BATS OF ANGUILLA, NORTHERN LESSER ANTILLES

HUGH H. GENOWAYS, SCOTT C. PEDERSEN, CARLETON J. PHILLIPS, AND LINDA K. GORDON

ABSTRACT

Five species of bats are known in the literature from Anguilla—Monophyllus plethodon, Brachyphylla cavernarum, Artibeus jamaicensis, Natalus stramineus, and Molossus molossus. These records are scattered in the literature as parts of simple reports of the species from the island or included in revisions of taxonomic groups that occur on the island, but the first comprehensive study of bats of Anguilla is presented herein. In addition to providing morphometric and natural history information for the five species of bats previously known from the island, records of a species of bat new to the fauna of the island of Anguilla—Tadarida brasiliensis—are documented. Based on data from this study, the conclusion is drawn that the Anegada Passage has had only a limited impact as a zoogeographic barrier for the chiropteran faunas of the Greater and Lesser Antilles, if a perspective of the last 10,000 years is taken.

Key words: Anegada Passage, Anguilla, Chiroptera, natural history, Tadarida brasiliensis

INTRODUCTION

The island of Anguilla is located at the northern end of the Leeward islands (18°13'12"N, 63°04'22"W), with only its political dependency, Sombrero Island, lying further to the north (58 km northwest). Because no bats have been reported from Sombrero Island, the chiropteran fauna of Anguilla is the northern-most population of bats in the Lesser Antilles. Currently, five species of bats are known from Anguilla—Monophyllus plethodon, Brachyphylla cavernarum, Artibeus jamaicensis, Natalus stramineus, and Molossus molossus. These records are scattered in the literature as parts of simple reports of the species from the island (J. A. Allen 1890; G. M. Allen 1911; Koopman 1968) or included in revisions of taxonomic groups that occur on the island (Goodwin 1959; Schwartz and Jones 1967; Swanepoel and Genoways 1978), but no comprehensive study of bats of Anguilla has appeared. Our field studies added a sixth species of bat—Tadarida brasiliensis—to the official total known from the island and we expect that a seventh species—Noctilio leporinus—eventually will be documented for the island.

Given the low, dry aspect of the island and degraded terrestrial habitats, a chiropteran fauna of six or seven species is surprisingly large for an island of this size in the Lesser Antilles. It is, therefore, a chi-
Invertebrate fauna of interest and deserving of additional study. With the results of our field studies on Anguilla in the mid-1980s and an intensive search of museum collections, we are able to present here for the first time a review focused on the bats of Anguilla.

**Methods and Materials**

_Study area._—Anguilla is 28 km long and approximately 8 km wide at its widest point, giving it an area of 90 square km. Anguilla is a low lying (maximum elevation is 59 m) island composed primarily of uplifted coral formations with some of the underlying igneous formations exposed. The island is situated just 10 km north of the island of St. Martin. The channel separating the islands is only 18 m deep so Anguilla was undoubtedly joined with St. Martin and St. Barthélemy during the Pleistocene into a much larger island. To the west of Anguilla are the British Virgin Islands, which are separated from it by the 166 km wide and 1,915 m deep Anegada Passage (Howard and Kellogg 1987; Frantantoni et al. 1997). It is only through this deep passage that cold water current moves in a southwesterly direction from the North Atlantic Deep Water in the western Atlantic entering the Caribbean Sea. From the Anegada Passage the water first enters the Virgin Island Basin lying to the north of St. Croix and from there it moves through the Jungfern Passage (1,815 m deep) in a southerly direction and Grappler Channel (1,710 m deep) to the southwest into the Venezuela Basin, which constitutes the eastern third of the Caribbean Sea (Frantantoni et al. 1997).

According to Beard (1949), the original vegetation of Anguilla was evergreen tropical bushland, but the island vegetation has been degraded to the point where the original habitat has been replaced by a combination of imported plants and agriculture. Indeed, during our visits to the island the damage from subsistence farming and especially over-grazing by goats and other domestic livestock was evident everywhere on the island—the contemporary terrestrial habitats could easily be considered a “goat climax.” The present vegetation of the island is characterized by dwarfism and shaping by the prevailing trade winds that sweep across the island from the east. The hottest months of the year are July to October and the coolest December to February, with a mean annual temperature of 27° C. Rainfall is relatively low and erratic with an average of 1,026 mm and ranging from 565 mm to 1,300 mm annually. Because the rock formations on the island are porous, the rainfall is only of limited value to the local plant communities (Howard and Kellogg 1987).

