	Saint Barthelémy	Saint Eustatius	Saint Kitts
Emballonuridae											
Peropteryx macrotis	AI	0	0	0	0	0	0	0	0	0	0
Phyllostomidae											
Brachyphyllinae											
Brachyphylla cavernarum	F	1	1	1	1	0	1	1	1	1	1
Brachyphylla nana	F	0	0	0	0	0	0	0	0	0	0
Phyllonycterinae											
Erophylla bombifrons	N	0	0	0	0	0	0	0	0	0	0
Erophylla sezekorni	N	0	0	0	0	0	0	0	0	0	0
Phyllonycteris aphylla	N	0	0	0	0	0	0	0	0	0	0
Phyllonycteris poeyi	N	0	0	0	0	0	0	0	0	0	0
Glossophaginae											
Anoura geoffroyi	N	0	0	0	0	0	0	0	0	0	0
Glossophaga longirostris	N	0	0	0	0	0	0	0	0	0	0
Glossophaga soricina	N	0	0	0	0	0	0	0	0	0	0
Monophyllus plethodon	N	0	1	1	1	0	1	1	1	0	1
Monophyllus redmani	N	0	0	0	0	0	0	0	0	0	0
Phyllostominae											
Lonchorhina aurita	F	0	0	0	0	0	0	0	0	0	0
Macrotus waterhousii	GA	0	0	0	0	0	0	0	0	0	0
Micronycteris megalotis	GA	0	0	0	0	0	0	0	0	0	0
Stenodermatinae											
Ardops nichollsi	F	0	1	1	1	0	1	1	0	1	1
Ariteus flavescens	GA	0	0	0	0	0	0	0	0	0	0
Artibeus glaucus	F	0	0	0	0	0	0	0	0	0	0
Artibeus jamaicensis	F	1	1	1	1	1	1	1	1	1	1
Artibeus lituratus	F	0	0	0	0	0	0	0	0	0	0
Chiroderma improvisum	F	0	0	0	1	0	0	0	0	0	0
Phyllops falcatus	F	0	0	0	0	0	0	0	0	0	0
Stenoderma rufum	F	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	F	0	0	1	0	0	0	0	0	0	0
Sturnira thomasi	F	0	0	0	1	0	0	0	0	0	0

Table A8.2. *(continued)*

Family/Subfamily/Species	Feeding guild	Lesser Antilles									
		La Désirade	Marie-Galante	Martinique	Montserrat	Mustique	Nevis	Saba	Saint Barthelémy	Saint Eustatius	Saint Kitts
Noctilionidae											
Noctilio leporinus	P	0	1	1	1	0	1	0	0	0	1
Mormoopidae											
Mormoops blainvillei	AI	0	0	0	0	0	0	0	0	0	0
Pteronotus davyi	AI	0	1	1	0	0	0	0	0	0	0
Pteronotus macleayii	AI	0	0	0	0	0	0	0	0	0	0
Pteronotus parnellii	AI	0	0	0	0	0	0	0	0	0	0
Pteronotus quadridens	AI	0	0	0	0	0	0	0	0	0	0
Natalidae											
Chilonatalus micropus	AI	0	0	0	0	0	0	0	0	0	0
Chilonatalus tumidifrons	AI	0	0	0	0	0	0	0	0	0	0
Natalus jamaicensis	AI	0	0	0	0	0	0	0	0	0	0
Natalus major	AI	0	0	0	0	0	0	0	0	0	0
Natalus primus	AI	0	0	0	0	0	0	0	0	0	0
Natalus stramineus	AI	0	1	1	1	0	1	1	0	0	0
Nyctiellus lepidus	AI	0	0	0	0	0	0	0	0	0	0
Molossidae											
Eumops auripendulus	HF	0	0	0	0	0	0	0	0	0	0
Eumops glaucinus	HF	0	0	0	0	0	0	0	0	0	0
Molossus molossus	HF	1	1	1	1	0	1	1	1	1	1
Mormopterus minutus	HF	0	0	0	0	0	0	0	0	0	0
Nyctinomops laticaudatus	HF	0	0	0	0	0	0	0	0	0	0
Nyctinomops macrotis	HF	0	0	0	0	0	0	0	0	0	0
Tadarida brasiliensis	HF	1	0	1	1	0	1	1	1	1	1
Vespertilionidae											
Antrozous pallidus	AI	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	AI	0	0	0	0	0	0	0	0	0	0
Eptesicus guadeloupensis	AI	0	0	0	0	0	0	0	0	0	0
Eptesicus lynni	AI	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	AI	0	0	0	0	0	0	0	0	0	0

