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Bats of Saba, Netherlands Antilles: a zoogeographic perspective

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Data presented herein provide records of four species of bats new to the fauna of the Antillean island of Saba — *Monophyllus plethodon*, *Ardops nichollsi*, *Tadarida brasiliensis*, and *Molossus molossus*. Together with three species previously recorded from the island – *Brachyphylla cavernarum*, *Artibeus jamaicensis*, and *Natalus stramineus* – the chiropteran fauna of the island is documented to be composed of seven species. Our analysis of species/area relationships for West Indian bats provides a slope value of $z = 0.177$ and $R^2 = 0.76$; therefore, the bat fauna of the West Indies has the flattest slope for this relationship of any West Indian group. This relationship is best explained by a propensity for over water dispersal by West Indian bats. We propose to unite the chiropteran faunas of the islands of Anguilla, Antigua, Barbuda, Nevis, Saba, St. Barthélemy, St. Eustatius, St. Kitts, and St. Martin by recognizing them as the Northern Antillean Faunal Area. Given the small size of Saba (12 km^2) and the even smaller effective habitat for non-molossid bats (4 km^2), conservation concerns are expressed for the future of the fauna and some recommendations are made for its preservation.

Key words: Caribbean, Chiroptera, conservation, Mammalia, Saba, zoogeography

INTRODUCTION

The island of Saba, a part of the Netherland Antilles, is the western-most of the Lesser Antillean islands lying about 150 kilometers to the east of St. Croix in the U.S. Virgin Islands. These islands are separated by the Anegada Passage that reaches a depth of 2,300 m marking the separation of the Virgin Islands of the eastern Greater Antilles from the islands of the Lesser Antilles that lie to the south and east. Saba is actually the emergent cone of an extinct volcano set on a seabed at a depth of 600 m and reaching an elevation of 887 m.

Until our work on the island in 2002 and 2003, the chiropteran fauna had not been the subject of systematic field studies. Previously, only three species of bats have been reported from Saba, including *Brachyphylla cavernarum*, *Artibeus jamaicensis*, and *Natalus stramineus*. Based on specimens collected by Dr. P. W. Hummelinck in June 1949 and by Dr. J. H. Ferwerda in May 1959, Husson (1960) reported *B. cavernarum* as the first species of bat known from the island. Koopman (1968) reported two additional species from Saba — *A. jamaicensis* and *N. stramineus* — based on specimens collected in January 1937 and deposited in the collections of the Field Museum of Natural History.

Our work has added four species of bats to the chiropteran fauna of Saba — *Monophyllus plethodon*, *Ardops nichollsi*, *Molossus molossus*, and *Tadarida brasiliensis* — bringing to seven the total number of species documented for the island. It is our belief that an eighth species, *Noctilio leporinus*, will be added to fauna with additional field studies. This report brings together the available information on the bats of Saba based on our studies, information gleaned from the re-examination of specimens previously deposited in museums, and data kindly shared with us by Mary Kay Clark, North Carolina State Museum of Natural Science, from her studies on the island in 1997.

MATERIALS AND METHODS

Study Area

Saba, located 17°37'–39'N, 63°13'–15'W, is a small island with an area of 12 km^2. The island is essentially round with an approximate diameter of 4 km (Fig. 1; numbers in text following localities refer to the numbering of the localities in this figure). The island is mountainous with extremely steep slopes and cliffs. We often commented that there were only two directions on this island — 'up' and 'down'. There are few beaches and these are covered with boulders. The highest point is Mount Scenery (887 m), which is the source of very steep and narrow valleys known as guts. These were all dry because there are no catchments and water quickly drains from these features (Stoffers, 1956). Saba lies in the Caribbean hurricane belt and was hit by Hurricane Debby in 2000 being buffeted by 75 mph winds on August 22nd. The last major hurricane to hit the island was the H4 Lenny with 150 mph winds on November 18th, 1999 (Caribbean Hurricane Network, 2005). Within the Lesser Antilles, Saba lies 45 km southwest of St. Martin and 25 km northwest of St. Eustatius. It is separated from both of these islands by channels that exceed 500 m. During the Pleistocene sea-level lowering, Saba was not joined with any other Antillean island, but it probably was united with an emergent Saba Bank to increase its size. The highest mean maximum temperatures are in August–September at 30.6°C and the coolest months are January–February with a mean value of 27.4°C. Saba averages over 1,000 mm of rainfall each year with September the wettest month and March the driest (Stoffers 1956).

The top of Mount Scenery is covered with elfin woodland composed of low, misshapen trees of less than 6 m in height. In many places this vegetation is impenetrable. Below the elfin woodland is palm brake down to 775 m in which mountain cabbage palm, *Euterpe globosa*, composes between 50–75% of the vegetation. Further down the mountain there is a band of tree-fern brake extending at least to 575 m. This area is dominated by two species — *Cyathea aborea* and *C. antillana*. None of these vegetative zones offers habitat for bats. There are few food plants present and the vegetation is so thick that it is impossible for bats to fly through it or beneath the canopy in most places.

On the drier, windward southeastern slopes of the mountain in the vicinity of Windwardside (9) and extending to Hell's Gate and Santa Cruz is one of the few areas on the island suitable for agricultural purposes. Here are small plantations of bananas, subsistence gardens, or areas covered by the introduced guinea grass. Another cultivated area is situated in the vicinity of The Bottom. In the lower areas along the southern coast is the driest vegetation on the island with areas of grass used for grazing and thickets of yellow balsam, *Croton flavens*.

The northern slopes of the mountain from just west of Upper Hell's Gate to as far west as Mary's Point are the wettest areas on Saba. At a place 0.25 km west of Upper Hell's Gate is the Saba National Park and the area known locally as the Ravine Rain Forest (2). This forest reaches to 600 m on the mountain and is associated with Island Gut. The primary rainforest is two storied with the upper being dominated by red rodwood, *Myrcia citrifolia*, that reaches a height of 10 m. The understory, reaching 5 to 7 m, is dominated by psychotria, one of the wild coffees, *Psychotria berteriana*, and dentate burr-wood, *Sloanea dentata*, with abundant tree ferns and mountain cabbage palms (Stoffers 1956). During our 2003 survey, we noted that many of the large trees near Mary's Point were either dead snags or reflected significant damage from Hurricane Lenny in 1999.

