Biodiversity, Biogeography, and Conservation of Bats in the Lesser An

Scott C. PEDERSEN, Hugh H. GENOWAYS, Gary G. KWIECINSKI, Peter A. LARSEN, and Roxanne J. LARSEN

he chiropteran fauna of the Lesser Antilles consists of 26 species. The diversity of this fauna is low when compared with Neotropical faunas of large continental islands or at sites on the adjacent mainland, however, the Lesser Antillean fauna contains 11 species endemic to these islands making it worthy of large-scale conservation efforts. At the southern end of the Lesser Antilles, the biological limit of the Lesser Antillean bat fauna is marked by Koopman's Line. To the south of this line, the bat faunas of the Grenadines and Grenada are composed of South American and widespread species of bats. The central Lesser Antillean islands have been grouped as the "Lesser Antillean Faunal Core." The bat faunas of these islands are characterized by the presence of 9 or more species and several endemic species that occur on only one or two of these islands. The faunas of the northern Lesser Antillean islands are united into the "Northern Antillean Faunal Area" and share the same eight species of bats. The conservation of bats is critical not only to the biodiversity that they represent, but to the maintenance of biodiversity of other fauna and flora. The maintenance of chiropteran fauna can best be served by three actions-preservation of caves, preservation of forest diversity, and restoration of hydrological systems.

Taxonomic Diversity in the Lesser Antilles

The chiropteran fauna of the Lesser Antilles consists of 26 species of bats representing 7 families (Table 1). The diversity of this fauna is low when compared with Neotropical faunas of large continental islands or sites on the adjacent mainland—Suriname (95 species), Nicaragua (85), Trinidad (64), Yucatan Peninsula (48), and coastal Venezuela (39) (Genoways et al., 2001). The Lesser Antillean bat fauna contains 11 species that are endemic to these islands and a 12th species— Brachyphylla cavernarum—that is endemic to the Antilles (Table 1). This represents a significant amount of biodiversity and is worthy of large-scale conservation efforts. These species of bats are not uniformly distributed throughout the Lesser Antilles, but occur in patterns that



provide insight into the development of the bat faunas of these islands (Table 2).

Table 1: List of the species of bats occurring on the Lesser Antillean islands.

> Family Emballonuridae *Peropteryx trinitatis*

Family Mormoopidae Pteronotus davyi Pteronotus rubiginosus

- Family Noctilionidae Noctilio leporinus
- Family Phyllostomidae Brachyphylla cavernarum * Anoura geoffroyi *Glossophaga longirostris* Monophyllus plethodon ** Micronycteris megalotis Ardops nichollsi * Dermanura bogotensis Artibeus jamaicensis Artibeus lituratus Artibeus planirostris Artibeus schwartzi ** Chiroderma improvisum ** Sturnira lilium Sturnira thomasi ** Family Vespertilionidae Eptesicus fuscus
 - Eptesicus guadeloupensis ** Myotis dominicensis * Myotis martiniquensis ** Myotis nigricans

Family Natalidae Natalus stramineus **

Family Molossidae Molossus molossus Tadarida brasiliensis

Restricted in distribution to the Lesser Antilles, Virgin Islands, and Puerto

** Endemic to the Lesser Antilles.

Table 2. Chiropteran species inventories for the Lesser Antilles. Species endemic to the Antilles are in bold and islands are arranged (approximately) from north to south. Solid circles show documentation of species by voucher specimens and/or genetic data. Asterisks indicate hybridization (H) among southern Lesser Antillean populations of *Artibeus jamaicensis, A. planirostris,* and A. schwartzi. Dashed lines define the Northern Antillean Faunal Area (Anguilla-Antigua) and Lesser Antillean Faunal Core (Montserrat–St. Vincent). Solid line identifies the southern Lesser Antillean location of Koopman's Line (east and south of Barbados westward through the Bequia Channel).

	Angli	112 .	atin	athelen	st. c	atius	c	,6 ³	1 ²	Guad	aloupe	ica.	ique	ja .	Incent Barb	ados nadines Grenadines	
	Angl	St. N	5°.	Saba	cz. c	atto Net	N ^S Balt	Antic Antic	Mont	SU80	Dout	Marti	nique St.L	5 [.]	"Bailo	Gler	adines Gren
Ardops nichollsi		•		•	•	•		•		•	•	•	•	•	!		
Artibeus schwartzi*									1				Н	٠	Η	•	Н
Brachyphylla cavernarum	•	٠	٠	•	•	•	٠	٠		•	•	•	•	٠	•		
Chiroderma improvisum										•					1		
Eptesicus guadeloupensis									1	•					!		
Monophyllus plethodon	•	•	•	•	•	•	•	•		•	•	•	•	•	•		
Myotis dominicensis									1	•	•				ļ		
Myotis martiniquensis									 			•			•		
Natalus stramineus	•	•		•		•	•	•	I I ●	•	•				1		
Sturnira thomasi										•					1		
Anoura geoffroyi									1						i i		•
Artibeus jamaicensis*	•	•	•	•	•	•	•	•	•	•	•	•	Н		İН	Н	
Artibeus lituratus									1					•	ļ	•	•
Artibeus planirostris*									1						Η	Н	•
Dermanura bogotensis									 						1		•
Eptesicus fuscus									 		•				1		
Glossophaga longirostris									1					•	i I	•	•
Micronycteris megalotis														•	į –		•
Molossus molossus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Myotis nigricans									1						1		•
Noctilio leporinus		•				•	•	•	I I ●	•	•	•	•	•	 ●	•	•
Peropteryx trinitatis									 						1		•
Pteronotus davyi									I I	•	•		•		1		•
Pteronotus rubiginosus									1					•	i I		
Sturnira lilium											•	•	•	•	į		•
Tadarida brasiliensis	•	•	•	•			•	•		•	•	•	•	•	1		

