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**ARTICLE**

**Abstract**

The chiropteran fauna of Barbados includes representatives of four families — Noctilionidae, Phyllostomidae, Vespertilionidae, and Molossidae — including 1 piscivore (*Noctilio leporinus*), 1 omnivore (*Brachyphylla cavernarum*), 1 pollenivore/nectarivore (*Monophyllus plethodon*), 1 frugivore (*Artibeus jamaicensis*), and 2 insectivorous species (*Myotis nyctor* and *Molossus molossus*). Despite an early report, we believe that preponderance of the evidence available at this time is that *E. fuscus* is not part of the fauna of Barbados. The Barbadian chiropteran fauna of 6 species is much smaller than those on the four neighboring Lesser Antillean islands to the west and north. We believe that this is primarily the result of two factors—geological age and geographic isolation. Our work indicates that populations of the 6 species of bats on Barbados are in good condition in all cases, but only for *Artibeus jamaicensis* and *Molossus molossus* are the populations large enough to not be of ongoing concern. The maintenance of the chiropteran fauna can best be served by three management actions — preservation of caves and associated gullies, forests, and hydrological systems.
**Keywords:** Barbados, biodiversity, Chiroptera, *Myotis nyctor*, systematics, zoogeography.

## Introduction

Barbados is the eastern-most of the Caribbean islands, with Bridgetown, Barbados, lying about 180 km to the southeast of Castries, St. Lucia, and 176 km east of Kingstown, St. Vincent. The Caribbean Sea touches the sandy beaches of western Barbados and the North Atlantic Ocean pounds the rocky eastern shore. With a population density of nearly 600 people per square kilometer, Barbados is among the most densely populated nations in the world. From 1625 until independence in 1966, Barbados was a British colony. Sugarcane was the basis of the economy of the island from near its founding, but has declined in recent years now primarily supplying the rum industry of the island. Tourism is now the mainstay of the economy.

The combination of a long history of intensive agricultural development of nearly the entire island and a high human population density has resulted in a considerable loss of biodiversity on Barbados. There have been no studies on the impact of this loss in biodiversity on the health and status of the chiropteran fauna of Barbados.

The first species of bat to be reported from Barbados was by Dobson (1878) who listed an *Eptesicus fuscus* from the island. The specimen that was the basis of this report is still available in the British Museum (Natural History), but based on our current studies, we believe that the species should be excluded from the fauna of the island. Records of six other species of bats from the island have appeared in the scattered scientific reports—*Noctilio leporinus, Monophyllus plethodon, Brachyphylla cavernarum, Artibeus jamaicensis, Myotis nyctor,* and *Molossus molossus* (Feilden 1890, Miller 1900, 1913, Jones 1951, Schwartz and Jones 1967, Koopman 1968, 1989, Jones and Phillips 1970, LaVal and Schwartz 1974, Buden 1977, Swanepoel and Genoways 1978, Jones 1989). With the exception of a recent natural history study of two areas on

the island (Grindal 2004), there have been no studies that have solely focused on the bats of Barbados.

Our research on the bat fauna of Barbados began with a brief visit in 1986, but was primarily focused in June 2007 and July 2008. These periods of field studies allowed us to visit 26 localities representing all 11 parishes of the island. Our 112 bat net nights of work allowed us to capture 933 individual bats and to gather data from them. These data allow us to assess the population status of each of the six species on Barbados. This information is arranged below in accounts for each species and is discussed to make overall conservation recommendations for this small but unique fauna.

**Material and Methods**

The island of Barbados (13°10' N, 59°32' W) is 34 km long and 23 km wide, giving an area of 432 square km. Barbados is a relatively low, flat island, rising in a series of limestone terraces to Mount Hillaby in St. Andrew Parish at 336 m in the northern half of the island. The warmest months are April to October with mean temperatures of 30°-31°C and the coolest are November to March with mean temperatures 28°-29°C. The mean annual rainfall is 1278 mm, with a dry season from December to May (driest month February, 28 mm) and a wet season from June to November (wettest month November, 206 mm). Barbados lies at the southern edge of the Caribbean hurricane zone so that hurricanes are rare occurrences. The largest hurricane to hit the island was the Great Hurricane of 1780 when over 4000 people were killed on 9-10 October 1780. In 1955, Hurricane Janet hit Barbados with winds up to 193 kph on 22 September. The last major hurricane to impact the island was Hurricane Allen, an h3 storm that hit on 4 August 1980. A smaller storm, Hurricane Marilyn (h1), passed to the north of the Barbados in September 1995 (Rappaport and Fernandez-Partagas 1995, Simmons and Associates 2000, Caribbean Hurricane Network 2010).

Although Barbados is often grouped with the Lesser Antillean islands, it is geologically and geographically unique. The distinct nature of Barbados can be observed by examining the basins and ridges in the southeastern Caribbean region. Beginning in the west and moving eastward, the following submarine and surface features are encountered: Caribbean Basin; Aves Ridge, running approximately north to south from near St. Croix to Margarita Island with the tiny rock, Isla de Aves, as the only emergent feature; Grenada Basin; Lesser Antilles Ridge, supporting the islands from Saba to Grenada, which are primarily volcanic in origin; Tobago Trench;

Barbados Ridge, with Barbados island being the only emergent land mass; and the Atlantic Ocean Basin. The Barbados Ridge extends from the point where it merges with the Lesser Antilles Ridge east of Martinique to near Tobago where it abuts the South American tectonic plate. Barbados lies in the boundary zone between the overriding Caribbean plate to the west and the subducting South American plate to the east. The Barbados Ridge is the accretionary wedge of the eastern Caribbean plate boundary zone. As the South American plate moves under the Caribbean plate the softer sedimentary materials of the Atlantic Ocean floor are scraped into a wedged-shaped ridge that is the Barbados Ridge. Thus the base material for Barbados Island is highly deformed sedimentary rock, which began accumulating 50 million years ago. Recent tectonic forces began acting below Barbados Island about a million years ago, bringing this portion of the ridge to the surface (Speed and Keller 1993, Speed 1994).

The steady rise of the island above sea level began about 700,000 years ago, making it the youngest island in the region. As it emerged, the island was covered with a layer of limestone ranging from 10 m to 100 m thick. This coral cap is composed of a succession of ancient coral reefs in which the fauna died as they rose above the sea. The coral cap is quite rigid and inclined from the high point in the northeastern part of the island (Scotland District) toward the three coasts (Speed and Keller 1993). Speed and Keller (1993) postulated that about 350,000 years ago the island extended several kilometers to the east and the entire island was covered with the coral cap. They suggest that tectonic faulting opened large fissures paralleling the east coast and the eastern walls of these openings slid down the eastern slope of the Barbados Ridge into the deep marine basin thus exposing the underlying rocks.

The coral cap has been shaped and modified by the action of groundwater flowing downhill within it. This groundwater causes dissolution of the limestone thereby forming caverns, which subsequently collapse to form sinkholes and "gullies" (Speed and Keller 1993). These caverns and gullies are vital to the health and future of bats on Barbados.

After three centuries of extensive agricultural development, the majority of the natural vegetation and the biodiversity that it represented have been lost. However, the gully system provides moist microenvironments in which small patches of natural forest and vegetation remain, which in turn provide important habitat to a variety of animals, including bats. This gully system has been estimated to include a total length of 430 km, 250 km of which is forested (Carrington 2007). The few areas of natural forest vegetation beyond the gully system are the coastal

wetlands and undercliff woods, which are well developed below Hackleton's Cliff (Gooding 1974, Simmons and Associates 2000, Carrington 2007). A small area of largely undisturbed mesophytic forest called Turner's Hall Woods can be found in the central part of the island, having escaped clearance for agriculture owing to its steeply sloping aspect. Today sugarcane production has been reduced to less than 9000 ha and secondary vegetation is reclaiming many of those areas that were removed from cultivation.

The forests of Barbados were classified by Beard (1949: 166) as "corresponding to that of evergreen seasonal forest in the more luxuriant parts and to semi-evergreen seasonal forest elsewhere." The highland areas of St. Thomas, St. Joseph, and St. Andrew parishes exhibit a mixture of secondary forest, introduced species of trees, and ornamental gardens. These areas are dominated by royal (*Roystonea regia*) and cabbage palm (*R. oleracea*), bamboo (*Bambusa*), introduced fruit trees (see below), and native trees, especially those typical of the gully system. Larger forest trees include locust (*Hymenacea courbaril*); Jack in the box (*Hernandia sonora*); sandbox, also called the monkey-no-climb tree (*Hura crepitans*); and silk cotton (*Ceiba pentandra*). Some of the important canopy trees that provide fruit for bats include wild clammy cherry (*Cordia collococca*) and fustic (*Maclura tinctoria*) that both produce small edible fruits; hogplum that produces large edible fruits (*Spondias mombin*); birch gum, also called gumbo-limbo (*Bursera simaruba*); poison tree (*Sapium hippomane*); and Barbados cedar (*Cedrela odorata*) (Beard 1949, Gooding 1974).

The south and west coasts of Barbados were originally characterized by mangrove swamps, but these have been drained leaving the largest remaining swamp at Graeme Hall where red mangrove (*Rhizophora mangle*) and white mangrove (*Laguncularia racemosa*) dominate (Carrington 2007). Small pockets of swamp habitat can still be found at the seaward ends of the gullies that empty along the west coast and at Chancery Lane on the south east coast. Another important forest type is the undercliff forest of the east coast occurring between the coral cliffs and the Atlantic coast. Some of the important undercliff trees include whitewood (*Tabebuia heterophylla*), poison tree, birch gum, and fiddle wood (*Citharexylum spinosum*), bearing fruit probably eaten by bats (Gooding 1974, Carrington 2007).

Additional sources of food for fruit-eating and nectar/pollen-feeding bats include the introduced fruit trees, such as banana (*Musa*), breadfruit (*Artocarpus altilis)*, mango (*Mangifera indica)*, almond (*Prunus dulcis*), genip, locally known as ackee (*Melicoccus bijugatus*), coconut (*Cocos nucifera*), guava (*Psidium guajava*), avocado (*Persea americana),* and soursop (*Annona muricata*).

Survey efforts on Barbados occurred during three periods—3-4 June 1986, consisting of 3 net nights; 22-26 June 2007, consisting of 37 net nights; and 20-27 July 2008, consisting of 72 net nights; giving a total of 112 net nights at 22 localities. Mist-netting for bats was conducted in a variety of habitats, including gullies, plantations, covered flyways, ornamental gardens, large ponds and streams, and access roads. Few of the locations had significant amounts of fruit in evidence. Five to eight mist-nets of varying lengths were erected at each location frequently situated diagonally across gullies or streams at 20 to 100 m intervals and monitored for four to six hours depending on activity and weather. Caves were surveyed for roosting bats. Three known cave roosts were surveyed—Coles Cave (St Thomas), Cave Hill (St. Lucy), and a cave along Culloden Road. Bats were netted in the gully adjacent to Harrison's Cave, which was closed to the public during 2008. We did not observe bat activity during our visit to Animal Flower Cave, St. Lucy.

Captured bats were measured and examined at the end of each evening—weight (g), length of forearm (mm), reproductive status, tooth wear, presence of scars, and external parasites. Bats were released or euthanized according to standard procedures.

Length of forearm and cranial measurements (mm) were taken from museum specimens using digital calipers and weights were recorded in grams. Measurements were taken following Hall (1946), except that greatest length of skull included the incisors, and length of forearm is the distance from elbow joint to tip of carpals with the wing in retracted position. StatView® software package (Sager 1992) provided standard statistics for each sample and paired t-tests were used to test for differences in group means.

A survey of existing collection materials in natural history museums (American Museum of Natural History, AMNH; [British] Natural History Museum, BMNH; Field Museum of Natural History, FMNH; Museum of Comparative Zoology, Harvard University, MCZ; National Museum of Natural History, NMNH; Royal Ontario Museum, ROM; University of Kansas, KU) yielded an additional 151 specimens of bats from Barbados. All voucher specimens from the 1986 survey (58 specimens) were deposited in the research collections at the Carnegie Museum of Natural History (CM) and those from 2007 and 2008 (220 specimens with associated tissues) were deposited in the mammal collections of the Museum of Texas Tech University (TTU), with a representative series deposited at the University of the West Indies-Cave Hill (UWI-CH) (8). This

made 437 voucher specimens available for our study.

**Results**

We captured a total of 933 bats during 3 field seasons—5 *Noctilio leporinus*, 103 *Brachyphylla cavernarum*, 25 *Monophyllus plethodon*, 659 *Artibeus jamaicensis*, 30 *Myotis nyctor*, and 111 *Molossus molossus*. Information from these specimens, the 151 museum specimens from ealier work, and the published literature have been combined to create the following Species Accounts for the 6 species of bats occurring on Barbados.

**Species Accounts**

*Noctilio leporinus mastivus* (Fig. 1)

*Specimens examined* (5).—**Christ Church Parish:** Graeme Hall Swamp, 0.5 km N St. Lawrence, 2 m [13°04'21.4" N, 59°34'44.1" W], 5 (4 TTU, 1 UWI-CH).

*Additional records.*—**Unknown Parish:** no specific locality (Jones 1951).

*Remarks.*—Our specimens from Graeme Hall Swamp are the first from a known locality on Barbados (Fig. 2). We have assigned these specimens to the subspecies *N. l. mastivus* following Davis (1973) who assigned all material from the West Indies, Mexico, Central America, and northern South America to this subspecies. Davis (1973) characterized this taxon based on its large size for the species, with the length of forearm in females more than 81.4, condylobasal length more than 22.8, and length of maxillary toothrow usually over 10.0. The forearm and cranial measurements of our specimens (Table 1) fit all of these criteria and they are within or above the range of measurement of specimens from Dominica (Genoways et al. 2001), the Grenadines (Genoways et al. 2010), and Grenada (Genoways et al. 1998), with the exception of mastoid breadth of the female from Barbados, which is smaller than in the other samples.