Mist-netting Efforts

The mist-netting surveys consisted of 11 nights of collecting during two periods, 25 June–2 July 2002 and 24–27 May 2003. Mist-netting for bats was conducted in a variety of habitats, including naturally vegetated guts, small fruit plantations, narrow openings planted with guinea grass, trails, covered flyways, access roads, and a swimming pool. Five to eight mist-nets were erected at 20 to 100 m intervals at each location and monitored for 4 to 6 hours depending on activity and weather. In both years, bats were measured and examined (weight, forearm length, reproductive status, tooth wear, presence of scars, and external parasites) at the end of the evening.

Voucher Specimens

Our work on Saba resulted in 62 voucher specimens of seven species of bats. A survey of existing collection materials in natural history museums (American Museum of Natural History, AMNH; Field Museum of Natural History, FMNH; Naturalis, Nationaal Natuurhistorisch Museum in Leiden, NNH; North Carolina State Museum of Natural Science, NCSM) yielded an additional 33 specimens of bats from Saba. All voucher specimens from the 2002 survey were deposited in the research collections at the University of Nebraska State Museum (UNSM) and those from 2003, with associated tissue samples, were deposited in the collections of the Museum of Texas Tech University. Length of forearm and cranial measurements were taken from museum specimens using digital calipers.

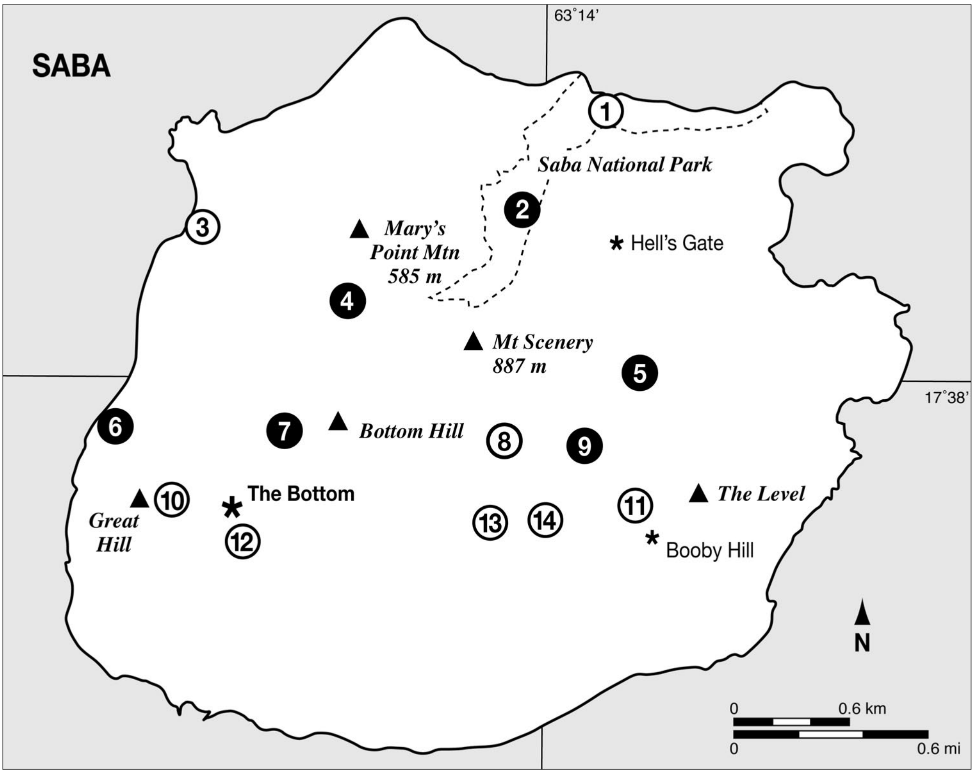

FIG. 1. Map of Saba indicating places where survey work for bats was conducted in 2002–2003. Closed circles are places where bats were obtained and open circles are places that were investigated but no bats were observed or obtained. The following numbers correspond to sites on the map: 1 — sulphur mine (abandoned walk-in mine in an area of sparse arid-adapted vegetation); 2 — Ravine Rain Forest (primary rain forest); 3 — cave in Well's Bay (small seaside overhang pocket); 4 — Mary's Point Mountain (secondary rain forest); 5 — English Quarter (private residential swimming pool surrounded by ornamental plantings); 6 — Ladderberg (old collecting site); 7 — Bottom Hill Trail (low secondary rain forest with a single story and dense ground cover); 8 — upper Mt. Scenery Trail (open agricultural area with guinea grass and adjacent banana groves surrounded by low tree fern brake vegetation); 9 — Windwardside (old collecting site); 10 — cave on top of Great Hill (deep descending cave); 11 — Booby Hill (banana plantation); 12 — cave in Bunker Hill (small overhang cave); 13 — Mt. Scenery Trail steps (trail cut through single story forest and dense ground cover); 14 — lower Mt. Scenery Trail (trail cut through single story forest and dense ground cover); Land Point (not found on our modern maps)

Measurements are given in millimeters and body masses are in grams.

Systematic Accounts

Monophyllus plethodon luciae Miller, 1902

Specimens examined (2) — Ravine Rain Forest, 0.25 km W Upper Hell's Gate, Saba National Park, 550 m, 17°38'17"N, 63°14'09"W, 1 (UNSM); Mary's Point Mountain, 0.6 km W Upper Hell's Gate, 557 m, 17°38'17"N, 63°14'32"W, 1 (TTU).

These two specimens represent the first records of the insular single-leaf bat from Saba (Schwartz and Jones, 1967). Living members of this species are confined to the Lesser Antilles, but a fossil subspecies (*M. p. frater*) is known from Puerto Rico. The insular single-leaf bat currently is known from the adjacent island of St. Martin (Genoways *et al.*, In press *a*); however, the species has not been reported from St. Eustatius, but it is known from St. Kitts the next island in the chain (Pedersen *et al.*, 2005). The length of forearm and seven cranial measurements for our two adult males (Table 1) fit well with samples of males from St. Martin (Genoways *et al.*, In press *a*) and St. Kitts (Pedersen *et al.*, 2005). However, it has been pointed out previously that this species is in need of taxonomic review now that much larger samples are available than were examined by Schwartz and Jones (1967).

Single individuals of the insular single-leaf bat were taken in both years of the survey. They were captured at sites less than 0.5 km apart on the northern slopes of Mount Scenery. The Ravine Rain Forest (2) is a restricted area associated with Island Gut that is primary rain forest. At Mary's Point Mountain (4), the area also is rain forest, but most of it is secondary because of subsistence garden plots created by the former residents of Mary's Point, which is now abandoned. There was a small banana plantation and a small opening with grass cover near where the bat was taken. Both nets were placed across the narrow footpath connecting the sites. The understory was far more open at the Ravine Rain Forest than at Mary's Point Mountain. At the Ravine Rain Forest, the insular single-leaf bat was taken along with *Brachyphylla cavernarum*, whereas at Mary's Point Mountain it was taken with *Artibeus jamaicensis*, *Ardops nichollsi*, and *Natalus stramineus*.