The Lesser Antilles chain is defined geologically by the Anegada Passage in the north and the southern end of the Grenada Bank in the south. When looking at the modern chiropteran fauna, the Anegada Passage would seem to be a zoogeographic barrier, but when the fossil evidence of the last 10,000 years is considered, this passage is less of a barrier (Genoways et al., 2007c). At the southern end of the Lesser Antilles, the biological limit of the Lesser Antillean bat fauna is marked by Koopman's Line, which passes through the Bequia Channel just south of St. Vincent (Figs. 1 and 2). South of this line (with the possible exception of Artibeus schwartzi), the bat faunas of the Grenadines and Grenada are composed of South American and widespread species of bats. These faunas can be classified as attenuated South American faunas (Genoways et al., 1998; Genoways et al., 2010). The chiropteran faunas of Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, and St. Vincent have been grouped as the "Lesser Antillean Faunal Core" and are characterized by the presence of nine or more species and several endemic species that occur on only one or two islands (Genoways *et al.*, 2001). The faunas of the islands of Anguilla, Antigua, Barbuda, Nevis, Saba, St. Barthélemy, St. Eustatius, St. Kitts, and St. Martin have been united into the "Northern Antillean Faunal Area." These island faunas share the same eight species of bats (Genoways *et al.*, 2007a). This faunal area can be seen as a transition zone between the Lesser Antillean Faunal Core and the Greater Antillean Faunal Core, which includes the bat fauna of Cuba, Hispaniola, Jamaica, and Puerto Rico. Barbados, at the southern end of the Lesser Antilles, has been in existence for

only 1 million years or less (Speed and Keller 1993), yet has been colonized and populated within this short period of time.



Antillean Endemics

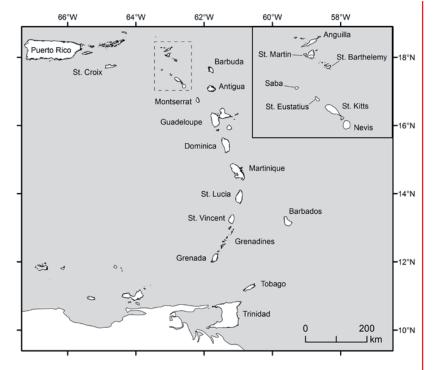


Figure 2. Map indicating the Northern Antilles Faunal Area, the Lesser Antilles Faunal Core, and Koopman's Line (Pedersen *et al.*).

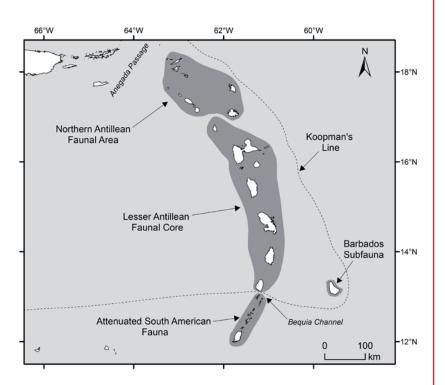


Figure 1. Map of the eastern Caribbean and the Lesser Antilles (Pedersen et al.).

Limitations On and the Complexity of **Biodiversity** Data

Before we can make broad statements aboutbatbiodiversity and batconservation, we must first re-visit the limitations and bias under which our data is collected.

Net Bias—Accurate species inventories for an island are hampered by the inadequacy ground-based netting of strategies, something that has been painfully obvious to field biologists who study speciesspecific responses to mist nets and species-specific ability to avoid mist nets (Barber *et al.*, 2003; Berry *et al.*, 2004; Lang *et al.*, 2004; R. Larsen *e t al.*, 2005, 2006, 2007; Simmons and Voss, 1998). Species that are not captured in surveys on a regular basis may simply be able to avoid mist nets, or fly where we cannot place mist nets, or are quite simply rare. Given this difficulty in accurately quantifying bat abundance and diversity, we have used a simple metric (bats per net-night: BNN) to approximate activity levels at our sampling sites on various islands throughout the region (Genoways et al., 2007a, 2007b, 2007c; P. Larsen et al., 2007; R. Larsen et al., 2005, 2006, 2007; Pedersen et al., 1996, 2003, 2005, 2006, 2007). The addition of other variables (e.g., net dimensions, net-hours, etc.) introduces false precision to the data and thereby increases bias in the survey data. BNN would seem therefore to be the most pragmatic metric with which to cross-evaluate historical data from numerous investigators and sampling protocols (Fenton et al., 1992; LaVal, 2004; Pedersen et al., 2005).

Survey Duration—Our efforts have shown that short-duration and/or single season surveys underestimate bat biodiversity; the capture of rare species requires a greater investment of time and effort. We conclude that without longduration/multi-year survey efforts, biodiversity estimates can only be approximations at best and guite probably underestimate the true faunal diversity of an island, thus providing a poor foundation for any subsequent conservation guidelines.

Survey Timing: Disturbance, Sex, and Time Frame—The severity and frequency of environmental disturbance has considerable influence on biodiversity in the eastern Caribbean. What appears to the human eye as a natural disaster, may be perceived by the biota on any one of these hurricane-dominated



volcanic islands as perfectly "normal," evolutionarily speaking. Indeed, despite the great fluctuations in bat abundance on Montserrat over the last 30 years, none of the 10 species of bats has been extirpated despite dramatic volcanic activity and a Category 5 hurricane (Pedersen *et al.*, 2009). During that time, some of our surveys yielded only 4 species of bat, and Chiroderma and Sturnira were not found from 1994 to 2004 despite extensive efforts. Had some of these species been extirpated by storms/ volcanic activity and then subsequently re-colonized the island, or had they simply became so rare as to have become "invisible" to our mist netting efforts (R. Larsen *et al.*, 2005, 2007)?

Fenton *et al.*, (1992) demonstrated that phyllostomid bats are indicators of habitat disruption, and island populations of fruit bats appear more susceptible to habitat disruption than are mainland populations (Barlow *et al.*, 2000). However, many bats in the Lesser Antilles seem stochastic events, should fossil data be included in an island's fauna (Pedersen *et al.*, 2006; Steadman *et al.*, 1984a, 1984b)? Is there a disturbance frequency/severity threshold for bat extirpation, or could it be that we must wrestle with a complicated and resilient metapopulation of bats throughout the Lesser Antilles?

