7-2010

Bats of the Grenadine Islands, West Indies, and Placement of Koopman's Line

Hugh H. Genoways
University of Nebraska - Lincoln, h.h.genoways@gmail.com

Gary G. Kwiecinski
University of Scranton

Peter A. Larsen
Texas Tech University, peter.larsen@duke.edu

Scott C. Pedersen
South Dakota State University, scott.pedersen@sdstate.edu

Roxanne J. Larsen
Texas Tech University, roxy.larsen@duke.edu

See next page for additional authors

Authors
Hugh H. Genoways, Gary G. Kwiecinski, Peter A. Larsen, Scott C. Pedersen, Roxanne J. Larsen, Justin D. Hoffman, Mark de Silva, Carleton J. Phillips, and Robert J. Baker

BATS OF THE GRENADINE ISLANDS, WEST INDIES, AND PLACEMENT OF KOOPMAN'S LINE

Hugh H. Genoways[1*], Gary G. Kwiecinski[2], Peter A. Larsen[3], Scott C. Pedersen[4], Roxanne J. Larsen[3], Justin D. Hoffman[5], Mark de Silva[6], Carleton J. Phillips[3], and Robert J. Baker[3]

1. University of Nebraska State Museum, W436 Nebraska Hall, Lincoln, NE 68588. U.S.A.
2. Biology Department, University of Scranton, 800 Linden Street, Scranton, PA 18510. U.S.A.
3. Department of Biological Sciences and Museum, Texas Tech University, Lubbock, TX 79409 . U.S.A.
4. Department of Biology and Microbiology, South Dakota State University, Brookings, SD 57007. U.S.A.
5. Department of Biological and Health Sciences, McNeese State University, MSU Box 92000, Lake Charles, LA 70609. U.S.A.
6. P.O. Box 860, Kingstown, St. Vincent and the Grenadines.

* Corresponding author. Email: hgenoways1@unl.edu

Abstract.
Almost nothing is known concerning the chiropteran fauna on the Grenadine Islands, a chain of islands between St. Vincent and Grenada located near the southern end of the Lesser Antilles. Previously, only a single species—*Glossophaga longirostris*—had been reported from the Grenadines. Our research, conducted on 4 occasions over the period of 1980 to 2006, provided museum vouchers and genetic specimens for the addition of 4 other species to the known fauna of these islands—*Noctilio leporinus*, *Artibeus lituratus*, *Artibeus schwartzi*, and *Molossus molossus*. The Grenadines, being situated between St. Vincent and Grenada, occupy an important zoogeographic position. None of the 12 species of bats occurring on Grenada are Antillean endemics, whereas on St. Vincent, to the north of the Grenadines, 3 of the 12 species are Antillean endemics. The boundary of the West Indian Subregion of the Neotropical Region based on the distribution of mammals has been designated as Koopman's Line. One of the areas where placement of Koopman's Line was unresolved was among the Grenadine Islands because the chiropteran fauna of this area was essentially unknown. Based on data reported herein, we place Koopman's Line along the 14-km wide Bequia Channel that separates St. Vincent and the northern-most Grenadine island of Bequia.
Keywords: biodiversity, Chiroptera, Grenadine Islands, Koopman's Line, systematics, zoogeography.

Introduction

The Grenadines are a series of nearly 200 islands, islets, cays, and rocks in the southern Lesser Antilles. Geographically, the Grenadines span a 110-km stretch of water between St. Vincent in the north and Grenada in the south. At least 7 of the islands have permanent settlements and some of the other smaller islets have been converted into resorts. Today, tourism is the main industry in the Grenadines and is the cause of considerable development on many of the islands. The Grenadines are divided politically, with those islands north of the Petite Martinique Channel (Fig. 1) being part of the nation of St. Vincent and the Grenadines—major islands including Bequia, Mustique, Canouan, Mayreau, and Union—and those south of the channel being part of the nation of Grenada—the only major island is Carriacou, whereas Petite Martinique is much smaller.

The Grenadine islands are primarily of volcanic origin, but many also include uplifted sedimentary elements (Beard 1949). Although politically divided, the Grenadines are geologically united along the narrow 4000 square km platform known as the Grenada Bank. The 14-km wide Bequia Channel separating St. Vincent and Bequia, which reaches a depth of 1100 m, marks the northern end of the Grenada Bank. Channels ranging from only 22 to 37 m deep separate the islands along this bank, which extends at this depth approximately 30 km to the southwest of Grenada, although without islands. The Grenadine islands were united with Grenada to form a single elongate island during the Last Glacial Maximum (26,500 to 19,000 years before present; Clark et al. 2009), resulting from a Pleistocene sea level lowering of 120 to 135 m (Watters 1989).

Although the chiropteran faunas of St. Vincent (Vaughan and Hill 1996) and Grenada (Genoways et al. 1998) have been studied in recent years, almost nothing is published concerning the intervening fauna on the

Grenadines. Allen (1908) was the first to record bats from the Grenadine islands when he presented data on a series of *Glossophaga longirostris* from Carriacou and Union Island deposited in the Museum of Comparative Zoology, Harvard University. These same vouchers were reported again by Allen (1911) in his classic "Mammals of the West Indies" and by Miller (1913b) in his revision of the genus *Glossophaga*. Miller (1913b) reported these specimens under the name *Glossophaga longirostris rostrata* (Miller 1913a). The only other mention of Grenadine bats was by Jones (1989) when he included 4 species from the islands in his table on the distribution of bats in the Lesser Antilles. These species occurrences were reported without reference to specific localities or islands, and were based on bats captured during the early phase of our research.

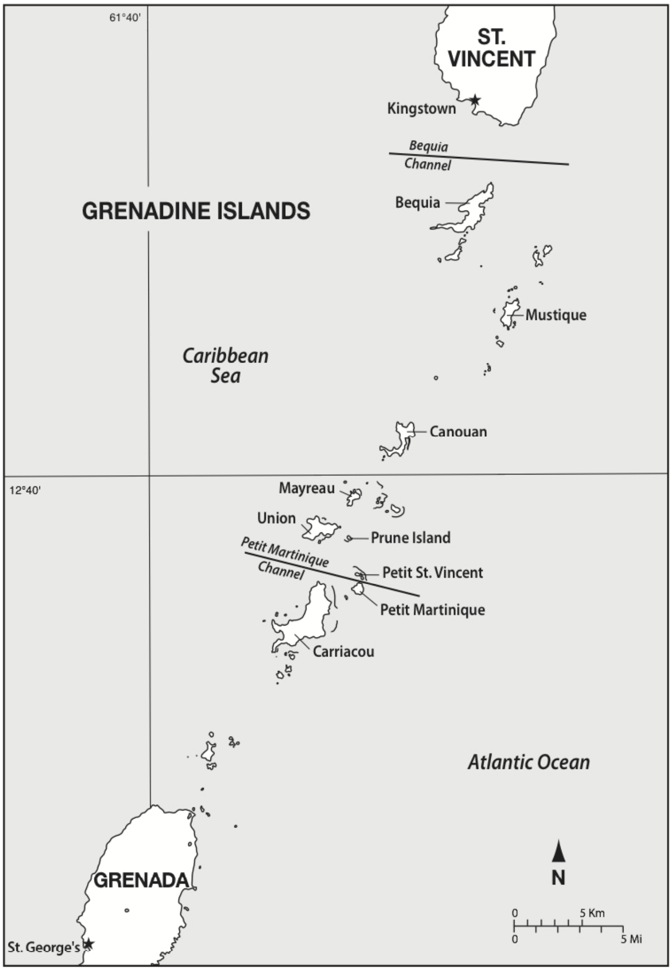

Figure 1. Map showing the Grenadine islands, St. Vincent, and Grenada at the southern end of the Lesser Antilles. The Bequia Channel marks the position of Koopman's Line. The Petit Martinique Channel is the dividing point between the nations of St. Vincent and the Grenadines and Grenada.

The Grenadines, being situated between St. Vincent and Grenada, occupy an important zoogeographic position (Genoways et al. 1998). In 1987-88, nucleotide restriction site mapping of bat mitochondrial genomes was employed for the first time on the Caribbean fauna, and based on these data it was hypothesized that the Grenadines acted as a "filter" to northward or southward dispersal by bats (Phillips et al. 1989). This was an important hypothesis because all current data support the conclusion that all species of bats inhabiting islands in the Caribbean region arrived by over water dispersal or evolved in place (Baker and Genoways 1978; Hedges 2006; Pregill 1981; Morgan and Woods 1986; Pumo et al. 1988, 1996; Phillips et al. 1989, 1991). To the south of the Grenadines, the chiropteran fauna of Grenada consists of species that either invaded from such areas as Trinidad or the South American mainland or are species that are so widespread in their distribution that no particular route of invasion can be determined at this time (Genoways et al. 1998). None of the species of bats occurring on Grenada are Antillean endemics, whereas on St. Vincent, to the north of the Grenadines, 3 of the 12 species are Antillean endemics that are characteristic of the Lesser Antilles (Vaughan and Hill 1996). Two of these species—*Monophyllus plethodon* and *Brachyphylla cavernarum*—occur from Puerto Rico southeastward to St. Vincent and Barbados. The third species—*Ardops nichollsi*—is a Lesser Antillean endemic, but does not occur on Barbados. The foregoing data and analyses led Genoways et al. (1998) to place the boundary of the West Indian Faunal Subregion, designated by them as Koopman's Line, between St. Vincent and Grenada. They opined that once the chiropteran fauna of the Grenadines was known, it could be "that Koopman's Line may eventually be found to bisect the Grenadines" (Genoways et al. 1998: 20).

The goals of our field research in the Grenadine islands were a) to describe the biodiversity of the chiropteran fauna occurring on the islands and b) to use this information to refine our understanding of West Indian zoogeography by determining the placement of Koopman's Line in the region. Refining our understanding of geographic placement of Koopman's Line or, alternatively, discovering that it is more of a region than a narrow zone, is the first step to testing hypotheses about ecological or other factors involved in the zoogeographic phenomenon. To this purpose, we conducted field research during 4 years in the Grenadines, including 1980, 1986, 2005, and 2006. Our work has resulted in the collection of 395 voucher specimens of 5 species. These data are reported herein.

Materials and Methods

Study area. The Grenadine islands are volcanic in origin, with many containing sedimentary components, but everywhere the soils are shallow (Graham 2003). Beard (1949) provided a discussion of the ecology and vegetation of the Grenadine islands. He concluded that all of the forests on these islands were secondary, classifying them as dry scrub woodlands. The largest trees are found on the slopes of Mount Royal on Canouan, on the slopes above Chatham Bay on Union Island, and in the forest reserve in central Carriacou. Among the dominant trees are gumbo-limbo (*Bursera simaruba*), white cedar (*Tabebuia pallida*), black mampoo (*Pisonia fragans*), locust (*Hymenaea courbaril*), and hog plum (*Spondia mombin*). In many places, the trees are badly deformed, branchy, and crooked; however, several of these species have large flowers used by pollen-feeding bats and small pod-like or plum-like fruits that are consumed by fruit-eating bats. A dense, shrubby under story is often dominated by rough velvet seed (*Guettarda scabra*), cucubano de vieques (*G. odorata*), false chiggergrape (*Coccoloba venosa*), and lancewood (*Nectandra coriacea*). Low lying coastal areas are dominated by red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and manchineel (*Hippomane mancinella*). A number of species of regional and introduced fruit trees add to the diversity of plants on the islands and foods available to bats, but nowhere in the Grenadines have we seen these trees occurring in managed plantations, including mangos (*Mangifera indica*), banana (*Musa* sp.), coconut palm (*Cocos nucifera*), guava (*Psidium guajava*), guinep (*Melicoccus bijugatus*), sapodilla (*Manilkara zapota*), nutmeg (*Myristica fragrans*), lime (*Citrus latifolia*), and soursop (*Annona muricata*).