The male taken on 25 May had testes that measured 4 in length, whereas the male taken on 30 June had testes that were 5 long. These males weighed, respectively, 15.4 and 15.3.

Brachyphylla cavernarum cavernarum Gray, 1834

Specimens examined (23) — Bat Hole near Land Point, 2 (NNH); Ladderberg, 6 (NNH); Ravine Rain Forest, 0.25 km W Upper Hell's Gate, Saba National Park, 550 m, 17°38'17"N, 63°14'09"W, 12 (8 TTU, 4 UNSM); Windwardside, 1 (AMNH); no specific locality, 2 (NNH).

Husson (1960) was the first to report the Antillean fruit-eating bat from Saba based on specimens from near Land Point. Husson (1960:70) states that Hummelinck found a chamber in a small cave, next to the coast at Land Point, in which he on 19 June 1949 collected a number of adult animals ($n = 21$) and juvenile individuals. Husson (1960: 155) describes the juveniles as 'hairless young'. In May 1959, Doctor J. H. Ferwerda collected the same species there ($n = 6$). Swanepoel and Genoways (1978) undertook a systematic review of the bats of the genus *Brachyphylla*, assigning material from Saba to *B. c. cavernarum*, which occurs from St. Croix to St. Vincent. We follow this arrangement here. The length of forearm and seven cranial measurements for two males and five females from Saba (Table 1) match closely the values given by Swanepoel and Genoways (1978) for their sample 15 based on material from Saba.

We took specimens of the Antillean fruit-eating bat in both years of our survey. All individuals were netted along a trail that proceeded through Island Gut (2), which contained the most undisturbed primary rain forest that we observed anywhere on the island. The bats were taken later in the evening (20:30 hrs) and most were netted as they flew up hill. In 2002, several of the *Brachyphylla* were eating/carrying small red berries 2–3 mm in diameter. A 'recent' landslide down this ravine opened up the canopy and the bats were clearly making use of this corridor in 2002. We searched three caves on Saba with no success in finding this or any other species of bat. Two of the caves were in the vicinity of The Bottom — but neither Deep Cave on Great Hill (10) nor the small overhang cave (12) south of The Bottom showed any evidence of bat habitation; however, the humidity and protection offered by these structures suggested that they would have made fine roosts. A seaside cave in Well's Bay (3) was said to have sheltered bats at one time but this feature was far too exposed to serve as a roost during our visit.

Testes lengths of three adult males were as follows (date of capture in parentheses): 9.5 (10 January); 9 (25 May); 7 (1 July). One female taken on 25 May evinced no gross reproductive activity. Two females taken on this same date carried embryos that measured 40 and 44 in crown-rump length. Another two females taken on 25 May give birth to living pups in the holding bags. Both pups were females, which weighed 11.3 and 15.1 (mothers, 51.0 and 44.2, respectively) and with length of forearm of 31.1 and 36.7 (mothers, 66.0 and 63.3, respectively). All three adult females taken on 1 July were lactating. Two adult males weighed 48.5 and 49.0. The non-reproductive female weighed 41.6, the three lactating females were 42.0, 45.0, and 46.8, and the two pregnant females were 58.6 and 61.8.

Three specimens of *B. cavernarum* collected from Saba in 2002 (UNSM 27927–27929) were included in a genetic analysis of Lesser Antillean bat populations by Carstens *et al.* (2004). Carstens *et al.* (2004) generated mitochondrial cytochrome *b* gene DNA sequence data from these specimens and identified two unique haplotypes. These haplotypes also were documented within the Montserrat and Nevis populations of *B. cavernarum*, suggesting recent gene flow between these islands.

Ardops nichollsi montserratensis (Thomas, 1894)

Specimen examined (1) — Mary's Point Mountain, 0.6 km W Upper Hell's Gate, 557 m, 17°38'17"N, 63°14'32"W, 1 (TTU).

Our specimen is the first record of the Antillean tree bat from Saba. Given the isolated position of the island, including isolation during the Pleistocene, we were surprised to discover this species. However, the species is known from the adjacent islands of St Martin (Genoways *et al.*, In press *a*) and St. Eustatius (Jones and Schwartz, 1967). The length of forearm and seven cranial measurements of our adult female specimen (Table 1) are in the range of females from St. Martin and St. Eustatius. Jones and Schwartz (1967) assigned specimens from St. Eustatius to *A. n. montserratensis* and we have followed that arrangement here pending a multivariate reevaluation of the geographic variation in this species.

Our Antillean tree bat was captured in a mist net set across a narrow walking trail (4) in an area consisting of secondary rain

TABLE 1. Length of forearm and seven cranial measurements (in mm) for seven species of bats from Saba, Netherlands Antilles