When we visited Graeme Hall Swamp, it was operated as the Graeme Hall Nature Sanctuary for public visitors and was designated as a wetland of international importance recognized by the Convention on Wetlands Treaty (Ramsar Convention). It consisted of mangrove swamps, freshwater pools, and a large open brackish lake, which had a connection to the ocean controlled by a sluice gate. We captured 4 specimens of the greater fishing bat in 2007 and a single individual in 2008 in mist nets set adjacent to the pools, whereas others were caught in nets set under trees and beside a bridge across the pools. We observed at least 12 additional individuals fishing over these small ponds.

Although we captured this species at a single site at the southern end of the island, we believe that it can be found on the island wherever there are quiet areas of open water with small fish and crustaceans present and appropriate day roosts nearby. It is difficult to properly survey this species because their open foraging areas are not easily sampled with mist nets. Notably we had a single individual of the greater fishing bat bounce off of one of our nets at Porters just north of Holetown along the west coast.



Figure 1. Photographs of the 6 species of bats occurring on Barbados as follows: *Noctilio leporinus*, greater fishing bat (upper left corner); *Monophyllus plethodon*, insular single-leaf bat (upper right corner); *Brachyphylla cavernarum*, Antillean fruit-eating bat (middle row left); *Artibeus jamaicensis*, Jamaican fruit-eating bat, (middle row right); *Myotis nyctor*, Schwartz's myotis (lower left corner); *Molossus molossus*, Pallas's mastiff bat (lower right corner).

Three males captured on 26 June 2007 had testes lengths of 3, 7, and 7 and the female taken on the same date was lactating. The males weighed 55.5, 59.4, and 61.7, whereas the female weighed 49.8.

*Monophyllus plethodon plethodon* (Fig. 1)

*Specimens examined* (42).—**St. Andrew Parish:** Grenade Hall, 227 m [13°15'58.6" N, 59°35'39.3" W], 4 (3 TTU, 1 UWI-CH). **St. James Parish:** Porters, 0.7 km N Holetown, 3 m [13°11'38.5" N, 59°38'13.3" W], 1 (TTU). **St. John Parish:** Martin's Bay, 34 m [13°11'47.9" N, 59°30'01.1" W], 1 (TTU). **St. Joseph Parish:** Horse Hill, 251 m [13°12'02.5″ N, 59°32'14.9"

W], 1 (TTU). **St. Thomas Parish:** Friendship Terrace, 54 m [13°08'24.4" N, 59°36'07.1" W], 1 (TTU); Harrison's Cave [13°12' N, 59°34' W], 16 (ROM); Jack in the Box Gully, 0.65 km S, 0.2 km E Ayshford, 156 m [13°10'15.9" N, 59°34'39.8" W], 18 (1 KU, 17 TTU).

*Additional records.*—**St. Michael Parish:** no specific locality (Miller 1900, Schwartz and Jones 1967). **St. Thomas Parish:** Cole's Cave (LaVal and Schwartz 1974); Harrison's Cave (Grindal 2004); Jack in the Box Gully (Timm and Genoways 2003).

*Remarks.*—The insular single-leaf bat was originally described by Miller based on a single specimen from St. Michael Parish (Miller 1900, Schwartz and Jones 1967). When Schwartz and Jones (1967) revised the genus *Monophyllus*, they had only 1 additional specimen from Barbados, a male from Jack in the Box Gully. Our survey clearly indicates that the species is widespread on the island, with the species now known from 9 locations in 6 parishes. The species was taken from sites at which the elevation ranged from 3 to 251 m; however, the species appeared to be more abundant at higher elevations, especially in St. Thomas Parish where there is a complex of caves and gullies (Fig. 2).
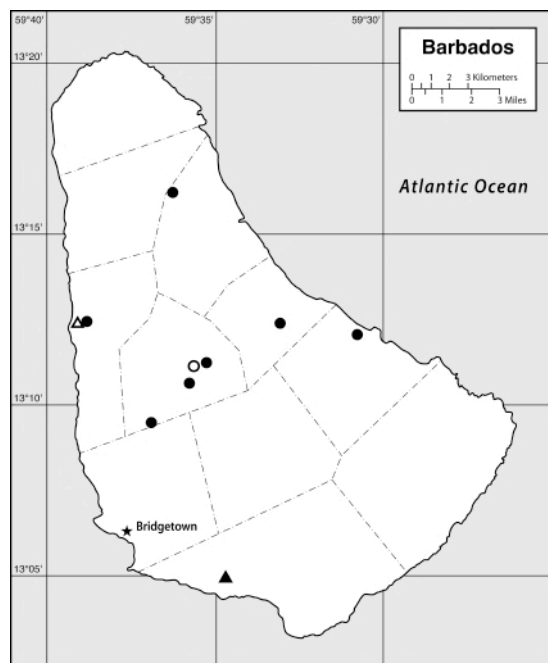


Figure 2. Map of the geographic distribution of *Noctilio leporinus* and *Monophyllus plethodon* on Barbados. Symbols represent: closed triangle, specimens examined for *Noctilio leporinus*; open triangle, other record of *Noctilio leporinus*; closed circles, specimens examined for *Monophyllus plethodon*; open circles, other records of *Monophyllus plethodon*.

Length of forearm and seven cranial measurements of 9 males and 10 females are given in Table 1. Males averaged significantly larger than females in 4 of the 8 measurements—greatest length of skull ($P \leq 0.05$), length of forearm ($P \leq 0.01$), and zygomatic breadth and mastoid breadth ($P \leq 0.001$). In the 4 non-significant measurements, males and females averaged the same in three measurements, with males averaging larger only in breadth across the upper molars.

When Schwartz and Jones (1967) studied *Monophyllus*, they stated: "It is purely on the basis of the holotype that we recognize *M. p. plethodon* as distinct from other Lesser Antillean populations." The holotype of *M. p. plethodon* was smaller than other specimens of *Monophyllus plethodon*, including the second specimen from Barbados. Schwartz and Jones (1967) were uncertain about their decision in recognizing both *M. p. plethodon* and *M. p. luciae* (type locality St. Lucia) and opined that additional material from these islands could alter their decision. With adequate samples available from both Barbados and St. Lucia, we have taken the opportunity to test the traditional morphometric difference between these populations (Table 2). Male and female samples were analyzed separately because of the amount of secondary sexual variation in size that was found previously in our sample from Barbados.

The morphometric results for males and females are shown in Table 2. Surprisingly, the males from Barbados are significantly different from males on St. Lucia in five of eight measurements, whereas the females are significantly different in only two measurements and, in fact, females from these 2 islands averaged the same in 4 measurements. The males from Barbados are significantly larger than those from St. Lucia in four (greatest length of skull and zygomatic breadth, $P \leq 0.05$; postorbital constriction and mastoid breadth, $P \leq 0.01$) of the five measurements. Males from Barbados are significantly smaller than those from St. Lucia in length of the maxillary toothrow ($P \leq 0.05$). The females from St. Lucia are significantly larger than those from Barbados in the two measurements—length of forearm ($P \leq 0.001$) and length of the maxillary toothrow ($P \leq 0.05$). Length of maxillary toothrow, therefore, seems to be the only point of agreement between the morphometric variation of sexes on the 2 islands and with what was initially anticipated from the analyses. Our conclusion from the analyses is that members of the population of *Monophyllus plethodon* from Barbados are not smaller than those on St. Lucia and in the case of males they are in fact significantly larger. The name of the nominate subspecies, *M. p. plethodon*, can be applied to the bats from Barbados, but the

Table 1. Length of forearm and seven cranial measurements for specimens of six species of bats from Barbados, Lesser Antilles.

| Statistics, catalogue no., and sex (sample size in parentheses) | Length of forearm | Greatest length of skull | Condylobasal length | Zygomatic breadth | Postorbital constriction | Mastoid breadth | Length of maxillary toothrow | Breadth across upper molars |
|---|---|---|---|---|---|---|---|---|
| ***Noctilio leporinus mastivus*** | | | | | | | | |
| TTU 110076, male | 84.7 | 28.8 | 24.6 | 19.8 | 7.4 | 17.8 | 10.3 | 12.9 |
| TTU 110079, male | 88.4 | 29.1 | 25.4 | 20.3 | 7.4 | 18.8 | 10.5 | 12.9 |
| TTU 110078, female | 86.0 | 26.7 | 24.1 | 18.9 | 7.2 | 15.5 | 10.1 | 12.5 |
| | | | | | | | | |
| ***Monophyllus plethodon plethodon*** | | | | | | | | |
| Males (N = 9) | | | | | | | | |
| Mean ± SE | 41.8±0.28 | 23.3±0.07 | 21.5±0.08 | 10.3±0.05 | 4.8±0.06 | 10.1±0.04 | 7.8±0.04 | 5.6±0.08 |
| Range | (40.8-43.4) | (23.0-23.6) | (21.2-21.9) | (10.1-10.6) | (4.6-5.1) | (9.9-10.3) | (7.7-8.0) | (5.2-5.9) |
| Females (N = 10) | | | | | | | | |
| Mean ± SE | 40.5±0.21 | 23.1±0.09 | 21.5±0.05 | 9.7±0.13 | 4.8±0.04 | 9.6±0.05 | 7.8±0.05 | 5.5±0.06 |
| Range | (39.3-41.4) | (23.0-23.6) | (21.3-21.7) | (8.9-10.4) | (4.6-5.0) | (9.4-10.0) | (7.5-8.1) | (5.2-5.7) |
| | | | | | | | | |
| ***Brachyphylla cavernarum minor*** | | | | | | | | |
| Males (N = 22) | | | | | | | | |
| Mean ± SE | 60.4±0.34 | 30.3±0.11 | 27.2±0.11 | 16.5±0.08 | 6.4±0.05 | 14.4±0.06 | 10.6±0.04 | 11.1±0.05 |
| Range | (57.0-63.0) | (29.1-31.1) | (26.1-28.1) | (16.0-17.7) | (6.0-6.8) | (13.8-15.1) | (10.2-10.9) | (10.5-11.5) |
| Females (N = 14) | | | | | | | | |
| Mean ± SE | 61.5±0.33 | 30.6±0.12 | 27.3±0.09 | 16.6±0.11 | 6.3±0.07 | 14.2±0.08 | 10.6±0.04 | 11.1±0.09 |
| Range | (59.9-63.3) | (29.7-31.9) | (26.7-27.6) | (15.9-17.3) | (5.8-6.8) | (13.7-14.7) | (10.3-10.8) | (10.6-11.8) |

Table 1. Length of forearm and seven cranial measurements for specimens of six species of bats from Barbados, Lesser Antilles (cont.).

| Statistics, catalogue no., and sex (sample size in parentheses) | Length of forearm | Greatest length of skull | Condylobasal length | Zygomatic breadth | Postorbital constriction | Mastoid breadth | Length of maxillary toothrow | Breadth across upper molars |
|---|---|---|---|---|---|---|---|---|
| ***Artibeus jamaicensis jamaicensis*** | | | | | | | | |
| Males (N = 16) | | | | | | | | |
| Mean ± SE | 58.7±0.43 | 28.7±0.11 | 25.2±0.11 | 17.1±0.09 | 7.2±0.05 | 14.9±0.10 | 10.1±0.04 | 12.8±0.07 |
| Range | (55.7-61.2) | (27.7-29.6) | (24.4-26.0) | (16.3-17.7) | (6.6-7.5) | (14.1-15.4) | (9.8-10.3) | (12.2-13.3) |
| Females (N = 22) | | | | | | | | |
| Mean ± SE | 60.0±0.53 | 29.2±0.10 | 25.6±0.10 | 17.5±0.07 | 7.2±0.06 | 15.0±0.08 | 10.1±0.05 | 12.9±0.06 |
| Range | (55.2-62.6) | (28.0-30.1) | (24.7-26.6) | (17.0-18.2) | (6.5-7.5) | (14.2-16.0) | (9.6-10.6) | (12.5-13.6) |
| ***Myotis nyctor*** | | | | | | | | |
| Males (N = 10) | | | | | | | | |
| Mean ± SE | 35.6±0.12 | 14.5±0.08 | 13.6±0.13 | 8.4±0.10 | 3.3±0.03 | 7.2±0.03 | 5.5±0.03 | 5.3±0.05 |
| Range | (35.1-36.3) | (14.2-14.9) | (13.1-14.3) | (7.9-8.9) | (3.2-3.5) | (7.0-7.3) | (5.4-5.7) | (5.1-5.6) |
| Females (N = 11) | | | | | | | | |
| Mean ± SE | 35.6±0.18 | 14.4±0.07 | 13.5±0.09 | 8.4±0.13 | 3.3±0.02 | 7.2±0.03 | 5.5±0.03 | 5.4±0.06 |
| Range | (34.7-36.6) | (14.0-14.8) | (13.1-13.9) | (7.5-8.9) | (3.2-3.4) | (7.0-7.4) | (5.3-5.6) | (4.9-5.6) |
| ***Molossus molossus molossus*** | | | | | | | | |
| Males ( N = 14) | | | | | | | | |
| Mean ± SE | 39.1±0.29 | 16.9±0.09 | 14.9±0.08 | 10.5±0.07 | 3.4±0.03 | 10.0±0.05 | 6.0±0.03 | 7.6±0.04 |
| Range | (36.2-40.4) | (16.1-17.4) | (14.1-15.3) | (10.0-10.7) | (3.2-3.5) | (9.7-10.3) | (5.8-6.1) | (7.3-7.8) |
| Females (N = 20) | | | | | | | | |
| Mean ± SE | 38.5±0.19 | 16.4±0.06 | 14.3±0.06 | 10.1±0.03 | 3.3±0.02 | 9.6±0.04 | 5.8±0.03 | 7.4±0.04 |
| Range | (36.9-40.2) | (15.9-16.8) | (13.9-14.8) | (9.8-10.5) | (3.1-3.4) | (9.4-10.0) | (5.6-6.0) | (7.2-7.7) |

Table 2. Comparisons of the morphological size of *Monophyllus plethodon* males from the Lesser Antillean islands of Barbados and St. Lucia and females from the same two islands. Measurements for samples from St. Lucia are from Kwiecinski et al. (in prep., St Lucia).

| Measurements | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | Barbados (N=9) | | St. Lucia (N=14) | Barbados (N=10) | | St. Lucia (N=15) |
| Length of forearm | 41.8±0.28 | ns | 41.7±0.17 | 40.5±0.21 | *** | 41.7±0.23 |
| Greatest length of skull | 23.3±0.07 | * | 22.9±0.09 | 23.1±0.09 | ns | 23.1±0.11 |
| Condylobasal length | 21.5±0.08 | ns | 21.4±0.11 | 21.5±0.05 | ns | 21.5±0.11 |
| Zygomatic breadth | 10.3±0.05 | * | 10.0±0.08 | 9.7±0.13 | ns | 9.8±0.07 |
| Postorbital constriction | 4.8±0.06 | ** | 4.6±0.03 | 4.8±0.04 | ns | 4.7±0.04 |
| Mastoid breadth | 10.1±0.04 | ** | 9.8±0.05 | 9.7±0.05 | ns | 9.7±0.05 |
| Length of the maxillary toothrow | 7.8±0.04 | * | 8.0±0.05 | 7.8±0.05 | * | 8.0±0.06 |
| Breadth across upper molars | 5.6±0.08 | ns | 5.7±0.07 | 5.5±0.06 | ns | 5.5±0.04 |

ns –not significant.
*--significant at the $P \leq 0.05$.
** --significant at the $P \leq 0.01$.
*** --significant at the $P \leq 0.001$.

question that now remains is what name should be applied to other populations of the species throughout the Lesser Antilles. Given these results, the validity of *M. p. luciae* must be seriously questioned and clearly calls for contemporary morphometric and molecular analyses of these bats from throughout their geographic range.