All of the islands are relatively low lying, with the highest elevation just over 300 m. Because of these low elevations, none of the islands creates its own weather, making all of the islands comparatively arid (Beard 1949), with annual rainfall being in the range of just over 100 cm. The islands do have arid-adapted thorny plants, including prickly pear cactus (*Opuntia dillenii*), century plants (*Agave caribaeicola*), and several species of acacia (*Acacia*). The driest part of the year is from December to late April. Annual temperatures range from 27º to 32º C.

The Grenadines lie near the southern boundary of the Caribbean hurricane belt, thus experience fewer hurricane-strength tropical storms than islands further to the north. Hurricane Janet in September 1955 caused major damage in the islands. More recently, Hurricane Ivan in September 2004 and especially Hurricane Emily in July 2005 caused damage in the Grenadines, particularly on Carriacou (Caribbean Hurricane Network 2008).

The following sketches of each island that we visited during our field studies were assembled from our field observations and a variety of internet and print sources (Daudin 2003; De Silva and Wilson 2006; Westercamp et al. 1985).

Bequia is the second largest and the northern-most of the Grenadine islands. It lies 14 km south of St. Vincent. The island covers 15.6 square km, being about 8 km long and 3.5 km wide, with a maximum elevation of 269 m. The island had a sugar economy until the mid 1800's, which was then replaced by cotton, fishing, and whaling. There are about 5000 human residents. The undeveloped portions of this island are covered primarily in thorny scrub forest. Several large concrete cisterns and 2 catchment ponds were noted adjacent to various housing developments, but these were dry during our survey of June 2006. Coconut, hog plum, and soursop trees were present around buildings and on property where irrigation had been provided. Well-tended banana patches were observed at Industry and at a small number of well-irrigated estates on the eastern half of the island. Several rock quarries and rock faces were investigated for potential roost sites without success.

Mustique is a privately owned island divided among less than 100 private *villas*. This island is more arid than Bequia. It covers 5.5 sq km, being 5 km long and 2 km wide, with a maximum elevation of 145 m. The island has a low plain in the north and to the south are 7 valleys that lead down to beaches. The hilly central area is wooded with low scrubby vegetation. Coconut trees are a dominant feature on the island, with the villas surrounded by ornamental plantings. The island produced cotton and sugar until the middle of the 19th century when the plantations were abandoned. In 1958, the island was purchased by private interests and developed in a controlled manner. Much of the island is now a wildlife sanctuary. There are about 500 permanent human residents.

Canouan is a crescent-shaped island about one-half of which is occupied by two major resorts. The island covers 7.3 square km, being 6 km long and 2 km wide, with a maximum elevation of 267 m. The high point, located in the north of the island, is Mount Royal where a small stand of large white cedars can be found. The remainder of the island is arid in aspect, although there are several human-made and maintained freshwater ponds. The population of the island is less than 2000.

Mayreau is one of the smallest of the permanently inhabited Grenadine islands (along with Petite Martinique, which is part of Grenada) with less than 300 residents. The hilltop village of Waterloo, with the colonial ruin at the top of the village called Old Wall, is the only settlement on the island. The island covers 3.76 square km, being 2.5 km long and 2 km wide, with a maximum elevation of 92 m. There is little development on the island, with a single road and an electrical power plant installed in 2004.

Union is the southern-most of the major islands belonging to the nation of St. Vincent and the Grenadines. The island covers 8.4 square km, being 5 km long and 2.5 km wide, with a maximum elevation of 305 m at Mount Taboi. The island had a cotton plantation economy until about the turn of the 20th century when it failed. The economy subsequently was dominated by sharecropping and subsistence farming, which is now being replaced by tourism. The island has approximately 3000 residents in the villages of Clifton and Ashton.

Prune Island is now most frequently called Palm Island because the entire island has been converted to the Palm Island Resort. The island covers 0.4 square km and has a maximum elevation of 45 m. Small areas of the original scrubby vegetation and palm groves still exist, separating various accommodations and along hiking and jogging trails.

Carriacou, part of the nation of Grenada, is the largest and the southern-most of the major Grenadine islands and lies 37 km north of Grenada. The island covers 31.6 square km, being 11.25 km long and 4 km wide, with a maximum elevation of 291 m at High Point North. The economy of the island originally was based on cotton and to a lesser extent on sugar until the 20th century, when limes and nutmeg have contributed to the economy from time to time. Currently, subsistence agriculture prevails on the island. The center of the island is a protected forest reserve that preserves the island's limited water resources. Carriacou has a population of about 6000.

Mist-netting efforts. The mist-netting surveys consisted of 21 nights of collecting during 4 periods, 28-31 May 1980 (4 nights), 17-19 (3 nights) and 22-23 May 1986 (2 nights), 4 August 2005 (1 night), and 26 May to 5 June 2006 (11 nights). Mist netting for bats was conducted in a variety of habitats, including naturally vegetated dry ravines, small fruit plantations, a botanical garden, covered flyways, access roads, and open freshwater ponds. Typically, 5 or 6 mist-nets (2 to 15 m in length depending on the situation) were erected at appropriate intervals at each location and monitored for 4 to 6 hours depending on activity and weather. In each survey period, bats were measured and examined (weight, forearm length, reproductive status, tooth wear, presence of scars, and external parasites) following the evening's work. Bats that were not taken as vouchers were released at the site of capture.

Voucher specimens. Our work on the Grenadine islands resulted in 395 voucher specimens of 5 species of bats (Carriacou, 161; Union, 71; Bequia, 65; Mustique, 55; Canouan, 37; Mayreau, 5; Prune Island, 1). All voucher specimens from the 1980 and 1986 surveys were deposited in the research collections at the Carnegie Museum of Natural History (CM), Pittsburgh, PA, under the care of John R. Wible and Suzanne B. McLaren and those from 2005-2006, with all associated tissue samples, were deposited in the collections of the Museum of Texas Tech University (TTU), Lubbock, under the care of Robert J. Baker and Heath Garner. Length of forearm and cranial measurements were taken from museum specimens using digital calipers. Measurements are given in millimeters and weights are in grams.

Species Accounts

Noctilio leporinus mastivus

Greater Fishing Bat

Specimens examined (5).—CARRIACOU: Botanical Gardens, Hillsborough, 20 m [12º29'02.8" N, 61º27'15.3" W], 1 (TTU); Craigston Estate, 4 (CM).

These 5 specimens represent the first documentation of occurrence of the greater fishing bat in the Grenadine islands. We follow Davis (1973) in using the subspecific name *mastivus* for this population. He used this trinomial for all circum-Caribbean populations.

The 4 specimens collected at the Craigston Estate were netted in 1980 over an open pond within sight of the coast. This part of the estate was an old lime orchard and factory, with many lime trees as well as some of the low thorny vegetation native to the island. Although only a single specimen was collected on Carriacou in 2006, at least 5 additional individuals were observed feeding on tadpoles in the Botanical Garden pond in Hillsborough.

Although the greater fishing bat was only taken on Carriacou during our survey, it can be expected on any island where there are rock outcroppings or small caves to provide day roosts and open water that is at least partly protected from the wind. This species is difficult to survey because of its open foraging habitat while its flight abilities are not conducive to being caught in mist nets. Observations by members of our team support a potentially wider distribution of this species in the Grenadines. On Canouan, 1 member of our field team (de Silva) watched a bat that appeared larger than an *Artibeus*, possibly a *Noctilio*, hawking large insects attracted to the bright floodlights at a basketball game.

Both nuclear (RAG-2) and mitochondrial (cytochrome-*b*) gene trees indicate a close genetic relationship between *N. leporinus* from Carriacou and conspecifics from northern South America (Lewis-Oritt et al. 2001). Although overall cytochrome-*b* sequence variation within *N. leporinus* is low, an individual from Carriacou clustered with those from Guyana, Venezuela, and Peru rather than with individuals from Montserrat, Grenada, and Panama (Lewis-Oritt et al. 2001). This observation is significant in that it indicates either multiple invasions by *N. leporinus* into the Caribbean or incomplete lineage sorting within the species.

A female captured on 30 May 1980 evinced no gross reproductive activity. Three males taken on this same date had testes lengths of 5, 5.5, and 6.5. The male taken 29 May 2006 had testes measuring 6.5 and weighed 52.6.

Length of forearm and 7 cranial measurements of 3 males (Hillsborough specimen first) and 1 female, respectively, are as follows: length of forearm, 88.5, 84.0, 88.1, 84.1; greatest length of skull, 28.4, 28.2, 28.9, 26.2; condylobasal length, 25.1, 24.4, 24.8, 23.7; zygomatic breadth, 19.5, 19.8, 19.9, 18.3; postorbital constriction, 7.3, 7.1, 7.8, 7.2; mastoid breadth, 16.7, 18.7, 19.8, 16.3; length of maxillary toothrow, 10.5, 10.3, 10.6, 9.8; breadth across upper molars, 12.9, 12.4, 12.6, 11.7.

Glossophaga longirostris rostrata

Miller's Long-tongued Bat

Specimens examined (139).—BEQUIA: Friendship Bay, 2.1 km S Port Elizabeth, 6 m [12º59'36.1" N, 61º14'08.9" W], 2 (TTU); Industry House, 2.3 km NE Port Elizabeth, 2 m [13º01'28.3" N, 61º13'10.6" W], 2 (TTU); 1.4 km N, 1.5 km E Port Elizabeth, 3 (CM); 2.1 km SW Port Elizabeth, 3 m [12º59'45.2" N, 61º14'42.5" W], 2 (TTU); St. Hilaire Hotel Ruins, 2.2 km SSE Port Elizabeth, 61 m [12º59'29.9" N, 61º13'51.6" W], 2 (TTU). CANOUAN: Archer Inn, 0.45 km N, 0.5 km E Charlestown, 13 m [12º42'12" N, 61º19'38.3" W], 14 (TTU); Carenage, 16 m [12º43'06.8" N, 61º19'29.2" W], 4 (TTU). CARRIACOU: Craigston Estate, 36 (30 CM, 6 TTU); Dumfries Lime Factory, 2.5 km S Hillsborough, 18 m [12º27'41.2" N, 61º27'20.8" W], 9 (TTU); Hillsborough, 34 m [12º28'41.9" N, 61º27'09.5" W], 2 (TTU); Hillsborough, 5 (CM); Limlair, Big Pond, 2.2 km N, 3.4 km E Hillsborough, 8 m [12º30'13.2" N, 61º25'37.8" W], 6 (TTU). MAYREAU: Catholic Church at Old Wall, 3 (TTU). MUSTIQUE: Adelphi, Bat Cave, 27 m [12º51'42.4" N, 61º10'54.0"W], 2 (TTU); Great House, 0.15 km N Lovell Village, 19 m [12º53'09.2" N, 61º11'12" W], 8 (TTU); 0.5 km S, 0.3 km W Point Lookout, 3 (CM); 0.3 km N South Point, 8 (CM); Star Groves, Residence of Mick Jagger, 3 m [12º53'30.9"N, 61º10'59.8" W], 1 (TTU). PALM [PRUNE] ISLAND: Palm Island Resort, 8 m [12º35'12.7" N, 61º24'03" W], 1 (TTU). UNION: 0.5 km N Clifton, 7 (CM); Big Sand Beach, 1 km N Clifton, 5 (CM); Noble Hill, 0.5 km S, 4.2 km W Clifton, 86 m [12º35'25.7" N, 61º27'20.5" W], 13 (TTU); Valley, 2.2 km W Clifton, 41 m [12º35'58.4" N, 61º26'17.1" W], 1 (TTU).

