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Bats of Sint Eustatius, Caribbean Netherlands

Front cover: Photograph of the island of St. Eustatius, Caribbean Netherlands. This view, taken at 0650 hr on 14 October 2015, is looking south from The Mountains in the Boven National Park near the northern end of the island. The nearest volcano is The Quill in The Quill National Park. Only a small portion of the city of Oranjestad can be seen along the lower slopes of The Quill. The volcano in the distance is Mount Liamuiga on the island of St. Kitts. Photograph by Wesley Overman.

Bats of Sint Eustatius, Caribbean Netherlands

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Abstract

The bat fauna of the Caribbean island of Sint Eustatius consists of five documented species—*Monophyllus plethodon*, *Brachyphylla cavernarum*, *Artibeus jamaicensis*, *Ardops nichollsi*, and *Molossus molossus*—and one provisional species—*Tadarida brasiliensis*. The Insular Single-leaf Bat, *M. plethodon*, is reported in the scientific literature for the first time from Sint Eustatius based on material presented herein. The bat fauna of the island is considered to be unbalanced because only three species, which are the environmental generalists, are abundant, whereas the more specialized species are rare or absent from the fauna. It is our hypothesis that the unbalanced bat fauna on St. Eustatius is the result of chronic environmental degradation and destruction due primarily to human activity.

Key words: anthropogenic impact, Chiroptera, distribution, environment, goat impacts, Mammalia, *Monophyllus*, natural history, Sint Eustatius

Introduction

The island of Sint Eustatius lies near the northern end of the Volcanic Caribbees in the Lesser Antilles. Dominated by the volcanic cone of The Quill, the island is covered primarily by low thorny vegetation and open grasslands. Only on the upper slopes of The Quill and in the bottom of its crater are larger, more tropical trees found. The flora has been highly impacted by human activities, beginning with the first permanent settlements by the Dutch in 1636. During this early period, the growing of sugar cane was extensive, using all available space. In the eighteenth century, St. Eustatius was an important trans-shipment point for the trans-Atlantic slave trade, making this the boom period for the economy of the island. The subsequent economic collapse has been reversed only recently with the appearance of Caribbean tourism activities on the island (Rojer 1997; Lindsay et al. 2005).

The flora and fauna of St. Eustatius has been the subject of considerable study by Dutch scientists (Rojer 1997), but for some reason bats have received little study. Not even Husson (1960) listed any bat specimens from St. Eustatius in his classic work "Mammals of the Netherlands Antilles." The first report of bats from the island was by Jones and Schwartz (1967) when they reported specimens of *Ardops nichollsi* from both the rim and the bottom of The Quill. In 1968, Koopman (1968) reported specimens of four additional species—*Brachyphylla cavernarum*, *Artibeus jamaicensis*, *Molossus molossus*, and *Tadarida brasiliensis*—without reference to any specific localities. Herein, we add *Monophyllus plethodon* as a sixth species of bat reported from St. Eustatius.

As part of our ongoing studies of the chiropteran fauna of the Lesser Antilles, the American field research teams visited the island on four occasions—3 to10 July 2002; 26 to 30 May 2003; 25 to 29 May 2004; and 19 to 23 March 2009. During these periods, the American team was able to sample 18 sites on the island and examined 375 individuals of four species of bats. The Dutch field research team visited St. Eustatius from 2 to 18 October 2015. They sampled nine sites on the island and examined 146 individuals of five species of bats. Combining these data allowed us to bring together for the first time all of the available information to develop a more complete understanding of the bat fauna of St. Eustatius.

The bat fauna of St. Eustatius is under stress from long-term environmental degradation due primarily to human impacts. The St. Eustatius National Parks

Foundation, known locally as Stenapa, was established in 1995 and is now responsible for environmental protection and monitoring of the island's flora and fauna. The Quill/Boven National Park—consisting of two sub-sectors, the dormant volcano "The Quill" and the "Boven" area covering five hills in the north of St. Eustatius—that was created to protect unique biodiversity may allow the island's bat populations to rebound in the future.

Methods and Materials

Study site.—St. Eustatius is one of the Volcanic Caribbees located in the northern Lesser Antilles—the neighboring islands are Saint Kitts (distant from 15 km; surface of 176 sq km), Nevis (distant from 47 km; surface of 93 sq km), Saba (distant from 28 km; surface of 12 sq km), Saint-Barthelemy (distant from 44 km; surface of 25 sq km), and Sint Maarten (distant from 56 km; surface of 85 sq km) (Fig. 1). During the Last Glacial Maximum, it was joined with St. Kitts and Nevis to form the St. Kitts bank. St. Eustatius, like its neighbor Saba just to the north, is of recent volcanic origin. The island has an area of 21 square km. Three landform types can be distinguished—the northwest hilly area of The Mountains consisting of five coalesced older volcanoes (late Pliocene), the flat center, and the southeast part with the dominant feature of the island,

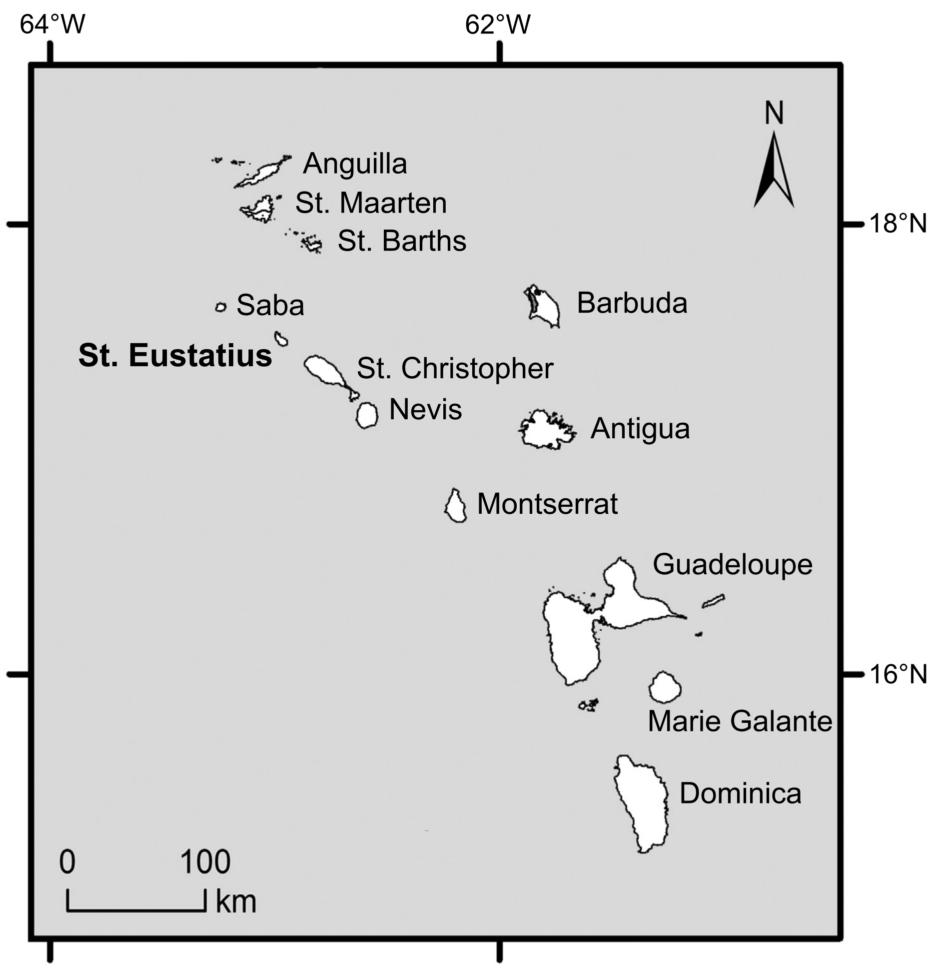

Figure 1. Map of the northern Lesser Antilles, showing the position of the island of Sint Eustatius in relation to other islands in the region.

The Quill. The Quill is a high cone-shaped stratovolcano with a round crater about 800 m wide (Lindsay et al. 2005). The rim of The Quill is highest on the eastern side at 600 m and lowest on the western side at 378 m with the bottom of the crater at 273 m. The Quill was a Holocene volcano, which was most recently active about 1600 years ago. The primary settlement, Oranjestad, is located along the west side of the island, to the northwest of The Quill. The lower flat parts of the island are used for grazing goats and cattle. An oil-trans-shipment company occupies a large part of The Mountains where oil from around the world is brought and mixed before shipping to its final destination (Rojer 1997; Lindsay et al. 2005).

St. Eustatius has a tropical climate with an average annual precipitation of 107.3 cm and a yearly average temperature of 25.7° C. The native flora of the island has been highly disturbed or destroyed by agricultural practices in the past and continued unrestricted grazing by goats and cattle. Old maps of the island indicate that plantations were growing sugar cane in every available area including the slopes of The Quill almost to its rim. Essentially all vegetation on the island should be considered to be secondary and much of it is in a pioneer state. In recent years, flora and vegetation types of St. Eustatius have come under considerable study (Rojer 1997; Helmer et al. 2008; de Freitas et al. 2014; Debrot et al. 2015; Posthouwer 2016; van Andel et al. 2016). These publications are in general agreement, but there are some specific disagreements and updating that occurs; therefore, we have followed van Andel et al. (2016).

Inside the crater of The Quill the flora is an evergreen seasonal forest, which is dominated by Cotton Tree (*Ceiba pentandra*), Yellow Plum (*Spondias mombin*), Trumpet Tree (*Cecropia schreberiana*), and Strangler Fig (*Ficus nymphaeifolia*). There is also evidence of past attempts to raise fruit trees in the crater with the presence of such trees as Coffee (*Coffea arabica*), Cocoa (*Theobroma cacao*), and Mammee Apple (*Mammea americana*). The dry evergreen forest of the crater rim has nearly three times as many plant species as the bottom of the crater. Among the trees that would provide valuable fruit for bats are West Indian Laurel Fig (*Ficus americana*), Serrettes (*Byrsonima spicata*), Swartz's Pigeonplum (*Coccoloba swartzii*), Smooth Star Apple (*Chrysophyllum argenteum*), and Pitch Apple (*Clusia major*). The dry evergreen forest extends down the slopes of The Quill to about 250 m with a different composition of species than the rim, including such species as White Cedar (*Tabebuia heterophylla*), Fiddlewood (*Citharexylum spinosum*), Gumbo-limbo (*Bursera simaruba*), Burn Nose (*Daphnopsis americana*), and White Pricklyash (*Zanthoxylum martinicense*). Thorny woodland prevails below 250 m, which is the area that continues to receive the greatest impact from humans. Depending upon the portion of the volcanic cone being studied, different plant species dominate, such as members of the genus *Acacia*, including Porknut (*A. macracantha*). In some areas Water Mampoo (*Pisonia subcordata*) comprises 62% of the canopy, whereas in other areas Black Scrub (*Quadrella cynophallophora*) comprises 41%. Other common species in these areas are White Indigoberry (*Randia aculeata*), Poisonberry (*Bourreria baccata*), Rough Velvetseed (*Guettarda scabra*), and Black Ironwood (*Krugiodendron ferreum*). In the northern hills, two vegetation types have been identified depending on their exposure. In more protected areas, Rat Apple (*Morisonia americana*) and Stinkwood (*Piscidia carthagenensis*) are among the common elements, whereas exposed areas of open grassy shrubland are dominated by a few trees including Braceletwood (*Jacquinia armillaris*), Falseteeth (*Cynophalla flexuosa*), and Guadeloupe Marlberry (*Ardisia obovata*). In the areas used for grazing of cattle and abandoned agricultural land, invasive Corallita Vine (*Antigonon leptopus*) smothers both natural and introduced vegetation. There are only scattered trees in these areas such as the invasive Bellyache Bush (*Jatropha gossypiifolia*) and the Whitelead Tree (*Leucaena leucocephala*), the latter having been imported to provide low-grade forage for animals.