Of the sites studied, the insular single-leaf bat appears to reach its highest population level in St Thomas Parish in the area of the Harrison's Cave, Cole's Cave, and Jack in the Box Gully. The structure of this gully system is complex with steep limestone sides, ledges, crevices, small cavities, fallen boulders, and populated with trees from the surrounding moist forest including such trees as Jack in the Box, sandbox, silk cotton, wild clammy cherry, and candlewood (*Cupania americana*). Harrison's Cave serves as a maternity colony site for the species, which underlines the importance of such cave habitats to these bats. Many areas beyond this complex are under cultivation, but there is secondary forest on steep hillsides and introduced fruit trees around the estates and homes. We netted several areas that could be described as foraging areas, such as inside the Grenade Hall forest and along the roads approaching this site. Adjacent to this area is the Grenade Hall Signal Station, which is sited at the edge of a steep forested escarpment. Four bats were caught in nets as they foraged along the road and the edge of the forest. At four sites, we netted single individuals of the insular single-leaf bat—Horse Hill where the bat was netted in thick, dry undercliff forest at the base of Hackleton's Cliff; Porters in an open ornamental garden with freshwater ponds surrounded by thickets of dry lowland scrub that included wild clammy cherries; Friendship Terrace, a dry gully/drainage with secondary forest and gully vegetation, including

two fig trees under which two nets were set; and Martin's Bay, a wet drainage with pools of fresh water, in secondary dry forest surrounded by areas of cultivation that included bananas (three nets in drainage, one net between banana plants).

Grindal (2004) observed hairless, non-flying young just inside the main entrance of Harrison's Cave in April 1998 and 2004. He estimated a total population at this site of 800 to 1000 bats in 1998, and 240 to 300 bats in 2004 (Grindal 2004). The 14 adults of the insular single-leaf bat taken at Harrison's Cave on 13 May 1975 were all females and all but one was lactating and this one individual evinced no gross reproductive activity. Two male neonates also are included in this collection—length of forearm, 18.4, 20.0; weight, 4.0, 5.0. Clearly at this time of year, Harrison's Cave was serving as a maternity roost for this species. Of five females taken on 23 June 2007 in Jack in the Box Gully, 4 were post-lactating and one revealed no gross reproductive activity. Six females were captured between 23-28 July 2008 of which 4 were lactating, 1 was post-lactating, and 1 showed no reproductive activity. These data for female *M. plethodon* on Barbados are not sufficiently complete to understand the entire reproductive cycle (Wilson 1979), but these data suggest a bimodal polyestrous cycle. Alternatively, populations belonging to different maternity colonies may not be synchronous in their reproductive cycles and young are produced over an expanded monoestrous cycle. Five males collected in late June had testes that averaged 2.9 (2-4) in length, whereas eight taken in late July averaged 3.3 (2-4) in length.

A female netted by Grindal (2004) in April weighed 15.5. The 14 females taken on 13 May weighed on average 13.4 (11.0-15.5); 5 taken on 23 June weighed 11.9 (11.5-12.4); and 6 from late July weighed 12.6 (11.9-13.7). The 5 males from late June weighed on average 14.3 (14.0-15.2) and

9 males from late July weighed 14.7 (12.9-16.1). Examining these data, it is interesting to note that the morphometric differences in the species also are reflected in these weight data, with males averaging larger than females.

Four individuals that we examined were missing teeth that appeared to be lost in life. Two individuals (TTU 109965, 109975) were missing both upper canines and the other two (TTU 109977, 109987) were missing the right upper canines. One of the individuals (TTU 109987) missing the right upper canine was also missing the left M1-M2 and m1and m2. TTU 109965 was missing the lower incisors with the remainder of the lower teeth being heavily worn, whereas TTU 109975 retained only left m1 and right p3-m2 in the mandible. Two males exhibited patches of white pelage. One (TTU 19979) from Jack in the Box Gully had a large white patch on its left shoulder. The other (TTU 109964) from Grenade Hall had a white patch on the dorsal surface in the lumbar region and another on the ventral surface near the pelvis.

### *Brachyphylla cavernarum minor* (Fig. 1)

*Specimens examined* (100).—**St. George Parish:** Brighton, 250 ft. [13.117° N, 59. 517° W], 3 (KU); Gun Hill, 153 m [13°08'33.7" N, 59°33'24.0" W], 1 (TTU). **St. James Parish:** Jamestown Park, Holetown, 9 m [13°11'12.9" N, 59°38'5.2" W], 1 (TTU); Spring Head [13°14' N, 59°36' W], 14 (ROM). **St. John Parish:** Codrington College [13°10' N, 59°29' W], 2
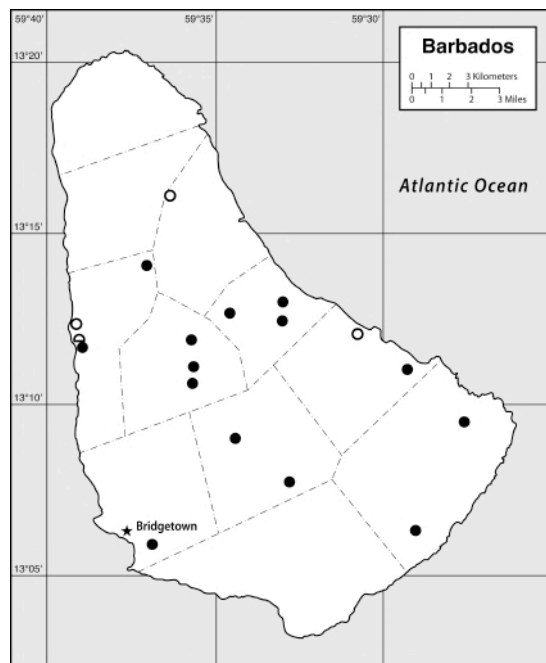


Figure 3. Map of the geographic distribution of *Brachyphylla cavernarum* on Barbados. Symbols represent: closed circles, specimens examined; open circles, other records.

(ROM). **St. Joseph Parish:** Flower Forest, 0.15 km S, 0.6 km W Melvin Hill, 233 m [13°12'12.3" N, 59°34'01.1" W], 4 (TTU); Horse Hill, 251 m [13°12'02.5″ N, 59°32'14.9" W], 1 (TTU); Joe's River, 1.2 km W Bathsheba, 80 m [13°12'40.7" N, 59°32'25.6" W], 7 (TTU). **St. Michael Parish:** Culloden Road, 9 (CM). **St. Philip Parish:** Golden Grove Plantation, 1 (CM); 0.3 km S, 0.5 km W Quarry, 46 m [13°05'33.3" N, 59°28'12.0" W], 2 (TTU). **St. Thomas Parish:** Cole's Cave, 184 m [13°10'48.1" N, 59°34'20.3" W], 21 (5 AMNH, 1 NMNH, 12 KU, 1 TTU, 2 UWI-CH); Jack in the Box Gully, 0.65 km S, 0.2 km E Ayshford, 156 m [13°10'15.9" N, 59°34'39.8" W], 15 (TTU); Welchman Hall Gully, 0.5 km N Welchman Hall, 290 m [13°11'40.1" N, 59°34'35.2" W], 4 (TTU); no specific locality, 1 (NMNH). **Parish Unknown:** no specific locality, 14 (1 BMNH, 2 FMNH, 11 KU).

*Specimens captured/released* (55).—**St. Andrew Parish:** Grenade Hall, 227 m [13°15'58.6" N, 59°35'39.3" W], 6. **St. George Parish:** Gun Hill, 153 m [13°08'33.7" N, 59°33'24.0" W], 4. **St James Parish:** Jamestown Park, Holetown, 9 m [13°11'12.9" N, 59°38'5.2" W], 1; Porters, 0.7 km N Holetown, 3 m [13°11'38.5" N, 59°38'13.3" W], 3. **St. John Parish:** Martin's Bay, 34 m [13°11'47.9" N, 59°30'01.1" W], 1. **St. Philip Parish:** 0.3 km S, 0.5 km W Quarry, 46 m [13°05'33.3" N, 59°28'12.0" W], 4. **St. Thomas Parish:** Jack in the Box Gully, 0.65 km S, 0.2 km E Ayshford, 156 m [13°10'15.9" N, 59°34'39.8" W], 35; Welchman Hall Gully, 0.5 km N Welchman Hall, 290 m [13°11'40.1" N, 59°34'35.2" W], 1.

*Additional records*.—**St. James Parish:** Folkestone Park and Marine Reserve, Holetown (Grindal 2004). **St. Thomas Parish:** Cole's Cave (Buden 1977, Timm and Genoways 2003, Grindal 2004). **Parish Unknown:** no specific locality (Feilden 1890).

*Remarks*.—The Barbadian endemic *Brachyphylla minor* was described as a distinct species by Miller (1913) with a type locality of Coles's Cave in St. Thomas Parish (Fig. 3). This taxon retained its specific status until 1968 when Koopman (1968) reduced it to a subspecies of the widespread *Brachyphylla cavernarum*. Swanepoel and Genoways (1978) reconfirmed the subspecific status of the Barbadian population and documented the morphometric distinctiveness of the taxon. Comparing *B. c. minor* to populations of *B. c. cavernarum* on St. Lucia and St. Vincent (type locality) in the length of forearm and 12 cranial measurements presented by Swanepoel and Genoways (1978), we find that on average males from Barbados are 4.66% and 4.31% smaller, respectively, and females are 5.20% and 4.65% smaller. Swanepoel and Genoways (1978: 39)

found that for at least one of the sexes there was no overlap in five of the 12 cranial measurements between the Barbados and St. Vincent populations of Antillean fruit-eating bat.

Table 1 presents length of forearm and 7 cranial measurements for 22 male and 14 female of *B. c. minor*. Only one measurement—length of forearm—evinced any significant ($P \leq 0.05$) morphometric secondary sexual variation. Females were significantly larger than males in this measurement and averaged larger than males in three others. Males averaged larger in two measurements and the sexes had the same means for two measurements.

The Antillean fruit-eating bat is an obligate cave dweller, living in colonies that usually occupy large, wet caves or similar human structures (Pedersen et al. 2007). However, individuals of *B. cavernarum* have been found only in Cole's Cave and the cave along Culloden Road (LaVal and Schwartz 1974, Grindal 2004). Grindal (2004) described the colonies in Cole's Cave, where two maternity groups were found— one along the left (upstream) passage from the main entrance and one along right (downstream) passage. A third cluster consisting of non-reproductive individuals was observed in the downstream passage. LaVal and Schwartz (1974) observed "large numbers of *Brachyphylla cavernarum* roosting in solution holes and crevices in the ceiling" when visiting Cole's Cave in February 1961. Grindal (2004) estimated the size of the populations of the Antillean fruit-eating bat in Cole's Cave as follows: upstream maternity colony, 1000 to 1200 (April 1998) and 1400 to 1600 (April 2004); downstream maternity colony, 500 to 600 and 1200 to 1440; and downstream non-reproductive colony, 20 to 30 and 80 to 100.

During our visit to the cave, *Brachyphylla cavernarum* were taken in hand nets from "chimney-like" ceiling holes in the left branch of the cave. We were unable to do a count because the holes were deep enough that we could not see the bats to make an estimate.

When the cave along Culloden Road was visited on 3 June 1986, it had been partially destroyed by a construction project. The remainder of the cave opened into the base of a nearly sheer cliff face of about 25 to 30 m in height. The area between the road and the cliff face had been leveled and was covered with limestone rubble. Bats were active inside the cave an hour before sunset and began to emerge just before dark. We placed two nets across the opening of the cave, catching 9 *B. cavernarum* and 31 *Artibeus jamaicensis* in about 45 minutes. We believe that this cave has been entirely destroyed because no evidence of it could be found during subsequent visits to the site.

Two of our larger samples come from Welchman Hall Gully (Fig. 4) and Jack in the Box Gully, both associated with Cole's Cave. Undoubtedly these bats were just emerging from the cave to begin foraging. Our data from Antigua shows that this species is capable of traveling up to 22 kilometers each night (Pedersen et al. 2006), which would put all of Barbados within range of bats from Cole's Cave. We would expect to find this species anywhere on Barbados, with activity concentrated around cultivated fruit trees, such as mangos, papaya, banana, genip, guava, and almond, and around native fruit trees, such as wild clammy cherry, fustic, and hogplum.