Specimens captured/released (18).—BEQUIA: Friendship Bay, 2.1 km S of Port Elizabeth, 6 m [12º59'36.1" N, 61º14'08.9" W], 4; Industry House, 2.3 km NE of Port Elizabeth, 2 m [13º01'28.3" N, 61º13'10.6" W], 10. CANOUAN: Carenage, 16 m [12º43'06.8" N, 61º19'29.2" W], 2. MUSTIQUE: Cotton House Pond, 0.7 km N, 0.4 km E Lovell Village, 19 m [12º53'22.9" N, 61º11'03.8" W], 2.

Additional records (Allen 1908, 1911; Miller 1913a, 1913b).—CARRIACOU: no specific locality. UNION: no specific locality.

Miller's long-tongued bat had been reported previously from Union and Carriacou islands (Allen 1908, 1911; Miller 1913a, 1913b), but it is reported here for the first time from 5 other Grenadine islands. The trinomial that apparently is available for these populations is *G. l. rostrata* described by Miller (1913a) from the island of Grenada. The most recent reviewers of this species (Webster and Handley 1986) continued to recognize *G. l. rostrata* as a valid subspecies. Length of forearm and 7 cranial measurements for individuals from 7 of the Grenadine islands are presented in Table 1. Comparing these measurements to those of specimens from Grenada (Genoways et al. 1998) reveals that the Grenadine specimens closely match those from Grenada. The range of measurements for the Grenada sample (12 specimens) completely encompasses that of the 32 specimens measured from the Grenadines (Table 1) for zygomatic breadth and mastoid breadth. No more than 6 individuals from the Grenadines fall outside of the range of measurements for the Grenada sample in all remaining characteristics—6 individuals fell below the range for greatest length of skull, 4 below for condylobasal length, 3 below for the length of maxillary toothrow, and 2 below for postorbital constriction, whereas 3 individuals fell above the range for breadth across the upper molars and 1 above for length of forearm. Certainly in morphometrics the specimens from the 7 Grenadine islands match closely *G. l. rostrata*.

Table 1.—Length of forearm and seven cranial measurements for specimens of *Glossophaga longirostris* from seven of the Grenadine Islands, Lesser Antilles. The islands are arranged from north to south.

Catalogue no. and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
				Bequia				
TTU 105203, male	38.3	22.5	21.4	9.9	4.8	9.3	7.9	5.8
TTU 105226, male	36.5	22.3	20.8	9.5	4.7	9.2	7.9	5.7
CM 83105, male	35.8	21.7	20.5	9.8	4.8	9.4	7.8	6.2
TTU 105215, female	38.5	23.0	21.4	9.8	4.8	9.4	8.0	6.1
TTU 105216, female	37.4	23.2	21.5	9.8	4.9	9.5	7.8	6.3
CM 83106, female	37.6	23.1	21.4	10.1	4.8	9.3	8.0	6.0
				Mustique				
TTU 105289, male	38.1	22.9	21.6	10.1	4.7	9.5	7.7	6.0
CM 83108, male	36.1	22.3	21.0	9.6	4.6	9.2	7.7	5.9
CM 83109, male	37.4	22.3	21.4	10.1	4.7	9.3	7.9	6.1
TTU 105284, female	38.0	23.1	21.4	10.0	4.7	9.5	7.8	5.7
TTU 105285, female	38.0	23.0	21.4	9.9	4.9	9.4	8.1	6.0
CM 83118, female	36.7	23.1	21.2	9.9	4.8	9.4	7.8	6.0
				Canouan				
TTU 105242, male	37.6	22.7	20.9	9.7	4.6	9.2	7.7	5.8
TTU 105248, male	37.7	23.1	21.4	10.2	4.8	9.6	8.0	6.3
TTU 105249, female	37.5	22.0	20.4	9.5	4.3	9.2	7.8	5.5
TTU 105250, female	38.6	23.4	21.6	9.6	4.6	9.2	8.2	5.9
TTU 105251, female	39.1	23.2	22.0	9.9	4.8	9.6	8.0	6.1

				Mayreau				
TTU 105266, male	37.7	23.0	21.2	10.1	4.6	9.5	7.7	5.9
TTU 105265, female	37.7	22.5	21.4	9.8	4.7	9.5	7.8	5.9
				Union Island				
TTU 105587, male	37.6	22.6	21.4	9.9	4.8	9.3	7.7	5.9
TTU 105588, male	37.0	22.5	21.2	10.0	4.6	9.3	7.6	5.7
CM 63272, male	37.4	22.1	20.5	9.7	4.6	9.3	7.6	5.8
TTU 105586, female	37.0	22.4	20.9	9.9	4.8	9.4	7.7	5.8
TTU 105590, female	37.9	23.3	21.6	10.2	4.8	9.4	8.3	6.1
CM 63273, female	38.4	23.1	21.7	9.7	4.7	9.3	7.8	5.8
				Prune Island				
TTU 105291, female	38.4	22.5	21.2	9.8	4.6	9.4	7.2	5.9
				Carriacou				
TTU 104585, male	38.6	23.2	21.8	9.7	4.6	9.5	8.0	5.7
TTU 104586, male	37.2	22.6	21.2	9.9	4.4	9.3	7.9	5.6
TTU 104587, male	37.1	22.9	21.1	9.9	4.7	9.3	7.9	5.7
TTU 35706, female	37.4	23.0	21.5	9.6	4.7	9.3	7.9	5.7
TTU 35707, female	38.2	22.9	21.4	9.7	4.7	9.2	7.7	5.6
TTU 35705, female	38.5	22.8	21.3	9.8	4.6	9.4	7.7	5.6

Hoffmann and Baker (2001) included 2 specimens of *G. longirostris* from the Grenadines (collected from Union and Carriacou) in their analysis of the genetic variation within the genus. Their results documented <1% variation in cytochrome-*b* gene sequence data among populations in the Grenadines, St. Vincent, Trinidad, and Tobago. Using the methods of Larsen et al. (2007b), we sequenced a portion of the cytochrome-*b* gene from 2 additional Grenadine specimens (Carriacou, TTU 104528; Canouan TTU 105251) and our results supported the hypothesis of a close genetic relationship among these populations.

Miller's long-tongued bat was the only species captured on each island visited during our studies. Based on our observations, this is probably the most abundant species of bat in the Grenadines and it was captured in a wide variety of situations. In several places, these bats were observed and taken from day roosts in man-made structures, including Star Groves, the residence of Mick Jagger, on Mustique where bats were pursued around a covered boardwalk between sections of the large multi-sectioned house. St. Hilaire Hotel, abandoned in the 1970s, is situated on top of a peninsula overlooking the ocean on the southeastern side of Bequia. Most walls of the hotel were torn down, and vegetation had encroached on the majority of the ruins; however, bats were present in several underground cisterns that remain. Long-tongued bats were taken from the stone Catholic Church at Old Wall on Mayreau. The interior of the church had a wooden-cathedral ceiling where *G. longirostris* roosted at corners of the roof boards and the ridge and truss beams. On Prune Island, 1 individual was captured from 5 or 6 observed in a 1 room storage shed for the golf course near the shore at the east end of the island. Several hundred *G. longirostris* were observed roosting within the rafters of the abandoned Dumfries Lime Factory on Carriacou. We observed approximately 10 Miller's long-tongued bats roosting within the sugar mill ruins just south of Mount Pleasant near Grand Bay on Carriacou, but were unable to obtain specimens from this colony.

The Adelphi Bat Cave on Mustique provided a more natural day roost. This "cave," located in the South Side Conservation Area, near Rabbit Island, was really more of a crevice, with the top covered with dense scrub vegetation that opened out over the rocky coast.

We also captured *Glossophaga* in a variety of foraging areas such as at the Anchor Inn, which is essentially in downtown Charlestown on

Canouan, where these bats were netted along with *A. schwartzi* between a banana and a mango tree in a small patch of fruit trees. At a nearby site, these 2 species also were captured along with *M. molossus* over an open pond, which was approximately 30 m in diameter. The same 3 species were taken further north on the island at the Raffles Resort in Carenage in nets set over 2 ponds at hole 17 on the golf course. Miller's long-tongued bats were taken on Union Island at Noble Hill where they were netted over a small (5 m by 6 m) livestock watering pond. Nearby, at Valley on Union Island, *G. longirostris* and *M. molossus* were collected at 1845 hrs followed by *A. schwartzi* at 1900 in a small grove of fruiting trees, including mango, papaya, and orange. Big Pond on Carriacou was another water source used for livestock, but it was a much larger reservoir (30 m by 60 m) than the 1 on Union. Two nets were set around the perimeter of the pond and 2 others in the surrounding low, thorny dry scrub forest, but bat activity was low throughout the night with the majority of our captures being *G. longirostris*.

Reproductive data for female and male *G. longirostris* are presented in Table 2. At the end of May and early June in the Grenadine islands, about two-thirds of the females were pregnant (34 of 50 females), indicating a high degree of synchronicity in the reproductive cycle. Weights of males from the Grenadine islands were as follows: Bequia, 9.8, 10.8, 10.9; Mustique, 9.3, 10.0; Canouan (9 individuals) 10.5 (9.6-11.9); Mayreau, 12.4; Union (9) 10.0 (9.2-12.1); Carriacou, (10) 10.2 (9.4-11.9). Weights of non-pregnant females from the Grenadine islands were as follows: Bequia, 9.2; Mustique (5) 9.5 (8.0-10.5); Canouan, 8.9, 9.6, 10.4; Union, 9.4, 9.9, 10.0; Carriacou, (4) 10.0 (9.4-11.2). Weights of pregnant females from the Grenadine islands were as follows: Bequia (4) 13.0 (12.0-13.8); Mustique, 10.5; Canouan (6) 11.3 (9.9-12.3); Mayreau, 12.4, 14.7; Union (5) 12.3 (11.5-13.7); Carriacou, 12.7, 13.7.

Table 2. Reproductive data for the females and males of three species of bats occurring on the islands of the Grenadines, Lesser Antilles. The islands are arranged from north to south.