Introductions of such carnivores as domestic cats undoubtedly have had a negative impact on bat populations by direct predation (Rodríguez-Durán et al. 2010; Welch and Leppanen 2017). Members of the American Team observed cats pulling bats out of mist nets. Feral domestic animals certainly have an impact on bat populations through habitat degradation, erosion, and competition for food resources. Debrot et al. (2015) conducted an extensive study of free roaming livestock on St. Eustatius in 2013, obtaining population estimates for the four most abundant feral animals on the island as follows: goats, 2470 ± 807; chickens, 2248 ± 668; cattle, 600; and sheep, minimum count

300. Their conclusion was that these population levels were beyond the carrying capacity of the island and a significant threat to its biodiversity and the restoration of natural vegetation. In a unique study, Posthouwer (2016) investigated the impact of human extraction on the wild plants of St. Eustatius, finding that the residents of St. Eustatius mentioned the names of 181 species of plants as being useful and that 66 species of those were harvested only from the wild. Although this level of extraction of wild resources must have an impact on the quality of local flora, they identified only four species that could encounter sustainability problems under their harvesting activity—Turk's Head Cactus (*Melocactus intortus*); Sweet Torchwood (*Nectandra coriacea*); Organ Pipe Cactus (*Pilosocereus royenii*); and West Indian Milkberry (*Chiococca alba*).

St. Eustatius lies in an active part of the Atlantic hurricane track. Major hurricanes that have impacted the island in recent years included Irma (h5) in September 2017, Lenny (h4) in November 1999, Jose (h1) in October 1999, Georges (h3) in September 1998, Luis (h4) and Marilyn (h1) both in September 1995, and Hugo (h4) in September 1989 (de Freitas et al. 2014; Caribbean Hurricane Network 2017). Although these storms most certainly impact bat populations, it is likely that bat species of the Lesser Antilles have adapted to such disturbances (Pedersen et al. in prep.).

Mist netting.—Mist netting was conducted in a variety of habitats including naturally vegetated ravines, access roads, trails, swimming pools and water catchments, fruit groves, secondary forest, a botanical garden, and the rim and bottom of The Quill. The American Team set five to eight mist nets (2.8, 6, 9, 12, or 18-m length by 2.8 m height) either singly or in groups at 20 to 100-m intervals, depending on local landscape features. Nets were opened near sunset (1800–1900 hr) and closed between 2100 and 2300 hr each night, depending on weather and activity. The Dutch Team set one to three nets of 3, 7, or 10-m length per night. Their nets were opened near sunset (1750–1800 hr) and closed between 2000 and 2340 hr each night, depending on weather and activity. Bats caught in nets were placed in holding bags and subsequently measured for: weight (given in grams), length of forearm (mm), reproductive condition, tooth wear, presence of ectoparasites, and scars. We followed R. Larsen et al. (2007; see also Findley and Wilson 1983) for determining capture rates of bats (bats per net per night or BNN). Together, we conducted 126 net-nights of work to capture 521 individuals of five species of bats at 26 sites (Fig. 2).

The American Team's designation of a few collecting sites on St. Eustatius varied between research seasons. Specimens cataloged at the University of Nebraska State Museum as "Emmaweg Street" from 2002 are from the exact same site as the specimens cataloged at the Museum of Texas Tech University as "Oranjestad Town Square" from 2003. We have used the latter designation throughout this paper. We collected at two sites related to the former medical school. One site was at the Golden Rock and the other was near the police station on Van Tonningenweg. The American and Dutch teams duplicated only two collecting sites—the Botanical Garden and Old Gin House. On the rim of The Quill, the teams collected at sites in close proximity to each other.

Museum voucher specimens.—We captured 521 bats, 371 of which were examined, measured, and released. We preserved 150 voucher specimens that were deposited in the mammal collections of the Museum of Texas Tech University (TTU) and the University of Nebraska State Museum (UNSM). We examined 12 additional specimens that were deposited in other museums: American Museum of Natural History (AMNH); Natural History Museum, University of Kansas (KU); and Museum of Comparative Zoology, Harvard University (MCZ).

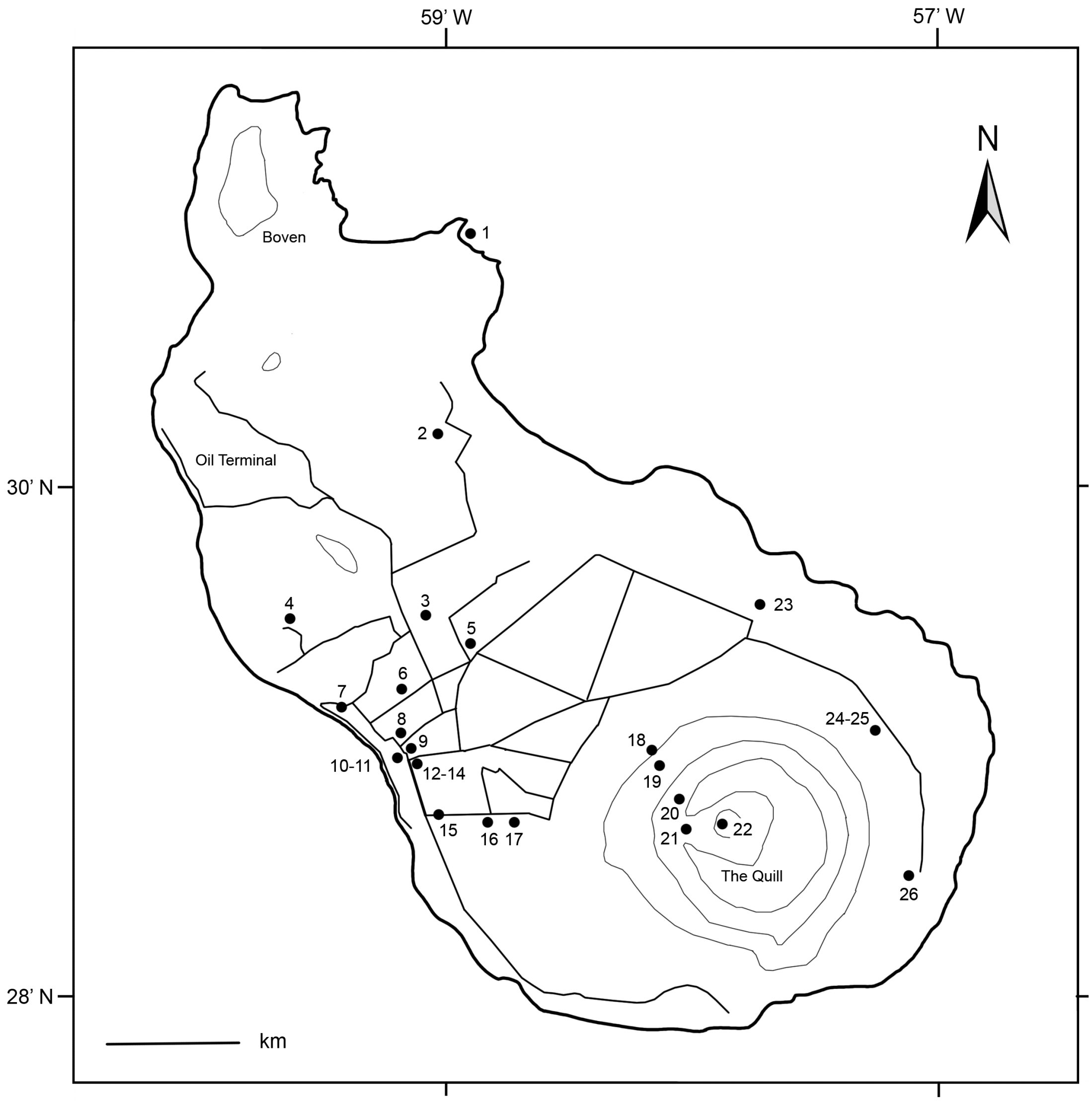

Figure 2. Map of Sint Eustatius showing the location of sites visited during field research on the bat fauna of the island. 1, sea caves, Venus Bay; 2, Solitude; 3, near F. D. Roosevelt Airport; 4, Billy's Gut; 5, Medical School Golden Rock; 6, Pond at New Ground; 7, Kings Well Resort; 8, Medical School on Van Tonningenweg; 9, Fort Oranje; 10, Old Gin House and Claes Gut; 11, Old Gin House; 12, Oranjestad Town Square; 13, Oranjestad; 14, Charlie's Place; 15, Tijgerweg; 16, intersection of Rosemarylaan and De Ruyterweg; 17, Garden Gilheads; 18, Mountain Piece; 19, 1.5 km E Oranjestad; 20, trail at edge of crater rim; 21, Rim of The Quill; 22, Bottom of The Quill; 23, English Quarter; 24, Knippenga Estate; 25, road to Botanical Garden; 26, Miriam C. Schmidt Botanical Garden. Dark lines on the island are roads and streets in Oranjestadt. The lighter lines are contour lines with the top of The Quill at 600 m. See text for the full description of work sites.

SPECIES ACCOUNTS

In the following six species accounts, we present the known information for each species of bat on St. Eustatius, including specimens examined, taxonomy, habitat preferences, reproduction, and weight data. Measurements of the length of forearm and seven cranial measurements are provided for males and females of four species for which we have specimens available for study. Weights were determined with a digital balance and recorded in grams (g). Forearms and crania were measured with digital calipers and recorded in millimeters (mm). All measurements of embryos are crown-rump length (mm) and testes measurements are of length (mm). Distances were recorded in kilometers (km) as they appeared on original specimen tags. All elevations are reported in meters (m). All times listed in text use a 24-hr clock.

Monophyllus plethodon plethodon Miller, 1900
Insular Single-leaf Bat

Specimen captured/released (1).—Near where the hiking trail from Yellow Rock comes to the edge of the crater of The Quill [17°28'42.1"N, 62°57'55.2"W], 1.

Remarks.—On 15 October 2015 the Dutch field research team captured a single adult female of this species at the edge of the crater of The Quill. This is the first record of the Insular Single-leaf Bat from St. Eustatius. The specimen was not preserved because of fear of damaging a small population, but there are excellent photographs available, which clearly reveal the characteristics typical of this species (Fig. 3). This individual weighed 15.5. Sunset on this date was 1750 hr and the bat was captured at 1820 hr. In addition to the *M. plethodon*, the Dutch Team also captured at this site one *B. cavernarum*, 21 *A. jamaicensis*, and one *A. nichollsi*. The vegetation in the area of the rim of The Quill was dry evergreen forest, with epiphytes and bromeliads as described in the Study Site section.

Figure 3. Photograph of a female *Monophyllus plethodon*, which was the first individual of this species captured on St. Eustatius. This bat was taken at the edge of the crater of The Quill. Note the elongated rostrum, simple noseleaf, and presences of a tail characteristic of this species.

On this evening the Dutch Team set a 3-m net at a height of 5 m in the middle of the hiking trail from Yellow Rock where it comes near to the edge of the crater of The Quill, and a 7-m net was placed at a right angle to the 3-m net along the rim of the crater. These nets were undoubtedly set near where the American Team had placed a 12-m net in both 2003 and 2004 without capturing this species. The net set by the American Team nearly filled the flyway created between a large, buttress-rooted fig tree and large boulder on the opposite side of the trail. This was the lowest point on the rim of the crater where the trail to the bottom of The Quill began its descent. A total of 109 bats were taken by the American Team at this location, capturing 16 *Brachyphylla*, 20 *Artibeus*, and 73 *Molossus*. Early in the evening netting, bats were captured exiting the crater, but within an hour bats were traversing in both directions. This graphically illustrates the difficulty of surveying these islands with small populations of some species of bats. As we have discussed previously, species on these small islands may occupy even a very small part of the area available (Genoways et al.