In addition to his observations on *Monophyllus*, Grindal (2004) observed two maternity colonies of *B. cavernarum* in Cole's Cave during visits in April 1998 and 2004. He described the juveniles as hairless and non-volant and recorded that 91% of the 70 females captured were lactating. No reproductive activity was observed during a survey in late September/early October 1998 (Grindal 2004). The only pregnant *B. cavernarum* that we have recorded from Barbados was taken on 28 February 1963 in Cole's Cave carrying an embryo with a 14.5 crown-rump length. A female obtained on 15 May 1975 was lactating, but 4 other females taken the following day were all noted as non-reproductive. A female caught on 3 June 1986 and 4 taken on 24-25 June 2007 were lactating. Of 13 females collected between 21 to 26 July 2008, 6 were lactating, 1 was post-lactating, and 6 evinced no gross reproductive activity. Average testes lengths for adult males were recorded as follows: 10 taken on 15-16 May 1975, 4.6 (3-8); 6 on 3-4 June 1986, 5.7 (4.5-7.5); 6 on 23-24 June 2007, 5 (4-7); 7 on 20-25 July 2008, 6 (5-7); and 2 on 21 August 1967, 2.5 and 5. These data give some insights into the reproductive cycle of *B. cavernarum* on Barbados but also raise questions. Breeding in the Antillean fruit-eating bat must occur in January and February with most births occurring in April, which is followed by an extended period of lactation, if all young are born in April as the data would seem to indicate. There does not appear to be any reproduction occurring in September/October. Whether or not a second young is produced at some point during the year is unclear.

Grindal (2004) studied mortality of bats in Cole's Cave. He found 145 dead *B. cavernarum* in the cave, with 143 being juveniles and 2 being adults. Based on population sizes he estimated the mortality rate for the upstream colony at 6.3 to 7.1% and for the downstream colony at 3.1 to 3.8%.

Twenty-seven adult males weighed on average 35.4 (29.1-40.0), whereas 21 adult, non-reproductive or lactating females had a mean

weight of 34.7 (30.5-40.5). A male (CM 83408) from a cave along Culloden Road was missing several lower teeth, including all incisors, right canine, right premolars, and first left premolar. The roots of the premolars are still visible so these teeth were lost in life. The lower left canine is present, but not in its normal position and the upper left canine exhibits far more wear than the right canine.

*Artibeus jamaicensis jamaicensis* (Fig. 1)

*Specimens examined* (184).—**Christ Church Parish:** Chancery Lane [10 mi. E Bridgetown, St. Michael Parish], 6 (AMNH); Graeme Hall Swamp, 0.5 km N St. Lawrence, 2 m [13°04'21.4" N, 59°34'44.1" W], 6 (TTU). **St. Andrew Parish:** 2 mi S, 0.75 mi W Belleplaine [13.221° N, 59.578° W], 6 (KU); cave near Gregg Farm [13°14' N, 59°35' W], 12 (ROM); Grenade Hall, 227 m [13°15'58.6" N, 59°35'39.3" W], 3 (TTU); Long Pond, 0.5 km E Belleplaine, 14 m [13°14'44.2" N, 59°33'32.1" W], 2 (TTU). **St. George Parish:** Brighton, 250 ft. [13.117° N, 59.517° W], 1 (KU); Gun Hill, 153 m [13°08'33.7" N, 59°33'24.0" W], 6 (TTU). **St. James Parish:** *Bellairs Research Station* [13°12' N, 59°39' W], 1 (ROM); Jamestown Park, Holetown, 9 m [13°11'12.9" N, 59°38'5.2" W], 6 (TTU); Lascelles [13°11' N, 59°38' W], 3 (ROM); Porters, 0.7 km N Holetown, 3 m [13°11'38.5" N, 59°38'13.3" W], 6 (TTU); *Saint James Church Yard, Holetown* [13°12' N, 59°38' W], 1 (ROM). **St. John Parish:** Codrington College [13°10' N, 59°29' W], 5 (ROM); Martin's Bay, 34 m [13°11'47.9" N, 59°30'01.1" W], 3 (TTU). **St. Joseph Parish:** Flower Forest, 0.15 km S, 0.6 km W Melvin Hill, 233 m [13°12'12.3" N, 59°34'01.1" W], 6 (TTU); Horse Hill, 251 m [13°12'02.5″ N, 59°32'14.9" W], 6 (TTU); Joe's River, 1.2 km W Bathsheba, 80 m [13°12'40.7" N, 59°32'25.6" W], 2 (TTU). **St. Lucy Parish:**



Figure 4. Photograph of an edge of Welchman Hall Gully, St. Thomas Parish, showing the native vegetation and rocky ledges and outcrops.

Bromefield Plantation, 35 m [13°17'47.9" N, 59°38'28.2" W], 5 (TTU); Cave Hill, 22 m [13°18'10.8" N, 59°35'06.7" W], 8 (6 TTU, 2 UWI-CH). **St. Michael Parish:** cave near Cave Hill [13°08' N, 59°37' W], 1 (ROM); Culloden Road, 31 (CM); no specific locality, 1 (AMNH). **St. Peter Parish:** The Whim, 1 km E Speightstown, 3 m [13°15'08.8″ N, 59°38'12.1″ W], 9 (TTU). **St. Philip Parish:** Golden Grove Plantation, 17 (CM); 0.8 km N Merricks, 22 m [13°08'43.6" N, 59°26'34.2" W], 2 (TTU); Oliver's Cave [13°06' N, 59°27' W], 1 (ROM); 0.3 km S, 0.5 km W Quarry, 46 m [13°05'33.3" N, 59°28'12.0" W], 2 (TTU). **St. Thomas Parish:**

Friendship Terrace, 54 m [13°08'24.4" N, 5936'07.1" W], 2 (TTU); Jack in the Box Gully, 0.65 km S, 0.2 km E Ayshford, 156 m [13°10'15.9" N, 59°34'39.8" W], 15 (3 KU, 12 TTU); 2 mi S Lammings [St. Joseph Parish] [13.154° N, 59.567° W], 2 (KU); Welchman Hall Gully, 0.5 km N Welchman Hall, 290 m [13°11'40.1" N, 59°34'35.2" W], 6 (TTU). **Unknown Parish:** no specific locality, 1 (MCZ).

*Specimens captured/released* (519).—**Christ Church Parish:** Graeme Hall Swamp, 0.5 km N St. Lawrence, 2 m [13°04'21.4" N, 59°34'44.1" W], 52. **St. Andrew Parish:** Grenade Hall, 227 m [13°15'58.6" N, 59°35'39.3" W], 6; Long Pond, 0.5 km E Belleplaine, 14 m [13°14'44.2" N, 59°33'32.1" W], 43. **St. George Parish:** Gun Hill, 153 m [13°08'33.7" N, 59°33'24.0" W], 4. **St James Parish:** Jamestown Park, Holetown, 9 m [13°11'12.9" N, 59°38'05.2" W], 8; Porters, 0.7 km N Holetown, 3 m [13°11'38.5" N, 59°38'13.3" W], 26. **St. John Parish:** Martin's Bay, 34 m [13°11'47.9" N, 59°30'01.1" W], 12. **St. Joseph Parish:** Flower Forest, 0.15 km S, 0.6 km W Melvin Hill, 233 m [13°12'12.3" N, 59°34'01.1" W], 22; Horse Hill, 251 m [13°12'02.5″ N, 59°32'14.9" W], 14; Joe's River, 1.2 km W Bathsheba, 80 m [13°12'40.7" N, 59°32'25.6" W], 26. **St. Lucy Parish:** Bromefield Plantation, 35 m [13°17'47.9" N, 59°38'28.2" W], 4; Cave Hill, 22 m [13°18'10.8" N, 59°35'06.7" W], 3; Paul's Point, 12 m [13°17'59.5" N, 59°34'31.4" W], 3. **St. Peter Parish:** The Whim, 1 km E Speightstown, 3 m [13°15'08.8″ N, 59°38'12.1″ W], 27. **St. Philip Parish:** 0.3 km S, 0.5 km W Quarry, 46 m [13°05'33.3" N, 59°28'12.0" W], 11. **St. Thomas Parish:** Friendship Terrace, 54 m [13°08'24.4" N, 59°36'07.1" W], 78; Jack in the Box Gully, 0.65 km S, 0.2 km E Ayshford, 156 m [13°10'15.9" N, 59°34'39.8" W], 149; Welchman Hall Gully, 0.5 km N Welchman Hall, 290 m [13°11'40.1" N, 59°34'35.2" W], 31.

*Additional records*.—**St. James Parish:** Folkestone Park and Marine Reserve, Holetown (Grindal 2004). **St. Michael Parish:** Carlisle Bay

(Grindal 2004). **St. Thomas Parish:** Jack in the Box Gully (Timm and Genoways 2003).

*Remarks.*—The Jamaican fruit-eating bat was by far the most commonly encountered species during our work on Barbados, although the mastiff bat is probably numerically dominant on the island. We encountered *A. jamaicensis* at every locality where mist nets were deployed to sample the chiropteran fauna of Barbados. Members of the genus *Artibeus* are among the most easily sampled species using mist nets, but it is also our assessment that the population of *A. jamaicensis* on Barbados is large and in excellent condition (Fig. 5).

The Barbados population of *Artibeus* is within a hybrid zone that is the result of multiple species coming into primary/secondary contact in the southern Lesser Antilles (Pumo et al. 1988, 1996, P. Larsen et al. 2010a). Both mitochondrial and nuclear DNA sequence data indicate that at least three species-level lineages of *Artibeus* colonized the Antilles from both northern South America (*A. planirostris* and a now extinct or genetically swamped species) and eastern Middle America (*A. jamaicensis*) during the mid to late Quaternary (see Phillips et al. 1989, 1991, P. Larsen et al. 2007, 2010a). These species subsequently came into contact in the southern Lesser Antilles and began hybridizing, with the present extent of the hybrid zone being from St. Lucia southward to
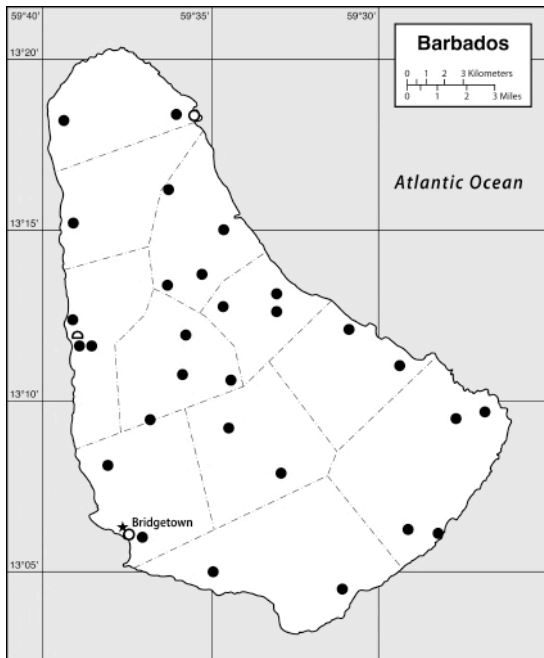


Figure 5. Map of the geographic distribution of *Artibeus jamaicensis* on Barbados. Symbols represent: closed circles, specimens examined; open circles, other records. Localities in italics in the list of specimens examined are not included in the map to prevent crowding of symbols.

Grenada, including Barbados. The available mitochondrial DNA sequence data (based on a representative sample and by using extrapolation) indicate that the Barbados population consists of 92% *A. jamaicensis* and 8% *A. schwartzi* mtDNA haplotypes. The neighboring population of *Artibeus* on St. Lucia consists of approximately 19% *A. jamaicensis* and 81% *A. schwartzi* mtDNA haplotypes and the St. Vincent population consists of 92% *A. schwartzi*, 7% *A. jamaicensis*, and 1% *A. planirostris* haplotypes. The mitochondrial DNA data indicate that the Barbados population is the result of colonization events by both *A. jamaicensis* and *A. schwartzi*. However, because of the potential for cytonuclear discordance resulting from hybridization, documentation of the presence/absence of *A. schwartzi* on Barbados requires additional analyses based on whole genome-scan data (e.g. Amplified Fragment Length Polymorphisms; Vos et al. 1995, P. Larsen et al. 2010a, 2010b). In the absence of genome-scan data the smaller morphological phenotype of the Barbados population (with respect to the St. Vincent population of *A. schwartzi*) indicates that *A. jamaicensis* would be the most appropriate taxon for the *Artibeus* of Barbados.

Table 1 presents data on the morphometrics of 16 male and 22 female *A. jamaicensis* from Barbados. Three measurements revealed significant secondary sexual dimorphism. Females averaged significantly larger than males at the $P \leq 0.05$ level for condylobasal length and at the $P \leq 0.01$ level for greatest length of skull and zygomatic breadth. Females averaged larger than males in three of the remaining measurements—length of forearm, mastoid breadth, and breadth across molars—and for the final two measurements (postorbital breadth and length of maxillary toothrow) the sexes have the same means. Although females from Barbados were significantly larger than males in only three measurements, this is more secondary sexual dimorphism than we have found in the members of this genus from 13 islands throughout the Antilles. On Anguilla, males (Genoways et al. 2007c) were significantly larger than females in breadth across upper molars and on Antigua females (Pedersen et al. 2006) were significantly larger than males in postorbital constriction. On none of the following islands was there significant secondary sexual dimorphism displayed by *Artibeus* in any measurement studied: Jamaica, St. Martin/St. Maarten, Saba, Nevis, Dominica, Bequia, Mustique, Canouan, Carriacou, and Grenada. The significance of this heightened morphological differentiation between the sexes on Barbados is not clear at this point, but this phenomenon should not be ignored given the large population size and limited natural resources and the potential for inter-species hybridization.