Island	Dates	Females					Males	
		Number females examined	Number pregnant	Crown-rump length of fetus	Number lactating	Number non-reproductive	Number males examined	Length of testes
				Glossophaga longirostris				
Bequia	23 May-5 June	7	6	16.0 (13.0-18.0)	0	1	4	3.8 (3.0-5.0)
Mustique	18-28 May	7	2	6.0, 12.0	1	4	10	3.3 (2.0-5.0)
Canouan	31 May	6	6	10.8 (4.0-16.0)	0	0	4	4.0 (3.5-4.6)
Mayreau	30 May	2	2	19.0, 20.0	0	0	1	3.5
Prune Island	30 May	1	1	15.0	0	0	0	---
Union Island	26-28 May	6	4	14.9 (14.7-15.0)	0	2	12	3.4 (2.0-4.6)
Carriacou	28-30 May	21	13	16.8 (8.0-22.5)	0	8	15	3.1 (2.0-4.5)
				Artibeus schwartzi				
Bequia	22 May-5 June	10	8	17.2 (7.0-27.0)	4[1]	1	11	7.5 (6.0-8.5)
Mustique	17-28 May	8	4	20.6 (9.5-30.0)	1	3	6	7.7 (7.2-8.8)
Canouan	31 May	6	4	11.3 (5.0-19.0)	1	1	4	7.4 (5.0-8.5)
Union Island	26 May	4	2	5.0, 11.0	1	1	2	6.0, 7.0
Carriacou	28-30 May	25	9	15.7 (9.0-22.0)	6	10	6	6.4 (4.0-8.1)
				Molossus molossus				
Bequia	23 May-5 June	5	5	12.6 (7.0-18.0)	0	0	2	3.5, 3.5
Mustique	28 May	1	0	--	1	0	0	---
Canouan	31 May	6	6	19.8 (18.0-21.0)	0	0	0	---

Mayreau	30 May	2	2	18.0, 21.0	0	0	0	---
Union Island	26-28 May	15	12	16.1 (14.0-18.8)	0	3	8	4.4 (3.0-5.0)
Carriacou	28-30 May	12	12	15.8 (12.0-20.5)	0	0	10	4.3 (2.5-5.5)

[1] Three pregnant females were also lactating (4-5 June).

Artibeus lituratus palmarum
Great Fruit-eating Bat

Specimens examined (14).—BEQUIA: Friendship Bay, 2.1 km S Port Elizabeth, 6 m [12º59'36.1" N, 61º14'08.9" W], 1 (TTU); Industry House, 2.3 km NE Port Elizabeth, 2 m [13º01'28.3" N, 61º13'10.6" W], 1 (TTU); 2.1 km SW Port Elizabeth, 3 m [12º59'45.2" N, 61º14'42.5" W], 1 (TTU). CARRIACOU: Botanical Gardens, Hillsborough, 20 m [12º29'02.8" N, 61º27'15.3" W], 3 (TTU); Hillsborough, 34 m [12º28'41.9" N, 61º27'09.5" W], 6 (TTU). UNION: Noble Hill, 0.5 km S, 4.2 km W Clifton, 86 m [12º35'25.7" N, 61º27'20.5" W], 2 (TTU).

We found the great fruit-eating bat sympatric with *Artibeus schwartzi* on 3 islands in the Grenadines. It seemed to us that it was improbable for 2 large frugivorous species to co-exist on these small, arid islands. Thus, we felt it necessary to document the 2 species-level entities coexisting here, rather than some type of hybrid swarm. To test this, Larsen et al. (in prep.) examined nuclear, mitochondrial, and morphological data generated from specimens collected on Carriacou and Union. Their results indicate an absence of hybridization between *A. lituratus* and *A. schwartzi*. Furthermore, the maintenance of diagnostic morphological characters in sympatry (see below) provides additional support for the hypothesis that this species is genetically isolated from its congeners. Therefore, in contrast to other species of *Artibeus* distributed in the southern Lesser Antilles (see *A. schwartzi* account), *A. lituratus* and *A. schwartzi* apparently have evolved isolating mechanisms that permit sympatry on ecologically limited islands.

Widespread populations of *A. lituratus* are known to the south of the Grenadines on the island of Grenada (Genoways et al. 1998) and a single individual has been reported to the north on St. Vincent (Jones and Phillips 1970). For the species to reach St. Vincent from Grenada, one would need to presume either a single long-distance movement or stepping-stone island hopping through the Grenadines, making the occurrence of the great fruit-eating bat in the Grenadines not unexpected.

With the congeneric *A. schwartzi* occurring on 3 islands in the Grenadines along with *A. lituratus*, the question arises of how to distinguish and recognize these species in the field. We were able to distinguish *A. lituratus* from *A. schwartzi* because all 14 of our specimens were correctly identified at the time of capture as later verified by our molecular data. Members of the team recalled the following characteristics of individuals of *A. lituratus* as aiding in recognizing the species: yellowish coloration of the tragus and pinnae; very well defined, bright white facial stripes; a distinctive russet orangey-brown pelage; a larger more robust body; an obviously aggressive attitude when being handled; the hide was harder to separate from the musculature compared to *A. schwartzi* when preparing voucher specimens as mentioned by earlier authors (Davis 1970: 106).

Analyses of morphometric differences (t-tests) between the 2 species also were performed on 3 sets of data (Tables 3 and 4)—Carriacou *lituratus* compared with *schwartzi*, Bequia *lituratus* compared with *schwartzi*, and combined samples of *lituratus* from Bequia, Union, and Carriacou compared with combined samples of *schwartzi* from these islands. The same pattern of results was obtained in all 3 analyses. *Artibeus lituratus* samples were significantly larger ($P \leq 0.05$) than *A. schwartzi* for 5 measurements (length of forearm, greatest length of skull, condylobasal length, zygomatic breath, and mastoid breadth). No significant differences ($P > 0.05$) between the species were found in length of the maxillary toothrow and breadth across upper molars. Postorbital constriction was significantly larger in *A. schwartzi* than in *A. lituratus* ($P \leq 0.01$). Despite these major morphometric differences between the species, there is no single measurement that separates the 2 species in the Grenadines because there is overlap in the range of values for each measurement. The primary difference in the crania of these 2 species is the proportionally narrower postorbital constriction in *A. lituratus*. This contributes to the prominent appearance of the postorbital processes (Davis 1970: 166-167) in *A. lituratus* and gives the interorbital region the shape of a shield.

Table 3 presents the length of forearm and 7 cranial measurements of the 14 *Artibeus lituratus* obtained from Grenadine islands. Comparing the measurements of these individuals with samples from Grenada (Genoways et al. 1998: 8) reveals that the values are similar, with broad overlap in the range of the measurements. One specimen from Bequia (TTU 105195) had larger measurements than any specimen from Grenada in 5 of the 7 cranial measurements (except postorbital constriction and breadth across upper molars). Four specimens from the Grenadines had broader postorbital constrictions than any individuals from Grenada, 3 Grenadine specimens had shorter forearms than Grenada specimens, and 1 had a shorter condylobasal length than specimens from Grenada. All other measurements of the Grenadine specimens fall within the range of variation of the Grenada sample. Clearly, the Grenadine populations of *Artibeus lituratus* are taxonomically close to the populations on Grenada to which Genoways et al. (1998) assigned the trinomial *A. l. palmarum*. This subspecies originally was described from Trinidad so its presence in the southern Lesser Antilles is not unexpected.

Hoofer et al. (2008) included a single specimen of *A. lituratus* (TTU 104511) collected from Union in their analysis of Artibeina. Four specimens from Carriacou (TTU 104553, TTU 104555, TTU 104556, TTU 104575) and 2 from Union (TTU 104511, TTU 105584) were included in Larsen et al. (in prep.). Using the methods of Larsen et al. (2007b), we identified 3 specimens from Bequia (TTU 105195, TTU 105204, TTU 105220), and 5 from Carriacou (TTU 104554, TTU 104557, TTU 104558, TTU 104576, TTU 104577) as *A. lituratus*.

The 3 *A. lituratus* captured on Bequia in 2006 were netted at 3 separate locations but always associated with mango trees. These bats were captured together with *G. longirostris* and *A. schwartzi* at all 3 netting locations. On Union Island, the 2 great fruit-eating bats were netted over a small (5 m by 6 m) livestock watering pond set in a dense acacia forest. There were no fruiting trees in the area so the presumption is that the bats were coming to the pond to drink. Six individuals of *A. lituratus* were collected in nets set under and between hog plum and mango trees along the edge of a small pasture near Hillsborough, Carriacou. The other 3 individuals from Carriacou were netted over a small pond of water adjacent to the Botanical Gardens in Hillsborough.

Table 3. Length of forearm and seven cranial measurements for 14 specimens of *Artibeus lituratus* from three of the Grenadine Islands, Lesser Antilles. The islands are arranged from north to south.

Catalogue no. and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
				Bequia				
TTU 105195, male	72.0	32.4	28.4	20.2	6.7	17.6	11.3	14.0
TTU 105204, male	72.8	30.9	27.2	18.1	6.3	16.8	10.8	13.3
TTU 105220, male	67.7	31.1	26.7	19.4	7.0	17.0	10.5	13.6
				Union Island				
TTU 104511, female	70.1	30.7	27.0	18.2	6.5	16.3	10.4	12.9
TTU 105584, female	70.2	30.8	27.1	18.3	6.8	16.8	10.6	13.4
				Carriacou				
TTU 104553, male	67.1	29.8	26.1	19.3	6.3	16.9	10.5	13.7
TTU 104554, male	64.1	30.4	25.7	17.9	6.4	16.8	10.2	12.8
TTU 104577, male	66.4	30.8	26.9	18.5	6.3	16.5	10.9	13.9
TTU 104555, female	64.3	30.9	26.6	19.4	6.8	16.5	10.6	13.3
TTU 104556, female	70.6	30.3	----	18.6	7.0	16.0	10.8	13.3
TTU 104557, female	72.0	31.6	27.8	19.1	6.4	16.9	10.7	13.6
TTU 104558, female	71.2	31.3	26.7	19.3	6.7	16.9	10.5	13.6
TTU 104575, female	66.8	30.3	26.6	18.2	6.3	16.0	10.8	13.3
TTU 104576, female	69.9	30.3	26.6	18.5	6.2	16.5	10.4	13.2

Despite the use of the same basic methods on all islands throughout this study, *A. lituratus* was captured only on the islands of Bequia, Carriacou, and Union. However, we were surprised to net the great fruit-eating bat during our 2006 survey because they had not been captured on these same islands in 1980 and 1986. In each instance, *A. lituratus* was outnumbered by its congener *A. schwartzi*. *Artibeus lituratus* comprised no more than 14 % (2-14%) of the fruit bat captures on Bequia, Carriacou, and Union, in 2006, wherein bats of the *A. schwartzi* complex outnumbered *A. lituratus* captures 131:3, 31:9, and 7:2 on Bequia, Carriacou, and Union, respectively.

However, observations by 1 of us (de Silva who is a resident of the Grenadines) may shed some light on this situation and provide insight in the movements of bats among Caribbean islands. On Mayreau in September 2004, about a week after the passage of Hurricane Ivan some unusual bats were observed. Although Hurricane Ivan destroyed many house roofs in the Grenadines, it completely devastated Grenada, with estimates of catastrophic losses of 90% of the trees being destroyed in the Great Etang Forest Reserve and National Park and the Annandale watershed (Ishmael 2004). The first reports of unusual bats came from a resident of Union stating that there were many strange bats eating his green guavas in broad daylight. A couple of days later on Mayreau, several bats that were larger than those normally observed were seen flying around the church buildings in Old Wall in the daytime. One of these bats was photographed hanging on the slender branch of a tall shrub alongside a well-worn path in daytime. The authors have examined this photograph and it is our consensus that the bat is an *A. lituratus* based on its overall light brown color, distinct facial stripes, and yellow edges of the ears, tragus, and noseleaf. The bats suddenly disappeared about 1 week after they appeared on Mayreau, but none were found dead. Although de Silva does receive natural history reports from residents on more northern islands in the Grenadines, he has received no reports of large bats appearing on those islands.

Three males from Carriacou taken 28-29 May 2006 had testes length of 6.5, 7.5, and 8.0 and 3 from Bequia taken 3-5 June 2006 had testes lengths of 4, 6, and 6. Two females from Union taken on 26 May 2006 evinced no gross reproductive activity. Five of the 6 females taken on Carriacou on the same dates as the males were lactating and the sixth female was an adult-sized, non-reproductive young of the year. From our limited sample it appears that parturition in *A. lituratus* occurs in early to mid-May. The 6 males weighed on average 57.1 (51.4-61.9), the 3 non-reproductive females weighed 48.0, 55.1, 57.0, and the 5 lactating females had a mean weight of 66.2 (61.1-72.6).