2007a, 2007b). It is worth noting that the American Team caught 73 *Molossus* while the Dutch Team caught none, although they did observe hundreds of *Molossus* flying in and out of the crater over the tops of the trees far and above their nets. This emphasizes the conclusions made by R. Larsen et al. (2007) regarding the inefficiency and idiosyncrasies of using mist nets to sample bat populations.

Schwartz and Jones (1967), who were the last revisers of the genus *Monophyllus*, would have included St. Eustatius within the geographic range of the subspecies *M. p. luciae*. However, Kwiecinski et al. (in prep.) demonstrated that there was "no continuing need to recognize the taxon *Monophyllus plethodon luciae* Miller 1902 and it should be placed as a junior synonym of *Monophyllus plethodon plethodon* Miller 1900." Thus, we provisionally recognize the St. Eustatius population as *M. plethodon plethodon*. We recommend future genetic analyses aimed at examining the presence or absence of phylogenetic and/or population structure across the Lesser Antillean distribution of *M. plethodon*.

Although this was the first record of the Insular Single-leaf Bat from the island, the species was expected to occur here because it is present on the surrounding islands of Saba (Genoways et al. 2007a), St. Kitts (Pedersen et al. 2005), and St. Maarten (Genoways et al. 2007b). This pollenivorous species will take insects in times of protein stress. We have found this species in good numbers in similar xeric habitats on other small islands such as Anguilla (Genoways et al. 2007c), Antigua (Pedersen et al. 2007), Barbuda (Pedersen et al. 2007), and Barbados (Genoways et al. 2011). Insular Single-leaf Bats may be far rarer on St. Eustatius than on other islands because of the widespread and prolonged human impact on the vegetation of the island. We expect that this species confines its day roosts to crevices and small pockets in the crater walls of The Quill. It probably leaves this area only when plants are flowering along the slopes of the cone or in small gardens and orchards surrounding Oranjestad.

Brachyphylla cavernarum cavernarum Gary 1834
Antillean Fruit-eating Bat

Specimens examined (31).—Billy's Gut, 50 m [17°29'23.8"N, 62°59'33.4"W], 3 (TTU 101974–76); Bottom of The Quill, 278 m [17°28'40"N, 62°57'51"W], 1 (TTU 102004); Garden Gilheads, 0.5 km S, 0.75 km E Oranjestad, 96 m [17°28'43.7"N, 62°56'46.0"W], 2 (TTU 111036–37); Miriam C. Schmidt Botanical Garden, 0.75 km S, 3.5 km E Oranjestad, 79 m [17°28'26.0"N, 62°57'05.9"W], 3 (TTU 111038–40); Mountain Piece, 196 m [17°28'59.3"N, 62°58'09.0"W], 1 (TTU 101994); Old Gin House, on coastal road, 0.5 km W Oranjestad [17°28'55.3"N, 62°59'14.0"W], 1 (UNSM 27979); Oranjestad Town Square [17°28'56.1"N, 62°59'10.3"W], 2 (UNSM 27962–63); Rim of The Quill, 400 m [17°28'40"N, 62°58'01"W], 15 (4 AMNH 213906–09; 11 TTU 102025, 102060–69); sea caves, Venus Bay, 3 m [17°31'21.7"N, 62°59'26.8"W], 2 (TTU 111041–42); no specific locality, 1 (MCZ 19500).

Additional records.—Rim of The Quill (Swanepoel and Genoways 1978); no specific locality (Koopman 1968).

Specimens captured/released (22).—Billy's Gut, 50 m [17°29'23.8"N, 62°59'33.4"W], 2; adjacent to F. D. Roosevelt Airport [17°29'25.5"N, 62°59'07.7"W], 1; Garden Gilheads, 0.5 km S, 0.75 km E Oranjestad, 96 m [17°28'43.7"N, 62°56'46.0"W], 9; Kings Well Resort [17°29'09.1"N, 62°59'27.2"W], 1; Mountain Piece, 196 m [17°28'59.3"N, 62°58'09.0"W], 3; near where the hiking trail from Yellow Rock comes to the edge of the crater of The Quill [17°28'42.1"N, 62°57'55.2"W], 1; Rim of The Quill, 400 m [17°28'40"N, 62°58'01"W], 5.

Remarks.—The genus *Brachyphylla* is endemic to the Antilles and includes two species (Swanepoel and Genoways 1978). The larger of the two, *B. cavernarum*, is known from Puerto Rico, the Virgin Islands, and the Lesser Antillean islands as far south as St. Vincent and Barbados (Fig. 4). The members of the nominate subspecies occur on St. Croix in the Virgin Islands and throughout the Lesser Antillean islands south to St. Lucia and St. Vincent. A small-sized subspecies, *B. c. minor*, occurs on Barbados (Genoways et al. 2011) and a third subspecies, *B. c. intermedia*, was found on Puerto Rico and all Virgin Islands, except St. Croix (Swanepoel and Genoways 1978). In their analysis of geographic variation in *B. cavernarum*, Swanepoel and Genoways (1978) grouped the individuals from St. Eustatius in their sample 16, which clustered most closely with samples from St. Croix, St. Martin, Barbuda, and

Figure 4. Photograph of a female *Brachyphylla cavernarum* taken from a mango tree near the F. D. Roosevelt Airport on the island of St. Eustatius. Note the greatly reduced nose-leaf and gray coloration characteristic of this species.

Martinique confirming the placement of St. Eustatius individuals in the nominate subspecies. Individuals from St. Eustatius and Barbuda averaged among the largest in measurements for the subspecies. Carstens et al. (2004) examined the genetic structure of northern Lesser Antillean populations of *B. cavernarum*, and they included two individuals collected from St. Eustatius in their analyses. Their results showed low genetic diversity (within the mitochondrial cytochrome-*b* gene) across the islands of St. Maarten, St. Eustatius, Saba, Nevis, and Montserrat. The two individuals examined from St. Eustatius differed by a single nucleotide in cyt-*b* sequences and these haplotypes were identified on neighboring islands (Carstens et al. 2004). Despite the lack of genetic structure observed in cyt-*b* gene variation, we recommend additional genetic analyses, perhaps using advanced genetic approaches appropriate for population-level genetic resolution (for example, high-throughput Restriction site Associated DNA Sequencing; RAD-seq), of Caribbean populations of *B. cavernarum*.

Analysis of length of forearm and seven cranial measurements for nine male and five female (Table 1) Antillean Fruit-eating Bats revealed only slight secondary sexual dimorphism. Of the eight measurements studied, only one, mastoid breadth, revealed a significant difference ($P \leq 0.05$ level) between males and females, with males averaging larger. Average male measurements were larger for four other measurements, whereas females averaged larger only in breadth across upper molars and the sexes average the same in greatest length of skull and postorbital constriction. Swanepoel and Genoways (1978) found males to be generally larger than females and concluded that there was sufficient secondary sexual dimorphism to analyze the sexes separately. This conclusion was not supported by our data; however, their sample from St. Eustatius was composed only of males.

Billy's Gut was a ravine situated between steep scrubby hillsides covered in scree fields. Five mist nets were placed amongst the sparse forest that covered the dry bottomlands of the gut. These nets captured five *Brachyphylla* and nine *Molossus*.

The site that we called Mountain Piece was located along a small gut that extended up on the lower northwestern slopes of The Quill centered at an elevation of 196 m. The vegetation was a mix of thorny woodland and semi-evergreen seasonal forest. There was evidence of cattle grazing in the area and the site was undoubtedly logged at some time in the past. Nine nets set in this area captured four *Brachyphylla*, six *Artibeus*, and nine *Molossus*.

Venus Bay is located on the northeast coast of St. Eustatius where several large erosion cavities were noted along the jagged beach, two of which were large enough (12 to 15 m deep with entrances of approximately 3 m in height) to shelter a colony of nearly 250 *Brachyphylla*. These caves were located on the east-facing side of the promontory at the southern edge of the bay.

Near the F. D. Roosevelt Airport on 14 October 2015, two 3-m nets were placed under a fruiting Mango Tree (*Mangifera indica*) in the backyard of a local home. These nets captured an adult female *B. cavernarum* and three *A. jamaicensis*, although many more bats were observed foraging on the ripe fruits in the tree. This *Brachyphylla* entered the net at 1910 hr, with sunset having occurred at 1751 hr. The airport was located in an open grassland area at the northern edge of Oranjestad in the lowland saddle in the middle

Table 1. Length of forearm and seven cranial measurements for specimens of four species of bats from Sint Eustatius, Caribbean Netherlands. ns = non–significant; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

Statistics 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
Brachyphylla cavernarum cavernarum								
Males (N = 9)								
Mean ± SE	65.1±0.49	31.8±0.08	28.7±0.0.4	17.2±0.13	6.4±0.04	14.9±0.08	11.2±0.09	11.6±0.06
Range	(63.5–67.4)	(31.4–32.2)	(28.5–28.9)	(16.6–17.9)	(6.3–6.7)	(14.5–15.3)	(10.8–11.7)	(11.2–11.8)
Females (N =5)	ns	ns	ns	ns	ns	*	ns	ns
Mean ± SE	64.6±0.45	31.8±0.15	28.6±0.13	17.1±0.12	6.4±0.09	14.6±0.13	11.2±0.11	11.7±0.08
Range	(63.2–65.9)	(31.4–32.1)	(28.3–29.0)	(16.8–17.4)	(6.2–6.7)	(14.2–15.0)	(10.9–11.5)	(11.5–11.9)
Artibeus jamaicensis jamaicensis								
Males (N =9)								
Mean ± SE	59.4±0.51	28.1±0.10	24.7±0.13	16.5±0.11	7.0±0.04	14.6±0.09	9.9±0.03	12.2±0.10
Range	(57.5–61.5)	(27.6–28.5)	(24.2–25.4)	(16.1–17.0)	(6.8–7.1)	(14.1–15.0)	(9.7–10.0)	(11.8–12.7)
Females (N = 9)	ns	ns	ns	ns	ns	ns	ns	ns
Mean ± SE	60.3±0.68	28.3±0.17	25.0±0.20	16.5±0.17	7.1±0.08	14.7±0.09	9.8±0.07	12.4±0.14
Range	(56.5–63.5)	(27.1–28.7)	(23.6–25.6)	(15.4–17.0)	(6.8–7.4)	(14.2–15.0)	(9.5–10.1)	(11.7–12.9)
Ardops nichollsi montserratensis								
Males (N = 6)								
Mean ± SE	48.5±0.50	22.9±0.10	20.1±0.06	15.1±0.09	5.9±0.06	12.4±0.07	7.5±0.04	9.9±0.08
Range	(47.2–51.1)	(22.6–23.3)	(20.2–21.4)	(14.8–15.4)	(5.7–6.1)	(12.2–12.6)	(7.3–7.6)	(9.7–10.2)
Females (N = 7)	**	***	***	**	ns	***	***	**
Mean ± SE	51.2±0.50	24.1±0.11	21.0±0.15	15.7±0.10	6.0±0.10	13.0±0.04	8.0±0.08	10.4±0.11
Range	(49.7–52.9)	(23.7–24.5)	(20.2–21.4)	(15.2–16.0)	(5.6–6.4)	(12.8–13.1)	(7.7–8.3)	(10.0–10.9)
Molossus molossus molossus								
Males (N = 7)								
Mean ± SE	38.7±0.31	16.9±0.12	14.7±0.05	10.3±0.07	3.4±0.03	9.8±0.07	5.8±0.04	7.3±0.05
Range	(37.7–40.2)	(16.5–17.5)	(14.5–14.9)	(10.2–10.7)	(3.2–3.4)	(9.5–10.1)	(5.6–6.0)	(7.2–7.5)
Females (N =7)	ns	***	***	**	***	***	**	***
Mean ± SE	37.9±0.34	16.1±0.12	14.0±0.10	9.9±0.07	3.2±0.04	9.4±0.06	5.5±0.04	7.0±0.06
Range	(36.5–39.1)	(15.7–16.7)	(13.6–14.3)	(9.7–10.2)	(3.2–3.3)	(9.1–9.5)	(5.4–5.7)	(6.8–7.2)

of the island. An adult male was taken over the swimming pool at Kings Well Resort at 2045 hr on 3 October (sunset at 1800 hr) and another male was taken at the edge of the crater at 1826 hr on 15 October (sunset at 1750 hr).