Table 3 presents a morphometric comparison of *Artibeus* from Barbados with populations on selected islands in other parts of the West Indies. Clearly *Artibeus* from Barbados are morphologically smaller than the population on the nearby island of St. Vincent in all measurements, whereas individuals in the population on the other nearby island, St. Lucia, are larger in only selected measurements such condylobasal length, zygomatic breadth, and length of maxillary toothrow. Further to the north on Dominica the results are much the same as St. Lucia except mastoid breadth is larger rather length of maxillary toothrow. In contrast, bats from Jamaica were smaller on average than those from Barbados in 5 of the 7 cranial measurements. At the southern end of the Lesser Antilles, *Artibeus* on Grenada (*A. planirostris*; *sensu* P. Larsen et al., 2007) show an unusual pattern where the males closely match the males from Barbados in most measurements, whereas the females from Grenada average smaller than females from Barbados in all measurements. The increased variability observed in the morphological data collected from southern Lesser Antillean populations of *Artibeus* lends support to the hypothesis of inter-specific hybridization across this region (Seehausen 2004, P. Larsen et al. 2010a). Clearly, a more detailed study covering all islands in the West Indies will be needed before we can fully understand the morphometric variation in these bats.

This species was abundant and widespread on Barbados, with the greatest concentrations of animals being found in the gully systems in association with imported fruit trees. These bats eat a wide range of fruits, including those of the non-native species such as mango, almond, banana, breadfruit, genip, guava, and soursop and the native fruits of silk cotton, wild clammy cherry, fustic, hogplum, birch gum, and fiddle wood. Jamaican fruiting-eating bats seek day roosts in a wide variety of situations and displays a relatively high level of light tolerance in many of these roosts, for example, rock ledges and overhangs, rock crevices, tree foliage, and buildings. It is a facultative cave roosting species and we have records from four caves on Barbados—Oliver's Cave, a cave near Gregg Farm, a cave near Cave Hill (Fig. 6), and the cave on Culloden Road. It is interesting that there are no records of *Artibeus* from the larger caves, such as Cole's, Harrison's, or Animal Flower.

It is difficult to determine exactly how many *A. jamaicensis* were captured by Grindal (2004), but the number exceeded 70. He noted that a relatively low proportion of captured females were reproductive during his surveys, but found reproductively active females in both the dry season (mid- to late April) and wet season (late September/early October), but slightly higher activity was during the wet season. Grindal (2004) also captured juvenile males in both the wet (2) and dry (1) seasons.



Figure 6. Photograph of the cave opening in Cave Hill, St. Lucy Parish.

Our collecting activities also provide insight on the reproductive cycle of female Jamaican fruit-eating bats. Of the 11 females taken on 13-14 May 1975, all were pregnant with single embryos that averaged 29.1 (18-30) in crown-rump length, whereas on 5 June 1986 only 2 (9 and 12 crown-rump length) of the 11 females were carrying embryos. In late June (23-26) 2007, 15 of the 17 netted females were pregnant with embryos averaging 30.9 (24-35). One female was of considerable interest because she was carrying twins (30 and 32 in crown-rump length) on 25 June, whereas all other females were carrying single embryos. Of the two non-pregnant females, one was lactating and its uterus was enlarged indicating she recently had given birth and the other female was a non-reproductive subadult. Twenty-seven females were obtained between 21 to 28 July 2008 of which 21 were lactating and 6 were pregnant with single embryos that averaged 35.5 (32-39) in crown-rump length. Finally, we have records of 4 females that evinced no reproductive activity on 19 August 1967. Our collection also includes three neonates, which had the following length of forearm and weight: 40.5, 15.2; 40, 14.6; 34, 12.3. These data indicate a high reproductive rate for female *A. jamaicensis*, with reproduction occurring in April, May, June, July, and late September/early October. Clearly females are producing at least two young per year and twinning would increase this reproductive rate further.

We recorded testes length of male *A. jamaicensis* on the following dates: 12-16 May 1975, 10 males, 7.5 (3-10); 5 June 1986, 6 males, 8.4 (5.5-10); 23-26 June 2007, 13 males, 9.6 (8-13); 16 July 1963, 11, 12; 21-28 July 2008, 28 males, 8.8 (4-12); 19-21 August 1967, 9, 9, 10. When the length of the testes of male *A. jamaicensis* reach 7

Table 3. Length of forearm and 7 cranial measurements for populations of *Artibeus* from selected islands in the West Indies.

| Sex, statistics, sample size | Length of forearm | Greatest length of skull | Condylobasal length | Zygomatic breadth | Postorbital constriction | Mastoid breadth | Length of maxillary toothrow | Breadth across upper molars |
|---|---|---|---|---|---|---|---|---|
| **Barbados** | | | | | | | | |
| Males | | | | | | | | |
| N | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| Mean ± SE | 58.7±0.43 | 28.7±0.11 | 25.2±0.11 | 17.1±0.09 | 7.2±0.05 | 14.9±0.10 | 10.1±0.04 | 12.8±0.07 |
| Range | (55.7-61.2) | (27.7-29.6) | (24.4-26.0) | (16.3-17.7) | (6.6-7.5) | (14.1-15.4) | (9.8-10.3) | (12.2-13.3) |
| Females | | | | | | | | |
| N | 22 | 22 | 22 | 22 | 22 | 22 | 22 | 22 |
| Mean ± SE | 60.0±0.53 | 29.2±0.10 | 25.6±0.10 | 17.5±0.07 | 7.2±0.06 | 15.0±0.08 | 10.1±0.05 | 12.9±0.06 |
| Range | (55.2-62.6) | (28.0-30.1) | (24.7-26.6) | (17.0-18.2) | (6.5-7.5) | (14.2-16.0) | (9.6-10.6) | (12.5-13.6) |
| **Jamaica** (Genoways et al. 2005) | | | | | | | | |
| Males | | | | | | | | |
| N | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Mean ± SE | 59.4±0.36 | 28.2±0.19 | 25.0±0.20 | 16.4±0.16 | 7.2±0.07 | 14.6±0.13 | 9.9±0.09 | 12.1±0.14 |
| Range | (57.8-61.9) | (27.4-29.0) | (24.1-26.1) | (15.9-17.3) | (7.0-7.6) | (14.1-15.4) | (9.7-10.5) | (11.4-12.9) |
| Females | | | | | | | | |
| N | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Mean ± SE | 60.5±0.80 | 28.4±0.23 | 25.2±0.20 | 16.9±0.23 | 7.2±0.04 | 14.8±0.17 | 9.8±0.10 | 12.3±0.13 |
| Range | (57.6-63.7) | (27.1-29.5) | (24.2-26.1) | (15.5-17.7) | (7.1-7.5) | (14.0-15.7) | (9.4-10.4) | (11.8-13.0) |
| **Dominica** (Genoways et al. 2001) | | | | | | | | |
| Males | | | | | | | | |
| N | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Mean ± SE | 59.9±0.48 | 29.2±0.19 | 26.0±0.18 | 17.8±0.12 | 7.1±0.05 | 15.4±0.11 | 10.2±0.10 | 12.9±0.10 |
| Range | 57.7-62.2 | 28.0-30.2 | 25.2-26.7 | 17.3-18.5 | 6.8-7.4 | 14.9-16.0 | 9.8-10.7 | 12.3-13.4 |
| Females | | | | | | | | |
| N | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Mean ± SE | 60.9±0.51 | 29.2±0.17 | 26.1±017 | 17.7±0.16 | 7.2±0.09 | 15.2±0.08 | 10.1±0.06 | 13.0±0.10 |
| Range | 58.5-64.3 | 28.5-30.0 | 25.2-27.0 | 17.0-18.5 | 6.9-7.6 | 14.8-15.6 | 9.7-10.3 | 12.5-13.6 |

Table 3. Length of forearm and 7 cranial measurements for populations of *Artibeus* from selected islands in the West Indies (cont.).

| Sex, statistics, sample size | Length of forearm | Greatest length of skull | Condylobasal length | Zygomatic breadth | Postorbital constriction | Mastoid breadth | Length of maxillary toothrow | Breadth across upper molars |
|---|---|---|---|---|---|---|---|---|
| **St. Lucia** (Kwiecinski et al. in prep., St. Lucia) | | | | | | | | |
| Males | | | | | | | | |
| N | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Mean ± SE | 60.3±0.60 | 29.3±0.22 | 26.2±0.23 | 17.4±0.13 | 7.3±0.08 | 15.1±0.15 | 10.5±0.10 | 12.8±0.08 |
| Range | (57.7-64.0) | (28.3-30.2) | (25.0-27.1) | (16.8-18.0) | (6.9-7.7) | (14.3-15.8) | (10.1-11.0) | (12.3-13.2) |
| Females | | | | | | | | |
| N | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 |
| Mean ± SE | 60.4±0.47 | 29.0±0.13 | 26.3±0.16 | 17.3±0.14 | 7.2±0.07 | 15.1±0.09 | 10.5±0.05 | 12.9±0.10 |
| Range | (56.3-62.9) | (28.4-29.8) | (25.5-27.9) | (16.3-18.3) | (6.8-7.6) | (14.5-15.6) | (10.1-10.7) | (12.4-13.8) |
| **St. Vincent** (Kwiecinski et al. in prep., St. Vincent) | | | | | | | | |
| Males | | | | | | | | |
| N | 17 | 21 | 21 | 21 | 21 | 21 | 21 | 21 |
| Mean ± SE | 64.1±0.43 | 30.7±0.16 | 27.4±0.13 | 19.3±0.14 | 7.3±0.04 | 16.3±0.10 | 11.2±0.06 | 14.1±0.10 |
| Range | (60.5-67.4) | (28.5-31.6) | (25.7-28.3) | (17.4-20.2) | (7.0-7.7) | (15.1-17.0) | (10.6-11.7) | (12.9-14.8) |
| Females | | | | | | | | |
| N | 25 | 31 | 31 | 31 | 31 | 31 | 31 | 31 |
| Mean ± SE | 64.7±0.59 | 30.6±0.14 | 27.4±0.13 | 19.1±0.15 | 7.4±0.03 | 16.0±0.09 | 11.1±0.07 | 14.0±0.09 |
| Range | (59.8-69.3) | (28.7-31.7) | (25.7-28.3) | (17.4-20.2) | (6.9-7.7) | (14.5-16.9) | (10.1-11.7) | (12.9-14.8) |
| **Grenada** (Genoways et al. 1998) | | | | | | | | |
| Males | | | | | | | | |
| N | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Mean ± SE | 58.0±0.62 | 28.2±0.19 | 25.3±0.17 | 17.5±0.14 | 7.1±0.07 | 15.0±0.11 | 10.1±0.08 | 12.8±0.11 |
| Range | (55.7-61.8) | (27.5-29.4) | (24.9-26.0) | (16.6-18.0) | (6.6-7.3) | (14.4-15.5) | (9.8-10.6) | (12.2-13.3) |
| Females | | | | | | | | |
| N | 32 | 32 | 32 | 32 | 32 | 32 | 32 | 32 |
| Mean ± SE | 58.1±0.27 | 28.2±0.10 | 25.0±0.09 | 17.2±0.08 | 6.9±0.03 | 15.0±08 | 10.0±0.05 | 12.6±0.06 |
| Range | (55.7-61.3) | (26.8-29.2) | (23.8-25.9) | (16.5-18.1) | (6.7-7.4) | (13.7-15.9) | (9.4-10.3) | (11.8-13.2) |

or 8, they are in full breeding condition; therefore, at least from mid-May until mid-August there are always males in the population that are capable of mating.

The mean weight of 53 adult males from Barbados was 38.4 (30.5-45.6). The mean weight of 22 lactating females was 40.2 (34.8-45.7), whereas 32 pregnant females had an average weight of 49.0 (42.0-60.1). The female that was carrying the twin embryos weighed 55.6 and the heaviest female was taken on 26 June 2007 carrying a single embryo that measured 33 in crown-rump length. Our records also indicate that the female carrying the largest embryo (39 crown-rump length) weighed 55.7.

Examination of the dentition of 31 specimens of *Artibeus* from Barbados revealed that all lacked both upper M3s and that all, but one, possessed both lower m3s. A female from the cave along Culloden Road (CM 83192) was missing the right lower m3. The presence/absence of the upper M3 is considered to be a species-level characteristic in some populations of *Artibeus*, whereas this pattern of variation in the lower m3 is believed to be a polymorphism (Genoways et al. 2010). The absence of the upper M3s allies the Barbados population of *Artibeus* with the *jamaicensis-schwartzi* complex and does not indicate any influence of *Artibeus planirostris* from the south on Grenada and Trinidad, where the upper M3 is present in 89% and 100%, respectively, of the populations (Genoways et al. 2010). Populations of *A. schwartzi* on Bequia, Canouan, and Union islands match the population from Barbados in 100% absence of M3, whereas the M3 is present in a small percentage of members of populations on Carriacou (5.3%), Mustique (9.1%), and St. Vincent (12.9%), indicating a potential genetic influence from *A. planirostris.*

The individuals from the cave on Culloden Road exhibit a high incidence of dental wear and loss, most notably in the mandible. Of the 18 specimens examined, 11 display highly worn teeth. In an extreme case (CM 83188), all of the lower teeth are worn to, or near, the mandible, whereas the upper dentition shows only limited wear but nothing approaching that observed in the lower teeth. At least 6 other individuals exhibit heavy wear to the cusps of the lower teeth to the point that most or all cusps are worn away. Four individuals are missing one or more of the lower incisors. A female from near Belleplaine (KU 110218) is missing the crown of the lower left m2, but two roots are still visible in the jaw.

*Myotis nyctor* (Fig. 1)

*Specimens examined* (39).—**St. Andrew Parish:** Grenade Hall, 227 m [13°15'58.6" N, 59°35'39.3" W], 2 (TTU). **St. George Parish:** Gun Hill, 153 m [13°08'33.7" N, 59°33'24.0" W], 1 (TTU). **St. John Parish:** Codrington College [13°10' N, 59°29' W], 1 (ROM). **St. Joseph Parish:** Flower Forest, 0.15 km S, 0.6 km W Melvin Hill, 233 m [13°12'12.3" N, 59°34'01.1" W], 1 (TTU); Horse Hill, 251 m [13°12'02.5″ N, 59°32'14.9" W], 3 (TTU); Joe's River, 1.2 km W Bathsheba, 80 m [13°12'40.7" N, 59°32'25.6" W], 12 (TTU). **St. Thomas Parish:** Cole's Cave, 8 (1 AMNH; 7 KU); Friendship Terrace, 54 m [13°08'24.4" N, 59°36'07.1" W], 4 (3 TTU, 1 UWI-CH); Welchman Hall Gully, 0.5 km N Welchman Hall, 290 m [13°11'40.1" N, 59°34'35.2" W], 7 (TTU).