Bat Biodiversity: Species-Area Curves—The number of species found on an island is correlated with the size (area) of the island, the distance from a source area (continental area) and the diversity of habitats available, which in most cases is directly affected by elevation of the island (MacArthur and Wilson, 1967). When looking at species-area curves for mammals, birds, lizards, and insects throughout the Caribbean, z-values (slope of the regression line) range from 0.48 to 0.20, with

to be disturbance adapted. Unlike their mainland congeners, these animals their reproductive and strategies have evolved in a region dominated by natural disasters. The low reproductive rates of most chiropteran taxa ("k-selected" organisms) are poorly suited for responding rapidly to disturbance in these complex, inherently unstable, tropical communities. Interestingly, Artibeus would seem to be capable of alternating between kand r-selected reproductive strategies (Kwiecinski and Pedersen, 2002), whereas other fruit bats (Monophyllus, Ardops, or Brachyphylla) are not. Our data suggest that Artibeus recovers quickly after a drought or a natural disaster, and can become numerically dominant on small islands. This is

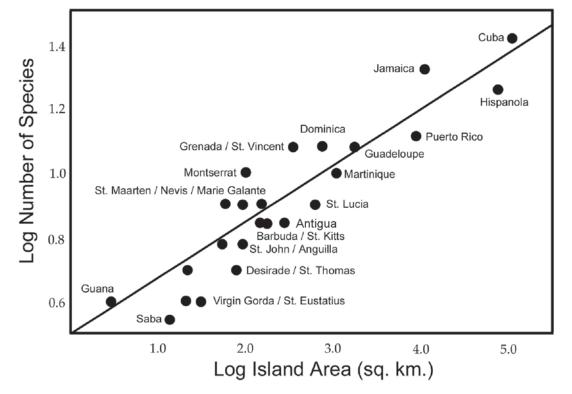


Figure 3. Species-area curve for the Lesser Antilles (after Pedersen *et al.*, 2009). Linear regression of log-transformed data: y = 0.17x + 0.49 (R2 = 0.81).

an interesting observation that bears further investigation—to what extent does reproductive strategy account for the contemporary community structure of bats throughout the Lesser Antilles?

So "when" do we perform a species inventory/ biodiversity survey on any one of these islands? What is the appropriate slice of time that should be used when constructing species-area curves? When was the most recent disturbance? Should human development/impact be factored-in? Assuming that time might ameliorate highly vagile species exhibiting low z-values (Davies and Smith, 1998; Griffiths and Klingener, 1988; Morgan and Woods, 1986; Wilcox, 1980). Low z-values suggest a greater propensity for dispersal or a reduced extinction rate relative to other West Indian biota (Davies and Smith,

1998). Not surprisingly, our z-value of 0.17 for bats is very low (Pedersen *et al.*, 2009; Fig. 3). We have also included fossil data, island elevation, and the treatment of different feeding guilds separately in our models, which has been productive



in some cases (Pedersen et al., 2005, 2006). Certainly, island elevation ameliorates the effect of small surface area on very small islands such as Saba (Genoways et *al.*, 2007a).

From the perspective of bat conservation, the relative position of an island above or below the "curve" is of great importance. Islands with relatively high levels of bat diversity appear above the line and can be attributed to (1) sufficient/diverse natural habitat; (2) close proximity to a source island; or (3) extensive biodiversity survey efforts. The position of an island below the "curve" may be attributed to (1) a dearth of habitat and/or habitat diversity due to island geology, history of natural disasters, or the impact of human activity; (2) the presence of an biological barrier that is difficult for bats to surmount; (3) a simple case of undersampling due to a variety of reasons (Pedersen et al., 2003), or even because (4) the demographics/natural history of each species is different and some species have yet to colonize the island (e.g., "old" invasions by Myotis and "recent" invasions like Artibeus).

Recent literature encourages the use of a new paradigm of island biogeography (Brown and Lomolino, 2000; Heaney, 2007; Lomolino, 2000a, b; Whittaker, 2000). Lomolino (2000a) and Brown and Lomolino (2000) list 3 limitations of equilibrium theory as species diversity (1) is not and may never be at equilibrium, (2) is shaped by variation in speciation, colonization, and extinction among taxa, and (3) is changed by differences among islands beyond area and isolation alone. With a better understanding of the complexity of the scales of nature (i.e. spatial, temporal, and ecological; Lomolino, 2000a; Whittaker, 2000), variables beyond the balance of immigration and extinction in island systems must be considered. Several alternatives and modifications to MacArthur and Wilson's (1967) equilibrium theory of island biogeography have been suggested within the last decade (see Lomolino 2000b - hierarchical speciesbased model) and include the addition of more complex variables (including evolution) into the simplistic equilibrium model (Lomolino, 2000a; Whittaker, 2000). Removing evolution from the original model allowed MacArthur and Wilson (1967) to assume variation in species richness was controlled by area and isolation alone, and species abilities to colonize and propagate different islands were equivalent (Lomolino 2000a). Additionally, Heaney (2007) comments on several the aspects of a new paradigm, which include frequency of dispersal, variation in gene flow, factors affecting species diversification, correlation of island age and inhabiting species' ages, species persistence on islands, and re-colonization of continents by island species.



Dispersal patterns in the Lesser Antilles—Terrestrial vertebrate movement along archipelagoes is thought to happen primarily by accidental rafting events (Censky et al., 1998; Raxworthy et

al., 2002; Schoener et al., 2001). For birds and bats, the question of dispersal is more complex because they are capable of flight (Fleming and Murray, 2009; Koopman, 1977; Whittaker, 1998). Pumo et al., (1996) and Carstens et al., (2004) imply restricted dispersal ability among the islands for the cave-roosting endemic, B. cavernarum, resulting in isolated intra-island gene pools, whereas the Caribbean eurytopic A. jamaicensis showed little isolation and apparently moves among the islands more often. As these genetic data imply, and with the possible except of *Noctilio leporinus*, Antillean bat species do not voluntarily move over water from one island to another on a regular basis (see also Fleming and Murray, 2009). Based on the available data, we conclude that tropical storms, not bat behavior, are responsible for insular dispersal and gene flow for bat populations living in the Lesser Antilles.

Genetic-Level Diversity and Phylogeographic Patterns

What follows is a brief review of recent studies of the molecular systematics and phylogeography of Lesser Antillean bats (*Table 2*).

Emballonuridae.—The Lesser Antillean representative of this family, Peropteryx trinitatis phaea (sensu Simmons, 2005) from Grenada, has not been examined genetically. Lim et al. (2008) included specimens of P. trinitatis collected from northern South America and Trinidad in their analysis of New World Emballonurid bats. Their data show that *P. trinitatus* is genetically distinct from *P. macrotis*, therefore providing further evidence that P. trinitatis is a taxonomically valid species (see Brosset and Charles-Dominique, 1990). A detailed genetic analysis of specimens from Grenada, Trinidad, and Tobago is clearly warranted based on the observations by Genoways et al., (1998) regarding the morphological variability exhibited throughout this region.