Five pregnant females were collected between 20 and 23 March, with two of the embryos measuring 10 and 22 in crown-rump length. Four females obtained 28–29 May were lactating. A female Antillean Fruit-eating Bat taken on the evening of 25 May gave birth overnight, with the neonate having a length of forearm 38.5 as compared to 66 for the mother. Females taken on 7 and 10 July were lactating. Two males taken on 9 March had testes length of 6 and 7.5, whereas five taken between 20 and 23 March had an average testes length of 5.8 (4–7). Although these are minimal reproductive data, they are in agreement with the findings of previous authors (Wilson 1979; Swanepoel and Genoways 1983; Kwiecinski et al. in prep.; Pedersen et al. in prep.) that the reproductive cycle of *B. cavernarum* was synchronous, seasonal monestry. The female reproductive cycle begins with breeding early in the dry season (December–January), with gestation occurring from January through April during the dry season and parturition starting at the beginning of the wet season in May.

The female and neonate from 25 May had a combined weight of 56.5, with the neonate weighing 15.1. Three lactating females obtained on 29 May had weights of 39.3, 41.6, and 44.2, and two lactating females obtained on 7 and 10 July weighed, respectively, 46.2 and 38.0. The average weight of nine non-pregnant females netted in late May was 43.3 (39.2–49.0) and one from 7 July weighed 42.2. Four male Antillean Fruit-eating Bats collected on 20 and 22 March had average weights of 46.0 (43.5–47.5). Seven males obtained in late May had an average weight of 44.1 (40.2–47.2). Two males taken in the first half of October weighed 45 and 46 and a female taken at this time weighed 56.

Artibeus jamaicensis jamaicensis Leach 1821
Jamaican Fruit-eating Bat

Specimens examined (56).—Bottom of The Quill, 278 m [17°28'40"N, 62°57'51"W], 32 (21 TTU 101981–90, 102000, 102005–14; 11 UNSM 27954–60, 27974–78); Fort Oranje [17°28'55.3"N, 62°59'12.3"W], 1 (TTU 101991); Garden Gilheads, 0.5 km S, 0.75 km E Oranjestad, 96 m [17°28'43.7"N, 62°56'46.0"W], 2 (TTU 110937–38); New Ground, N end Oranjestad [17°29'26.2"N, 62°59'14.0"W], 1 (UNSM 27978); Miriam C. Schmidt Botanical Garden, 0.75 km S, 3.5 km E Oranjestad, 79 m [17°28'26.0"N, 62°57'05.9"W], 1 (TTU 110939); Mountain Piece, 196 m [17°28'59.3"N, 62°58'09.0"W], 1 (TTU 101992); 1.5 km E Oranjestad, 236 m [17°28'58.8"N, 62°58'03.3"W], 2 (TTU 110935–36); Oranjestad Town Square [17°28'56.1"N, 62°59'10.3"W], 2 (UNSM 27972–73); Rim of The Quill, 400 m [17°28'40"N, 62°58'01"W], 12 (2 AMNH 213923–24; 10 TTU 101995–97, 102024, 102054–59); Solitude, 2 km N, 0.4 km E Oranjestad, 26 m [17°30'09.4"N, 62°59'00.6"W], 1 (TTU 110940); Tijgerweg, Oranjestad [17°28'46.5"N, 62°59'03.2"W], 1 (UNSM 27961).

Additional record.—No specific locality (Koopman 1968).

Specimens captured/released (124).—Bottom of The Quill, 278 m [17°28'40"N, 62°57'51"W], 11; adjacent to F. D. Roosevelt Airport [17°29'25.5"N, 62°59'07.7"W], 3; Garden Gilheads, 0.5 km S, 0.75 km E Oranjestad, 96 m [17°28'43.7"N, 62°56'46.0"W], 53; Kings Well Resort [17°29'09.1"N, 62°59'27.2"W], 5; Old Gin House [17°28'55.3"N, 62°59'14.1"W], 2; Mountain Piece, 196 m [17°28'59.3"N, 62°58'09.0"W], 5; near where the hiking trail from Yellow Rock comes to the edge of the crater of The Quill [17°28'42.1"N, 62°57'55.2"W], 21; 1.5 km E Oranjestad, 236 m [17°28'58.8"N, 62°58'03.3"W], 11; Rim of The Quill, 400 m [17°28'40"N, 62°58'01"W], 10; Solitude, 2 km N, 0.4 km E Oranjestad, 26 m [17°30'09.4"N, 62°59'00.6"W], 2; near corner of Rosemarylaan and De Ruyterweg, Oranjestad [17°28'43.0"N, 62°59'04.2"W], 1.

Remarks.—This fruit-eating species was particularly abundant in The Quill and around its rim and upper slopes (Fig. 5). It is tolerant of light in its day roosts so the small crevices and holes in the inner wall of the crater would have provided excellent spaces. Genoways et al. (2001) reviewed morphological variation in selected Antillean populations of this species. Our St. Eustatius sample (Table 1) closely matches the measurements of other samples of *A. j. jamaicensis* from Jamaica,

Figure 5. Photograph of a male *Artibeus jamaicensis* from swimming pool of the Kings Well Resort on the island of St. Eustatius. Note the large nose-leaf, white stripe over the eye, and brown coloration, all characteristic of this species.

Hispaniola, Puerto Rico, St. John, and Dominica (Genoways et al. 2001). P. Larsen et al. (2007) included 10 individuals of *A. jamaicensis* collected from St. Eustatius in their phylogenetic analysis of the *Artibeus jamaicensis* complex. Their results show a single mitochondrial cytochrome-*b* haplotype shared among the 10 individuals and this haplotype was also shared with individuals collected from a wide geographical distribution, ranging from Quintana Roo, Mexico, eastward to Jamaica and Puerto Rico, throughout the northern Lesser Antilles, and as far south as Carriacou in the Grenadines. The results of P. Larsen et al. (2007) support the hypothesis of a recent Caribbean colonization by *A. jamaicensis* (perhaps within the last ~25,000 years) originating from Central American populations and expanded rapidly to the east across the Greater Antilles and Lesser Antilles. Carstens et al. (2004) identified a similar lack of genetic variation across the northern Lesser Antilles; however, their analyses also identified three *A. schwartzi* mitochondrial haplotypes on the islands of Montserrat, Nevis, and St. Kitts (see P. Larsen et al. 2007 and P. Larsen et al. 2010). The existence of *A. schwartzi* mitochondrial haplotypes circulating in northern Lesser Antillean populations of *A. jamaicensis* provides evidence of historical or ongoing hybridization (P. Larsen et al. 2010). Moreover, this observation suggests gene-flow from southern Lesser Antillean islands to the north. In light of this, we recommend additional studies aimed at quantifying population structure and directional gene flow across Caribbean populations of *A. jamaicensis*.

An analysis of the length of forearm and seven cranial measurements for nine male and nine female Jamaican Fruit-eating Bats revealed no secondary sexual dimorphism in the St. Eustatius population (Table 1). Females average larger than males in six measurements, whereas males averaged larger for length of maxillary toothrow and the sexes averaged the same for zygomatic breadth.

Garden Gilheads was a privately owned truck garden, which was producing a variety of fruits and vegetables. It was located in a suburban area to the south of Oranjestad. Six nets were placed throughout this beautifully maintained facility among Guava (*Psidium guajava*), Bananas in flower (*Musa* sp.), Mango Trees, Star Fruit (*Averrhoa carambola*), Avocado (*Persea americana*), Pomegranate (*Punica granatum*), Soursop (*Annona muricata*), Papaya (*Carica papaya*), and several vegetable crops. We captured a total of 69 bats during one of our most successful nights on the island. Of these, 55 Jamaican Fruit-eating Bats were netted under and around Mango Trees.

The Solitude site was adjacent to two private residences at the southern edge of the northern volcanic hills. In March 2009, their adjoining front yards were covered in dry grass but both buildings abutted a rocky outcrop that was covered primarily by shrubby trees including Porknut, Water Mampoo, Swartz's Pigeon-plum, and Gumbo-limbo. Five nets were set between the buildings and in the surrounding thorny vegetation. Nine bats were captured in these nets with three being *Artibeus* and six *Molossus*.

On three occasions two nets were placed in the neighborhood immediately east of the Fort Oranje. The site consisted of several old buildings with fruit trees surrounding a small park that was framed by the intersection of three roads, the largest of which being Emmaweg. On 7 July 2002, two *B. cavernarum* and 12 *M. molossus* were taken here and on the following day two *A. jamaicensis* were captured, while a year later on 27 May just two *M. molossus* were the only bats obtained. In Oranjestad, near the corner of Rosemarylaan and De Ruyterweg two nets were placed under a large tamarind tree. On the evening of 5 October 2015, one adult male *A. jamaicensis* and a male and seven female *M. molossus* were taken in these nets.

Capture times for *A. jamaicensis* on St. Eustatius were as follows (sunset times in parentheses): 3 October, 2015, 2040 (1800); 5 October, 1829 (1756); 10 October, 2045, 2105 (1754); 13 October, 1825 (1752); 14 October, 1915, 1930, 1930 (1751); 15 October, 21 individuals were captured—the first at 1800 and last at 2130 (1750); 17 October, 1815, 2000 (1750). Typically, the earliest that a fruit bat arrived at a net was 10 minutes after sunset.

Twelve pregnant females were taken between 20 to 23 March, with one having an embryo that measured 5 in crown-rump length. One female taken 23 March was post-lactating. In the period of 27 to 29 May, we obtained nine pregnant female Jamaican Fruit-eating Bats of which five had embryos that averaged 18.6 (14–25) in crown-rump length. During this same period of May, two lactating females and four young females with open phalangeal epiphyses were collected. Two pregnant females and a lactating female were obtained on 9 July. An adult male taken on 9 March had testes that were 8 in length. In the period between 20 and 23 March, 21 male Jamaican Fruit-eating Bats presented as having their testes in a scrotal position. Three of these individuals had testes lengths of 7, 8, and 8. Ten scrotal males were obtained from 27 to 29 May, with one having testes that measured 10 in length. In addition, four young males with open phalangeal epiphyses were taken during this period. Between 3 and 9 July, five males with testes in a scrotal position and two with testes in an inguinal position were netted. The Jamaican Fruit-eating Bat is known to follow a bimodal polyestrous reproductive cycle in Central America (Wilson 1979) and Jamaica (Genoways et al. 2005). Timing of the reproductive cycle may vary depending on geography and environmental conditions, but pregnant females can be expected in February to April and late May to early August and parturition can be expected in March–April and early May and late June to August.