*Additional records.*—**St. Thomas Parish:** Cole's Cave (LaVal and Schwartz 1974, Timm and Genoways 2003, Grindal 2004); Harrison's Cave (Grindal 2004).

*Remarks.*—This species was originally described as *Myotis martiniquensis nyctor* by LaVal and Schwartz (1974) based on 8 specimens from Cole's Cave, St. Thomas Parish, Barbados (Fig. 7). Only recently have R. Larsen et al. (2012) presented morphological and molecular data demonstrating that this is a distinct species representing a third Lesser Antillean endemic *Myotis* to be known under the name, *Myotis nyctor*. Overall, structure in the nuclear,
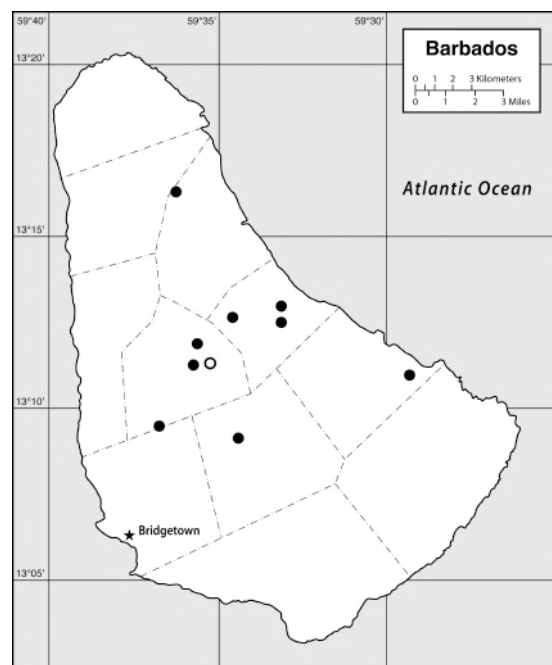


Figure 7. Map of the geographic distribution of *Myotis nyctor* on Barbados. Symbols represent: closed circles, specimens examined; open circles, other records.

mitochondrial, and morphological datasets reveal that *M. nyctor* is on a separate and unique evolutionary trajectory from *M. martiniquensis* and *M. dominicensis* and has been for quite some time.

Mitochondrial cytochrome-*b* sequence indicates specimens of *M. nyctor* are paraphyletic with respect to *M. martiniquensis*. The genetic distance separating *nyctor* from *martiniquensis* is approximately 9.0%, a value typical of (or greater than) species-level genetic distances within *Myotis*. Additionally, nuclear AFLP data indicate *M. nyctor* has a distinct nuclear genome from *M. martiniquensis* (see R. Larsen et al. 2012). Although *Myotis nyctor* is the only known species of *Myotis* on Barbados, a close genetic relationship between a specimen from Grenada (Genoways et al., 1998) and *M. nyctor* from Barbados (0.4% genetic distance) was recovered and measurements of this specimen are below the range of *M. nyctor* from Barbados (R. Larsen et al. 2012). Additional voucher specimens with genetic data are needed to test for a close genetic relationship between *Myotis* from Barbados and Grenada.

Compared to other Lesser Antillean *Myotis* morphologically, *M. nyctor* is almost uniformly larger externally and smaller cranially than *M. martiniquensis*. *Myotis nyctor* is significantly larger than *M. martiniquensis* in total length, length of tail vertebrae, and length of tibia, yet significantly smaller than *M. martiniquensis* in length of forearm, postorbital constriction, mastoid breadth, and breadth across the upper molars. These results match those of LaVal and Schwartz (1974) for length of forearm and breadth across the upper molars. Additionally, *M. nyctor* and *M. dominicensis* (endemic to Dominica and Guadeloupe) do not overlap in 9 of 13 cranial and external measurements (Table 3), with *M. dominicensis* being smaller in all nine measurements. They overlap in range of measurements in length of forearm, length of hind foot, postorbital constriction, and breadth across the upper molars. *Myotis dominicensis* does not overlap the range of measurements for length of tibia to length of forearm ratio in *M. nyctor*, but does have smaller average values for all 13 measurements and the length of tibia to length of forearm ratio (R. Larsen et al. 2012).

Table 1 presents values for length of forearm and 7 cranial measurements for samples of 10 males and 11 females. No secondary sexual variation was detected in these measurements. Males averaged larger than females in greatest length of skull and condylobasal length and females were larger in breadth across upper molars, however, in each case the differences were only 0.1. For the other 5 measurements, the means for the sexes are equal.

Prior to our work on Barbados, *M. nyctor* was reported only from specimens from Cole's Cave (LaVal and Schwartz 1974), although Grindal (2004) thought that it could have been present in a former colony "approximately 30 m in from the entrance of the north inlet passage of Harrison's Cave in October 1998." Our records of *M. nyctor* from 2007 and 2008 are concentrated in the central highlands and northeastern portions of the island and were associated with caves, gullies, and rocky outcrops in combination with stands of larger trees.

LaVal and Schwartz (1974) netted the type series at the mouth of Cole's Cave after 2000 hrs on 16 February 1961 (Fig. 8). We observed these bats as they foraged on insects among the trees in both Jack in the Box Gully and Welchman Hall Gully. Our experience, unlike that of LaVal and Schwartz (1974), was that this bat was active early, between 1730 and 1800, when dusk was about 1900. Our largest sample was netted along Joe's River in St. Joseph Parish at a location where the river was not flowing, but there were numerous freshwater pools along the riverbed. The area was densely covered in short (4-6 m) thorny trees, dominated by members of the genus *Acacia*. Nearby, the northern end of Hackleton's Cliff easily provides sufficient rock crevices and small caves that *Myotis* uses for day roosts. The bats were netted over the small freshwater pools as they came to drink and foraging on small insects. The Horse Hill site, at a higher elevation and nearer to Hackleton's Cliff, was located in a typical undercliff forest.



Figure 8. Photograph of the gully leading up to the entrance of Cole's Cave, St. Thomas Parish. The opening of the cave can be seen near the center of the picture.

The northern-most site where we captured this species was Grenade Hall, which is situated at the crest of an escarpment covered in a mahogany forest. Two individuals of *M. nyctor* were netted in flyways at the edge of this forest. Flower Forest is located in western St. Joseph Parish at the edge of the Scotland District at the site of the former

Richmond sugar plantation. The immediate environs of the visitors' center are flower gardens, with plantings of non-native species, including a large collection of palms dominated by a group of Royal Palms and dense stands of bamboo. Our specimen was netted in a canopied flyway under a large stand of bamboo. The specimen (ROM 74379) from Codrington College in St. John Parish provides some interesting data about *M. nyctor* because it was reportedly taken on 15 May 1975 from the attic of one of the buildings at the college. If this species is capable of using human habitations as day roosts as do many temperate species of *Myotis*, it will have a much broader range of day roosts available than previously thought. The two southern-most sites where we captured *M. nyctor* were Friendship Terrace and Gun Hill. The four captures at Friendship Terrace were taken at the confluence of two drainage culverts under a bridge for Highway H2A. Only individuals of *Myotis* were seen using the culvert contributing to the Friendship Terrace gully before sunset and seemingly coming from forested areas because no roosting individuals were observed in the culverts. We subsequently observed *Myotis* utilizing the entire culvert system throughout the time of our netting. The individual from Gun Hill was taken in nets set across a road under a row of mature mahogany trees near the base of the hill. The escarpment of Gun Hill is the highest point in central Barbados and is covered in short, dense secondary forest encircled entirely by urban development.

Of the 21 females captured by Grindal (2004), some were reproductively active in both the dry (April) and wet season (late September/early October) sampling periods. Unfortunately, Grindal does not give specific numbers of individuals exhibiting each category of reproductive activity—pregnant, lactating, and post-lactating—but indicates that there was slightly more activity in the dry season than in the wet season. Grindal (2004) did capture a flying juvenile with a length of forearm of 35.6 during the wet season. Our reproductive data from June and July helps fill part of the gap in Grindal's sampling periods. All five of the females captured on 24 June 2007 were lactating. Of the 7 females netted on 23 July 2008, 5 evinced no gross reproductive activity, 1 was lactating, and 1 carried an embryo measuring 8 in crown-rump length. Three females were taken on 27 July 2008 of which 2 were non-reproductive and 1 carried an embryo measuring 14 in crown-rump length. A male from 15 May 1975 had a testes length of 3 and one from 24 June 2007 had a testes length of 4. Eleven males netted between 23 to 25 June 2008 had a mean testes length of 2.7 (1-4). Although the reproductive data for this species are still incomplete, its pattern, with reproductively active females in April, June, July,

and late September/early October, may represent an aseasonal breeding cycle (Wilson, 1979).

Fifteen adult males capture in June and July weighed on average 4.1 (3.6-4.5) and thirteen non-reproductive and lactating females weighed on average 4.1 (3.6-4.6). Two pregnant females taken on 23 July and 25 July weighed 4.9 and 5.6, respectively. Grindal (2004) reported a mean weigh of 5.3 (4.25-6.5) for 11 females of unknown reproductive status.

***Molossus molossus molossus*** (Fig. 1)

*Specimens examined* (66).—**Christ Church Parish:** Graeme Hall Swamp, 0.5 km N St. Lawrence, 2 m [13°04'21.4" N, 59°34'44.1" W], 8 (TTU); Hastings, 2 (AMNH). **St. Andrew Parish:** Grenade Hall, 227 m [13°15'58.6"N, 59°35'39.3" W], 1 (TTU); Long Pond, 0.5 km E Belleplaine, 14 m [13°14'44.2" N, 59°33'32.1" W], 7 (6 TTU, 1 UWI-CH). **St. James Parish:** *Bellairs Research Station* [13°12' N, 59°39' W], 1 (ROM); Jamestown Park, Holetown, 9 m [13°11'12.9" N, 59°38'5.2" W], 2 (TTU); *Saint James Church, Holetown* [13°12' N, 59°38' W], 15 (ROM); *Saint James Church Yard, Holetown* [13°12' N, 59°38' W], 8 (ROM). **St. John Parish:** Codrington College [13°10' N, 59°29' W], 1 (ROM). **St. Lucy Parish:** Bromefield Plantation, 35 m [13°17'47.9" N, 59°38'28.2" W], 7 (TTU); Paul's Point, 12 m [13°17'59.5" N, 59°34'31.4" W], 3 (TTU). **St. Thomas Parish:** Welchman Hall Gully, 0.5 km N Welchman Hall, 290 m [13°11'40.1" N, 59°34'35.2" W], 10 (TTU). Parish Unknown: no specific locality, 1 (MCZ).

*Specimens captured/released* (73).— **Christ Church Parish:** Graeme Hall Swamp, 0.5 km N St. Lawrence, 2 m [13°04'21.4" N, 59°34'44.1" W], 28. **St. James Parish:** Jamestown Park, Holetown, 9 m [13°11'12.9" N, 59°38'5.2" W], 3; Porters, 0.7 km N Holetown, 3 m [13°11'38.5" N, 59°38'13.3" W], 35. **St. Lucy Parish:** Bromefield Plantation, 35 m [13°17'47.9" N, 59°38'28.2" W], 7.

*Additional records.*—**St. James Parish:** Folkestone Park and Marine Reserve, Holetown (Grindal 2004). **Parish Unknown:** no specific locality (Feilden 1890).

*Remarks.*—A number of scientific names have been applied to this 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 1 provides the length of forearm and 7 cranial measurements of 14 males and 20 females from Barbados. Males on average were larger than females in length of forearm, which was the only measurement that did not differ significantly between the sexes. Males were significantly larger

than females at the $P \leq 0.01$ level for three measurements—postorbital constriction, length of maxillary toothrow, and breadth across upper molars. Males were significantly larger than females at the $P \leq 0.001$ level for the remaining four cranial measurements. Comparing these measurements to samples from Grenada (Genoways et al. 1998), Dominica (Genoways et al. 2001), and the Grenadines (Genoways et al. 2010), the sample from Barbados matches closely in means and ranges the samples from Dominica and Grenada. However, comparison with the samples from Grenadines reveals that individuals from the Grenadines tend to be smaller than individuals from any of the other 3 samples. Until thorough morphological analyses of geographic variation of this species from throughout the Antilles are undertaken, we will not be able to interpret the meaning of this pattern of geographic variation.

These insectivorous bats were observed at each site (Fig. 9) and were readily identified by their rapid and darting flight as they hawked their prey in the twilight. This may be the most abundant species of bat on the island of Barbados, but our sampling with mist nets clearly underestimates their populations because we observe many more at altitudes above the reach of our nets (R. Larsen et al. 2007). Our largest collections came from Graeme Hall Swamp (Fig. 10) and Porters where these bats were netted as they hawked insects or came to drink at open ponds. The specimens from Long Pond were taken under some short trees where a road crossed a small stream. At Welchman Hall Gully these bats were flying under the native trees canopy in this park-like setting. The Bromefield Plantation net site was located in the gully south of the plantation house. The gully was moist with standing pools of freshwater, and mixed gully vegetation and secondary forest, including manchineel. Our specimens of *Molossus* were taken in a net that was set near a highway and in a large open area under a mango tree. At Paul's Point, nets were set near two livestock ponds in open pasture with a view of the Atlantic Ocean.

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. We noted this species to be especially abundant in Holetown where they were associated with buildings that were empty or under renovation, in particular Saint James Church. Before human settlement, mastiff bats would have found day roosts in holes in trees and rock crevices and were probably much less common than at present.