Lasiurus degelidus	AI	0	0	0	0	0	0	0	0	0	0
Lasiurus intermedius	AI	0	0	0	0	0	0	0	0	0	0
Lasiurus minor	AI	0	0	0	0	0	0	0	0	0	0
Lasiurus pfeifferi	AI	0	0	0	0	0	0	0	0	0	0
Myotis dominicensis	AI	0	0	0	0	0	0	0	0	0	0
Myotis martiniquensis	AI	0	0	1	0	0	0	0	0	0	0
Myotis nigricans	AI	0	0	0	0	0	0	0	0	0	0
Nycticeius cubanus	AI	0	0	0	0	0	0	0	0	0	0
Island bat species richness		4	8	11	10	1	8	7	5	5	7

Family/Subfamily/Species	Feeding guild	Lesser Antilles				San Andrés*	Providencia*	Total number of islands
		St. Lucia	St. Martin	St. Vincent	Union			
Emballonuridae								
Peropteryx macrotis	AI	0	0	0	0	0	0	1
Phyllostomidae								
Brachyphyllinae								
Brachyphylla cavernarum	F	1	1	1	0	0	0	26
Brachyphylla nana	F	0	0	0	0	0	0	6
Phyllonycterinae								
Erophylla bombifrons	N	0	0	0	0	0	0	2
Erophylla sezekorni	N	0	0	0	0	0	0	23
Phyllonycteris aphylla	N	0	0	0	0	0	0	1
Phyllonycteris poeyi	N	0	0	0	0	0	0	3
Glossophaginae								
Anoura geoffroyi	N	0	0	0	0	0	0	1
Glossophaga longirostris	N	0	0	1	1	0	0	4
Glossophaga soricina	N	0	0	0	0	0	0	1
Monophyllus plethodon	N	1	1	1	0	0	0	16
Monophyllus redmani	N	0	0	0	0	0	0	11
Phyllostominae								
Lonchorhina aurita	F	0	0	0	0	0	0	1
Macrotus waterhousii	GA	0	0	0	0	0	0	26
Micronycteris megalotis	GA	0	0	1	0	0	0	2
Stenodermatinae								
Ardops nichollsi	F	1	1	1	0	0	0	12
Ariteus flavescens	GA	0	0	0	0	0	0	1

Table A8.2. *(continued)*

Family/Subfamily/Species	Feeding guild	Lesser Antilles				San Andrés*	Providencia*	Total number of islands
		St. Lucia	St. Martin	St. Vincent	Union			
Artibeus glaucus	F	0	0	0	0	0	0	1
Artibeus jamaicensis	F	1	1	1	1	1	1	48
Artibeus lituratus	F	0	0	1	0	0	0	2
Chiroderma improvisum	F	0	0	0	0	0	0	2
Phyllops falcatus	F	0	0	0	0	0	0	4
Stenoderma rufum	F	0	0	0	0	0	0	5
Sturnira lilium	F	1	0	1	0	0	0	5
Sturnira thomasi	F	0	0	0	0	0	0	2
Noctilionidae								
Noctilio leporinus	P	1	1	1	0	0	0	28
Mormoopidae								
Mormoops blainvillei	AI	0	0	0	0	0	0	6
Pteronotus davyi	AI	0	0	0	0	0	0	4
Pteronotus macleayii	AI	0	0	0	0	0	0	3
Pteronotus parnellii	AI	0	0	1	0	0	0	6
Pteronotus quadridens	AI	0	0	0	0	0	0	4
Natalidae								
Chilonatalus micropus	AI	0	0	0	0	0	1	5
Chilonatalus tumidifrons	AI	0	0	0	0	0	0	1
Natalus jamaicensis	AI	0	0	0	0	0	0	1
Natalus major	AI	0	0	0	0	0	0	1
Natalus primus	AI	0	0	0	0	0	0	2
Natalus stramineus	AI	0	1	0	0	0	0	11
Nyctiellus lepidus	AI	0	0	0	0	0	0	7
Molossidae								
Eumops auripendulus	HF	0	0	0	0	0	0	1