Mormoopidae.-Lewis-Oritt et al., (2001a) and Davalos (2006) examined phylogenetic variation in both mitochondrial and nuclear DNA datasets from several species of *Pteronotus*. Davalos (2006) elevated the subspecies P. parnellii rubiginosus to species status and our molecular identifications of specimens from St. Vincent are congruent with this taxonomic arrangement. Thus, P. rubiginosus is the appropriate binomial for Lesser Antillean populations formally identified as P. parnellii on St. Vincent. Moreover, our analyses indicate a close relationship between St. Vincent and Suriname populations of P. rubiginosus (< 1% in cytochrome-b gene variation). This indicates colonization of the Lesser Antilles from northern South America by *P. rubiginosus*. Davalos (2006) also examined genetic variation within Pteronotus davyi and included specimens collected from Dominica in her analyses. The results of Davalos (2006) indicate a close relationship between *Pteronotus davyi* on Dominica and Trinidad, also indicating a northern South American origin for Lesser Antillean populations of this species.

Noctilionidae.—Lesser Antillean populations of Noctilio leporinus exhibit low (< 1.5%) mitochondrial DNA sequence variation across their distribution (Lewis-Oritt *et al.*, 2001b). This result indicates a fairly recent colonization of the Lesser Antilles by this species, most likely originating from northern South America. Moreover, the genetic data indicate multiple colonization events by *N. leporinus* into the Lesser Antilles (see Genoways *et al.*, 2010).

Phyllostomidae.—Of the Lesser Antillean representatives of the family Phyllostomidae, the most detailed phylogenetic analyses have been performed on the genus Artibeus (P. Larsen et al., 2007; P. Larsen et al., 2010; Phillips et al., 1989; Phillips et al., 1991; Pumo et al., 1996). Collectively the data from Artibeus indicate recent (late Pleistocene/Holocene) colonization events by A. jamaicensis from Central America and A. planirostris and A. lituratus from northern South America (Genoways et al., 2005; Genoways et al., 2010; P. Larsen et al., 2007; P. Larsen et al., 2010). Perhaps the most interesting aspect of the genetic variation present in Lesser Antillean populations of Artibeus is found with the endemic A. schwartzi. Mitochondrial, nuclear, and morphological data indicate that contemporary populations of A. *schwartzi* on St. Vincent and throughout the Grenadines are the product of extensive hybridization among multiple species of Artibeus (see P. Larsen et al., 2010). The potential hybrid origin for A. schwartzi and evolutionary significance of hybridization among multiple lineages of Artibeus is discussed in detail by P. Larsen *et al.*, (2010). It should also be noted that the hybrid zone within Lesser Antillean populations of Artibeus coincides with the geographic position of Koopman's Line (Genoways et al., 2010).

Relatively few studies have examined the patterns of genetic variation within the Lesser Antillean endemics Brachyphylla cavernarum, Ardops nichollsi, Monophyllus plethodon, Chiroderma improvisum, and Sturnira thomasi. Carstens et al. (2004), Davalos (2004), and Murray (2008) did examine genetic variation within B. cavernarum. Their results indicate (1) a close genetic relationship between *B. cavernarum* and *B. pumila* (<3%) in cytochrome-b gene sequence data), and (2) a recent expansion by *B. cavernarum* throughout the Lesser Antilles. The population genetic structure and molecular systematics of Ardops nichollsi has been investigated by Carstens et al. (2004), Davalos (2004), and Davalos (2007). Collectively the data from these studies indicate low sequence variation within Ardops nichollsi and a close genetic relationship between Ardops and Ariteus. These results are consistent with the hypothesis of a relatively recent origin (~ 2 million years ago) of the genus Ardops (Baker et al., in press). Baker et al.(1994) used cytochrome-b sequence data to examine interspecific relationships within the genus Chiroderma. This molecular marker inferred a sister relationship between *C. improvisum* and *C. villosum* (distributed in Central and South America), whereas the most basal species in the genus, *C. salvini*, is found throughout Middle, Central and South America. This may indicate the ancestor of the Lesser Antillean lineage originated from Central or South America. Additional studies of *M. plethodon* and *S. thomasi* are ongoing.

Genetic data from Glossophaga longirostris (Hoffmann and Baker, 2001) indicate a close relationship among populations distributed from St. Vincent southward to Trinidad and Tobago, thus suggesting a colonization of the southern Lesser Antilles from northern South America. Robust genetic analyses of the remaining Lesser Antillean phyllostomids Anoura geoffroyi, Dermanura bogotensis, Micronycteris megalotis, and Sturnira lilium, are either absent or ongoing.

Vespertilionidae.—Ruedi and Mayer (2001) and Stadelmann et al., (2007) included the Lesser Antillean endemics *Myotis dominicensis* and *M. martiniquensis* in their analyses of New World species of Myotis. Collectively, their data show a sister relationship between *M. dominicensis* and *M. martiniquensis*. However, these existing molecular datasets fail to elucidate the biogeographic origins of the Caribbean populations of Myotis. This failure is attributable to saturation of molecular markers and/or poor taxonomic sampling throughout Central and South America. Previous authors (using morphological data) have suggested the origins of Lesser Antillean Myotis are from South America (Baker and Genoways, 1978; LaVal, 1973; LaVal and Schwartz, 1974). The taxonomic status of the subspecies *M. martiniquensis nyctor* from Barbados, as well as *M. nigricans* from Grenada, is currently under investigation.

Natalidae.—Davalos (2005) included specimens of *Natalus stramineus* collected from Dominica and Marie Galante in her examination of the genetic variation within Natalidae. Her results show that the mitochondrial lineages (cytochrome-b gene sequence data) within *N. stramineus* are paraphyletic with respect to *N. tumidirostris* from Trinidad. Several hypotheses could account for this result and include, (1) incomplete lineage sorting, (2) mitochondrial introgression subsequent to hybridization, or (3) multiple species exist within the *N. stramineus* complex (Davalos, 2005). Additional studies of the genetic variation within Lesser Antillean populations of *Natalus*

stramineus are required to test these alternative hypotheses.





Molossidae.—Phylogenetic analyses using molecular data from Lesser Antillean populations referable to Molossus molossus and Tadarida brasiliensis remain to be conducted. Genoways et al., (1981) and Timm and Genoways (2003) identified significant morphological variability among Antillean populations of *M. molossus* indicating that the species complex was in need of taxonomic revision. With respect to T. brasiliensis, there are subtle morphological differences that separate the subspecies T. b. antillularum and T. b. constanzae (Timm and Genoways, 2003). However, the significance of this variation remains to be determined and requires a taxonomic assessment of the entire Tadarida brasiliensis complex using molecular data.