Grindal (2004) recorded that 4 adult females taken in mid-April were non-pregnant; however, 2 juvenile females also were taken at this time. Thirteen females that we examined in this study

taken between 12 to 16 May 1975 were all pregnant with embryos that had a mean crown-rump length of 19.5 (13-22.5). Examination of 2 females from 9 June 1912 revealed no reproductive activity. Of 10 females netted on 24 to 25 June 2007, 2 evinced no reproductive activity, 2 were post-lactating, and the remaining 6 females were pregnant with embryos measuring a mean crown-rump length of 14.5 (2-24). Four of the 17 females that we obtained between 22 to 28 July 2008 were lactating but also carried small embryos with crown-rump lengths of 5, 5, 9, and 10. Another female was carrying an embryo with crown-rump length of 7, but was not lactating. Seven of the remaining 12 females were lactating and the other 5 evinced no gross reproductive activity.
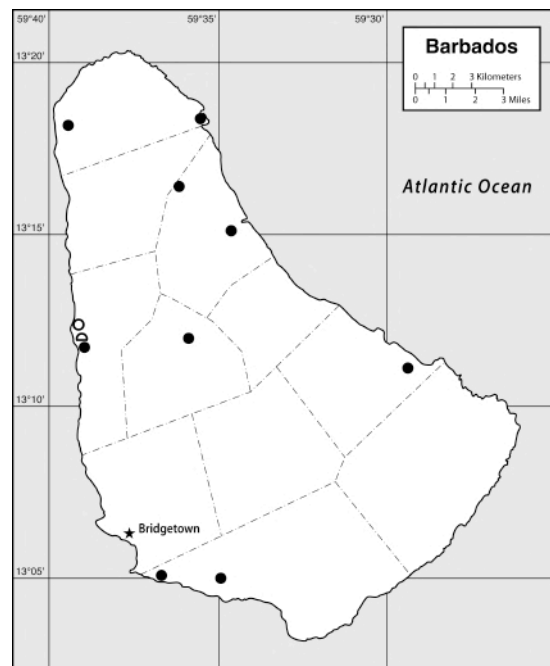


Figure 9. Map of the geographic distribution of *Molossus molossus* on Barbados. Symbols represent: closed circles, specimens examined; open circles, other records. Localities in italics in the list of specimens examined are not included in the map to prevent crowding of symbols.

Genoways et al. (2005) found a lack of synchrony displayed by female *Molossus molossus* on Jamaica, "with some individuals at various stages of reproduction and others reproductively inactive during the same period, a reproductive pattern of aseasonal polyestry or continuous breeding is suggested" (Wilson 1979). At the end of May and early June in the Grenadine islands, we found (Genoways et al. 2010) "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." Our female reproductive data from Barbados, although

limited, seems to more closely resemble that observed on Jamaica, with females at various stages of reproduction from mid-April until the end of July. The May sample indicates a high level of synchronicity of pregnancy, but this is not true of our other samples in our study. Our data do not indicate a reproductive pattern that differs from aseasonal polyestry or continuous breeding.



Figure 10. Photograph of one of the brackish ponds in Graeme Hall Swamp, Christ Church Parish.

Of note, 4 females in the July sample that were lactating also were carrying small embryos, thereby indicating to us that a postpartum estrus and breeding had occurred in these individuals. This characteristic along with continuous breeding gives this species an extremely high potential fecundity rate. Therefore, it should be no surprise that *Molossus molossus* is probably the most abundant species on most, if not all, the islands in the Caribbean. This species is especially suited to succeed in an ecosystem controlled by disturbances, such as hurricanes, earthquakes, volcanoes, changing sea levels, and human impacts. Even if large numbers of individuals are killed by these disasters, populations can respond quickly and re-populate the island.

Reproductive data (average testes length) for male *Molossus* on Barbados are available from three months as follows: 14 to 16 May 1975, (10 individuals) 5.1 (3-9); 24 to 26 June 2007, (3) 2, 2.5, 4; 22 to 28 July 2008, (4) 2, 3, 3, 4. Grindal (2004) found the weight of 4 females taken in April to average 11.4 (10.0-13.0) and 2 juvenile females taken at this time to weigh 11.0, 12.0. Thirteen non-reproductive or lactating females weighed an average of 9.8 (8.7-11.6), whereas 21 pregnant females weighed on average 11.8 (9.7-14.5). The mean weight of 17 adult male mastiff bats was 11.4 (10.0-13.0).

An individual from Graeme Hall Swamp exhibited extensive depigmentation of its flight membranes. Four other specimens displayed areas of white pelage—2 individuals from Paul's Point had a white spot on their muzzles and 2 others

from Long Pond and Bromefield Plantation exhibited white fur on the lower abdomen.

**Species Excluded from Fauna**
***Eptesicus fuscus***
*Specimen examined* (1).—Parish unknown: no specific locality, 1 (BMNH).

This was the first species of bat to be reported from Barbados when Dobson (1878: 194) listed a specimen of *Vesperugo serotinus* var β (*Vesperus fuscus*) from the island. The only additional information that Dobson (1878) presented for the specimen was that it was an adult prepared as a skin. The individual (BMNH 1975.568) that was the basis of this report is still available for study in the British Museum (Natural History). It consists of a "live" mount with the wings spread and at least a portion of the cranium in the mount. The cranium could not be removed without destroying most of the specimen. The only measurements that could be obtained from the individual were length of ear (dry), 13.0, and length of forearm, approximately 47.1.

There are two known populations of *Eptesicus* in the Lesser Antilles—*E. guadeloupensis* (Genoways and Baker, 1975, Baker et al. 1978) from Guadeloupe and *Eptesicus fuscus* (Hill and Evans 1985) from Dominica. Hill and Evans (1985) believed that the population on Dominica was most closely related to that on Puerto Rico and tentatively assigned the specimens to *E. f. wetmorei*. The length of the ears of the Barbados specimen clearly allies it with *E. fuscus* and not the large-eared species, *E. guadeloupensis*.

No additional specimens of this big brown bat have been obtained over the years, including during our work and Grindal's (2004) study. Koopman (1968) postulated that the specimen was an accidental occurrence, however, other authors (Baker and Genoways 1978; Hill and Evans 1985) believed that the species should be excluded from the fauna of the island. According to Hill and Evans (1985), the specimen in question was obtained from a dealer by the name of Cuming and he may have mislabeled the specimen or alternatively, he may have received the specimen from Barbados and assumed that the island was its place of origin. Indeed, in the mid 1800s, Barbados was a busy center of commerce, with ships arriving from throughout the New World.

Although it is impossible to prove that this species is not present on the island, we believe that preponderance of the evidence available at this time is that *E. fuscus* is not part of the fauna of Barbados. This conclusion will remain open to review whenever field research concerning bats is conducted on Barbados.

**Discussion**
Presently, the Barbadian chiropteran fauna

includes representatives of four families — Noctilionidae, Phyllostomidae, Vespertilionidae, and Molossidae—including 1 piscivore (*Noctilio leporinus*), 1 omnivore (*Brachyphylla cavern-arum*), 1 pollenivore/nectarivore (*Monophyllus plethodon*), 1 frugivore (*Artibeus jamaicensis*), and 2 insectivorous species (*Myotis nyctor* and *Molossus molossus*). This chiropteran fauna of 6 species is much smaller than those on the four neighboring Lesser Antillean islands to the west and north (Table 4)—Dominica (12), Martinique (11), St. Lucia (9), and St. Vincent (12). We believe that this is primarily the result of two factors—geological age and geographic isolation.

The geological history of the Caribbean region is complex and is still not fully understood (Hedges 2001). The Lesser Antillean arc of islands is relatively old having appeared by the Eocene (50 mya); however, it is not possible to trace the history of individual islands and when they were emergent above sea level. The Lesser Antillean islands are situated along the eastern and leading margin of the Caribbean plate. These islands are of volcanic origin, with the newer deposits burying the old; however, there are exposures on the St. Lucia and Martinique that date as old as the Oligocene/Miocene (20 mya) (Wadge 1994). As discussed previously, the island of Barbados is much younger being brought to the ocean surface by tectonic forces that began acting below the Barbados Ridge about a million years ago (Speed and Keller 1993, Speed 1994). The steady rise of the island of Barbados above sea level began about 700,000 years ago, making it the youngest island in the region.

Barbados is geographically isolated from other islands in the Lesser Antilles—Barbados to Dominica, 270 km; Martinique, 175 km; St. Lucia, 142 km; and St. Vincent, 146 km. These distances are considerably greater than the distances between these same islands—Dominica to Martinique, 40 km; Martinique to St. Lucia, 34 km; St. Lucia to St. Vincent, 42 km. The distances to be overcome by bats by over water dispersal to reach Barbados is about 4 times the distances between the islands in the main Lesser Antillean chain and is against the prevailing winds. This isolation is an imposing filter that would restrict immigration of bats and restrict gene flow between populations on Barbados and the other islands.

What are the characteristics of the species of bats that have overcome the obstacles and reached Barbados? The greater fishing bat, *N. leporinus*, is a large, strong flying species that regularly feeds over estuaries and coastal areas. The species is present on most of the islands in the West Indies and the circum-Caribbean mainland. The mastiff bat, *M. molossus*, is a small, but fast flying species that feeds on insects as they ascend to high altitudes in the evening. The history and relationships of *A. jamaicensis* are unique and complicated, being a member of a complex of three species—*A. jamaicensis*, *A. planirostris,* and *A. schwartzi*—with *A. jamaicensis* occurring in the Greater Antilles and the Lesser Antilles as far south as Martinique and Barbados. The members of this complex are large, strong-flying, fruit-eating species. Two species, *M. plethodon* and *B. cavernarum*, both are strong fliers and both feed on nectar, flowers, and small fruits. These two species occur from St. Vincent northward to Puerto Rico. Finally, *M. nyctor* is the most enigmatic of the species to reach Barbados (R. Larsen et al. 2012). It is a small species with a fluttering flight that pursues insects in rather cluttered habitats. Its distribution is not well understood. The common characteristic among these species with the exception of *M. nyctor* is strong flight ability, particularly as indicated by their broad geographic distribution and their ability to overcome large water gaps within this distribution.

Several species of bat are notable by their absence from Barbados. Table 4 lists 13 species that occur on islands immediately to the west and north but have not been recorded on Barbados. Four of these would head our list of "missing" species on Barbados—*Pteronotus davyi, Ardops nichollsi, Sturnira lilium,* and *Tadarida brasiliensis*. The first species, *P. davyii*, is a swift flying insectivorous species, which reached the Lesser Antilles from South America and is known as far north as Marie Galante. As a Lesser Antillean endemic, *A. nichollsi*, is a fruit-eating species with a distribution similar to *M. plethodon*, except it is not known from Puerto Rico. The yellow-shouldered bat, *Sturnira lilium*, invaded the Lesser Antilles from South America (Baker and Genoways, 1978), reaching as far north as Dominica but is then replaced by a similar endemic species, *Sturnira thomasi*, on Guadeloupe and Montserrat. For *S. lilium* to reach the Lesser Antilles, it over came a greater distance, if coming from the South American mainland (225 km), or about the same distance, if coming from Trinidad (147 km), as from St. Vincent or St. Lucia to Barbados. The Brazilian free-tailed bat, *T. brasiliensis*, shares many characteristics with *M. molossus* as a high, fast-flying insectivore and occupies a larger geographic area in the United States and through much of the Neotropics.

Table 4. Composition of the chiropteran fauna of five islands in the southern Lesser Antilles. Asterisk (*) indicates the potential for hybridization between *A. jamaicensis* and *A. schwartzi* (P. Larsen et al. 2010a).

| Species | Barbados (6) Present study | Dominica (12) Genoways et al. 2001 | Martinique (11) Issartel et al. 2008 | St. Lucia (9) Kwiecinski et al. in prep., St. Lucia | St Vincent (12) Kwiecinski et al. in prep., St Vincent |
|---|---|---|---|---|---|
| *Pteronotus davyi* | - | + | + | + | - |
| *Pteronotus rubiginosus* | - | - | - | - | + |
| *Noctilio leporinus* | + | + | + | + | + |
| *Micronycteris buriri* | - | - | - | - | + |
| *Brachyphylla cavernarum* | + | + | + | + | + |
| *Monophyllus plethodon* | + | + | + | + | + |
| *Glossophaga longirostris* | - | - | - | - | + |
| *Artibeus jamaicensis** | + | + | + | - | - |
| *Artibeus lituratus* | - | - | - | - | + |
| *Artibeus schwartzi** | - | - | - | + | + |
| *Ardops nichollsi* | - | + | + | + | + |
| *Sturnira lilium* | - | + | + | + | + |
| *Natalus stramineus* | - | + | + | - | - |
| *Eptesicus fuscus* | - | + | - | - | - |
| *Myotis dominicensis* | - | + | - | - | - |
| *Myotis martiniquensis* | - | - | + | - | - |
| *Myotis nyctor* | + | - | - | - | - |
| *Tadarida brasiliensis* | - | + | + | + | + |
| *Molossus molossus* | + | + | + | + | + |

We are unable to discern any characteristics that distinguish our 4 absentee species from the 6 species that have arrived on Barbados. The absentee species all have demonstrated ability to overcome water gaps such as the one separating Barbados from its neighboring islands; the ability to colonize and establish populations on multiple islands in the Lesser Antilles; and there is nothing unique about their food or foraging habits. Based on these considerations, it is our working hypothesis that the relatively young geological age of Barbados and the distance separating Barbados from neighboring islands have dually contributed to the small chiropteran fauna of Barbados. In fact, it is our contention that this is not a fully developed fauna and as such we designate it as the "Barbados subfauna" of the Lesser Antillean chiropteran fauna. We do see some of the effects of the geographic isolation of Barbados as well, especially in *Brachyphylla cavernarum* in which animals from the island are about 5% smaller than those of the main islands of the adjacent Lesser Antilles. However, until we understand the relationship of Barbadian populations of *M. plethodon* and *M. nyctor* to those on other islands, we will not be able to give a full assessment of the impact of the geographic isolation of Barbados.