Statistics, catalog numbers, and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
Monophyllus plethodon luciae								
TTU 101953, ♂	42.1	23.7	21.1	10.3	4.6	10.0	8.0	5.5
UNSM 27926, ♂	40.9	22.7	21.0	10.3	4.5	9.8	7.5	5.4
Brachyphylla cavernarum cavernarum								
TTU 101966, ♂	69.2	32.1	28.9	17.0	6.9	14.8	11.0	11.6
UNSM 27929, ♂	68.5	32.2	29.4	17.5	6.2	15.2	11.4	11.9
♀♀ ($n = 5$)								
x̄ ± SE	65.0 ± 0.70	31.9 ± 0.20	28.4 ± 0.10	17.4 ± 0.10	6.6 ± 0.10	14.8 ± 0.10	11.0 ± 0.10	11.5 ± 0.04
Range	63.4–67.0	31.3–32.4	28.1–28.9	16.9–17.6	6.3–6.7	14.5–15.0	10.8–11.1	11.5–11.7
Ardops nichollsi montserratensis								
TTU 101954, ♀	51.8	24.3	21.3	16.1	6.2	13.3	7.9	10.5
Artibeus jamaicensis jamaicensis								
♂♂ ($n = 5$)								
x̄ ± SE	61.5 ± 0.53	28.1 ± 0.19	24.6 ± 0.15	16.8 ± 0.16	7.2 ± 0.09	15.0 ± 0.11	9.7 ± 0.11	12.4 ± 0.13
Range	59.7–62.7	27.6–28.6	24.2–24.9	16.3–17.2	6.8–7.3	14.7–15.4	9.4–9.9	12.1–12.9
♀♀ ($n = 4$)								
x̄ ± SE	63.1 ± 0.56	28.4 ± 0.13	24.7 ± 0.44	16.8 ± 0.14	7.3 ± 0.07	14.9 ± 0.26	9.7 ± 0.11	12.5 ± 0.13
Range	61.5–64.1	28.0–28.6	23.4–25.3	16.4–17.0	7.2–7.5	14.1–15.2	9.4–9.9	12.4–12.9
Natalus stramineus stramineus								
♂♂ ($n = 4$)								
x̄ ± SE	39.2 ± 0.48	16.4 ± 0.11	15.0 ± 0.03	8.4 ± 0.04	3.1 ± 0.05	7.5 ± 0.09	7.1 ± 0.07	5.5 ± 0.05
Range	38.2–40.2	16.1–16.6	14.9–15.0	8.3–8,5	3.0–3.2	7.3–7.7	7.0–7.3	5.4–5.6
♀♀ ($n = 5$)								
x̄ ± SE	38.6 ± 0.13	16.2 ± 0.06	14.8 ± 0.08	8.2 ± 0.03	3.1 ± 0.02	7.5 ± 0.05	7.0 ± 0.04	5.3 ± 0.04
Range	38.1–38.9	16.0–16.3	14.5–15.0	8.1–8.3	3.0–3.1	7.3–7.6	6.9–7.1	5.2–5.4
Molossus molossus molossus								
♂♂ ($n = 3$)								
x̄ ± SE	38.7 ± 0.35	16.6 ± 0.09	14.5 ± 0.12	10.2 ± 0.12	3.2 ± 0.06	9.5 ± 0.23	5.7 ± 0.10	7.3 ± 0.12
Range	38.2–39.4	16.4–16.7	14.3–14.7	10.0–10.4	3.1–3.3	9.0–9.7	5.5–5.8	7.1–7.5
♀♀ ($n = 5$)								
x̄ ± SE	37.7 ± 0.31	15.7 ± 0.24	14.0 ± 0.11	9.8 ± 0.08	3.2 ± 0.04	9.3 ± 0.10	5.5 ± 0.04	7.0 ± 0.11
Range	36.6–38.2	15.0–16.3	13.6–14.3	9.5–9.9	3.1–3.3	9.0–9.6	5.4–5.6	6.6–7.2

TABLE 1. Continued

Statistics, catalog numbers, and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
Tadarida brasiliensis antillularum								
♂♂ (*n* = 5)								
x̄ ± SE	37.6 ± 0.06	15.8 ± 0.11	14.8 ± 0.11	9.2 ± 0.04	3.6 ± 0.03	8.9 ± 0.07	5.6 ± 0.02	6.5 ± 0.11
Range	37.5–37.8	15.5–16.1	14.5–15.2	9.1–9.3	3.5–3.7	8.7–9.1	5.5–5.6	6.1–6.7
♀♀ (*n* = 5)								
x̄ ± SE	37.7 ± 0.34	15.7 ± 0.15	14.4 ± 0.12	9.1 ± 0.16	3.7 ± 0.04	8.7 ± 0.09	5.6 ± 0.05	6.5 ± 0.05
Range	36.5–38.4	15.3–16.2	14.1–14.8	8.5–9.4	3.6–3.8	8.6–9.0	5.4–5.7	6.4–6.7

forest. It was captured in the same net as the *Monophyllus plethodon* discussed above. This female specimen carried a single embryo measuring 14 in crown-rump length and weighed 25.9.

Artibeus jamaicensis jamaicensis
Leach, 1821

Specimens examined (24) — Bottom Hill Trail, 0.5 km N The Bottom, 2 (UNSM); Mary’s Point Mountain, 0.6 km W Upper Hell’s Gate, 557 m, 17°38’17”N, 63°14’32”W, 7 (5 TTU, 2 UNSM); no specific locality, 15 (FMNH).

The Jamaican fruit-eating bat was first reported from Saba by Koopman (1968) based on ‘15 specimens in the Field Museum of Natural History’, which are those listed above. The length of forearm and cranial measurements for five males and four females (Table 1) reveal no significant secondary sexual differences between individuals in this sample. Females did average slightly larger than males in five measurements, whereas males were larger in mastoid breadth and the mean for the sexes was equal for zygomatic breadth and length of the maxillary toothrow. Genoways *et al.* (2001) have reviewed morphological variation in Antillean populations of this species. Our sample from Saba (see Table 1) most closely matches the measurements of other samples of *A. j. jamaicensis* (Genoways *et al.*, 2001).

Although *A. jamaicensis* is generally a common species in most tropical habitats, we did not find it to be abundant on Saba wherein we captured only nine individuals at two sites. Two individuals were taken in nets set over the Bottom Hill Trail (7) and an adjacent small gut. The nets were placed in an area of secondary rain forest having a single canopy, with a heavy understory, primarily of ferns, although one net was set over a stand of piper (*Piper dilatum*).

The first Jamaican fruit-eating bat was taken at approximately 20:15 and the second at 22:45; both were males. The first individual was carrying a fig with it when netted and the second individual's face was covered with fruit juice. On the night of 30 June 2002, two Jamaican fruit-eating bats were caught in a mist net set near an old plot of banana plants at Mary's Point Mountain (4). Five additional individuals were captured near this same place on the night of 25 May 2003. The general vegetation in this area was secondary rain forest as described previously.

The sulphur mine (1) on the northeast coast near the airport was visited in 2002. This mine consisted of several short straight interconnected tunnels and a unique climbing spiral tunnel composed of several coils that resembled a huge snails' shell. The entrance to the mine was surrounded by xeric habitat and was exposed to very strong prevailing winds at this exposed location. A small amount of fruit bat guano was identified in a small protected alcove at the back of the mine, but there was no indication that this location was used as a permanent roost by bats. Subsequent to our surveys, several Jamaican fruit bats were observed and photographed roosting in this mine in late 2006 by Allyson Walsh of Lubee Bat Conservancy.

Four adult males captured on 25 January 1937 had testes length of 4.5, 4.5, 5.5, and 8. Two males taken on 25 May had testes lengths of 5 and 6, whereas two taken on 28 June and one from 30 June had testes lengths of 8, 8, and 7, respectively. Eight females taken on 25 January 1937 evinced no gross reproductive activity as was found for two individuals obtained on 25 May. Another female netted on 25 May was carrying a single embryo measuring 40 in crown-rump length and one taken 30 June was lactating. The average body mass of five adult males was 36.8 (34.8–40.3), whereas two non-pregnant females weighed 35.7 and 37.7. The lactating female weighed 43.4 and the pregnant female weighed 53.3.