Table 4. Length of forearm and seven cranial measurements for male and female specimens of *Artibeus schwartzi* from five of the Grenadine Islands, Lesser Antilles. The islands are arranged from north to south.

Sex, sample size, and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
				Bequia				
Males (N = 11)								
Mean ± SE	62.1± 0.55	30.1±0.20	26.4±0.18	18.5±0.16	7.1±0.06	15.8±0.19	10.6±0.10	13.6±0.14
Range	59.3-65.3	28.6-30.9	25.4-27.5	17.3-19.2	6.9-7.6	14.5-16.7	10.2-11.0	12.8-14.4
Females (N = 8)								
Mean ± SE	63.1±0.84	30.1±0.13	26.7±0.11	18.5±0.09	7.1±0.08	15.8±0.14	10.7±0.05	13.6±0.12
Range	60.1-68.1	29.7-30.8	26.0-27.1	18.1-18.9	6.9-7.5	15.2-16.3	10.6-10.9	13.3-14.2
				Mustique				
Males (N = 12)								
Mean ± SE	62.9±0.85	30.1±0.34	26.5±0.28	18.5±0.32	7.3±0.09	15.8±0.19	10.5±0.13	13.6±0.20
Range	58.0-68.1	28.6-32.9	25.0-28.6	17.0-20.0	6.8-7.9	15.0-17.3	9.8-11.1	12.3-14.6
Females (N= 10)								
Mean ± SE	63.1±0.89	30.2±0.21	26.6±0.17	18.5±0.12	7.2±0.04	15.8±0.14	10.6±0.09	13.7±0.12
Range	56.7-65.9	29.5-31.3	25.9-27.5	18.0-19.2	6.9-7.3	15.2-16.6	10.2-11.0	13.1-14.4
				Canouan				
Males (N = 4)								
Mean ± SE	61.6±1.86	30.0±0.40	26.4±0.40	18.2±0.19	7.4±0.04	15.5±0.19	10.6±0.13	13.6±0.18
Range	58.3-66.7	29.2-31.1	25.6-27.5	17.8-18.7	7.3-7.5	15.0-15.8	10.3-10.9	13.2-13.9
Female (N = 4)								
Mean ± SE	63.3±1.51	29.9±0.46	26.2±0.38	18.4±0.41	7.3±0.24	15.7±0.27	10.6±0.22	13.9±0.31
Range	60.6-66.5	28.6-30.7	25.1-26.9	17.3-19.1	6.6-7.7	15.0-16.2	10.0-10.9	13.3-14.7

Union Island								
Males (N = 7)								
Mean ± SE	59.0±0.78	29.3±0.26	25.7±0.20	17.6±0.24	7.3±0.09	15.5±0.20	10.4±0.07	13.2±0.15
Range	56.2-61.9	28.6-30.3	25.0-26.3	16.9-18.7	7.0-7.6	15.0-16.6	10.0-10.6	12.8-13.8
Females (N = 8)								
Mean ± SE	60.6±0.71	29.7±0.22	26.2±0.20	18.0±0.18	7.3±0.09	15.6±0.20	10.4±0.15	13.5±0.21
Range	58.1-62.8	28.6-30.4	25.3-27.0	16.9-18.6	6.8-7.6	14.5-16.3	9.7-11.0	12.4-14.5
Carriacou								
Males (N = 9)								
Mean ± SE	60.3±0.92	29.5±0.29	26.0±0.25	17.9±0.21	7.3±0.09	15.5±0.23	10.5±0.17	13.2±0.18
Range	57.3-64.0	28.5-30.6	24.6-26.7	17.2-18.8	6.8-7.5	14.9-16.8	9.8-11.2	12.5-13.8
Females (N= 10)								
Mean ± SE	61.3±0.48	29.3±0.16	25.8±0.18	17.7±0.13	7.1±0.09	15.4±0.12	10.2±0.09	13.2±0.11
Range	58.9-63.6	28.4-30.1	25.1-26.9	16.9-18.3	6.7-7.6	14.7-15.9	9.8-10.6	12.6-13.5

Artibeus schwartzi
Schwartz's Fruit-eating Bat

Specimens examined (155).—BEQUIA: Friendship Bay, 2.1 km S Port Elizabeth, 6 m [12º59'36.1" N, 61º14'08.9" W], 4 (TTU); Industry House, 2.3 km NE Port Elizabeth, 2 m [13º01'28.3" N, 61º13'10.6" W], 10 (TTU); 1.4 km N, 1.5 km E Port Elizabeth, 14 (CM); 2.1 km SW Port Elizabeth, 3 m [12º59'45.2" N, 61º14'42.5" W], 4 (TTU); 1.1 km S, 0.5 km E Port Elizabeth, 10 (CM). CANOUAN: Archer Inn, 0.45 km N, 0.5 km E Charlestown, 13 m [12º42'12" N, 61º19'38.3" W], 12 (TTU); Carenage, 16 m [12º43'06.8" N, 61º19'29.2" W], 1 (TTU). CARRIACOU: Botanical Gardens, Hillsborough, 20 m [12º29'02.8" N, 61º27'15.3" W], 12 (TTU); Craigston Estate, 4 (CM); Hillsborough, 34 m [12º28'41.9" N, 61º27'09.5" W], 18 (TTU); Hillsborough, 17 (CM); Limlair, Big Pond, 2.2 km N, 3.4 km E Hillsborough, 8 m [12º30'13.2" N, 61º25'37.8" W], 1 (TTU). MUSTIQUE: Great House, 0.15 km N Lovell Village, 19 m [12º53'09.2" N, 61º11'12" W], 13 (TTU); 0.4 km S Point Lookout, 19 (CM). UNION: Big Sand Beach, 1 km N Clifton, 5 (CM); 0.5 km N Clifton, 4 (CM); Noble Hill, 0.5 km S, 4.2 km W Clifton, 86 m [12º35'25.7" N, 61º27'20.5" W], 1 (TTU); Valley, 2.2 km W Clifton, 41 m [12º35'58.4" N, 61º26'17.1" W], 6 (TTU).

Specimens captured/released (120).—BEQUIA: Friendship Bay, 2.1 km S Port Elizabeth, 6 m [12º59'36.1" N, 61º14'08.9" W], 27; Industry House, 2.3 km NE Port Elizabeth, 2 m [13º01'28.3" N, 61º13'10.6" W], 67; 2.1 km SW Port Elizabeth, 3 m [12º59'45.2" N, 61º14'42.5" W], 19. MUSTIQUE: Cotton House Pond, 0.7 km N, 0.4 km E Lovell Village, 19 m [12º53'22.9" N, 61º11'03.8" W], 7.

Jones (1978) originally described this taxon as a subspecies of the widespread Jamaican fruit-eating bat, *Artibeus jamaicensis*, and restricted its distribution to the island of St. Vincent. However, Larsen et al. (2007b; using mitochondrial cytochrome-*b* sequences) concluded that *A. jamaicensis*, *A. schwartzi*, and *A. planirostris* are each species-level lineages. Although several hypotheses exist regarding the evolutionary history of *A. schwartzi* (Jones 1989; Phillips et al. 1989; Pumo et al. 1996; see Larsen et al. 2007b), recent analyses provide support for the hypothesis that *A. schwartzi* is of hybrid origin subsequent to extensive hybridization among *A. jamaicensis*, *A. planirostris,* and an extinct or uncharacterized species of *Artibeus* (Larsen et al. in prep.). This unique hybridization event is likely the result of primary contact among multiple species of *Artibeus* in the southern Lesser Antilles (Larsen et al. in prep.), with the hybrid zone extending from St. Lucia southward to Grenada. Given genetic and morphological data, we conclude that *A. schwartzi* is the appropriate name applied to the populations on St. Vincent southward throughout the Grenadine islands.

The genetic data from *Artibeus* presented in Pumo et al. (1988), Phillips et al. (1989), Phillips et al. (1991), Larsen et al. (2007b), and Larsen et al. (in prep.) provide an interesting zoogeographic perspective of gene flow across the southern Lesser Antilles. Collectively these data indicate: 1) a Caribbean colonization by *A. jamaicensis* from the Yucatan Peninsula eastward across the Greater and northern Lesser Antilles, and southward to St. Lucia and Barbados, 2) a Caribbean colonization by *A. planirostris* from mainland South America, northward from Trinidad and Tobago to Grenada, and 3) a distribution of *A. schwartzi* in the southern Lesser Antilles from St. Lucia southward to Carriacou. Within the Caribbean, mtDNA haplotypes representative of *A. jamaicensis*, *A. planirostris*, and *A. schwartzi* that are identified outside of these general distributions are likely mitochondrial introgression events resulting from earlier hybridization (Larsen et al. in prep.). For example, Larsen et al. (in prep.) identified 6 specimens from Carriacou as *A. planirostris* using mtDNA sequence data, yet nuclear AFLP and morphological data indicated that the nuclear genome and cranial phenotype were typical of *A. schwartzi*. Given hybridization among these species, identifications based exclusively on mtDNA data must be approached with caution. Nonetheless, frequencies of mtDNA haplotypes of *A. jamaicensis*, *A. planirostris*, and *A. schwartzi* in the southern Lesser Antilles provide important insight into the potential of the Grenadines as a barrier to gene flow (see Phillips et al. 1989, Genoways et al. 1998; Larsen et al. in prep.).

We compared the mean values of all measurements of the Grenadine samples (Table 4) with values given by Genoways et al. (1998: 15) for a sample of *A. schwartzi* from St. Vincent and a sample of *A. planirostris* from Grenada (Larsen et al. 2007b). Mean values for all measurements of the Grenadine samples are less than the means for the sample from St. Vincent, except the Canouan sample has the same mean value (7.4) for postorbital constriction as the St. Vincent sample. Mean values for all measurements of the Grenadine samples are larger than the means for the sample from Grenada. Although these morphometric data are equivocal on the specific identity of the Grenadine populations, the preponderance of the information places them with *A. schwartzi*.

Table 4 presents the morphometric data for male and female *A. schwartzi* from each of the 5 Grenadine islands where we captured this species. Using t-tests, samples from each island were tested for secondary sexual variation. There were no significant differences between males and females for any measurement for samples from any island; therefore, we combined males and females for all subsequent analyses. Comparisons for geographical variation were made between samples from the following islands: Bequia versus Mustique; Mustique versus Canouan; Canouan versus Union; Union versus Carriacou. There were no significant differences for any measurement for any of the island comparisons made. However, when data from the northern-most 2 islands—Bequia and Mustique—are combined and compared (using t-tests) with the combined sample of the southern-most 2 islands—Union and Carriacou—some significant results were obtained. The only measurement in which these 2 samples did not differ significantly was postorbital constriction. The other measurements differed at the following levels: $P \leq 0.0001$, length of forearm and zygomatic breadth; $P \leq 0.001$, greatest length of skull and condylobasal length; $P \leq 0.01$, length of maxillary toothrow and breadth across upper molars; $P \leq 0.05$, mastoid breadth. In all measurements, except postorbital constriction in which the samples averaged the same, the northern sample had a higher average than the southern sample.