Bat Conservation Issues in the Lesser Antilles

The conservation of bats is not only important to maintain their contribution to island biodiversity, but because they are linked to the maintenance of other aspects of the region's fauna and flora. The maintenance of chiropteran fauna can best be served by three conservation actions treated separately below—preservation of caves, preservation of forests, and restoration of hydrological systems.

Preservation/Protection of Caves—At least 10 species of bats occurring in the Lesser Antilles are obligate cave roosters, or will roost in rock fissures/ over-hangs if caves are not available. Caves and their man-made equivalents (mines, wells, cisterns, abandoned buildings) provide critical refugia in times of natural disaster (Gannon and Willig, 1994; Pedersen et al., 1996), and are one of the most critical limiting factors for several bat species (Genoways et al., 2007a, 2007b, 2007c; Pedersen et al., 2003, 2005, 2006). Conversely, cave roosts pose a risk to their occupants if the cave is destroyed suddenly (e.g., earthquakes, volcanic activity, human action; Genoways et al., 2007b). Our observations indicate that most caves throughout the region are heavily impacted by human activities (vandalism, used as garbage dumps, buried beneath housing developments and roads, used as housing for livestock, and even modified for human habitation).

Conservation efforts often underestimate or even ignore the fragility of cave systems and the valuable hidden levels of biodiversity therein. Guano produced by cave roosting bats is the primary energy source for entire ecosystems of obligate cave vertebrates, invertebrates, plants, and fungi. The protection of caves should be a priority for any island conservation effort.



Preservation/Protection of Forests-Several bat species utilize caves in a facultative manner, but more commonly roost in the cavities of large trees (living or dead), or in foliage roosts such as beards of several types of palm-tree. Foliage roosts pose a very different kind of conservation problem that involves the protection of forests. Healthy forests require healthy bat populations and healthy bat populations require healthy forests. Forests provide roosts, protection, and food resources for bats, in return, bats provide several vital functions for the forests, including insect control, pollination of a wide-variety of plant species, and the subsequent dispersal of plant seeds.

The 12 species of insectivorous bats occurring in the Lesser Antilles consume a wide variety of nocturnal insects and help control these insect populations. The nutrients represented by these insects are transported by insectivorous bats from the foraging areas back to their roosting sites thus contributing to the cycling of energy and nutrients through forest and cave ecosystems (Jones *et al.*, 2009).

More than 350 species of plant representing 44 plant families are bat-pollinated (Fleming et al., 2009); bats play a vital role in maintaining the genetic diversity in tropical plant communities (Fleming et al., 2009; Quesada et al., 2004). Bat-pollinated plants include large tropical forest trees, such as kapok (*Ceiba pentandra*), sandbox tree (Hura crepitans), and royal palm (Roystonea regia), to cactus (Neobuxbaumia euphorbioides), and agave (Agave angustifolia) (Fleming et al., 2009). Native fruit trees, such as guava (Psidium guajava) and the introduced banana (Musa paradisiaca) also are pollinated by bats (Soto-Centeno and Kurta, 2006). Bats do not specialize in pollinating a single species of plant, but visit a range of species available in their habitat (Heithaus et al. 1975; Muchhala and Jarrín-V., 2002; Nassar et al., 2003; Soto-Centeno and Kurta, 2006; Tschapka et al., 2008; Quesada et al., 2004). Bats are excellent pollinators because they readily overcome distances between various plants and carry heavier pollen loads than other pollinators (e.g., insects, birds).

The 14 species of phyllostomid bats occurring in the Lesser Antilles are involved in the pollination and seed dispersal of some ecologically and economically important plant species (Howe and Miriti, 2004; Jones et al., 2009). Bats frequently disperse seeds of pioneer plants (e.g., Cecropia, Solanum, Piper) critical to the revegetation of areas that had been cleared for agriculture or that have been heavily damaged by hurricanes or volcanic eruptions (Jones *et al.*, 2009; Kelm *et al.*, 2008; Martínez-Garza and González-Montagut, 2002; Medellín and Gaona, 1999). Although birds have long been credited as seed dispersers, Medellín and Gaona (1999) found that bats account for more than half of the "seed rain" in a variety of tropical forest habitats in southern Mexico. **Protection and Restoration of Hydrological Systems**— Perhaps most importantly, healthy forests are vital to the maintenance of an island's hydrologic system of small streams, aquatic habitats, soil moisture levels, the humidity of numerous microhabitats and ecological niches, and all of the biodiversity that these represent.

Many hydrological systems throughout the Lesser Antilles have been dramatically altered for human consumption and irrigation of crops, sometimes with great damage to the entire ecosystem (Genoways *et al.*, 2007b). Protection of fresh water resources is imperative for any and all conservation efforts. Real estate development and road construction must be done more carefully with consideration for deforestation and water runoff if sedimentation is reduced, we can limit damage to natural springs and natural hydrological cycles. Healthy hydrologic systems help insure clean water resources and this benefits forests, wildlife, and the human populations on these islands.

Our use of molecular-based studies adds to the previous faunal and ecological surveys (at various time frames and in variable environmental conditions and habitats) by increasing our understanding of the genetic variation in the bat fauna of the Lesser Antilles, in light of a modern theory of island biogeography. This broadens our understanding of the complex patterns and processes influencing island systems and island biota.

The conservation needs of bats are relatively straightforward; their foraging areas and roost sites must be preserved. Where possible, forests should be protected. This could be accomplished in several ways: land purchase by local governments/NGOs, or by reforestation programs as part of a wildlife management option. Forests could also be preserved by establishing wildlife management zones according to areas of conservation priority, species priority, landownership, etc. Where possible forest enrichment could be achieved by planting native species and forest habitat could be enhanced by creating corridors between forest fragments. Where possible, water resources should be maintained or restored to support plant and animal communities that are not only vital to the health of bats and forests, but to that of humans as well. Roost sites such as caves must also be protected but deep sheltered ravines on some of the more mountainous islands also provide significant roosting options and refuge during large storms. Perhaps deep ravines and caves should be viewed as ecological equivalents from both evolutionary and animal conservation perspectives.

There is a tremendous need to increase awareness and to educate the public about local bats. Without public involvement in conservation, bat populations and everything that relies on them will suffer. Awareness and education can be accomplished by creating displays and information kiosks at local festivals and agricultural fairs. Wildlife management agencies can work with local schools to develop youth-based conservation programs for native species and sustainable development. Simple information booklets can be printed and distributed to encourage the planting of native fruit trees on both public and private lands that will in turn support a wide range of native bird and bat species.