Because the presence/absence of the third molar of this species is known to vary, we examined nine individuals for these characteristics (Genoways *et al.*, 2001). All nine individuals were missing both upper third molars, whereas in eight individuals both lower third molars were present. These results are consistent with those found in other populations of *A. j. jamaicensis*. The one individual that was missing both lower third molars was an adult male taken at Mary's Point Mountain on 25 May 2003 (TTU 101957). An adult female (TTU 101959) taken at the same time and place was noted as having heavily worn teeth, probably as the result of old age.

Two studies have analyzed genetic data from the Saba population of *A. jamaicensis*. First, in their analysis of population genetics of Lesser Antillean bats, Carstens *et al.* (2004) included sequence data of the entire mitochondrial cytochrome *b* gene from four individuals of *A. jamaicensis* collected in 2002 (UNSM 27924, UNSM 27925, UNSM 27931, and UNSM 27932). Of these four individuals, Carstens *et al.* (2004) identified three unique haplotypes that were shared with populations of *A. jamaicensis* on Montserrat, Nevis, St. Eustatius, St. Kitts, and St. Maarten. Their results are indicative of frequent gene flow amongst these populations. Second, Larsen *et al.* (2007*b*) included cytochrome *b* gene sequence data from five individuals of *A. jamaicensis*, collected from Saba in 2003 (TTU 101955–101959), in their analysis of the phylogenetics and phylogeography of the *A. jamaicensis* complex. Of these five individuals Larsen *et al.* (2007*b*) identify a single haplotype, which is shared amongst populations of *A. jamaicensis* ranging from Quintana Roo, Mexico, throughout the Greater Antilles and in the Lesser Antilles as far south as Grenada. Their results are very similar to those of Pumo *et al.* (1988, 1996) and Phillips *et al.* (1989) who documented a similar lack of genetic diversity within Caribbean populations of *A. jamaicensis*. The concordance between the studies of Larsen *et al.* (2007*b*), Pumo *et al.* (1988, 1996), and Phillips *et al.* (1989) regarding the lack of genetic diversity in populations of *A. jamaicensis* throughout the Greater and Lesser Antilles, lends additional support to the hypothesis of a recent invasion by this species into the Caribbean (Phillips *et al.*, 1991; Genoways *et al.*, 2005).

Natalus stramineus stramineus
Gray, 1838

Specimens examined (10) — Mary's Point Mountain, 0.6 km W Upper Hell's Gate, 557 m, 17°38'17"N, 63°14'32", 9 (8 TTU, 1 UNSM); no specific locality, 1 (FMNH).

Koopman (1968) was the first to report the greater funnel-eared bat from Saba based on the specimen deposited in the Field Museum of Natural History. We took this species in both years of our survey at the same location on the island. The length of forearm and seven cranial measurements for four males and five females (Table 1) reveal no significant secondary sexual variation except for zygomatic breadth where males were significantly larger at the $P \leq 0.01$ level.

Dávalos (2005) and Tejedor *et al.* (2005) presented evidence that unrecognized taxa of *Natalus* exist within currently named populations in the West Indies. Goodwin (1959), in his revision of members of the subgenus *Natalus*, restricted the type locality of *Natalus stramineus* to Antigua rather than Lagoa Santa, Minas Gerais, Brazil, as was done by earlier authors. This decision later was reconfirmed by Handley and Gardner (1990) and Tejedor (2006). Tejedor (2006) restricted *N. stramineus* to the northern Lesser Antilles, ranging from Dominica to Anguilla, and in a canonical analysis of external and cranial characters, demonstrated that 'the sample from Dominica is morphometrically distinct from that of the remaining islands'. Although Tejedor (2006) did not use it, the name *N. s. dominicensis* Shamel (1928) is available for the population on Dominica, leaving the nominate subspecies, *N. s. stramineus*, as the appropriate name to apply to the other populations in the northern Lesser Antilles, including those on Saba.

Our specimens were netted over a foot trail along the southern side of Mary's Point Mountain (4) in secondary rain forest and near a small grove of banana trees. To the north side of the trail was an outcrop of eroded lava that was overgrown by the secondary rain forest. It was from these rocks that funnel-eared bats appeared each year; no cave was ever found despite an extended search. Several of these bats were observed flying no more than a meter above the trail, giving the impression that they were large moths emerging just at dusk.

A female captured in January 1937 evinced no gross reproductive activity. Of four females netted on 25–26 May, one carried a single embryo that measured 21 in crown-rump length and the other three were lactating as was a female obtained on 30 June. Testes lengths of four males taken on 26 May were 1, 1, 2, and 2. These males weighed an average of 4.8 (4.5–5.1). The pregnant female weighed 6.3 and the four lactating females averaged 4.6 (4.4–4.8) in body mass.

Tadarida brasiliensis antillularum
(Miller, 1902)

Specimens examined (24) — 100 m NW English Quarter, 370 m, 17°38'04"N, 63°13’47”W, 19 (9 TTU, 10 UNSM); Windwardside, 5 (NCSM).

These specimens represent the first record of the Brazilian free-tailed bat from Saba. Although our collection of 24 specimens would seem to indicate this species is relatively abundant on Saba, we believe that all specimens came from a single place, with all being netted over a small man-made swimming pool. Length of forearm and cranial measurements for five males and five females are reported in Table 1. These samples reveal no significant secondary sexual variation in these measurements. Measurements of the specimens from Saba closely match those of individuals from Sint Maarten/Saint Martin (Genoways *et al.*, In press *a*). We continue to follow Schwartz (1955) in assigning all Lesser Antillean populations of this species to the subspecies *T. b. antillularum* until a comprehensive study of geographic variation in Antillean populations is undertaken. Owen *et al.* (1990) presented evidence of a close relationship between *T. b. cynocephala* from the southeastern United States and Antillean populations of *T. brasiliensis*. Further data are needed to fully explore the taxonomic and biogeographic implications if such a relationship exists.

All specimens examined were netted over a private swimming pool that was approximately 3 m wide and 7 m long (5). This pool had residential buildings on two sides and dense ornamental plantings on the other two sides. The pool was located at a residence on the windward side of the island, with winds being most significant just before and after dark. We suspect that this species was roosting in steep lava cliffs located within 500 m of the pool. The Brazilian free-tailed bat out-numbered the other free-tailed bat, *M. molossus*, taken at this location by about 4 to 1.