With only 8 individuals, the size of the sample from Canouan is small compared to the other samples. The status of this population lying between the northern and southern Grenadines is still unclear; however, because it showed no significant differences with either the Union or Mustique samples, thus it probably is best considered as a transitional population. Inspection of the mean values, places the Canouan population, in our opinion, nearer to the northern populations than the southern populations in the Grenadines. Morphometric analyses of populations of *A. planirostris*, *A. schwartzi*, and *A. jamaicensis* extending from northeastern South America to as far north as the island of Dominica will be needed to fully understand variation among these taxa.

Many of the sites where *A. schwartzi* were captured are discussed in the accounts of other species in this article. A total of 77 specimens were captured (using 8 mist nets) at Industry House on Bequia where a local resident's property included an open swimming pool and a large well-manicured lawn, with an abundance of mango, coconut, and banana trees. At the Great House on Mustique, a sample of 13 individuals was taken from a gated estate with manicured lawns where 3 mist nets were placed between and under a sapodilla, 3 mango, and 2 fruiting palm trees. At Big Sand Beach on the island of Union, 5 nets were placed among and between arid adapted acacia and other trees, resulting in the capture of 5 *A. schwartzi*, 5 *G. longirostris*, and 1 *M. molossus*. At 2 other sites—0.5 km N Clifton and Noble Hill—on Union, Schwartz's fruit-eating bats were netted over small catchment ponds. These bats appeared to be drinking from the ponds. On Carriacou, *A. schwartzi* also was captured over a small pond next to the Botanical Garden in Hillsborough and at the edge of town where hog plum and mango trees grew along the edge of a small pasture. Most of our records of this species are based on individuals captured during foraging. Although no specimens were collected, a few *A. schwartzi* were observed roosting among hundreds of *G. longirostris* in the abandon Dumfries lime factory on Carriacou.

It has long been considered (see Genoways et al. 2001) that presence/absence of the upper M3 and lower m3 were geographically variable characters in the *A. jamaicensis* complex. However, based on our new understanding of the relationships of these populations, it now appears that at least the presence/absence of the upper M3 is a species-level character (Table 5). Populations from the Bahamas to Dominica to which we would now apply the name *A. jamaicensis*, lack the upper third molars. Populations on Trinidad are now considered to be *A. planirostris* and 100% of the individuals have the upper M3. In the Grenada population, 89% of the individuals have the upper M3 indicating a strong relationship with *A. planirostris*, but also suggesting some genetic introgression from *A. jamaicensis*. The hybrid nature of *A. schwartzi* is supported by this character, because the upper M3 is present in low numbers of individuals from St. Vincent (12.9%). It should be noted that the upper M3 is absent in the Barbados material that has been studied to date, indicating a relationship with *A. jamaicensis*, although some molecular data would place this population with *A. schwartzi* (Pumo et al. 1988, 1996). The relationship of Grenadine populations with *A. schwartzi* is indicated by the presence of the upper M3 in 2 individuals from Mustique and 1 from Carriacou; however, the overall rate is only 3.6% (3 of 83). This is a lower rate than was seen in the St. Vincent population and supports the somewhat puzzling idea that the Grenadine populations have a closer relationship with *A. jamaicensis* than does the St. Vincent population.

Table 5. Presence/absence* of M3/m3 in Antillean and Trinidadian populations of *Artibeus jamaicensis/planirostris/schwartzi* complex. Data drawn from the current study and from Genoways et al. (2001, 2007a, 2007b, 2007c), Larsen et al. (2007a), Pedersen et al. (2003, 2005, 2006, 2007), and some unpublished data for Barbados and St. Vincent. The islands are arranged in a north to south pattern.

Island	Presence of upper third molar (M3)		Presence of lower third molar (m3)	
	N	Percentage present	N	Percentage present
Bahamas	6	0	6	83%
Cuba	81	0	80	98%
Hispaniola	33	0	20	95%
Jamaica	11	0	11	100%
Puerto Rico	61	0	63	92%
St. John	45	0	45	89%
Anguilla	16	0	16	100%
St. Martin/St. Maarten	10	0	10	70%
St. Barts	5	0	5	100%
Saba	9	0	9	88.9%
St. Kitts	6	0	6	67%
Nevis	10	0	10	100%
Barbuda	6	0	6	67%
Antigua	8	0	8	87.5%
Dominica	97	0	97	94%
Barbados	18	0	18	95.2%
St. Vincent	31	12.9%	21	100%
Bequia	19	0	19	100%
Mustique	22	9.1%	22	95.5%
Canouan	8	0	8	100%
Union	15	0	15	100%
Carriacou	19	5.3%	19	100%
Grenada	18	89%	18	100%
Trinidad	8	100%	8	100%

* Considered as "absent" if one of the pair of teeth is missing.

Examination of Table 5 leads us to believe that presence or absence of the lower third molars (m3) in this *Artibeus* complex is neither an indication of geographic variation or a species-level character. This appears to us to be a low occurrence polymorphism in *A. jamaicensis* and *A. schwartzi*.

Reproductive data for females and males of *A. schwartzi* are presented in Table 2. At the end of May and early June in the Grenadine islands, 50 % of the females were pregnant (27 of 54 females) and an additional 13 were lactating, indicating a high degree of synchronicity in the reproductive cycle. Weights of males from the Grenadine islands were as follows: Bequia (9 individuals) 45.0 (38.6-54.3); Mustique (6) 40.4 (32.9-45.2); Canouan (4) 45.2 (39.0-54.9); Union, 39.4, 40.6, 49.7; Carriacou (7) 43.1 (39.7-46.5). Weights of non-pregnant females from the Grenadine islands were as follows: Bequia, 41.6, 42.2; Mustique, 43.8, 44.2, 44.6; Canouan, 51.5; Union, 46.0, 52.7; Carriacou (14) 43.8 (29.6-48.8). Weights of pregnant females from the Grenadine islands were as follows: Bequia (7) 49.1 (44.3-57.4); Mustique (4) 51.5 (46.1-54.3); Canouan (4) 42.1 (37.0-48.6); Union, 49.6, 51.7; Carriacou (6) 46.7 (38.3-51.3).

Molossus molossus molossus

Pallas's Mastiff Bat

Specimens examined (82).—BEQUIA: Industry House, 2.3 km NE Port Elizabeth, 2 m [13º01'28.3" N, 61º13'10.6" W], 3 (TTU); 1.4 km N, 1.5 km E Port Elizabeth, 6 (CM). CANOUAN: Archer Inn, 0.45 km N, 0.5 km E Charlestown, 13 m [12º42'12" N, 61º19'38.3"

W], 6 (TTU). CARRIACOU: Botanical Gardens, Hillsborough, 20 m [12º29'02.8" N, 61º27'15.3" W], 2 (TTU); Craigston Estate, 20 (14 CM, 6 TTU); Hillsborough, 34 m [12º28'41.9" N, 61º27'09.5" W], 2 (TTU); Hillsborough, 12 (CM); Limlair, Big Pond, 2.2 km N, 3.4 km E Hillsborough, 8 m [12º30'13.2" N, 61º25'37.8" W], 1 (TTU). MAYREAU: Fresh Water Pond, 0.5 km N, 0.25 km E Old Wall, 12 m [12º38'39.7" N, 61º23'27" W], 2 (TTU). MUSTIQUE: Cotton House Pond, 0.7 km N, 0.4 km E Lovell Village, 19 m [12º53'22.9" N, 61º11'03.8" W], 1 (TTU). UNION: Big Sand Beach, 1 km N Clifton, 1 (CM); 0.5 km N Clifton, 18 (CM); Noble Hill, 0.5 km S, 4.2 km W Clifton, 86 m [12º35'25.7" N, 61º27'20.5" W], 7 (TTU); Valley, 2.2 km W Clifton, 41 m [12º35'58.4" N, 61º26'17.1" W], 1 (TTU).

A number of scientific names have been applied to this bat in the Antillean islands. It is now believed that the most appropriate name is *Molossus molossus*, which is a widespread Neotropical species. Husson (1962) restricted the type locality of *M. molossus* to the island of Martinique, which lead Dolan (1989) to apply the name *M. m. molossus* to this species in the Lesser Antilles.

Table 6 provides the length of forearm and 7 cranial measurements of 9 males and 15 females from 6 islands in the Grenadines. Comparing these measurements to samples from Grenada (Genoways et al. 1998) and Dominica (Genoways et al. 2001), reveals that individuals from the Grenadines tend to be smaller than individuals in either of the other 2 samples. Only 1 individual (from Carriacou) had a measurement (mastoid breadth) that was above the range of measurements of the Grenada sample. Individuals from Carriacou (1 individual each) were larger than the range of measurements for the Dominica sample in length of forearm and postorbital constriction and 3 from Union were above the range for postorbital constriction. However, when the number of individuals (sample of 24) from the Grenadines with measurements below the range of the measurements from the 2 other samples are considered, the following results are obtained (number below range of the Grenada sample followed by number below range of the Dominica sample): length of forearm, 6, 0; greatest length of skull, 10, 16; condylobasal length, 7, 3; zygomatic breadth, 8, 3; postorbital constriction, 3, 0; mastoid breadth, 3, 8; length of maxillary toothrow, 2, 6; breadth of upper molars, 7, 8. Until thorough analyses of geographic variation of samples of this species from throughout the Antilles are undertaken, we will not be able to interpret the meaning of the smaller sized individuals from the Grenadines.

This insectivorous bat was seen regularly on the 6 largest islands in the Grenadines at evening twilight as they were hawking their prey. These mastiff bats in modern times find day roosts under the tile and corrugated steel roofs and in the attics of homes and other buildings. Before the settlement of these islands, mastiff bats probably found day roosts in holes in palm trees and rock crevices and were less common than at present. We were able to reliably mist net these bats over freshwater ponds and swimming pools throughout the Grenadine islands.

Table 6.—Length of forearm and seven cranial measurements for specimens of *Molossus molossus* from six of the Grenadine Islands, Lesser Antilles. The islands are arranged from north to south.

Catalogue no. and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
				Bequia				
TTU 105217, male	37.6	15.9	13.9	10.0	3.4	9.6	5.5	7.0
TTU 105218, male	37.4	16.4	14.7	10.0	3.4	9.5	5.6	7.2
CM 83419, male	37.6	15.9	14.1	10.0	3.2	9.7	5.6	7.1
TTU 105219, female	36.5	15.7	13.7	9.4	3.4	9.1	5.4	6.8
CM 83420, female	38.0	15.7	14.0	9.7	3.3	9.6	5.6	6.9
CM 83421, female	37.4	15.7	13.9	9.8	3.5	9.2	5.2	6.9
				Mustique				
TTU 105269, female	37.9	16.2	14.1	10.0	3.4	9.6	5.6	7.2

				Canouan				
TTU 105253, female	38.2	16.2	14.4	9.9	3.5	9.7	5.8	6.9
TTU 105254, female	39.1	16.2	14.2	10.1	3.3	9.6	5.6	7.1
TTU 105255, female	37.1	16.2	14.0	10.0	3.5	9.5	5.8	7.3
				Mayreau				
TTU 105267, female	37.7	16.2	14.0	10.0	3.4	9.6	5.7	7.1
TTU 105268, female	38.3	15.9	13.8	9.7	3.4	9.2	5.5	7.0
				Union Island				
CM 63478, male	38.7	16.8	14.9	10.4	3.5	10.0	5.7	7.5
CM 63479, male	37.9	17.0	14.7	10.2	3.6	9.9	5.8	7.2
CM 63480, male	38.4	16.7	14.9	10.2	3.6	9.7	5.8	7.3
TTU 105600, female	38.8	15.8	14.0	10.2	3.5	9.7	5.7	7.1
TTU 105601, female	39.0	16.2	14.2	10.1	3.6	9.7	5.7	7.2
CM 63470, female	38.7	16.3	14.2	10.0	3.5	9.7	5.6	7.1
				Carriacou				
TTU 35735, male	38.5	16.6	14.7	10.3	3.5	9.9	5.7	7.2
TTU 104579, male	39.3	16.9	15.0	10.4	3.7	10.2	5.8	7.4
TTU 104588, male	37.3	16.8	14.6	10.2	3.5	9.6	5.8	6.9
TTU 35736, female	37.7	15.7	13.9	9.8	3.4	9.5	5.4	6.9
TTU 35737, female	37.4	15.7	13.6	9.8	3.4	9.5	5.6	7.0
TTU 10478, female	38.2	15.8	13.8	9.9	3.5	9.4	5.5	6.9

Good examples of these sites include the place where our only *M. molossus* specimen from Mustique was taken over the Cotton House Pond. This was a highly manicured estate with a pond (40-50 m diameter) in front of the main entrance to the house. The pond was surrounded by lawns except for a banana patch near the east end of a pond while the west end of pond was near a road. The net that captured the bat was set near the road at one end of the pond. Another good example is the freshwater pond near the Catholic Church at Old Wall on Mayreau where the only 2 *M. molossus* were taken on the island. The pond, about 20 m in diameter, was fed by a drainage ditch from a nearby road. It was surrounded by a nearly impenetrable growth of scrub and cacti. Other sites where this species was captured are discussed elsewhere in this article.