Genoways et al. (2010) reviewed data concerning variation in the presence/absence of the upper M3 and lower m3 in Antillean populations of the *Artibeus jamaicensis* complex, but did not have information for the St. Eustatius population. They concluded that the presence/absence of the upper M3 was a species-level character, whereas presence/absence of the lower m3 in this *Artibeus* complex was neither an indication of geographic variation nor a species-level character, but rather it was a low occurrence polymorphism. We examined 18 individuals from St. Eustatius finding all lacking the upper M3. Populations of *Artibeus* from the Bahamas through the Greater Antilles and south at least far as Dominica in the Lesser Antilles also uniformly lacked the upper third molars. Therefore, the St. Eustatius material fits perfectly within this geographic grouping of populations to which we now apply the name *A. jamaicensis*. We also examined these 18 individuals for the occurrence of the lower m3, finding that 16 had both lower m3 present. This gave a result of 88.9% presence of the m3 in the St. Eustatius population, which was the rate for this polymorphism to similar populations on Antigua, Saba, and St. Lucia (Genoways et al. 2010; Pedersen et al. in prep.). Of the two individuals missing lower m3, one male (TTU 102007) was missing both teeth, whereas the other male (TTU 102011) was missing the left m3 and the right m3 was present, but it was minute.

Eight non-pregnant females collected on 20–21 March weighed on average of 36.6 (35.0–38.9); 10 from late May averaged 36.1 (33.4–40.3); and two from 6 July weighed 30.5 and 37.1. A pregnant female obtained on 21 March weighed 38.9; nine pregnant females collected on 28 May had an average weight of 41.3 (35.1–50.7); and two pregnant females taken on 9 July weighed 44.6 and 55.7. A lactating female captured on 27 May weighed 30.5 and one captured on 9 July weighed 40.4. Seven males taken on 20 March weighed on average 35.1 (34.0–36.2); 10 males taken on 27–29 May had an average weight of 35.5 (32.6–37.5); and 11 males taken on 6–10 July weighed an average of 35.6 (31.7–40.0). Six males taken between 3 and 17 October weighed on average 42.0 (40–46), whereas 10 females from this time period weighed on average 43.3 (39.5–46).

Ardops nichollsi montserratensis (Thomas, 1894)
Antillean Tree Bat

Specimens examined (15).—Bottom of The Quill, 278 m [17°28'40"N, 62°57'51"W], 7 (5 TTU 101978–80, 102002–03; 2 UNSM 27952–53); Miriam C.

Schmidt Botanical Garden, 0.75 km S, 3.5 km E Oranjestad, 79 m [17°28'26.0"N, 62°57'05.9"W], 1 (TTU 110931); 1.5 km E Oranjestad, 236 m [17°28'58.8"N, 62°58'03.3"W], 6 (TTU 110925–30); Rim of The Quill, 400 m [17°28'40"N, 62°58'01"W], 1 (AMNH 213925).

Additional records.—Floor of crater of The Quill (Jones and Schwartz 1967); rim of crater of The Quill (Jones and Schwartz 1967); no specific locality (Koopman 1968).

Specimens captured/released (3).—Near where the hiking trail from Yellow Rock comes to the edge of the crater of The Quill [17°28'42.1"N, 62°57'55.2"W], 1; 1.5 km E Oranjestad, 236 m [17°28'58.8"N, 62°58'03.3"W], 2.

Remarks.—Previously, Jones and Schwartz (1967) recognized five subspecies of *Ardops nichollsi*, where the subspecies *montserratensis* was comprised of individuals of *Ardops nichollsi* from Montserrat and St. Eustatius (Fig. 6). Subsequently, this subspecies was reported from Saba (Genoways et al. 2007a), St. Martin (Genoways et al. 2007b), St. Kitts (Pedersen et al. 2005), and Nevis (Pedersen et al. 2003). In the most recent molecular analyses of *Ardops*, R. Larsen et al. (2017) provided evidence that specimens from St. Eustatius grouped with populations from Dominica northward in two critical characteristics—within highly conserved ZFY intron sequence data northern male *Ardops nichollsi* differed from populations in the southern Lesser Antilles at seven nucleotide positions, and males and females from northern populations had a combination of nuclear AFLPs that distinguish them as significantly different at the molecular level from the southern populations. Morphologically, the northern populations were divided into two groups, with the small-sized individuals occurring on Dominica and the larger individuals, approaching those on Martinique and St. Lucia in size, occurring from Guadeloupe and Marie Galante north to Saba and St. Martin to which R. Larsen et al. (2017) applied the name *A. n. montserratensis*. Potentially, Pleistocene island banks (Rojas et al. 2011; Baker et al. 2012) would have contributed to gene flow among populations of *A. nichollsi* in the northern Lesser Antilles, but may have limited gene flow in populations distributed in the southern Lesser Antilles (for example, St. Lucia and St. Vincent). In a 40,000-year fossil record on the small island of Marie Galante in the central Lesser Antilles, *Ardops nichollsi* does not appear until the Pleistocene-Holocene transition about 15,000 years ago (Stoetzel et al. 2016). Carstens et al. (2004) included a single individual of *A. nichollsi* from St. Eustatius in their analysis of genetic structure in the northern Lesser Antilles. The mitochondrial haplotype of this individual differed by only a single nucleotide (in cyt-*b* data) from individuals examined from Nevis and St. Kitts. These results are consistent with the hypothesis of enhanced gene flow in the northern Lesser Antilles (R. Larsen et al. 2017).

Figure 6. Photograph of a female *Ardops nichollsi* from the edge of the crater of The Quill on St. Eustatius. Note the large, complex nose-leaf, the white shoulder spot that is visible above the left wing, and the long, grayish pelage characteristic of this species.

Table 1 presents length of forearm and seven cranial measurements for six male and seven female Antillean Tree Bats from St. Eustatius. There was considerable secondary sexual dimorphism in these bats on St. Eustatius, as we have found in many other islands in the Lesser Antilles (Baker et al. 1978; Genoways et al. 2001; R. Larsen et al. 2017; Kwiecinski et al. in prep.; Pedersen et al. in prep.). Females averaged larger than the males in all eight measurements. These differences were significant at $P \leq 0.01$ level for three measurements (length of forearm, zygomatic breadth, and breadth across upper molars) and at the $P \leq 0.001$ level for four other measurements, with the postorbital constriction not testing to be significantly different.

The bottom of The Quill had the appearance of a well-manicured campground, scavenged clean by the large numbers of hermit crabs. Large 2-m diameter Strangler Fig trees (25 to 30 m tall) and several large buttressed Silk Cotton trees dominated the vegetation at the bottom. Rock scree against the volcanic walls should have provided exceptional roosting opportunities for crevice and small cave bats. We placed nets in this area on five separate evenings, giving a total of 23 net-nights, which resulted in the capture of 58 bats of four species (*B. cavernarum*, 1; *A. jamiacensis*, 43; *A. nichollsi*, 7; *M. molossus*, 7).

The Miriam C. Schmidt Botanical Garden was a nascent botanical garden established in an area known locally as Behind the Mountain. In this place, a small area of pioneer and thorny dry vegetation, dominated by Black Scrub, Shortleaf Fig (*Ficus citrifolia*), and Spiny Fiddlewood (*Citharexylum spinosum*), had been cleared from the hillside to make way for the planting of small trees, shrubs, and ornamental plants. The vegetation in the upper extent of this property merged into thorny woodland. Six mist nets were placed around the edges of the property and among the larger plantings on 20 March 2009. Only five bats were captured during this evening, including three *B. cavernarum*, one *A. jamaicensis*, and one *A. nichollsi*. This was the furthest distance from The Quill's crater rim and upper slopes where the Antillean Tree Bat was obtained on St. Eustatius. This species finds it day roosts in the foliage of trees, which tend to be larger and denser at these higher elevations (Garbino and Tavares 2018). At this same site on the night of 6 October 2015, only two *M. molossus* were captured in two 7-m and one 10-m nets.

Our location designated as 1.5 km east of Oranjestad, which was worked on 19 March 2009, was located at the head of the same gut as Mountain Piece, which we worked on 29 May 2004. Five nets were set in 2009 primarily across a new hiking trail (centered at an elevation of 236 m) that passed south to The Quill and north to a large radio reflector that overlooked Mountain Piece and the airport. The vegetation in the area was primarily semi-evergreen seasonal forest with some tall trees. We took 21 bats in our nets—13 *Artibeus* and eight *Ardops*. It should be noted that we caught no Antillean Tree Bats in this gut centered at an elevation 196 m, whereas higher up the slope at an elevation of 236 m, we took the largest sample of this species on St. Eustatius. This concentration of activity by the Antillean Tree Bat at higher elevations on Lesser Antillean islands has been documented previously (R. Larsen et al. 2017; Kwiecinski et al. in prep.; Pedersen et al. in prep.). An adult female taken at the edge of the crater was netted at 1820 hr about 30 minutes after sunset on 15 October.

Four pregnant Antillean Tree Bats were taken during our work on St. Eustatius, with three taken on 20 March having embryos with crown-rump lengths of 3, 4, and 5 and one taken on 27 May with an embryo measuring 16 in crown-rump length. Three males taken on 20 March had testes lengths of 5, 6, and 7 and one obtained 22 March had testes measuring 7. These limited reproductive data do fit with the bimodal polyestry involving a postpartum estrus exhibited by other populations of Antillean Tree Bats elsewhere in the Lesser Antilles (Pedersen et al. 2005; Kwiecinski et al. in prep.).

Weights of non-pregnant females were obtained on the following dates: 20 March, 25.1, 28.6, 30.3; 28 May, 23.0, 25.9; 6 July, 23.3; 15 October, 33. Three pregnant females caught on 20 March weighed 23.7, 25.4, and 29.6, and one taken on 27 March weighed 27.6. Weights of males were obtained on the following dates: 20 March, 22.6, 23.5, 25.8; 28 May, 19.9, 22.2; 6 July, 22.7.

Molossus molossus molossus (Pallas, 1766)
Pallas's Mastiff Bat

Specimens examined (60).—Billy's Gut, 50 m [17°29'23.8"N, 62°59'33.4"W], 1 (TTU 101977); Bottom of The Quill, 278 m [17°28'40"N, 62°57'51"W], 1 (TTU 102001); English Quarter, 1 (KU 152114); Garden Gilheads, 0.5 km S, 0.75 km E Oranjestad, 96 m [17°28'43.7"N, 62°56'46.0"W], 2 (TTU 111446–47); Mountain Piece, 196 m [17°28'59.3"N, 62°58'09.0"W], 1 (TTU 101993); New Ground, N end Oranjestad [17°29'26.2"N, 62°59'14.0"W], 6 (UNSM 27964–69); Oranjestad, 40 m [17°28'40"N, 62°58'01"W], 9 (3 AMNH 213942–44; 6 TTU 102015–20); Old Gin House, on coastal road, 0.5 km W Oranjestad

[17°28'55.3"N, 62°59'14.0"W], 2 (UNSM 27970–71); Oranjestad Town Square, 40 m [17°28'56.1"N, 62°59'10.3"W], 5 (3 TTU 102021–23; 2 UNSM 27972–73); Rim of The Quill [17°28'40"N, 62°58'01"W], 30 (TTU 101998–99, 102026–53); Solitude, 2 km N, 0.4 km E Oranjestad, 26 m [17°30'09.4"N, 62°59'00.6"W], 2 (TTU 111448–49).

Additional records.—English Quarter (Timm and Genoways 2003); no specific locality (Koopman 1968).