A female taken in the last week of April 1997 was lactating. Six females taken on 26 May evinced no gross reproductive activity as did two females from 1 July. However, two females from 1 July were carrying single embryos measuring each 4 in crown-rump length. Males from 26 May had testes lengths of 4, 4, and 5, whereas eight males from 1 July had a mean testes length of 4.1 (3–7). Five females taken on 26 May weighed an average of 10.4 (10.1–10.7) and were noted by the preparator as being excessively fat, whereas a sixth female from this same date weighed only 7.8 and was not fat. Four females from 1 July weighed an average of 7.9 (7.7–8.0). Three males captured on 26 May weighed 8.0, 8.4, and 9.3, whereas eight males taken on 1 July had a mean body mass of 7.4 (6.5–9.5).

Molossus molossus molossus
(Pallas, 1766)

Specimens examined (11) — Bottom Hill Trail, 0.5 km N The Bottom, 5 (UNSM); 100 m NW English Quarter, 370 m, 17°38’04”N, 63°13’47”W, 5 (3 TTU, 2 UNSM); Windwardside, 1 (NCSM).

Our specimens of Pallas’s mastiff bat are the first to be reported from Saba. 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 throughout the Lesser Antilles. Length of forearm and seven cranial measurements for three males and five females from Saba are given in Table 1. Males averaged significantly larger than females at the $P \leq 0.01$ level in three (greatest length of skull, condylobasal length, and zygomatic breadth) of the eight measurements examined. Males averaged larger than females in all other measurements except postorbital constriction in which the values were equal.

Along the Bottom Hill Trail (7), the first bats were observed flying at 19:00. Three mastiff bats were caught at 19:15 in a net set across a small gut adjacent to the trail. The vegetation in this area was a single canopy secondary rain forest with heavy undergrowth. Two additional individuals were taken at 20:50 and 21:30 in nets set across the trail in more open areas. This collection site was located between The Bottom and Troy and bats were probably roosting in buildings in these settlements. The remaining 6 specimens were captured over the same small residential swimming pool described in the account for the Brazilian free-tailed bat. Over this pool mastiff bats were outnumbered by Brazilian free-tailed bats each year of our survey. We suspect mastiff bats were roosting in buildings in the neighboring settlements of English Quarter (5) and Windwardside (9). On 1 July the first bats over the pool were captured at 18:55.

The female taken on 26 May evinced no gross reproductive activity as did two captured on 28 June; however, three additional females obtained on 28 June each carried a single embryo measuring 7, 8, and 11 in crown-rump length. A female caught on 1 July also was pregnant with an embryo measuring 5. Two males netted on 26 May had testes length of 4 and 5 and one taken 1 July had testes measuring 5. Three males had weights of 9.5, 11.3, and 13.1, and three non-pregnant females weighed 8.9, 9.2, and 12.7. The four pregnant females had a mean body mass of 9.1 (7.9–9.9).

DISCUSSION

Data presented herein provide records of four species of bats new to the fauna of the island of Saba — *Monophyllus plethodon*, *Ardops nichollsi*, *Tadarida brasiliensis*, and *Molossus molossus.* This brings the known chiropteran fauna of the island to seven species. We are confident that with additional work an eighth species, *Noctilio leporinus*, will be added to this fauna. There are sufficient seaside caves to provide shelter for this species, albeit there are very few locations that bat biologists might place their mist nets in order to capture this species. Presently, this simple chiropteran fauna includes representatives of three families — Phyllostomidae, Natalidae, and Molossidae — including one omnivore (*B. cavernarum*), one pollenivore/nectarivore (*M. plethodon*), two frugivores (*A. nichollsi*, *A. jamaicensis*), and three insectivorous species (*N. stramineus*, *T. brasiliensis*, and *M. molossus*).

Given the small size and rather isolated position of Saba, we were surprised by the size of this fauna. It matches the size and diversity of the chiropteran fauna (12 km^2 with seven species) of other much larger islands in the northern Lesser Antilles such as Anguilla (91 km^2 with six species) (Genoways *et al.*, In press *b*); Antigua (280 km^2 with seven species) (Pedersen *et al.*, 2006); Barbuda (162 km^2 with seven species) (Pedersen *et al.*, In press); Nevis (93 km^2 with eight species) (Pedersen *et al.*, 2003); St. Barthélemy (18 km^2 with five species) (Larsen *et al.*, 2007*a*); St. Kitts (168 km^2 with seven species) (Pedersen *et al.*, 2005); St. Martin (96 km^2 with eight species) (Genoways *et al.*, In press *a*).

Species-area analyses have been used to examine the relationship between island area and the number of species present on an island (MacArthur and Wilson 1963, 1967; MacArthur, 1972; Wright, 1981) with the corollary that as island size decreases, extinction rates increase. We have examined this relationship as it applies to the chiropteran fauna on islands of the northern Lesser Antilles, in particular, Nevis (Pedersen *et al.*, 2003). In that analysis, we found a slope value of $z = 0.206$ and $R^2 = 0.74$, where z is the slope of the log species-area relationship and R^2 indicates the amount of species diversity that is explained by area of the islands. In a more recent analysis of West Indian bat faunas, with a focus on the bats of Jamaica. Genoways *et al.* (2005) provided a slope value of $z = 0.21$ with $R^2 = 0.76$. Morgan and Woods (1986) and Griffiths and Klingener (1988) also reported slopes of $z = 0.21$ for West Indian mammal and bat faunas, whereas Wilcox (1980) noted $z = 0.24$ for bats, and 0.48 for land mammals in the West Indies. Wilcox (1980) went on to calculate a slope of $z = 0.24$ for breeding land birds and 0.38 for herpetofauna, observing that 'more highly vagile' species produce lower z-values. This pattern was also noted by Davies and Smith (1998) who reported z-values of 0.34 for beetles and 0.20 for butterflies in the West Indies. They noted that the relationship/slope for butterflies was the lowest/flattest thus far reported for West Indian biota and interpreted their data to mean that butterflies had a propensity for dispersal and colonization, or alternatively, that butterflies have low extinction rates relative to other West Indian animals.