We are left with a great many questions with regards to conservation efforts and biodiversity survey data for Lesser Antillean bats. Many of these questions relate to how our survey data can be integrated into conservation and management decisions that impact a broad range of biodiversity. We have a great deal of work yet to do.

Acknowledgments—Our thanks go to innumerable Forestry and Environment Officers on over a dozen islands for providing their support over the last 20 years. Material and curatorial support was provided primarily by the Division of Zoology of the University of Nebraska State Museum and by the Natural Science Research Laboratory of the Museum of Texas Tech University.

Literature cited

BAKER R. J., BININDA-EMONDS O. R. P., MAN-TILLA-MELUK H., PORTER C. A., VAN DEN BUSS-CHe R. A., In press, "Molecular timescale of diversification of feeding strategy and morphology in New World leaf-nosed bats (Phyllostomidae): a phylogenetic perspective. In Evolutionary history of bats: fossils, molecules and morphology", in Gunnell G. F, Simmons N. B. (eds.), *Cambridge Studies in Molecules and Morphology – New Evolutionary Paradigms*, Cambridge, Cambridge University Press.

BAKER R. J., GENOWAYS H. H., 1978, "Zoogeography of Antillean bats. Academy Natural Science of Philadelphia Special Publications", *Special Publication*, No. 13, 563-597.

BAKER R. J., TADDEI V. A. HUDGEONS J. L., VAN DEN BUSSCHE R. A., 1994, "Systematic relationships within *Chiroderma* (Chiroptera: Phyllostomidae) based on cytochrome-B sequence variation", Journal of Mammalogy, vol. 75, No. 2, 321-327.

BARBER J. R., RAZAK K. A., FUZESSERY Z. M., 2003, "Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus", Journal Compara-tive Physiology* A, vol. 189, 843–855.



BARLOW K. E., VAUGHAN N., JONES K. E., RODRÍGUEZ-DURÁN A., GANNON M. R., 2000, "Are bats which pollinate and disperse forest plants particularly sensitive to disturbance? A case study on the effects of Hurricane Georges on bats of Puerto Rico", *Bulletin of the British Ecological Society*, vol. 31, 36-37.

BERRY N., O'CONNOR W., HOLDERIED M. W., JONES G., 2004, "Detection and avoidance of harp traps by echolocating bats", *Acta Chiropterologica*, vol. 62, 335-346.

BROSSET A., CHARLES-DOMINIQUE P., 1990, "The bats from French Guiana: a taxonomic, faunistic and ecological approach", *Mammalia*, vol. 54, No. 4, 509-560.

BROWN J. H., LOMOLINO M. V., 2000. "Concluding remarks: Historical perspective and the future of island biogeography theory", Global Ecology and Biogeography, vol. 9, 87-92.

CARSTENS B. C., SULLIVAN J., DÁVALOS L. M., LARSEN P. A., PEDERSEN S. C., 2004, "Exploring population and genetic structure in three species of Lesser Antillean bats", *Molecular Ecology*, vol. 13, No. 9, 2557-2566.

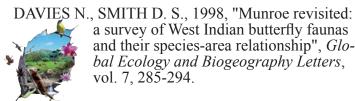
CENSKY E. J., HODGE K., DUDLEY J., 1998, "Over-water dispersal of lizards due to hurricanes", *Nature*, vol. 395, 556.

DAVALOS L. M., 2004, "Phylogeny and biogeography of Caribbean mammals", *Biological Journal of the Linnean Society*, vol. 81, No. 3, 373-394.

DAVALOS L. M., 2005, "Molecular phylogeny of funnel-eared bats (Chiroptera: Natalidae), with notes on biogeography and conservation", *Molecular Phylogenetics and Evolution*, vol. 37, No. 1, 91-103.

DAVALOS L. M., 2006, "The geography of diversification in the mormoopids (Chiroptera: Mormoopidae)", *Biological Journal of the Linnean Society*, vol. 88, No. 1, 101-118.

DAVALOS L. M., 2007, "Short-faced bats (Phyllostomidae: Stenodermatina): a Caribbean radiation of strict frugivores", *Journal of Biogeography*, vol. 34, No. 2, 364-375.



FENTON M. B., ACHARYA L., AUDET D., HICKEY M. B., MERRI-MAN C., OBRIST M. K., SYME D., 1992, "Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics", *Biotropica*, vol. 24, 440-446.

FLEMING T. H., GEISELMAN C., KRESS W. J., 2009, "The evolution of bat pollination: a phylogenetic perspective", *Annals of Botany*, vol. 104, 1017-1043.

FLEMING T. H., MURRAY K. L., 2009, "Population and Genetic Consequences of Hurricanes for Three Species of West Indian Phyllostomid Bats", *Biotropica*, vol. 41, 250–256.

GANNON M. R., WILLIG M. R., 1994, "The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico", *Biotropica*, vol. 26, 320-331.

GENOWAYS H. H., 1998, "Two new species of bats of the Genus Sturnira from the Lesser Antilles, West Indies", *Occasional Papers of the Museum, Texas Tech University*, No. 176, 1-7.

GENOWAYS H. H., BAKER R. J., BICKHAM J. W., PHILLIPS C. J., 2005, "Bats of Jamaica". *Special Publications, Museum of Texas Tech University*, No. 48, 1-155.

GENOWAYS H. H., DOWLER R. C., CARTER C. H., 1981, "Intraisland and interisland variation in Antillean populations of *Molossus molossus* (Mammalia: Molossidae)", *Annals of Carnegie Museum*, vol. 50, No. 20, 475-492.

GENOWAYS H. H., KWIECINSKI G. G., LARSEN P. A., PEDERSEN S. C., LARSEN R. J., HOFFMAN J. D., DE SILVA M., PHILLIPS C. J., BAKER R. J., 2010, "Bats of the Grenadine islands, West Indies, and placement of Koopman's Line", *Chiroptera Neotropical*, vol. 16, No. 1, 501-521.

GENOWAYS H. H., LARSEN P. A., PEDERSEN S. C., HUEBSCHMAN J. J., 2007a. "Bats of Saba, Netherlands Antilles". *Acta Chiropterologica*, vol. 9, 91-114.

GENOWAYS H. H., PEDERSEN S. C., LARSEN P. A., KWIECINSKI G. G., HUEBSCHMAN J. J., 2007b, "Bats of Saint Martin, French West Indies/Sint Maarten, Netherlands Antilles", *Mastozoologia Neotropical*, vol. 14, No. 2,169-188.