The trees commonly present on the island include loblolly (_Pisonia subcordata_), tamarind (_Tamarindus indica_), and cedar (_Tabebuia pallida_), with _Acacia_ forming open thickets in the less disturbed areas. Some of the other species of trees that are probably valuable as food for the three phyllostomid bat species are _Chinaberry_ (_Bourreria succulenta_), _genip_ (_Meliococcus bijugatus_), _almond_ (_Terminalia catappa_), _wild guava_ (_Guettarda scabra_), _white cedar_ (_Tabebuia heterophylla_), _turpentine tree_ (_Bursera simaruba_), _maidenberg_ (_Crossopetalum rhacoma_), and _seaside mahoe_ (_Thespesia populnea_). An entire street in the village, which serves as the capital of the island, “The Valley” (Fig. 1) is lined with old mahogany trees (_Swietinia mahogani_). The introduced neem tree (_Azadirachta indica_) is a popular, but aggressive, invader on the island. There also are introduced fruit trees on the island such as _papaya_ (_Carica papaya_), _breadfruit_ (_Artocarpus altilis_), and _mango_ (_Mangifera indica_). The manchineel (_Hippomane mancilla_) occurs in coastal areas and around salt ponds (Howard and Kellogg 1987).

_Voucher specimens._—A survey of specimens in existing natural history museum collections—American Museum of Natural History, AMNH; National Museum of Natural History, NMNH; University of Nebraska State Museum, UNSM—yielded a total of 129 specimens of bats from Anguilla available for study. Length of forearm and cranial measurements were taken from museum specimens using digital calipers. Measurements are given in millimeters and weights are in grams.
Monophyllus plethodon luciae
Miller 1902

Specimens examined (11).—Chalvilles, 1 (UNSM); cave at the head of Katouche Bay, 1.5 km NE North Hill Village, 7 (NMNH); “Apple Hole” Cavern, 1 km NE North Side Village, 1 (NMNH); Small Fountain Cave, Little Bay, 1 (AMNH); Wattices, 1 (UNSM).

Miller’s long-tongued bat has been reported from Anguilla by Schwartz and Jones (1967) and Koopman (1968). Schwartz and Jones (1967) in their revision of the genus assigned a single specimen from Anguilla to M. p. luciae, which has a geographic range from Anguilla southward to St. Vincent. Koopman (1968) mentions this specimen from Small Fountain Cave without giving its precise locality. Currently, this species occurs only in the Lesser Antilles, but five fossil specimens of an extinct subspecies (M. p. frater) are known from west of the Anegada Passage on Puerto Rico (Schwartz and Jones 1967).

Length of forearm and seven cranial measurements for three males and three females are presented in Table 1. Females averaged smaller than males in all measurements except postorbital constriction where the sexes averaged the same. These differences were significant at $P \leq 0.05$ for three of the measurements—zygomatic breadth, mastoid breadth, and breadth across the upper molars.

The cave at the head of Katouche Bay is probably the one known locally as Iguana Cave (see map published by the Government of the United Kingdom for the Government of Anguilla, 1997). This is a simple cave in the rock with two rooms, which were mined for phosphate in the past. A fig tree (probably Ficus citrifolia) grows through an opening in the cave. Miller’s long-tongued bats were captured in mist nets at the entrance of Iguana Cave as well as Pitch Apple Hole (see description in Brachyphylla account). Individuals from Chalvilles and Wattices were netted as they foraged in an area of pasture with a single large fig tree.
Table 1.—Length of forearm and cranial measurements of six species of bats occurring on the West Indian island of Anguilla.

<table>
<thead>
<tr>
<th>Statistics, catalog numbers, and sex</th>
<th>Length of forearm</th>
<th>Greatest length of skull</th>
<th>Condylorbasal length</th>
<th>Zygomatic breadth</th>
<th>Postorbital constriction</th>
<th>Mastoid breadth</th>
<th>Length of maxillary toothrow</th>
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and in a subsistence garden with a few banana trees, respectively. We have not found the precise location of Small Fountain Cave.

Single females taken on May 21 and October 10 evinced no gross reproductive activity. The testis length of a male taken on May 22 was 4 and for three males taken on October 10 was 4, 4, and 4.5. Weights of three males and a female taken on October 10 were, respectively, 16.0, 16.5, 18.3, and 14.5.