Our recent survey work has concentrated on the islands that lie to the north of what Genoways *et al.* (2001) defined for bats as the Lesser Antillean Faunal Core, covering the islands Montserrat and Guadeloupe in the north to St. Vincent in the south. The chiropteran fauna of islands in this region are composed of at least 12 species of bats, with endemic species such as *Sturnira thomasi*, *Chiroderma improvisum*, *Eptesicus guadeloupensis*, *Myotis dominicensis*, and *M. martiniquensis* as well as the Antillean endemic species *Ardops nichollsi*, *Monophyllus plethodon*, and *Brachyphylla cavernarum.* Of the islands positioned to the north of Guadeloupe in the Lesser Antilles, only Montserrat qualifies as a member of the Lesser Antillean Faunal Core and even this island has only 10 species present (Pedersen *et al.*, 1996), but two of these are endemics — *S. thomasi* and *C. improvisum*.

Now that our survey of the bats of the islands to the north of the Lesser Antillean Faunal Core is concluded, we re-analyzed the data for the species/area relationship for West Indian bats, as shown in Fig. 2 (Genoways *et al.*, In press *a*, In press *b*; Larsen *et al.*, 2007*a*; Pedersen *et al.*, 1996, 2003, 2005, 2006, In press). Our new analysis provides a slope value of $z = 0.177$ and $R^2 = 0.76$; therefore, the bat fauna of the West Indies has the flattest slope for this relationship of any West Indian group. The reason our work in the northern Lesser Antilles has resulted in the depression of the slope of the species/area curve for bats is that these islands basically share the same number of species regardless of island size (Saba at 12 km^2 up to Antigua at 280 km^2). The prediction that smaller islands will have fewer species of bats is not operating in these islands. Indeed, the position of Saba in Fig. 2 indicates that there are many more species of bats on this island than the species-area curve would predict.

Following the proposal of Davies and Smith (1998) these data could be interpreted to mean that bats have a propensity for dispersal and colonization or alternatively that bats have low extinction rates relative to other West Indian biota. Based on our knowledge of the fossil record for Antillean bats (Pregill *et al.*, 1994), extinctions of bats are known to have occurred on the northern Lesser Antillean islands of Anguilla (*Macrotus waterhousii* and *Mormoops blainvillii*), St. Martin (*M. waterhousii*), and Antigua (*M. blainvillii*, *Pteronotus parnellii*, and *Phyllonycteris major*). This makes the explanation of a lowered extinction rate seem less plausible. However, there are at least two lines of evidence that appear to argue in favor of the explanation that this pattern has developed because of the propensity of Antillean bats for dispersal and colonization.

During the height of sea level depression in the Pleistocene, it is believed that only five islands existed to the north of

Guadeloupe in the northern Lesser Antilles. These islands were Montserrat (which we believe shares its chiropteran fauna most closely with Guadeloupe), Saba (which may have been somewhat larger because of the emergence of part of the Saba bank), the St. Martin bank (incorporating St. Martin, St. Barthélemy, and Anguilla), the St. Kitts bank (including St. Kitts, Nevis, and St. Eustatius), and the Barbuda bank (consisting of Antigua and Barbuda). Although these geological changes would have reduced the need for dispersal to explain the development of these island faunas, the fauna on Saba is instructive because this fauna developed in a relatively isolated position and without a major increase in geographic size. Clearly, this fauna on the smallest island that we have surveyed, matches the diversity of other islands in the northern Lesser Antilles and is best explained by over-water dispersal by these bats.

The islands of the Caribbean archipelago exhibit levels of endemism and taxonomic composition that are characteristic of more isolated, oceanic islands (Hedges, 1996). For example, 99% of the 166 native species of amphibians, 93% of the 449 species of reptiles and 80% of the 145 species of mammals are endemic (Hedges, 1996). However, none of the species of bats occurring in the northern Lesser Antilles are endemic to that region and among the eight species present four species (*Noctilio leporinus*, *A. jamaicensis*, *Molossus molossus*, and *Tadarida brasiliensis)* are widespread in distribution, two species (*M. plethodon*, *B. cavernarum*) occur from Puerto Rico to Barbados and St. Vincent, and *A. nichollsi* and *Natalus stramineus* (following the current taxonomic arrangement) are Lesser Antillean endemics. This lack of endemism also seems to argue against isolation and in favor of enough dispersal to maintain the populations of these eight species.

When considering insular patterns of animal dispersal, these movements may be result of either deterministic (Crowell, 1986; Lawlor, 1986; Lomolino, 1986; Patterson and Atmar, 1986) or stochastic factors (Simberloff, 1978, 1980; Connor and Simberloff, 1978, 1979; Connor and

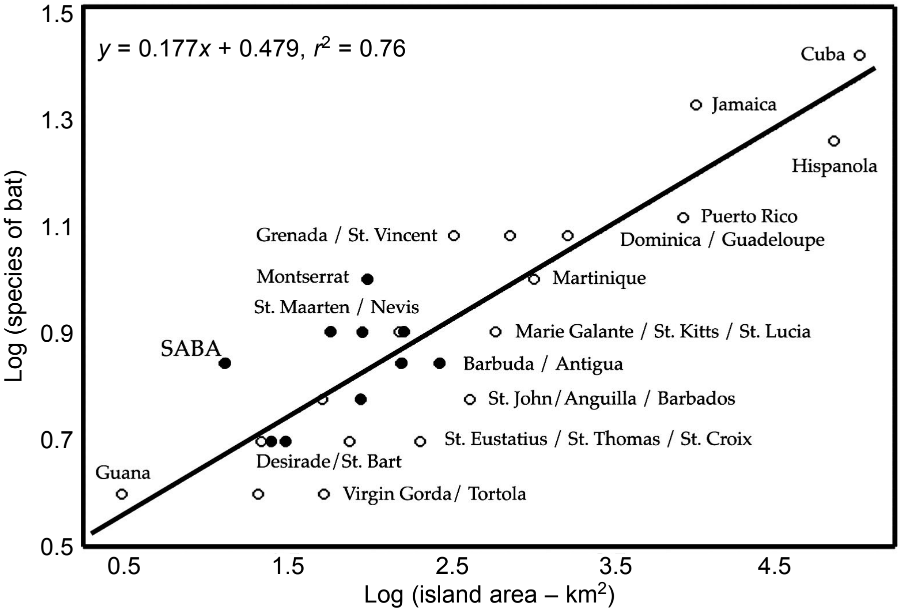

FIG. 2. Species/area curve based on the published data for the chiropteran fauna on islands in the West Indies