GENOWAYS H. H., PEDERSEN S. C., PHILLIPS C. J., GORDON L. K., 2007c, "Bats of Anguilla, Northern Lesser Antilles". *Occasional Papers of the Museum, Texas Tech University*, No. 270, 1-12.

GENOWAYS H. H., PHILLIPS C. J., BAKER R. J., 1998, "Bats of the Antillean island of Grenada: a new zoogeographic perspective", *Occasional Papers, Museum of Texas Tech University*, No. 177, 1-32.

GENOWAYS H. H., TIMM R. M., BAKER R. J., PHILLIPS C. J., SCHLITTER D. A., 2001, "Bats of the West Indian island of Dominica: natural history, areography, and trophic structure", *Special Publication*, *Museum of Texas Tech University*, No. 43, 1-44.

GRIFFITHS T. A., KLINGENER D., 1988, "On the distribution of Greater Antillean bats". *Biotropica*, vol. 20, 240-251.

HEANEY L. R., 2007, "Is a new paradigm emerging for oceanic island biogeography?", *Journal of Biogeography*, vol. 34, 753-757.

HEITHAUS E. R., FLEMING T. H., OPLER P. A., 1975, "Foraging patterns and resources utilization in seven species of bats in a seasonal tropical forest", *Ecology*, vol. 56, 841-854.

HOFFMANN F. G., BAKER R. J., 2001, "Systematics of bats of the genus Glossophaga (Chiroptera: Phyllostomidae) and phylogeography in G. soricina based on the cytochrome-b gene", *Journal of Mammalogy*, vol. 82, No. 4, 1092-1101.

HOWE H. F., MIRITI M. N., 2004, "When seed dispersal matters", *BioScience*, vol. 54, 651-660.

JONES G., JACOBS D. S., KUNZ T. H., WILLIG M. R., RACEY P. A., 2009, "Carpe noctem: importance of bats as bioindicators", *Endangered Species Research*, vol. 8, 93-115.

KELM D. H., WIESNER K. R., VON HELVERSEN O., 2008, "Effects of artificial roosts for frugivorous bats on seed dispersal in a Neotropical forest pasture mosaic", Conservation Biology, vol. 22, 733-741.

KOOPMAN K. F., 1977, "Zoogeography", in Baker R. (ed.), *Biology of the bats of the New World Family Phyllostomatidae, Special Publication of the Museum*, *Texas Tech University*, Lubbock, 39-47.

KWIECINSKI G. G., PEDERSEN S. C., 2002, "Montserrat redux-recovery: role of reproduction in plant-visiting bats". *Bat Research News*, vol. 43, 159A. LANGA. B., WEISE C. D., KALKO E. K. V., ROEMER H., 2004, "The bias of bat netting". *Bat Research News*, vol. 45, 235A.

LARSEN P. A., GENOWAYS H. H., PEDERSEN S. C., 2007, "New records of bats from Saint Barthélemy, French West Indies," *Mammalia*, vol. 70, 321-325.

LARSEN P. A., HOOFER S. R., BOZEMAN M. C., PEDERSEN S. C., GENOWAYS H. H., PHILLIPS C. J., PUMO D. E., BAKER R. J., 2007, "Phylogenetics and phylogeography of the *Artibeus jamaicensis* complex based on cytochrome-b DNA sequences", *Journal of Mammalogy*, vol. 88, No. 3, 712-727.

LARSEN P. A., MARCHAN-RIVADENEIRA M. R., BAKER R. J., 2010, "Natural hybridization generates mammalian lineage with species characteristics", *Proceedings of the National Academy of Sciences*, vol. 107, No. 25, 11447-11452.

LARSEN R. J., BOEGLER K. A., CUDMORE K. W., KOLBA J. C., PEDERSEN S. C., 2006, "Montserrat: Mist-Net Bias and Accumulation Curves", *Bat Research News*, vol. 47, 121A.

LARSEN R. J., BOEGLER K. A., GENOWAYS H. H., MASEFIELD W. P., KIRSCH R. A., PEDERSEN S. C., 2007, "Mist-net bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles)", *Acta Chiropterologica*, vol. 9, 423-435.

LARSEN R. J., BOEGLER K. A., PEDERSEN S. C., 2005, "Mist Netting Bias on Montserrat", Bat Research News, vol. 46, 191A.

LAVAL R. K., 1973, "A revision of the neotropical bats of the genus Myotis", *Bulletin of the Natural History Museum of Los Angeles County*, No. 15, 1-54.

LAVAL R. K., 2004, "Impact of global warming and locally changing climate on tropical cloud forest bats", *Journal of Mammalogy*, vol. 85, 237-244.

LAVAL R. K., Schwartz A., 1974, "A new bat of the genus *Myotis from Barbados*", *Caribbean Journal of Science*, vol. 14, No. 3-4, 189-191.

LEWIS-ORITT N., PORTER C. A., BAKER R. J., 2001a, "Molecular systematics of the family Mormoopidae (Chiroptera) based on cytochrome b and recombination activating gene 2 sequences", *Molecular Phylogenetics and Evolution*, vol. 20, No. 3, 426-436.



LEWIS-ORITT N., VAN DEN BUSSCHE R. A., BAKER R. J., 2001b, "Molecular evidence for evolution of piscivory in Noctiliio (Chiroptera: Noctilionidae)", Journal of Mammalogy, vol. 82, No. 3, 748-759.

LIM B. K., ENGSTROM M. D., BICKHAM J. W., PATTON J. C., 2008, "Molecular phylogeny of New World sheath-tailed bats (Emballonuridae: Diclidurini) based on loci from the four genetic transmission systems in mammals", *Biological Journal of the Linnean Society*, vol. 93, No. 1, 189-209.

LOMOLINO M. V., 2000a, "A call for a new paradigm of island biogeography", Global Ecology and Biogeography, vol. 9, No. 1, 1-6.

LOMOLINO M. V., 2000b, "A species-based theory of insular zoogeography", Global Ecology and Biogeography, vol. 9, No. 1, 39-58.

MACARTHUR R. H., WILSON E. O., 1967, The theory of island biogeography, Princeton, NJ, Princeton University Press.

MARTÍNEZ-GARZA C., GONZÁLEZ-MONTAGUT R., 2002, "Seed rain of fleshy-fruited species in tropical pastures in Los Tuxtlas, Mexico", Journal of Tropical Ecology, vol. 18, 457-462.