Reproductive data for females and males of *M. molossus* are presented in Table 2. At the end of May and early June in the Grenadine islands, over 90% of the females were pregnant (37 of 41 females), indicating the highest degree of synchronicity in the reproductive cycle of any species examined from the islands. Weights of males from the Grenadine islands were as follows: Bequia, 9.7, 9.9; Carriacou, 10.0, 11.4, 11.4. The weight of a non-pregnant female from Mustique was 10.7. Weights of pregnant females from the Grenadine islands were as follows: Bequia 8.9; Canouan (6) 12.6 (11.4-14.2); Mayreau, 10.7, 11.0; Union, 10.7, 11.2; Carriacou (8) 9.9 (9.5-10.5).

Discussion

The documented chiropteran fauna of the small, arid islands of the Grenadines is limited to 5 species—*N. leporinus* (piscivore/insectivore), *G. longirostris* (nectarivore/pollenivore), *A. lituratus* (frugivore), *A. schwartzi* (frugivore), and *M. molossus* (insectivore). With this low number of species, there is also a limited systematic representation in the fauna with only 3 chiropteran families being represented—Noctilionidae, 1 species; Phyllostomidae, 3; and Molossidae, 1.

The degree to which various feeding guilds are represented on each island provides interesting insights into island biogeography, but poses additional biological questions for future inquiry.

Specifically, there does not seem to be a clear pattern between the number of species found on these islands with regard to their north-south position in the group nor with their elevation. The major surprise of our work is that 2 large frugivores can co-exist on these small, ecologically limited, arid islands where the fruit supply is at best limited at least to the human eye. There are several possible explanations for this situation, such as food sources for these species are broader than we recognize or that their ranges of food taken do not significantly overlap. Another possible explanation as suggested by our observations is that this dynamic is a transitory situation, with *A. lituratus* having recently arrived and that it eventually will move on to 1 of the larger islands or will be out-competed on these small islands by *A. schwartzi*.

The largest island of Carriacou has all 5 species representing 4 feeding guilds (trophic niches): carnivore, frugivore, nectivore, and insectivore. However, it was difficult to assess the presence/absence of *N. leporinus* on the other islands, because these bats are not readily surveyed with mist nets and their day roosts are often difficult to locate. Fishing bats normally would be expected on any Neotropical island where food—fish, crustaceans, and insects—and day roosts (trees, caves, and rock crevices) are available.

The bat faunas of Bequia and Union match the trophic relationship of bats on Carriacou, except the piscivore is missing. The faunas on Mustique and Canouan are composed of a nectivore/pollenivore, a frugivore, and an insectivore. Finally, the fauna of Mayreau may demonstrate the most basic chiropteran fauna for a small, arid Neotropical island, with a single nectivorous/pollenivorous species and a single insectivorous species. Our information documents that a frugivorous species did arrive on Mayreau, but was gone within a matter of a week. Genoways et al. (2001) demonstrated that insectivorous bats tend to dominate the faunas of the Lesser Antillean islands and the Netherland Antilles off of the north coast of South America; however, as the evidence presented here indicates, this is not true for the Grenadine islands.

Genoways et al. (1998) redefined the zoogeographic boundary of the West Indian Subregion of the Neotropical Region based on the distribution of mammals (Hershkovitz 1958). The mammalian boundary of the West Indian Subregion was designated Koopman's Line (Genoways et al. 1998) to differentiate it from Bond's Line, which is the boundary based on the distribution of birds (Lack 1976) but lies to the south between Tobago and Grenada. One of the areas where Genoways et al. (1998) questioned the placement of Koopman's Line was between Grenada and St. Vincent—the Grenadine Islands—because the chiropteran fauna of the Grenadines was essentially unknown at the time of their work. Based on data reported herein, we place Koopman's Line along the Bequia Channel that separates St. Vincent and the northern-most Grenadine island of Bequia (Fig. 1). The 14-km wide Bequia Channel separating St. Vincent and Bequia is not an impressive zoogeographic barrier, at least to the human map-reader. Boaters, however, know that the deep but narrow channel is characterized by an exceptionally stiff east-west current and by prevailing east to southeast wind that typically is between 15-30 knots. This current and airflow is adverse to both water-borne and air-borne transit of the channel. Moreover, because Bequia is wetter than the Grenadine islands just to the south, it is not surprising that cloud-bursts over the channel, Bequia, and St. Vincent are common in summer time.

The zoogeographic importance of the Bequia Channel also makes geological sense. The Grenadine islands sit on the Grenada bank and all were connected to Grenada during the Last Glacial Maximum. St. Vincent was never connected to this complex because the Bequia Channel is 700 m deep or deeper. The only Antillean endemic species of bats that occurs south of the Bequia Channel is *Artibeus schwartzi*, a species hypothesized to be of hybrid origin and may have developed both north and south of the Bequia Channel. On St. Vincent, there are healthy populations of 3 other Antillean endemics—*Monophyllus plethodon*, *Brachyphylla cavernarum*, and *Ardops nichollsi*. We have records of these 3 species from the Kingstown area, easily within human visual distance of Bequia. The distributional pattern is consistent with the hypothesis that the typical east-west airflow and weather over the channel are adverse factors in southward movement by bats.

The Bequia Channel also might delineate an ecological barrier for these 3 Antillean endemic species. The Grenadine islands are all small, arid, and relatively low in elevation, with a flora composed primarily of plants adapted to these arid conditions, hence they lack the plant diversity of St. Vincent and St. Lucia. Species that are nectivores/pollenivores tend to be well represented on arid islands (Genoways et al. 2001), so *Monophyllus plethodon* would have been a likely candidate to cross the barrier. The closely related *G. longirostris* is present in large numbers on Bequia and may out compete *M. plethodon*, although both species are present on the more diverse St. Vincent. In developing the original hypothesis that the Grenadines might be a "filter" barrier to dispersal, it was pointed out that because of the aridity and small size of most of the islands, bat populations might be subject to periodic local species extinctions (Phillips et al. 1989). Under this scenario, it was imagined that bats might occasionally colonize islands, gradually increase in numbers to the point of having a potentially stable population, but then die out during especially adverse conditions. The Grenadines thus would act as effective sinks, with the bat populations blinking on and off over time. More important, if this were the case, the occasional presence of a species on an island in the Grenadine chain would not matter to overall dispersal because the population density would never reach the point of forcing or promoting dispersal (Phillips et al. 1989).

From the top of the cliff near a southern cave on St. Vincent where we found *Brachyphylla cavernarum* roosting during the day, one can see Bequia. Our experience with the Antillean fruit-eating bat elsewhere in the Lesser Antilles is that it is a robust, strong flying omnivore. We have taken it on other low, dry islands in the Lesser Antilles—for example, Anguilla (Genoways et al. 2007b), Barbuda (Pedersen et al. 2007), and St. Barts (Larsen et al. 2007a). The 1 limiting factor that may have prevented both *M. plethodon* and *B. cavernarum* from establishing permanent populations on Bequia is the lack of appropriate day roosts. *Brachyphylla* prefer relatively large, humid caves as day roosts, whereas *Monophyllus* find day roosts in a broader range of caves, but is an obligate cave roosting species. During our work on Bequia, we did not find any caves that could serve as day roosts for these species.

On the other hand, the endemic tree bat, *Ardops nichollsi*, is a species that we would not expect to find on the Grenadine islands. It is a tree roosting species that eats small native and introduced fruits. Tree bats tend to occur at higher elevations, usually above 300 m.

The chiropteran fauna of the Grenadines is best considered to be an attenuated or depauperate representation of the South American bat fauna. The representatives of this fauna decrease from the South American mainland northward to Trinidad, Tobago, Grenada, and finally in the Grenadines. Two species in the Grenadines—*Artibeus lituratus* and *Glossophaga longirostris*—are definitely related to populations to the south on the South American mainland. This fauna also includes 2 other species—*Noctilio leporinus* and *Molossus molossus*—that are widespread in their distribution. Now we know, based on molecular data, that the greater fishing bat has its relationship to populations in northeastern South America. The invasion route cannot be determined for certain at this time for Pallas' mastiff bats, but the South American mainland would be the closest source area.

The fifth species in the Grenadine fauna—*Artibeus schwartzi*—presents some challenges to zoogeographic interpretation. Recent molecular studies provide support for the hypothesis that *A. schwartzi* is of hybrid origin resulting from extensive hybridization among *A. jamaicensis*, *A. planirostris*, and an extinct or uncharacterized species of *Artibeus* (Larsen et al. in prep.). This would mean that this species has zoogeographic components that represent South American origins (*A. planirostris*), Central American and northern Antillean origins (*A. jamaicensis*), and possibly *in situ* origins (an extinct or uncharacterized species of *Artibeus*). The interpretation is further complicated by the fact that morphometrically the St. Vincent populations are much larger than those in the Grenadines and that morphometrically northern Grenadine populations are significantly larger than the southern populations. We must await further information on these relationships before final conclusions can be drawn, but *A. schwartzi* is currently under intensive study by a team headed by 1 of us (P. Larsen).

In addition to more work on the status and evolution of *A. schwartzi*, more work is needed in the Grenadines to determine the full distribution of *N. leporinus* and to determine the relationship and origins of populations of *M. molossus*. It will be interesting to learn when several species—*Pteronotus davyi*, *P. parnellii*, *Micronycteris megalotis*, and *Sturnira lilium*—presumably passed through the Grenadines from the south and established populations further north in the Lesser Antilles. Did these passages all occur during the same time period? Did they occur during, following, or before the Last Glacial Maximum? It is interesting to us that even with this very small chiropteran fauna that many questions have been answered, while others have been raised.

Genetic data used to define species and species boundaries (see Baker and Bradley 2006 for a review) have contributed substantially to understanding the relationships proposed herein and combined with more classical type studies present a more complete understanding of the bat fauna of the Antilles. Our study provides strong evidence that voucher specimens with tissues for genetic studies are critical to the reconstruction of the natural history and evolution of the faunas of these islands.