Specimens captured/released (221).—Billy's Gut, 50 m [17°29'23.8"N, 62°59'33.4"W], 8; Bottom of The Quill, 278 m [17°28'40"N, 62°57'51"W], 6; Charlie's Place (across from Madam Theatre at 11 Fort Oranjestraat), Oranjestad [17°28'56.4'"N, 62°59'07.5"W], 3; Fort Oranje [17°28'55.3"N, 62°59'12.3"W], 8; Garden Gilheads, 0.5 km S, 0.75 km E Oranjestad, 96 m [17°28'43.7"N, 62°56'46.0"W], 1; Kings Well Resort [17°29'09.1"N, 62°59'27.2"W], 69; Knippenga Estate [17°29'00.8"N, 62°57'7.5"W], 17; Medical School Golden Rock, Oranjestad [17°28'58.9"N, 62°58'58.9"W], 5; Medical School on Van Tonningenweg near police station[17°29'01.1"N, 62°59'12.5"W], 2; Miriam C. Schmidt Botanical Garden, 0.75 km S, 3.5 km E Oranjestad, 79 m [17°28'26.0"N, 62°57'05.9"W], 2; Mountain Piece, 196 m [17°28'59.3"N, 62°58'09.0"W], 8; Old Gin House, on coastal road, 0.5 km W Oranjestad [17°28'55.3"N, 62°59'14.0"W], 22; Oranjestad Town Square, 40 m [17°28'56.1"N, 62°59'10.3"W], 9; Rim of The Quill, 400 m [17°28'40"N, 62°58'01"W], 43; Road to Botanical Garden, just S of Knippenga Estate [17°29'01.9"N, 62°57'10.0"W], 6; Solitude, 2 km N, 0.4 km E Oranjestad, 26 m [17°30'09.4"N, 62°59'00.6"W], 4; near corner of Rosemarylaan and De Ruyterweg, Oranjestad [17°28'43.0"N, 62°59'04.2"W], 8.

Remarks.—This common "house bat" is widely distributed throughout the archipelago and was expected on St. Eustatius (Fig. 7). Koopman (1968) first reported specimens of this species from St. Eustatius without reference to specific specimens or localities. Husson (1962) restricted the type locality of *M. molossus* to the island of Martinique, which led Dolan (1989) based on morphometrics to apply the name *M. m. molossus* to this species throughout the Lesser Antilles. Lindsey and Ammerman (2016) included specimens from the Lesser Antilles, although not St. Eustatius, in their analysis of the pattern of diversification in the mitochondrial gene cytochrome-*b* from throughout the geographic range of *M. molossus*. They found that Lesser Antillean specimens clustered in a large polytomy, including material from Puerto Rico, Guyana, Suriname, Bolivia, and eastern Ecuador. Genetic divergence values (1.2%) were low within this cluster. This was one of three lineages recovered in their analysis, with the other two consisting of individuals from western Ecuador and from Brazil and Central America. We agree with Dolan (1989) and Lindsey and Ammerman (2016) in applying the name *M. m. molossus* to this species on St. Eustatius.

Figure 7. Photograph of *Molossus molossus* from swimming pool of the Kings Well Resort on the island of St. Eustatius. Note the short, rounded ears, nearly naked face, and chestnut-black coloration characteristic of this species. The tail that is free beyond the edge of the uropotagium, characteristic of all bats of the family Molossidae, is difficult to see between the feet of this individual.

The results of an analysis of secondary sexual variation in the length of forearm and seven cranial measurements of seven male and seven female Pallas's Mastiff Bats are presented in Table 1. Males averaged larger in all cranial measurements, being significantly larger at the $P \leq 0.01$ level for zygomatic breadth and length of maxillary toothrow and at $P \leq 0.001$ level for the remaining cranial measurements. Males averaged larger than females in length of forearm, but not significantly.

These bats routinely exit their day roosts early enough each evening to be seen clearly. In October 2015, careful records were kept of the time of sunset and the times that bats were captured in the mist nets. The first *M. molossus* to be captured each evening were taken at the following times after sunset (time is in minutes): 3 October, 45; 4 October, 29; 5 October, 32; 6 October, 39; 7 October, 19; 9 October, 40; 10 October, 31; 11 October, 32; 12 October, 17; 13 October, 33; 17 October, 30. This gives a mean time of 31.5 minutes after sunset for the arrival of the first mastiff bat at a netting site.

At New Ground, nets were strung across one of two man-made cattle ponds surrounded by open, overgrazed pasture. In two nets on one evening, six Pallas's Mastiff Bats were taken, whereas on a second night one net was placed across the pond, catching a single *Artibeus*.

On a number of evenings, we placed mist nets in a variety of situations within Oranjestad with the purpose of catching free-tailed bats, including both *Molossus* and *Tadarida*. Unfortunately, we were able to catch only the former. Nets were set at two sites associated with the former medical school on the island. On 10 July 2002, a single net was set over the swimming pool at the Golden Rock dormitory buildings, resulting in the capture of five mastiff bats. On 29 May 2003, two nets were placed around the classroom building located near the new police station, resulting in the taking of only two *M. molossus*. In the Old Gin House, on two occasions nets were set across the hotel swimming pool, which was located in an enclosed courtyard, open only to the sky, above this two-story building. On 29 May 2003, 17 *Molossus* were taken in a single net in less than an hour. On 10 October 2015, four *M. molossus* and two *A. jamaicensis* were taken in two nets between 1754 hr and 2300 hr. The Old Gin House records associated with the coastal road in 2002 refer to a small ravine named Claes Gut that intersects the road and runs just south of the hotel. This gut is occupied by a large water catchment that sits on top of a large covered cistern (known locally as the "Steps"). This place was located at the base of the Fort Oranje rampart and was a relatively recent water catchment for the city. In 2002, there was water in the catchment, but not in subsequent years. Nets were set across this catchment on two evenings, catching two *Molossus* the first evening and one *Brachyphylla* and one *Molossus* on the second. On four occasions, mist nets were placed within the fortress grounds of Fort Oranje, which was located on a 40-m bluff overlooking the Oranjestad Bay. Nets were set either adjacent to the moat (water catchment for the fort) or between buildings adjacent to and within the fort grounds. The following bats were taken at this location as follows: 7 July 2002, 1 *M. molossus*; 27 May 2003, 1 *M. molossus*; 30 May 2003, 2 *M. molossus*; 27 May 2004, 8 *M. molossus* and 1 *A. jamaicensis*. On the night of 12 October 2015, three nets (two 3-m, one 10-m) were situated at Charlie's Place in downtown Oranjestad, catching threee mastiff bats at 1810 hr.

On five nights in the first half of October 2015, a 7-m net was placed over the swimming pool at Kings Well Resort, located on the bluff overlooking Oranjestad Bay where Van Tonningenweg curves sharply to the south to enter Lower Town. These netting efforts resulted in the capture of 69 *M. molossus*, five *A. jamaicensis*, and one *B. cavernarum*. On the night of 9 October 2015, one 3-m and two 7-m nets were placed over the swimming pool at Knippenga Estate. This relatively new high-end resort was located along the road to Behind the Mountain near the east coast of the island. This area was covered in thorny woodland similar to the area around the Botanical Garden. Between 1754 hr and 2340 hr, 17 female *M. molossus* were netted. On the night of 7 October 2015, two 7-m nets were set in scrub and thorny vegetation just south of the Knippenga Estate along the road to the Botanical Gardens. Between 1756 hr and 2230 hr, one male and five female mastiff bats were taken in these nets.

Ten pregnant female mastiff bats were captured from 26 to 29 May, with two having embryos that measured 7 and 9 in crown-rump length. A female taken on 27 May was lactating. Between 3 to 10 July, we captured an additional 17 pregnant females. Bats judged to be juveniles with unfused phalangeal epiphyses were obtained on the following dates: 3 October, 1; 4 October, 5; 5 October, 3; 12 October, 1; 17 October, 1. Three male mastiff bats taken on 21 and 23 March all had testes that were 3 in length. Genoways et al. (2005) concluded that *M. molossus* on Jamaica displayed an aseasonal polyestry with some individuals involved in reproductive activity throughout most of the year. However, elsewhere in the Antilles, these bats appear to breed at various times during the year, but will become quiescent when local conditions are not favorable (Pedersen et al. in prep.).

Three non-pregnant females caught on 21 March had body weights of 9.8, 9.9, and 10.6. Thirteen non-pregnant females obtained in late May had an average body weight of 11.6 (10.6–12.3), whereas two non-pregnant females from the first week of July weighed 11.3 and 14.4. Eight pregnant females taken at the end of May weighed on average 12.8 (11.3–13.7), whereas 14 pregnant females netted in the first week of July weighed on average 14.4 (11.9–18.6). Three males taken on 21 March weighed 10.4, 10.6, and 12.4. Ten males netted in late May had an average body weight of 14.4 (13.0–16.5) and five from the first week of July averaged 12.9 (11.1–14.8). Ten males taken in the first half of October weighed on average 13.0 (9–15), whereas 10 females from this same time period weighed on average 12.6 (11–15.5).

Tadarida brasiliensis antillarum (Miller, 1902)
Brazilian Free-tailed Bat

Additional record.—No specific locality (Koopman 1968).

Remarks.—The sole record of this free-tailed bat from St. Eustatius is based on a statement by Koopman (1968): "The United States National Museum has material from St. Eustatius." Our subsequent search for this museum material has been unsuccessful. A search of the online catalogue of mammal collections of the National Museum of Natural History returned no results for St. Eustatius. Linda Gordon, a long time collection manager for the mammal collections, made a thorough review of their catalogue and collections and reported that she was unable to find any *Tadarida* from St. Eustatius. Considering that Dr. Koopman may have listed the incorrect institution for these specimens, we have searched the online catalogues of other museum collections, including VertNet.org, with no success.

Based on these results, we believe that *T. b. antillarum* should only provisionally be considered to be a member of the bat fauna of St. Eustatius. We had expected to find *Tadarida* on St. Eustatius because the species has been reported from St. Kitts, the island immediately to the south (Pedersen et al. 2005) and from Saba, the island immediately to the north (Genoways et al. 2007a). In fact on a clear day, from Oranjestad one can see the area on Saba where we collected the species. However, we handled 277 free-tailed bats while working on St. Eustatius without finding a single Brazilian Free-tailed Bat.

DISCUSSION

There are five documented species of bats in the fauna of Sint Eustatius, including *Monophyllus plethodon* first reported here—four species in the family Phyllostomidae and one in the Molossidae. We have tentatively included a second species in the family Molossidae (*Tadarida brasiliensis*) in the fauna based on a literature record, but without a known voucher. This is a small and an unbalanced chiropteran fauna for an island in the northern Lesser Antilles. There is the potential for at least two more species of bats being present on the island—the Greater Fishing Bat (*Noctilio leporinus*), and the Gray's Funnel-eared Bat (*Natalus stramineus*). These species are known from Saba (Genoways et al. 2007a) and St. Martin (Genoways et al. 2007b) to the north and the other islands on the St. Kitts bank to the south (Pedersen et al. 2003, 2005). There seems to be adequate day roosts for the Greater Fishing Bat such as the sea caves that we searched at Venus Bay and the shear cliffs at the northern tip of the Boven where vertical crevices in the towering wall would provide ideal roost sites. These bats do prefer to "fish" over relatively calm water and there are not many protected coves and bays on St. Eustatius and those, such as Tumble Down Dick Bay and Gallows Bay, have considerable human activity. The Gray's Funnel-eared Bat roosts in a narrow range of humid microhabitats, which seemed abundant in the interior of The Quill, and their insect diet potentially should be met on the island. A third and less likely species, *Chiroderma improvisum*, could be present on St. Eustatius because it is present on the other islands on the St. Kitts bank (Beck et al. 2016; Pedersen et al. in prep.). However, it is extremely rare wherever the species occurs.