Our work indicates that populations of the 6 species of bats on Barbados are in good condition in all cases, but only for *Artibeus jamaicensis* and *Molossus molossus* are the populations large enough to not be of ongoing concern. The conservation of these 6 species of bats is not only important to maintain their contribution to the biodiversity of Barbados, but because they are linked to the maintenance of many other aspects of the island's fauna and flora. The maintenance of the chiropteran fauna can best be served by three management actions—preservation of caves and associated gullies, forests, and hydrological systems.

The cave and gully systems are a national treasure and their value goes far beyond their significance to the bat fauna of the island on Barbados. 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. On Barbados, 3 species of bats (*B. cavernarum*, *M. plethodon*, and *M. nyctor*) are obligate cave roosting species and two others (*N. leporinus* and *A. jamaicensis*) will

roost in rock features commonly found in gullies, if caves are not available. Caves and presumably gullies provide critical refugia in times of natural disaster such as hurricanes (Gannon and Willig, 1994; Pedersen et al., 1996), and these roosts are one of the most critical limiting factors during reproduction (Pedersen et al. 2003, 2005, 2006, Genoways et al. 2007a, 2007b, 2007c). Our observations show that Cole's, Harrison's, and Animal Flower caves have been heavily impacted by human activities. Given that these caves contain the only known maternity colonies for *B. cavernarum*, *M. plethodon*, and *M. nyctor*, their successful management in the future is critical to bat conservation efforts on Barbados.

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 (Jones et al. 2009). Therefore, the preservation of native habitat such as those found in the undercliff forest associated with Hackleton's Cliff, or those confined to the various gully systems on Barbados will serve to conserve both trees and bats.

There are approximately 650 species of plants found in the wild on Barbados (Carrington 2007) and many of these are often pollinated by 3 of the species of fruit bats on the island—*M. plethodon*, *B. cavernarum,* and *A. jamaicensis*. Indeed, bats pollinate more than 350 species of plant representing 44 plant families throughout the Neotropics (Fleming et al. 2009). Therein, bats play a vital role in maintaining the genetic diversity in tropical plant communities (Quesada et al. 2004, Fleming et al. 2009). On Barbados, bat-pollinated plants include tropical forest trees, such as silk cotton (*Ceiba pentandra*), sandbox (*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 rarely specialize in pollinating a single species of plant, but visit a range of species available in their habitat (Muchhala and Jarrín-V. 2002, Quesada et al. 2004, Soto-Centeno and Kurta 2006, Tschapka et al. 2008).

Fruit-eating bats regularly disperse seeds of pioneer plants (for example, *Cecropia, Solanum,* and *Piper*) that are critical to the re-vegetation of areas that have been cleared for agriculture or that have been heavily damaged by hurricanes (Medellín and Gaona 1999, Martínez-Garza and González-Montagut, 2002, Jones et al. 2009). 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.

The undercliff forest that we observed in the vicinity of Bathsheba appeared to be in good condition, but it is being cleared as development in the area is progressing. It will be important in the future for bat and other ecosystems that large and continuous tracks of this forest are preserved. The gully system and the associated forests on Barbados have been heavily impacted by human activities. Some of these such as Welchman Hall Gully, Sailors Gully, and The Whim have been developed for tourism and local leisure activities. Some of the gullies have been cleared for agriculture and other purposes. A good example of some of the problems that we observed are illustrated by Jack in the Box Gully, which is a very important gully associated with Cole's Cave and Harrison's Cave. The road right of way across the gully has resulted in clearing of some forest, allowed large amounts of garbage to be dumped into the gully, and we noted a number of invasive plant species invading the native forest. The presence of bat species in gullies that are documented in this paper further reinforces the intrinsic value of gullies for Barbadian biodiversity. Protection of fresh water resources benefit forests, wildlife, and the human populations on islands, such as Barbados. The forests and limestone cap of Barbados are integral to the maintenance of the hydrologic system of small streams, aquatic habitats, and soil moisture levels.

**Acknowledgements**

## References

Baker R.J. & Genoways H.H. 1978. Zoogeography of Antillean bats. Special Publication of the Academy of Natural Sciences of Philadelphia, 13: 53-97.

Baker R.J., Genoways H.H. & Patton J.C. 1978. Bats of Guadeloupe. Occasional Papers of the Museum, Texas Tech University, 50: 1-16.

Beard J.S. 1949. The natural vegetation of the Windward & Leeward islands. Oxford, UK: Clarendon Press, 192 pp.

Buden D.W. 1977. First records of bats of the genus *Brachyphylla* from the Caicos Islands, with notes on geographic variation. Journal of Mammalogy, 58: 221-225.

Caribbean Hurricane Network. 2010. Barbados (TNCM). Accessed March 10 at <http://stormcarib.com/climatology/>.

Carrington S. 2007. Wild plants of Barbados. Second edition. Oxford: Macmillan Caribbean, v + 242 pp.

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

Dobson G.E. 1878. Catalogue of the Chiroptera in the collection of the British Museum. London: Trustees of the British Museum, xlii + 567 pp.

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

Feilden H.W. 1890. Notes on terrestrial mammals from Barbados. The Zoologist, series 3, 14: 52-55.

Fleming T.H., Geiselman C. & Kress W.J. 2009. The evolution of bat pollination: a phylogenetic perspective. Annals of Botany, 104: 1017-1043.

Gannon M.R. & Willig M.R. 1994. The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. Biotropica, 26: 320-331.

Genoways H.H. & Baker R.J. 1975. A new species of *Eptesicus* from Guadeloupe, Lesser Antilles (Chiroptera: Vespertilionidae). Occasional Papers of the Museum, Texas Tech University, 34: 1-7.

Genoways H.H., Baker R.J., Bickham J.W. & Phillips C.J. 2005. Bats of Jamaica. Special Publications of the Museum, Texas Tech University, 48:1-155.

Genoways H.H., Kwiecinski G.G., Larsen P.A., Pedersen S.C., Larsen R.J., Hoffman J.D., Silva M. de, Phillips C.J. & Baker R.J. 2010. Bats of the Grenadine Islands, West Indies, and placement of Koopman's Line. Chiroptera Neotropical, 16: 501-521.

Genoways H.H., Larsen P.A., Pedersen S.C. & Huebschman J.J. 2007a. Bats of Saba, Netherlands Antilles. Acta Chiropterologica, 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, 14: 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, 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 of the Museum, Texas Tech University, 177: 1-28.

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 Publications of the Museum, Texas Tech University, 43: 1-43.

Gooding E.G.B. 1974. The plant communities of Barbados. Ministry of Education, Bridgetown, Barbados, xi + 243 pp.

Grindal S.D. 2004. Notes on the natural history of bats on Barbados. Journal of the Barbados Museum and Historical Society, 50: 9-27.

Hall E.R. 1946. Mammals of Nevada. University of California Press, Berkeley, xi + 710 pp.

Hedges S.B. 2001. Biogeography of the West Indies: an overview. Pp. 15-33, Biogeography of the West Indies: patterns and perspectives, 2nd edition (Woods C.A. & Sergile F.E., eds.), Boca Raton, LA: CRC Press, 582 pp.

Hill J.E. & Evans P.G.H. 1985. A record of *Eptesicus fuscus* (Chiroptera: Vespertilionidae) from Dominica, West Indies. Mammalia, 49: 133-136.

Husson A.M. 1962. The bats of Suriname. Zoölogische Verhandelingen, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands, 58: 1–282.

Issartel G., Lebanc F., Vincent S. & Favre P. 2008. Inventaires des Chiropteres de Martinique – Mission 2006. Rapport SFEPM-DIREN Martinique, Paris – Fort de France, 67 pp. + unnumbered tables.

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, 8: 93-115.

Jones J.K. Jr. 1989. Distribution and systematics of bats in the Lesser Antilles. Pp. 645-660 in Biogeography of the West Indies: past, present, and future (Woods C.A., ed.). Sandhill Crane Press Inc., Gainesville, FL, 878 pp.

Jones J. K. Jr. & 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.

Jones T.S. 1951. Bat records from the islands of Grenada and Tobago, British West Indies. Journal of Mammalogy, 32: 223-224.

Koopman K.F. 1968. Taxonomic and distributional notes on Lesser Antillean bats. American Museum Novitates, 2333: 1–13.

Koopman K.F. 1989. A review and analysis of the bats of the West Indies. Pp. 635-643 in Biogeography of the West Indies: past, present, and future (Woods C.A., ed.). Sandhill Crane Press Inc., Gainesville, FL, 878 pp.

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, 88: 712-727.

Larsen P.A., Marchan-Rivadeneira M.R. & Baker R.J. 2010a. Natural hybridization generates mammalian lineage with species characteristics. Proceedings of the National Academy of Sciences of the USA, 107: 11447-11452.

Larsen P.A., Marchan-Rivadeneira M.R. & Baker R.J. 2010b. Taxonomic status of Anderson's fruit-eating bat (*Artibeus jamaicensis aequatorialis*) and revised classification of *Artibeus* (Chiroptera: Phyllostomidae). Zootaxa, 2648: 45–60.

Larsen R.J., Boegler K.A., Genoways H.H., Masefield W.P., Kirsch R.A. & Pedersen S.C. 2007. Mist netting bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). Acta Chiropterologica, 9: 423-435.

Larsen R.J., Larsen P.A., Genoways H.H., Catzeflis F.M., Geluso K., Kwiecinski G.G., Pedersen S.C., Simal F. & Baker R.J. 2012. Evolutionary history of Caribbean *Myotis* and evidence of a third Lesser Antillean endemic. Mammalian Biology, 77: 124-134.

LaVal R.K. & Schwartz A. 1974. A new bat of the genus *Myotis* from Barbados. Caribbean Journal of Science, 14: 189-191.

Martínez-Garza C. & González-Montagut, R. 2002. Seed rain of fleshy-fruited species in tropical pastures in Los Tuxtlas, Mexico. Journal of Tropical Ecology, 18: 457-462.

Medellín R.A. & Gaona O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica, 31: 478-485.

Miller G.S. Jr. 1900. The bats of the genus *Monophyllus*. Proceedings of the Washington Academy of Sciences, 2: 31-38.

Miller G.S. Jr. 1913. Notes on bats of the genus *Molossus*. Proceedings of the United States National Museum, 46: 85-92.

Muchhala N. & Jarrín-V. P. 2002. Flower visitation by bats in cloud forests of western Ecuador. Biotropica, 34: 387-395.

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, 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, 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, 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, 249: 1-18.

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, 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. Pp. 661-684, in Biogeography of the West Indies (Woods C.A., eds.). Gainesville, FL: Sandhill Crane Press, xvii + 878 pp.

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*. Pp. 97-123, in Latin American mammalogy: history, biodiversity, and conservation (Mares M.A. & Schmidly D.J., eds.). Norman: University of Oklahoma, xviii + 468 pp.

Pumo D.E., Goldin E.Z., Elliot B., Phillips C.J. & 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. & Genoways H.H. 1996. Molecular systematics of the fruit bat, *Artibeus jamaicensis*: origin of an unusual island population. Journal of Mammalogy, 77: 491-503.

Quesada M., Stoner K.E., Lobo J.A., Herrerias-Diego Y., Palacios-Guevara C., Munguia-Rosas M.A.O., Salazar K.A. & Rosas-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, 36:131-138.

Rappaport E.N. & Fernandez-Partagas J. 1995. The deadliest Atlantic tropical cyclones, 1492-1996. National Weather Service, National Hurricane Center, Miami, FL <http://www.nhc.noaa/pastdeadly.shtml>, accessed 12 October 2011.

Sager S. 1992. StatView®. Abacus Concepts, Inc., Berkeley, CA, x + 466 pp.

Schwartz A. & Jones J.K. Jr. 1967. Bredin-Archbold-Smithsonian Biological Survey of Dominica. 7. Review of bats of the endemic Antillean genus *Monophyllus*. Proceedings of the United States National Museum, 124: 1–20.

Seehausen O. 2004. Hybridization and adaptive radiation. Trends in Ecology and Evolution, 19: 198–207.

Simmons and Associates Inc. 2000. First national report to the Conference of Parties to the Convention on Biological Diversity. Report to the Ministry of Environment, Energy and Natural Resources, Government of Barbados, 67 pp.

Soto-Centeno J.A. & Kurta A. 2006. Diet of two nectarivorous bats, *Erophylla sezekorni* and *Monophyllus redmani* (Phyllostomidae), on Puerto Rico. Journal of Mammalogy, 87: 19-26.

Speed R.C. 1994. Barbados and the Lesser Antilles forearc. Pp. 179-192, in Caribbean geology: an introduction (Donovan S.K. & Jackson T.A., eds). Kingston, Jamaica: University of the West Indies Publishers' Association, iii + 289 pp.

Speed R.C. & Keller C.A. 1993. Synopsis of the geological evolution of Barbados. Journal of the Barbados Museum and Historical Society, 41: 113-139.

Swanepoel P. & Genoways H.H. 1978. Revision of the Antillean bats of the genus *Brachyphylla* (Mammalia: Phyllostomatidae). Bulletin of the Carnegie Museum of Natural History, 12: 1-53.

Timm R.M. & Genoways H.H. 2003. West Indian mammals from the Albert Schwartz Collection: biological and historical information. Scientific Papers, Natural History Museum of the University of Kansas, 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, 89: 924-932.

Vos P., Hogers R., Bleeker M., Reijans M. van de, Lee T. Hornes M., Frijters A., Pot J., Peleman J., Kuiper M. & Zabeau M. 1995. AFLP: a new technique for DNA fingerprinting. Nucleic Acids Research, 23: 4407–4414.

Wadge G. 1994. The Lesser Antilles. Pp. 167-177, in Caribbean geology: an introduction (Donovan S.K. & Jackson T.A., eds.). Kingston, Jamaica: University of the West Indies Publishers' Association, iii + 289 pp.

Wilson D. E. 1979. Reproductive patterns. Pp. 317-378, in Biology of bats of the New World Family Phyllostomatidae, Part III (Baker R.J., Jones J.K. Jr. & Carter D.C., eds.). Special Publication of the Museum, Texas Tech University, 16: 1-441.