Acknowledgments

We wish to express our sincere appreciation to the following people who gave us permission or allowed us access to their property in the Grenadines: Gary Ruskin, Director of Security, Raffles Resort, Canouan; Jim Boos, Charlie "Nolly" Simons, and the Hughes family (Industry House Estate) for granting access to their property on Bequia; Claude Ambrose for allowing us to mist net at his residence on Union. We also wish to acknowledge the field assistance of Chris Cudmore, Brent Gooding, Paul Homnick, Joe Kolba, and John Larsen. Matthew Harvey provided logistical support on Union and Carriacou, Raven Hoflund on Mustique, and Charmine Simmons on Canouan provided similar support. Dr. Kathian Herbert-Hackshaw, Chief Veterinary Officer, Ministry of Agriculture, St. Vincent and the Grenadines, provided logistical assistance for the 2005-2006 field work. We thank local authorities for their assistance in arranging collecting permits: L. McPhail of the Ministry of Agriculture, Grenada; Brain Johnson, Director of Forestry, and Cornelius Richards, Chief Forestry Officer, Ministry of Agriculture, St. Vincent.

We appreciate access to the collection of mammals of the Carnegie Museum of Natural History (CM), with John R. Wible, Curator, and Suzanne B. McLaren, Collection Manager, and The Museum of Texas Tech University (TTU), with Robert J. Baker, Curator, and Heath Garner, Collection Manager. Nicole Cook assisted in extracting cranial material from fluid prepared specimens. Angie Fox, Technical Artist for the University of Nebraska State Museum, prepared Figure 1.

South Dakota State University provided some financial assistance through the Research/Scholarship Support Fund. The University of Scranton provided financial assistance through Faculty and Student Development Grants. J. Sowell provided financial support for travel and archiving of specimens through the Natural Science Research Laboratory of the Museum of Texas Tech University. The biological database program at Texas Tech provided funds for some of the molecular studies.

References

Allen G.M. 1908. Notes on Chiroptera. Bulletin of the Museum of Comparative Zoology, Harvard College 52: 25-62.

Allen G.M. 1911. Mammals of the West Indies. Bulletin of the Museum of Comparative Zoology, Harvard College 54: 175-263.

Baker R.J. and Bradley R.D. 2006. Speciation in mammals and the Genetic Species Concept. Journal of Mammalogy 87: 643-662.

Baker R.J. and Genoways H.H. 1978. Zoogeography of Antillean bats. In: Zoogeography in the Caribbean (edited by Gill F.B.), pp. 53-97. Special Publication, Academy of Natural Sciences of Philadelphia, 13: iii + 1-128.

Beard J.S. 1949. The natural vegetation of the Windward and Leeward islands. Clarendon Press, Oxford, UK.

Caribbean Hurricane Network. 2008. St. Vincent (TVSV) and Grenada (TGPY). Accessed 1 September at <http://stormcarib.com/climatology/>.

Clark P.U.; Dyke A.S.; Shakun J.D.; Carlson A.E.; Clark J.; Wohlfarth B.; Mitrovica J.X.; Hostetler S.W. and McCabe A. M. 2009. The Last Glacial Maximum. Science 325: 710-714.

Daudin J. (editor). 2003. A natural history monograph of Union Island. Desormeaux, Martinique.

Davis W.B. 1970. The large fruit bats (genus *Artibeus*) of Middle America, with a review of the *Artibeus jamaicensis* complex. Journal of Mammalogy 51: 105-122.

Davis W.B. 1973. Geographic variation in the fishing bat, *Noctilio leporinus*. Journal of Mammalogy 54: 862-874.

De Silva M. and Wilson D. 2006. A natural history of Mustique. The Mustique Company Ltd., St. Vincent and the Grenadines.

Dolan P.G. 1989. Systematics of Middle American mastiff bats of the genus *Molossus*. Special Publication of the Museum, Texas Tech University 29: 1-71.

Genoways H.H.; Larsen P.A.; Pedersen S.C. and Huebschman J.J. 2007a. Bats of Saba, Netherland Antilles: a zoogeographic perspective. Acta Chiropterologica 9: 97-114.

Genoways H.H.; Pedersen S.C.; Larsen P.A.; Kwiecinski G.G. and Huebschman. J.J. 2007b. Bats of Saint Martin, French West Indies/Sint Maarten, Netherlands Antilles. Mastozoología Neotropical 14: 169-188.

Genoways H.H.; Pedersen S.C.; Phillips C.J. and Gordon L.K. 2007c. Bats of Anguilla, northern Lesser Antilles. Occasional Papers of the Museum, Texas Tech University 270: 1-12.

Genoways H.H.; Phillips C.J. and Baker R.J. 1998. Bats of the Antillean island of Grenada: A new zoogeographic perspective. Occasional Papers of the Museum, Texas Tech University 177: 1-28.

Genoways H.H.; Timm R.M.; Baker R.J.; Phillips C.J. and Schlitter D.A. 2001. Bats of the West Indian island of Dominica: Natural history, areography, and trophic structure. Special Publications of the Museum, Texas Tech University 43: 1-43.

Graham A. 2003. Geohistory models and Cenozoic paleoenvironments of the Caribbean region. Systematic Botany 28: 378-386.

Hedges S.B. 2006. Paleogeography of the Antilles and origin of West Indian terrestrial vertebrates. Annals of the Missouri Botanical Garden 93: 231-244.

Hershkovitz P. 1958. A geographic classification of Neotropical mammals. Fieldiana: Zoology 36: 581-620.
Hoffmann F.G. and 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 82: 1092-1101.
Hoofer S.R.; Solari S.; Larsen P.A.; Bradley R.D. and Baker R.J. 2008. Phylogenetics of the fruit-eating bats (Phyllostomidae: Artibeina) inferred from mitochondrial DNA sequences. Occasional Papers of the Museum, Texas Tech University 277: 1-15.
Husson A.M. 1962. The bats of Suriname. Zoölogische Monographierën, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands, 2: xxxiv + 1-569.
Ishmael L. (Director General). 2004. Grenada: Macro-socio-economic assessment of the damages caused by Hurricane Ivan, September 7, 2004. Organisation of Eastern Caribbean States.
Jones J.K. Jr. 1978. A new bat of the genus *Artibeus* from the Lesser Antillean island of St. Vincent. Occasional Papers of the Museum, Texas Tech University 51: 1-6.
Jones J.K. Jr. 1989. Distribution and systematics of bats in the Lesser Antilles. In: Biogeography of the West Indies: Past, present, and future (edited by Woods C.A.), pp. 645-660. Sandhill Crane Press, Inc., Gainesville, Florida.
Jones J.K. Jr. and Phillips C.J. 1970. Comments on systematics and zoogeography of bats in the Lesser Antilles. Studies on the Fauna of Curaçao and other Caribbean Islands 32: 131-145.
Lack D. 1976. Island biology: Illustrated by the land birds of Jamaica. University of California Press, Berkeley and Los Angeles.
Larsen P.A.; Genoways H.H. and Pedersen S.C. 2007a. New records of bats from St. Barthélemy, French West Indies. Mammalia 70: 321-325.
Larsen P.A.; Hoofer S.R.; Bozeman M.C.; Pedersen S.C.; Genoways H.H.; Phillips C.J.; Pumo D.E. and Baker R.J. 2007b. Phylogenetics and phylogeography of the *Artibeus jamaicensis* complex based on cytochrome-*b* DNA sequences. Journal of Mammalogy 88: 712-727.
Larsen P.A.; Marchán M.R. and Baker R.J. In preparation. Natural hybridization generates novel mammalian lineage with species characteristics.
Lewis-Oritt N.; Van Den Bussche R.A. and Baker R.J. 2001. Molecular evidence for evolution of piscivory in *Noctilio* (Chiroptera: Noctilionidae). Journal of Mammalogy 82: 748-759.
Miller G.S. Jr. 1913a. Five new mammals from tropical America. Proceedings of the Biological Society of Washington 24: 31-33.
Miller G.S. Jr. 1913b. Revision of the bats of the genus *Glossophaga*. Proceedings of the United States National Museum 46: 413-429.
Morgan G.S. and Woods C.A. 1986. Extinction and zoogeography of West Indian mammals. Biological Journal of the Linnean Society 28: 167-203.
Pedersen S.C.; Genoways H.H.; Morton M.N.; Swier V.J.; Larsen P.A.; Lindsay K.C.; Adams R.A. and Appino J.D. 2006. Bats of Antigua, northern Lesser Antilles. Occasional Papers of the Museum, Texas Tech University 249: 1-18.
Pedersen S.C.; Genoways H.H.; Morton M.N.; Johnson J.W. and Courts S.E. 2003. Bats of Nevis, northern Lesser Antilles. Acta Chiropterologica 5: 251-267.
Pedersen S.C.; Genoways H.H.; Morton M.N.; Kwiecinski G.G. and 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 41: 744-760.
Pedersen S.C.; Larsen P.A.; Genoways H.H.; Morton M.N.; Lindsay K.C. and Cindric J. 2007. Bats of Barbuda, northern Lesser Antilles. Occasional Papers of the Museum, Texas Tech University 271: 1-19.
Phillips C.J.; Pumo D.E.; Genoways H.H. and Ray P.E. 1989. Caribbean island zoogeography: A new approach using mitochondrial DNA to study Neotropical bats. In: Biogeography of the West Indies (edited by Woods C.A.), pp. 661-684. Sandhill Crane Press, Gainesville, Florida.
Phillips C.J.; Pumo D.E.; Genoways H.H.; Ray P.E. and Briskey C.A. 1991. Mitochondrial DNA evolution and phylogeography in two Neotropical fruit bats, *Artibeus jamaicensis* and *Artibeus lituratus*. In: Latin American mammalogy: History, biodiversity, and conservation (edited by Mares M.A. and Schmidly D.J.), pp. 97-123. University of Oklahoma Press, Norman.
Pregill G.K. 1981. An appraisal of Caribbean biogeography and its application to West Indian terrestrial vertebrates. Systematic Zoology 30: 147-155.
Pumo D.E.; Goldin E.Z.; Elliot B.; Phillips C.J. and Genoways H.H. 1988. Mitochondrial DNA polymorphism in three Antillean island populations of the fruit bat, *Artibeus jamaicensis*. Molecular Biology and Evolution 5: 79-89.
Pumo D.E.; Kim I.; Remsen J.; Phillips C.J. and Genoways H.H. 1996. Molecular systematics

of the fruit bat, *Artibeus jamaicensis*: Origin of an unusual island population. Journal of Mammalogy 77: 491-503.

Vaughan N. and Hill J.E. 1996. Bat (Chiroptera) diversity and abundance in banana plantations and rain forest, and three new records for St. Vincent, Lesser Antilles. Mammalia 60: 441-447.

Watters D.R. 1989. Archaeological implications for the Lesser Antilles biogeography: The small island perspective. In: Biogeography of the West Indies: Past present and future (edited by Woods C.A.), pp. 153-166. Sandhill Crane Press, Inc., Gainesville, Florida.

Webster W.D. and Handley C.O. Jr. 1986. Systematics of Miller's long-tongued bat, *Glossophaga longirostris*, with description of two new subspecies. Occasional Papers of the Museum, Texas Tech University 100: 1-22.

Westercamp D.; Andreieff P.; Bouysse P.; Mascle A. and Baubron J.C. 1985. Géologie de l'archipel des Grenadines (Petites Antilles méridionales). Bureau de recherches géologiques et minières, Service géologique national, Orléans, France.

Associate Editor: Felipe de Melo Martins.