We consider this chiropteran fauna to be unbalanced because only five species have been documented, whereas most of the other islands in the Lesser Antilles from Montserrat northward have faunas that include eight to 10 species. The number of species found on an island is correlated with land area and with the diversity of habitats available on the island (equated to the elevation of the island). The fauna of St. Eustatius was included in a recent study in which the relationships among the bat faunas of the Lesser Antilles were compared via simple species-elevation and species-area regression analyses (Pedersen et al. in prep.). In that study the St. Eustatius fauna falls along the 95% confidence limit above the curve in the species-area analysis and it falls just outside the lower 95% confidence limit in species-elevation curve. This indicates that the fauna is larger than would be predicted by the small area of the island, but fauna is much smaller than would be predicted by habitat diversity (elevation). This result would support the idea that St. Eustatius lacks habitat diversity, which we believe indicates chronic environmental degradation due to human activity.

Of the species on St. Eustatius, only three occur in significant numbers—*Brachyphylla cavernarum*, *Artibeus jamaicensis*, and *Molossus molossus*. Two of these (*Artibeus* and *Molossus*) are generalists, which are widespread in their geographic distribution and have a broad environmental tolerance. The Jamaican Fruit-eating Bat uses caves, crevices, and rock ledges as day roosts, but will also roost in trees when other sites are not available. Pallas's Mastiff Bats probably were originally a tree hole roosting species that also used small rock crevices, but have greatly expanded their population numbers by adopting human-made structures as day roosts. These two species fill the role of being bat "weeds" or pioneer species capable of living in habitats that are heavily impacted by human activity and natural disasters. The third of these species, *Brachyphylla cavernarum*, is an Antillean endemic occurring from Puerto Rico and the Virgin Islands southward to St. Vincent and Barbados. This species is also an environmental generalist. It prefers dark caves and caverns but will roost in areas with indirect sunlight, in human-constructed structures, dense trees, and tree holes. Antillean Fruit-eating Bats do eat a wide variety of fruits, such as Sapodilla (*Manilkara zapota*), Mango, Papaya, Manjack (*Cordia* sp.), and Royal Palm (*Roystonea boringuena*); flowers such as the Silk Cotton (*Ceiba pentandra*), Royal Palm, Portia Tree (*Thespesia populnea*), and West Indian Locust (*Hymenaea courbaril*); and insects (Swanepoel and Genoways 1983; Lenoble et al. 2014).

Given the amount of effort invested in these surveys, the other two species documented for St. Eustatius can only be rated as rare (*Ardops nichollsi*) and extremely rare (*Monophyllus plethodon*). Extant members of these species are endemic to the Lesser Antilles. Antillean Tree Bats are frugivores and roost in trees, whereas Insular Single-leaf Bats are primarily nectivorous/pollenivorous but will take insects in times of environmental stress. Both of these species are associated with higher elevations (above 250 m) on other islands (Pedersen et al. in prep.).

Since the Last Glacial Maximum, the islands of the northern Lesser Antilles have undergone significant environmental changes. The Pleistocene Banks began breaking up as the sea level rose, thereby isolating the islands that we see today. There were concomitant climate shifts during the Pleistocene transition into the Holocene, where alternating periods of wet and dry produced "more variable environmental conditions during this period compared to present-day." (Royer et al. 2017).

Sint Eustatius has not been blessed with an overabundance of natural resources. Despite the presence of the majestic Quill with its elevation of 600 m, there is insufficient topography to create island-generated weather (rainfall) on St. Eustatius. In concert, these natural forcing events impacted not only the environment, but also the fauna and flora on these islands. However, it is our hypothesis that the unbalanced bat fauna on St. Eustatius is the result of chronic environmental degradation and destruction due to human activity.

Archaeological data indicate that the first wave of archaic peoples entered the Lesser Antilles as early as 5600 years ago (Fitzpatrick and Keegan 2007; Siegel et al. 2015). An increasing number of studies are reporting new fossil records of bats attributing initial population declines, extirpations, and extinctions of Caribbean bats to the impact of these early peoples (Steadman et al. 1984, 2015; Pregill et al. 1988; Rick et al. 2013; Bailon et al. 2015; Soto-Centeno and Steadman 2015; Boudadi-Maligne et al. 2016; Stoetzel et al. 2016; Valente et al. 2017). Unfortunately, there are currently no fossil records of mammals from St. Eustatius, but we believe that it can be assumed that similar impacts occurred on all of the islands. Then beginning in the middle of the seventeenth century, European agriculture has been practiced extensively on the St. Eustatius. In the early 19th century, there were 40 plantations and nearly every hectare was put into production—forests were cleared nearly to the top of The Quill for the planting of sugar cane. In the late 1800's, plantation agriculture declined. Efforts to revive agriculture continued, however, until nearly 1950 (Rojer 1997), but presently there is essentially no agricultural activity on the island. In 1952 and 1953, felling of trees still took place on the slopes and rim of The Quill and charcoal production was a frequent activity in The Mountains (de Freitas et al. 2014). Van Andel et al. (2016) recently studied the vegetation types on the island and concluded: "Due to centuries of anthropogenic disturbance, none of the original lowland forests are left."

In the Caribbean Netherlands, overgrazing by feral livestock is one of the most serious threats to biodiversity. On St. Eustatius the severe consequences of feral animals were obvious and included, for example, the lack of undergrowth in The Quill-slope woodlands and coppice formation with stunted bonsai-like growth of trees due to chronic ungulate grazing pressure (Debrot et al. 2015). The preference of grazers for tree saplings and seedlings has enabled the spread of invasive species, including spiny plants (for example, *Acacia* sp. and White Indigoberry, *Randia aculeata*), toxic plants (for example, Bellyache Bush, *Jatropha gossypiifolia* and Buttonsage, *Lantana involucrata*) or even plants that are both prickly and poisonous (Christmas Bush, *Comocladia dodonaea*). Commenting on the central plain of the island, Van Andel et al. (2016) stated that it "suffers from the deleterious effects of invasive species and free roaming cattle, but most of the officially protected vegetation types on the island, also suffer from overgrazing, particularly by goats."

Feral cats and dogs may directly feed on bats when the opportunity is presented (Rodríguez-Durán et al. 2010; Welch and Leppanen 2017). In fact, we have watched cats consume bats out of mist nets. The introduced Black Rats (*Rattus rattus*) on the island may compete directly with the frugivorous bats for wild and domestic fruits, and indirectly by consuming the seeds needed to regenerate the native plants and fruit trees. Elsewhere, we have seen bat roosts that have been disrupted by humans and livestock, especially by goats. However, we did not observe this directly on St. Eustatius. Finally, the human residents of the St. Eustatius compete with bats by gathering native plant resources for their consumption thus taking these resources away from the bats and slowing the restoration of native vegetation (Posthouwer 2016). These activities should not be permitted in the national parks.

The anthropogenic disturbances on St. Eustatius have impacted bat populations in two primary areas—food and shelter. Logging and clearing land for agriculture reduces tree species and maturity that these bats depended upon for food and shelter. In some cases, invasive species have come to replace native trees and in others the grazing of feral animals has kept important trees from maturing. Fruit- and pollen-feeding bats depend upon a diverse collection of tree species providing a year-round supply of fruit, pollen, and nectar. Several species of tropical bats seek primary day roosts in the foliage of trees or in tree holes. The best advantages for such uses are larger more mature trees. It is difficult for these native forests to recover, because invasive species may outcompete some native plants, while other natives may never mature due to the uncontrolled grazing by livestock.

The insectivorous species of bats on St. Eustatius (*M. molossus*, abundant; *T. brasiliensis*, a possible rare species; *N. stramineus*, potential third species) have been impacted by the shifting of the insect fauna as is known to occur in both temperate and tropical rain forests with logging, including selective logging (Holloway et al. 1992; Bawa and Seidler 1998; Summerville and Crist 2002). For tropical birds, logging had the greatest impacts on those species that selectively forage on the ground or in the understory of the forest interior. Similarly, Peters et al. (2006) found a reduced number of gleaning and aerial insectivorous bats in parts of the southeastern Amazon that had been selectively logged. These decreases in bat diversity were thought to be due to decreases in insect diversity rather than insect abundance, because secondary growth forests are known to typically have higher insect densities (Fenton 1990). However, the primary forests on St. Eustatius were not replaced by secondary forest but rather by sugar cane and other agriculture. In this situation, the generalist insectivore, *M. molossus*, benefitted from these anthropogenic changes.

It was in recognition of these anthropogenic impacts on St. Eustatius that the St. Eustatius National Parks Foundation (STENAPA) was established with responsibility for both marine and terrestrial natural resources. The major accomplishment for terrestrial natural resources was the establishment of The Quill/Boven National Park, consisting of both the cone of "The Quill" and the area of the five hills in the north of the island. The motivation for this action was to preserve untouched and intact for future generations the integrity of the landscape, nature, and history of the island. However, challenges certainly remain for STENAPA to reach these lofty goals. Certainly chief among these challenges is dealing with the free-roaming livestock on the island. The goal of removing all feral animals from the island is a daunting one, but inspiration can be drawn from the successful Project Santiago in the Galápagos Islands (Cruz et al. 2009).

We have made specific recommendations for the conservation of bats in the Lesser Antilles that would pertain to the future of bats on St. Eustatius (see Pedersen et al. 2013). In that publication, we recommend the preservation/protection of all caves, which would include caves, rock fissures, and rock shelters as well as man-made equivalents of these such as mines, wells, and cisterns. These serve as roosts and may become vital refugia during natural disasters. Many of the bat species known from St. Eustatius use caves as day roosts—*Monophyllus*, *Brachyphylla*, *Artibeus*, *Molossus*, as well as potential species such as *Noctilio* and *Natalus*. We recommend the preservation/protection of forests because "Healthy forests require healthy bat populations and healthy bat populations require healthy forests." Indeed, the future of forests and bats in the tropics are intertwined—forests provide "roosts, protection, and food resources," whereas the forests receive "insect control, pollination of a wide-variety of plant species, and the subsequent dispersal of plant seeds." We recommend the protection/restoration of hydrological systems. Healthy freshwater hydrologic systems are necessary for forests and wildlife populations including bats. Finally, we recommend additional field research to determine whether the unreported bat species are indeed present on the island and to shed additional light on the genetic variation within species.

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LITERATURE CITED

Bailon S., C. Bochaton, and A. Lenoble. 2015. New data on Pleistocene and Holocene herpetofauna of Marie Galante (Blanchard Cave, Guadeloupe Islands, French West Indies): Insular faunal turnover and human impact. Quaternary Science Reviews 128:127–137.

Baker, R. J., O. R. P. Bininda-Emonds, H. Mantilla-Meluk, C. A. Porter, and R. A. Van Den Bussche. 2012. Molecular timescale of diversification of feeding strategy and morphology in New World leaf-nosed bats (Phyllostomidae): A phylogenetic perspective. Pp. 385–409 in Evolutionary history of bats: Fossils, molecules and morphology (G. F. Gunnell and N. B. Simmons, eds.). Cambridge University Press, New York.

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

Bawa, K. S., and R. Seidler. 1998. Natural forest management and conservation of biodiversity in tropical forests. Conservation Biology 12:46–55.

Beck, J. D., A. D. Loftis, J. L. Daly, W. K. Reeves, and M. V. Orlova. 2016. First record of *Chiroderma improvisum* Baker & Genoways, 1976 (Chiroptera: Phyllostomidae) from Saint Kitts, Lesser Antilles. Check List 12:1854.