Eumops glaucinus	HF	0	0	0	0	0	0	2
Molossus molossus	HF	1	1	1	1	0	0	37
Mormopterus minutus	HF	0	0	0	0	0	0	1
Nyctinomops laticaudatus	HF	0	0	0	0	0	0	1
Nyctinomops macrotis	HF	0	0	0	0	0	0	3
Tadarida brasiliensis	HF	1	1	1	0	0	0	32
Vespertilionidae								
Antrozous pallidus	AI	0	0	0	0	0	0	1
Eptesicus fuscus	AI	0	0	0	0	0	0	17
Eptesicus guadeloupensis	AI	0	0	0	0	0	0	1
Eptesicus lynni	AI	0	0	0	0	0	0	1
Lasionycteris noctivagans	AI	0	0	0	0	0	0	1
Lasiurus degelidus	AI	0	0	0	0	0	0	1
Lasiurus intermedius	AI	0	0	0	0	0	0	2
Lasiurus minor	AI	0	0	0	0	0	0	11
Lasiurus pfeifferi	AI	0	0	0	0	0	0	1
Myotis dominicensis	AI	0	0	0	0	0	0	2
Myotis martiniquensis	AI	0	0	0	0	0	0	2
Myotis nigricans	AI	0	0	0	0	0	0	1
Nycticeius cubanus	AI	0	0	0	0	0	0	1
Island bat species richness		8	8	12	3	1	2	

Sources: Species composition of islands determined from Allen 1911; Anderson and Nelson 1965; Baker and Genoways 1978; Baker et al. 1984; Breuil and Masson 1991; Buden 1974, 1975a, 1975b, 1976, 1977, 1985, 1986; CITES 1992; Clark and Lee 1999; Convention on Migratory Species 2005; Dávalos 2004; Dávalos and Eriksson 2003; Gannon et al. 2005; Genoways and Baker 1975; Genoways et al. 1998; Genoways et al. 2001; Genoways et al. 2005; Genoways et al. 2007a; Genoways et al. 2007b; Genoways et al. 2007c; Griffiths and Klingener 1988; Hamas and Zusi 1992; Handley and Webster 1987; Hill 1985; IUCN 1996; Jennings et al. 2004; Jones 1989; Klingener et al. 1978; Kock and Stephan 1986; Koopman 1955, 1989; Koopman et al. 1957; Kwiecinski and Coles 2007; Larsen et al. 2006; Lazell and Jarecki 1985; Lorvelec et al. 2001; Mancina and Rivera 2000; Masson et al. 1990; McCarthy and Henderson 1992; McFarlane 1991; Morgan 1989; Ottenwalder and Genoways 1982; Pedersen et al. 1996; Pedersen et al. 2003; Pedersen et al. 2005; Pedersen et al. 2006; Pierson et al. 1986; Pinchon 1967; Shamel 1931; Silva-Toboado 1979; Simmons and Conway 2001; Timm and Genoways 2003; Vaughan and Hill 1996.

Note: AI = aerial insectivore; F = frugivore; GA = gleaning animalivore; P = piscivore; HF = high-flying insectivore; N = nectarivore.

*Islands excluded from analyses because they are not in the Bahamas, Greater Antilles, or Lesser Antillies and islands excluded from analyses because of concerns that records do not represent resident, breeding populations.

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