MEDELLÍN R. A., GAONA O., 1999, "Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico", Biotropica, vol. 31, 478-485.

MORGAN G. S., WOODS C. A., 1986, "Extinction and the zoogeography of West Indian land mammals", Biological Journal of the Linnaean Society, vol. 28, 167-203.

MUCHHALA N., JARRÍN-V, P., 2002, "Flower visitation by bats in cloud forests of western Ecuador", Biotropica, vol. 34, 387-395.

MURRAY K. L., 2008, "The genetic structure and mating systems of the buffy flower bat (Erophylla *sezekorni*)", PhD dissertation, University of Miami, Miami, FL, USA.

NASSAR J. M., BECK H., DA S. L. STERNBERG L., FLEMING T. H., 2003, "Dependence on cacti and agaves in nectar-feeding bats from Venezuelan arid zones", Journal of Mammalogy, vol. 84, 106-116.



PEDERSEN S. C., GENOWAYS H. H., FREEMAN P. W., 1996, "Notes on the bats from Montserrat (Lesser Antilles), with comments concerning the effects of Hurricane Hugo", Caribbean Journal of Science, vol. 32, 206-213.

PEDERSEN S. C., GENOWAYS H. H., MORTON M. N., JOHNSON J. W., COURTS S. E., 2003, "Bats of Nevis, northern Lesser Antilles", Acta *Chiropterologica*, vol. 5, 251-267.

PEDERSEN S. C., GENOWAYS H. H., MORTON M. N., KWIECINSKI G. G., COURTS S. E., 2005, "Bats of St. Kitts (St. Christopher), northern Lesser Antilles, with comments regarding capture rates of Neotropical bats", Caribbean Journal of Science, vol. 41, 744-760.

PEDERSEN S. C., GENOWAYS H. H., MORTON M. N., SWIER V. J., LARSEN P. A., LINDSAY K. C., ADAMS R. A., APPINO J. D., 2006, "Bats of Antigua, northern Lesser Antilles", Occasional Papers of the Museum, Texas Tech University, No. 249, 1-18.

PEDERSEN S. C., KWIECINSKI G. G., LARSEN P. L., MORTON M. N., ADAMS R. A., GENOWAYS H. H., SWIER V. J., 2009, "Bats of Montserrat: Population fluctuation in response to hurricanes and volcanoes, 1978-2005", in Fleming T. H., Racey P. A. (eds.), Island Bats, Evolution, Ecology and Conservation, Chicago, University of Chicago Press, 302-340.

PEDERSEN S. C., LARSEN P. A., GENOWAYS H. H., MORTON M. N., LINDSAY K. C., CINDRIC J., 2007, "Bats of Barbuda, Northern Lesser Antilles". Occasional Papers of the Museum, Texas Tech University, No. 271, 1-19.

PHILLIPS C. J., PUMO D. E., GENOWAYS H. H., RAY P. E., 1989, "Caribbean island zoogeography: a new approach using mitochondrial DNA to study Neotropical bats", in Woods C. A., (ed.), Biogeography of the West Indies, Gainseville, Florida, Sandhill Crane Press.

PHILLIPS C. J., PUMO D. E., GENOWAYS H. H., RAY P. E., BRISKEY C. A., 1991, "Mitochondrial DNA evolution and phylogeography in two neotropical fruit bats, Artibeus jamaicensis and Artibeus lituratus", in Mares, M. A., Schmidly, D. J., (eds.), Latin American Mammalogy: history, biodiversity, and conservation, Norman, Oklahoma, University of Oklahoma Press.



PUMO D. E., REMSEN K. I., PHILLIPS C. J., GENOWAYS H. H., 1996, "Molecular systematics of the fruit bat, *Artibeus jamaicensis*: origin of an unusual island population", *Journal of Mammalogy*, vol. 77, No. 2, 491-503.

QUESADA M., STONER K. E., LOBO J. A., HER-RERIAS-DIEGO Y., PALACIOS-GUEVARA C., MUNGUIA-ROSAS M. A., O-SALAZAR K. A., RO-SAS-GUERRERO V., 2004, "Effects of forest fragmentation on pollinator activity and consequences for plant reproductive success and mating patterns in bat-pollinated Bombacaceous trees", *Biotropica*, vol. 36, 131-138.

RAXWORTHY C. J., FORSTNER M. R. J., NUSS-BAUM R. A., 2002, "Chameleon radiation by oceanic dispersal", *Nature*, vol. 415, 784-786.

RUEDI M., MAYER F., 2001, "Molecular systematics of bats the genus Myotis (Vespertilionidae) suggests deterministic ecomorphology convergences", *Molecular Phylogenetics and Evolution*, vol. 21, No. 3, 436-448.

SCHOENER T. W., SPILLER D. A., LOSOS J. B., 2001, "Natural restoration of the species-area relation for a lizard after a hurricane", *Science*, vol. 294, 1525-1528.

SIMMONS N. B., 2005, "Order Chiroptera", in Wilson D. E., Reeder D. M. (eds.), *Mammal species of the world: a taxonomic and geographic reference*, 3rd ed., Baltimore, Maryland, Johns Hopkins University Press.

SIMMONS N. B., Voss R. S., 1998, "The mammals of Paracou, French Guiana, a Neotropical lowland rainforest fauna. Part 1, Bats", *Bulletin American Museum of Natural History*, No. 237.

SOTO-CENTENO J. A., KURTA A., 2006, "Diet of two nectarivorous bats, *Erophylla sezekorni* and *Monophyllus redmani* (Phyllostomidae), on Puerto Rico", *Journal of Mammalogy*, vol. 87, 19-26.

SPEED R. C., KELLER C. A., 1993, "Synopsis of the geological evolution of Barbados", *Journal of the Barbados Museum and Historical Society*, vol. 61, 113-139.

STADELMANN B., LIN L. -K., KUNZ T. H., RUEDI M., 2007, "Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes", *Molecular Phylogenetics and Evolution*, vol. 43, No. 1, 32-48. TIMM R. M., GENOWAYS H. H., 2003, "West Indian mammals from the Albert Schwartz collection: biological and historical information", *Scientific Papers, Natural History Museum, The University of Kansas*, No. 29, 1-47.

TSCHAPKA M., SPERR E, B., CABALLERO-MARTÍNEZ L. A., MEDELLÍN R. A., 2008, "Diet and cranial morphology of *Musonycteris harrisoni*, a highly specialized nectar-feeding bat in western Mexico", *Journal of Mammalogy*, vol. 89, 924-932.