McCoy, 1979; Brown, 1986). Movement of terrestrial vertebrates along archipelagoes is thought to happen primarily by accidental rafting events (Censky *et al.*, 1998; Schoener *et al.*, 2001; Raxworthy *et al.*, 2002). For birds and bats, the question of dispersal is more complex because flight could promote inter-island dispersal (Whittaker, 1998). Movement patterns of bats in the Lesser Antilles are poorly known, but have been thought to be limited because inter-island distances present barriers to dispersal (Koopman, 1976; Genoways *et al.*, 1998). However, Klein and Brown (1994) believe data from recent studies provide evidence of frequent and multiple colonizations of islands by bats throughout the Lesser Antilles. Indeed, based on genetic data, Pumo *et al.* (1996) and Carstens *et al.* (2004) imply restricted dispersal ability among the islands for the cave-roosting endemic *B. cavernarum* resulting in isolated intra-island gene pools, whereas the Caribbean eurytopic *A. jamaicensis* showed little isolation and apparently moves among the islands more freely. As these genetic data imply, we do not believe that Antillean bat species, with the possible exception of *N. leporinus*, strike out on their own on a regular basis to move over water from one island to another. It is our conclusion based on the available data that the stochastic events of tropical storms and hurricanes moving primarily from southeast to northwest effect insular dispersal, contemporary and historical biogeography, and gene flow for bat populations living in the Lesser Antilles.

The coefficient of determination (R^2) estimates the amount of species diversity that can be explained by the independent variable alone. Our value of 76% for West Indian bats falls between the values of 69% for West Indian mammals generally (Morgan and Woods, 1986) and 88% for West Indian bat faunas (Griffiths and Klingener, 1988). In comparison, the variance for West Indian butterflies (64%) was lower than any of the mammalian values. With 24% of the variance dependent on factors other than area, it is interesting to examine a species/altitude curve (Fig. 3, log of species number versus log of altitude in meters) for

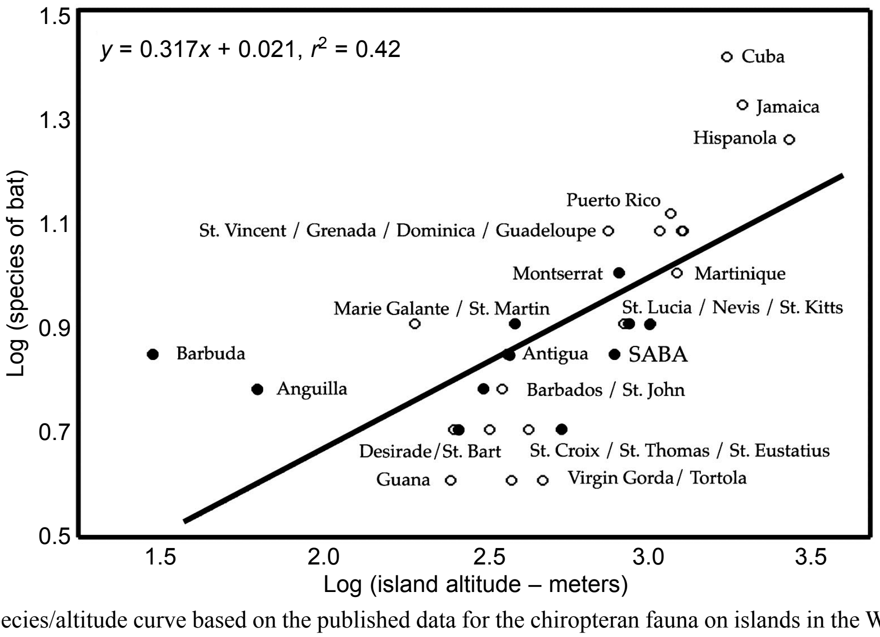

FIG. 3. Species/altitude curve based on the published data for the chiropteran fauna on islands in the West Indies

West Indian bats. This analysis should give a better estimate of available habitat diversity than would the area of the island alone because plant communities in the West Indies are greatly influenced by altitude. Our analysis gives a $z = 0.32$ and $R^2 = 0.42$. Although this indicates that altitude can certainly influence the number of species of bats on islands, altitude has less influence than does area. Indeed, Fig. 3 shows that Saba has fewer species than would be predicted by its elevation. However, habitat diversity associated with high elevations may ameliorate the effect of small geographic area available to bats on small islands such as Saba.

In summary, we propose to unite the chiropteran faunas of the islands of Anguilla, Antigua, Barbuda, Nevis, Saba, St. Barthélemy, St. Eustatius, St. Kitts, and St. Martin into the “Northern Antillean Faunal Area.” These island faunas share the eight species of bats and no endemic taxa. This faunal area can be seen as a transition zone between the Lesser Antillean Faunal Core and the Greater Antillean Faunal Core, which includes the bat fauna of Cuba, Hispaniola, Jamaica, and Puerto Rico.

On an island as small as Saba, there must be a basic underlying concern about the conservation of all members of the flora and fauna. Despite bat diversity, we encountered low population numbers. Several local biologists even commented to us that both the bird and bat populations had been seriously depressed since Hurricane Lenny in 1999. Our own experiences in 2002 confirm the lack of birds. We believe that the area problem faced by bats on Saba is even more severe than would be initially anticipated because most of the species restrict their activity to the northern third of the island. This part of the island offers the best forests on the island, which provide foraging and roosting opportunities for bats, are less affected by the trade winds, and offer the most protection from tropical storms and hurricanes. This leaves phyllostomid populations on Saba with as little as 4 km^2 of effective area on the island.

Human activity or the lack thereof provides little concern for the conservation status of bats on Saba. The small settlements on the island are confined primarily to the southern and eastern parts of the island where we found only low-levels of bat activity and we believe that this was historically the situation as well. There has been no large-scale agricultural development on the island to alter the available habitat and most of the subsistence farming has been conducted in the areas adjacent to human settlements. In the Caribbean, there is always the threat of natural disasters, such as hurricanes and volcanic activity, which may lead to extinction events, but it must be remembered that this chiropteran fauna evolved in this disaster-dominated ecosystem. However, if human activity is factored into the conservation status of this fauna, we would urge the Government to expand the Saba National Park to the west to include Mary’s Point Mountain and if possible to extend as far west as Bottom Hill. This would protect not only the primary areas used by the bat fauna of the island but also some of the important floral elements as well. Central to the conservation of bat faunas throughout the Caribbean is the protection of caves and habitats that surround cave entrances. On Saba, this is not so much an issue as it is elsewhere (for example, St. Maarten, Nevis), nevertheless, we are convinced that all natural rock shelters and caves should be safeguarded as they are vital to the protection of bats, if only during those times of natural disasters.

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