Boudadi-Maligne M., S. Bailon, C. Bochaton, F. Casagrande, S. Grouard, N. Serrand, and A. Lenoble. 2016. Evidence for historical human-induced extinctions of vertebrate species on La Désirade (French West Indies). Quaternary Research 85:54–65.

Caribbean Hurricane Network. 2017. Climatology of Caribbean hurricanes: St. Eustatius. Accessed at <http://stormcarib.com/climatology/TNCE_all_isl.htm> on 11 September 2017.

Carstens, B. C., J. Sullivan, L. M. Dávalos, P. A. Larsen, and S. C. Pedersen. 2004. Exploring population and genetic structure in three species of Lesser Antillean bats. Molecular Ecology 13:2557–2566.

Cruz, F., V. Carrion, K. J. Campbell, C. Lavoie, and C. J. Donlan. 2009. Bio-economics of large-scale eradication of feral goats from Santiago Island, Galápagos. Journal of Wildlife Management 73:191–200.

Debrot, A. O., J. C. J. Hazenbosch, S. Piontek, C. Kraft, J. van Belle, and A. Strijkstra. 2015. Roaming livestock distribution, densities and population estimates for St. Eustatius, 2013. Institute for Marine Resources & Ecosystem Studies, Wageningen University and Research C088.15:1–27.

de Freitas, J. A., A. C. Rojer, B. S. J. Nijhof, and A. O. Debrot. 2014. Landscape ecological vegetation map of Sint Eustatius (Lesser Antilles). Royal Netherlands Academy of Arts and Sciences, Amsterdam.

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

Fenton, M. B. 1990. The foraging behavior and ecology of animal-eating bats. Canadian Journal of Zoology 68:411–422.

Findley, J. S., and D. E. Wilson. 1983. Are bats rare in tropical Africa? Biotropica 15:299–303.

Fitzpatrick, S. M., and W. F. Keegan. 2007. Human impacts and adaptations in the Caribbean islands: An historical ecology approach. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 98:29–45.

Garbino, G. S. T., and V. C. Tavares. 2018. Roosting ecology of Stenodermatinae bats (Phyllostomidae): Evolution of foliage roosting and correlated phenotypes. Mammal Review doi: 10.1111/mam.12114.

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

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

Genoways, H. H., P. A. Larsen, S. C. Pedersen, and J. J. Huebschman. 2007a. Bats of Saba, Northern Lesser Antilles. Acta Chiropterologica 9:91–114.

Genoways, H. H., R. J. Larsen, S. C. Pedersen, G. G. Kwiecinski, and P. A. Larsen. 2011. Bats of Barbados. Chiroptera Neotropical 17:1029–1054.

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

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

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

Helmer, E. H., T. A. Kennaway, D. H. Pedreros, M. L. Clark, H. Marcano-Vega, L. L. Tiezen, T. R. Ruzycki, S. R. Schill, and C. M. Sean Carrington. 2008. Land cover and forest formation distributions for St. Kitts, Nevis, St. Eustatius, Grenada and Barbados from decision tree classification of cloud-cleared satellite imagery. Caribbean Journal of Science 44:175–198.

Holloway, J. D., A. H. Kirk-Spriggs, and C. V. Khen. 1992. The response of some rain forest insect groups to logging and conversion to plantation. Philosophical Transactions of the Royal Society of London, Biological Sciences 335:425–436.

Husson, A. M. 1960. De Zoogdieren van de Nederlandse Antillen. Uitgaven van de Natuurwetenschappelijke Werkgroep Nederlandse Antillen, Curaçao 12:1–83.

Husson, A. M. 1962. The bats of Suriname, Vol. 2. Zoölogische Monographieën, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

Jones, J. K., Jr., and A. Schwartz. 1967. Bredin-Archbold-Smithsonian Biological Survey of Dominica. 6. Synopsis of bats of the Antillean genus *Ardops*. Proceedings of the United States National Museum 124(3634):1–13.

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

Kwiecinski, G. G., S. C. Pedersen, H. H. Genoways, P. A. Larsen, R. J. Larsen, J. D. Hoffman, F. Springer, C. J. Phillips, and R. J. Baker. in prep. Bats of Saint Vincent, Lesser Antilles. Occasional Papers, Museum of Texas Tech University.

Larsen, P. A., S. R. Hoofer, M. C. Bozeman, S. C. Pedersen, H. H. Genoways, C. J. Phillips, D. E. Pumo, and R. J. Baker. 2007. Phylogenetics and phylogeography of the *Artibeus jamaicensis* complex based on the cytochrome-*b* DNA sequence. Journal of Mammalogy 88:712–727.

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

Larsen R. J., K. A. Boegler, H. H. Genoways, W. P. Masefield, R. A. Kirsch, and S. C. Pedersen. 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., P. A. Larsen, C. D. Phillips, H. H. Genoways, G. G. Kwiecinski, S. C. Pedersen, C. J. Phillips, and R. J. Baker. 2017. Patterns of morphological and molecular evolution in the Antillean tree bat, *Ardops nichollsi* (Chiroptera: Phyllostomidae). Occasional Papers, Museum of Texas Tech University 345:1–28.

Lenoble, A., B. Angin, J-B. Huchet, and A. Royer. 2014. Seasonal insectivory of the Antillean fruit bat (*Brachyphylla cavernarum*). Caribbean Journal of Science 48:127–131.

Lindsay, J. M., R. E. A. Robertson, J. B. Shepherd, and S. Ali. 2005. Volcanic hazard atlas of the Lesser Antilles. St. Augustine, Trinidad and Tobago: Seismic Research Unit, University of the West Indies.

Lindsey, L. L., and L. K. Ammerman. 2016. Patterns of diversification in a widely distributed species of bat, *Molossus molossus*. Occasional Papers, Museum of Texas Tech University 339:1–15.

Pedersen, S. C., H. H. Genoways, G. G. Kwiecinski, P. A. Larsen, and R. J. Larsen. 2013. Biodiversity, biogeography, and conservation of bats in the Lesser Antilles. Pp. 62–73, 330 in Biodiversité insulaire: La flore, la faune et l'homme dans les Petites Antilles (J.-L. Vernier and M. Burac, eds.). Schoelchers, Martinique, Direction de l'Environnement, de l'Aménagement et du Logement de Martinique et Université des Antilles et de la Guyane, France.

Pedersen, S. C., H. H. Genoways, M. N. Morton, J. W. Johnson, and S. E. Courts. 2003. Bats of Nevis, northern Lesser Antilles. Acta Chiropterologica 5:251–267.

Pedersen, S. C., H. H. Genoways, M. N. Morton, G. G. Kwiecinski, and S. E. Courts. 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., H. H. Genoways, M. N. Morton, V. J. Swier, P. A. Larsen, K. C. Lindsay, R. A. Adams, and J. D. Appino. 2006. Bats of Antigua, northern Lesser Antilles. Occasional Papers, Museum of Texas Tech University 249:1–18.

Pedersen, S. C., G. G. Kwiecinski, H. H. Genoways, R. J. Larsen, P. A. Larsen, C. J. Phillips, and R. J. Baker. in prep. Bats of Saint Lucia, Lesser Antilles. Occasional Papers, Museum of Texas Tech University.

Pedersen, S. C., P. A. Larsen, H. H. Genoways, M. N. Morton, K. C. Lindsay, and J. Cindric. 2007. Bats of Barbuda, northern Lesser Antilles. Occasional Papers, Museum of Texas Tech University 271:1–19.

Peters, S. L., J. R. Malcolm, and B. L. Zimmerman. 2006. Effects of selective logging on bat communities in the southeastern Amazon. Conservation Biology 20:1410–1421.

Posthouwer, C. 2016. Sustainability of wild plant extraction on the Dutch Caribbean island Sint Eustatius. Unpublished Masters of Science Research Project, Leiden University, Leiden, The Netherlands.

Pregill, G. K., D. W. Steadman, S. L. Olson, and F. V. Grady. 1988. Late Holocene fossil vertebrates from Burma Quarry, Antigua, Lesser Antilles. Smithsonian Contributions to Zoology 463:iv + 1–27.

Rick, T. C., P. V. Kirch, J. M. Erlandson, and S. M. Fitzpatrick. 2013. Archeology, deep history, and the human transformation of island ecosystems. Anthropocene 4:33–45.

Rodríguez-Durán, A., J. Pérez, M. A. Montalbán, and J. M. Sandoval. 2010. Predation by free-ranging cats on an insular population of bats. Acta Chiropterologica 12:359–362.

Rojas, D., A. Vale, V. Ferrero, and L. Navarro. 2011. When did plants become important to leaf-nosed bats? Diversification of feeding habits in the family Phyllostomidae. Molecular Ecology 20:2217–2228.

Rojer, A. 1997. Biological inventory of Sint Eustatius. Carmabi Foundation, Curaçao, Netherlands.

Royer, A., B. Malaizé, C. Lécuyer, A. Quefflec, K. Charlier, T. Caley, and A. Lenoble. 2017. A high-resolution temporal record of environmental changes in the eastern Caribbean (Guadeloupe) from 40 to 10 ka BP. Quaternary Science Reviews 155:198–212.

Schwartz, A., and J. K. Jones, 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(3635):1–20.

Siegel P. E., J. G. Jones, D. M. Pearsall, N. P. Dunning, P. Farrell, N. A. Duncan, J. H. Curtis, and S. K. Singh. 2015. Paleoenvironmental evidence for first human colonization of the eastern Caribbean. Quaternary Science Reviews 129:275–295.

Soto-Centeno, J. A., and D. W. Steadman. 2015. Fossils reject climate change as the cause of extinction of Caribbean bats. Science Reports 5:7971.

Steadman D. W., N. A. Albury, B. Kakuk, J. I. Mead, J. A. Soto-Centeno, H. M. Singleton, and J. Frankling. 2015. Vertebrate community on an ice-age Caribbean island. PNAS 112:44 E5963–E5971.

Steadman, D. W., G. K. Pregill, and S. L. Olson. 1984. Fossil vertebrates from Antigua, Lesser Antilles: Evidence for late Holocene human-caused extinctions in the West Indies. Proceedings of the National Academy of Science 81:4448–4451.

Stoetzel, E., A. Royer, D. Cochard, and A. Lenoble. 2016. Late Quaternary changes in bat palaeobiodiversity and palaeobiogeography under climatic and anthropogenic pressure: New insights from Marie-Galante, Lesser Antilles. Quaternary Science Review 143:150–174.

Summerville, K. S., and T. O. Crist. 2002. Effects of timber harvest on forest Lepidoptera: Community, guild, and species responses. Ecological Applications 12:820–835.

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

Swanepoel, P., and H. H. Genoways. 1983. *Brachyphylla cavernarum*. Mammalian Species 205:1–6.

Timm, R. M., and H. H. Genoways. 2003. West Indian mammals from the Albert Schwartz collection: Biological and historical information. Scientific Papers of the Natural History Museum, University of Kansas 29:1–47.

Valente L, R. S. Etienne, and L. M. Dávalos. 2017. Recent extinctions disturb path to equilibrium diversity in Caribbean bats. Nature Ecology and Evolution 1:26. doi:10.1038/s41559–016–0026.

van Andel, T., B. van der Hoorn, M. Stech, S. B. Arostegui, and J. Miller. 2016. A quantitative assessment of the vegetation types on the island of St. Eustatius, Dutch Caribbean. Global Ecology and Conservation 7:59–69.

Welch, J. N., and C. Leppanen. 2017. The threat of invasive species to bats: a review. Mammal Review, doi: 10.1111/mam.12099.

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

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