**Brachyphylla cavernarum cavernarum**
Gray 1834

*Specimens examined (60).—Fountain Cave, Island Harbour, 7 (AMNH); “Apple Hole” Cavern, 1 km NE North Side Village, 3 (NMNH); “The Fountain” Cavern, 0.5 km SW Shoal Village, 46 (8 NMNH, 38 UNSM); The Valley, 4 (AMNH).*

*Additional record.—Cavannagh Cave (McFarlane and MacPhee 1989).*

This Antillean endemic fruit-eating bat has been reported previously from Anguilla without specific localities by Koopman (1968) and the specimens in the American Museum of Natural History were included in the revision of the genus by Swanepeol and Genoways (1978). Swanepol and Genoways (1978) assigned material from St. Croix in the Virgin Islands and Anguilla southward through the Lesser Antilles to St. Vincent to the nominate subspecies, which has a type locality of St. Vincent. Forearm and cranial measurements of seven males and four females fall well within the range of samples presented by Swanepol and Genoways (1978) for this subspecies (Table 1). No statistically significant secondary sexual variation was found in our sample, which agrees with the results of Swanepol and Genoways (1978). Males averaged larger than females in six measurements, whereas females averaged larger in postorbital constriction and the sexes averaged the same in breadth across upper molars.

The majority of our specimens came from two of the well-known caves on Anguilla—The Fountain and “Apple Hole” Cavern, which is known locally as Pitch Apple Hole. Both caves are dome-type caverns with small entrances located near the top of the dome. At the Fountain the drop to the floor is 10 m and at Pitch Apple the drop is 15 m. The Fountain is composed of two chambers of a total length of 50 m and a width of 30 m. There are two pools of freshwater in the cavern (Hummelinck 1979; Watters 1991). A pitch apple tree (*Clusia rosea*) is located at the entrance of each of these caverns. The roots of these trees, which reach to the floor of the cavern, provided access to the caves’ interiors during early explorations. *Brachyphylla* were netted at the entrance of these two caverns. At Pitch Apple Hole, individuals of *M. plethodon* and *A. jamaicensis* were taken along with the *B. cavernarum*, whereas at The Fountain, a single *N. stramineus* was netted along with the *B. cavernarum* (see also Genoways 1989; McFarlane and MacPhee 1989).

On the evening following netting at the entrance of The Fountain, we took the permanently installed 10-m steel ladder to the floor of the cavern and searched for bats. We saw a few individuals of *Brachyphylla* moving about the large rooms of the cavern, but the majority of the colony was inaccessible because of the pools of water and the crevices they occupied were too narrow for us to explore. The pools of water helped keep the level of humidity high in the cavern, but much of the floor was covered with loose, dry soil, which was easily disturbed.

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**Table 1 (cont.).**

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<tr>
<th>Statistics, catalog numbers, and sex</th>
<th>Length of forearm</th>
<th>Greatest length of skull</th>
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<th>Zygomatic breadth</th>
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Nine males collected on May 19 had testes that averaged 7.9 (5-10) long and three males collected on October 6-7 had testes that were 8, 8, and 9 long. Single females taken on April 1, April 7, October 6, and October 8 evinced no gross reproductive activity. Among 28 females collected on May 19 at The Fountain, 21 were lactating, 5 evinced no gross evidence of being pregnant or lactating, one carried a fetus that measured 40.5 in crown-rump length, and one gave birth in captivity to a male neonate with a forearm length of 36.3. Six males captured on October 6-7 had an average weight of 53.3 (46-59.5), whereas five females taken on these dates weighed an average of 48.8 (42-52.5).

*Artibeus jamaicensis jamaicensis*

Leach 1821

Specimens examined (45).—Chalvilles, 13 (UNSM); Flat Cap Caves, 10 (AMNH); “Apple Hole” Cavern, 1 km NE North Side Village, 5 (NMNH); Isaac’s Cave, ca. 2 km NE North Side Village, 1 (NMNH); 0.5 km S South Hill Village, 16 (NMNH).

The Jamaican fruit-eating bat was the first species of bat reported from Anguilla when J. A. Allen (1890) reported a single specimen without specific locality under the designation *Artibeus* “perspicillatus (Linn.).” Later G. M. Allen (1911) referred this specimen to *A. j. jamaicensis*. Koopman (1968) mentions “a series now in the American Museum” of *A. j. jamaicensis* from Anguilla. Genoways et al. (2001) have reviewed morphological variation in Antillean populations of this species. Our Anguillan sample (Table 1) closely matches the measurements of other samples of *A. j. jamaicensis*; in fact, the mean of greatest length of skull of specimens from Anguilla at 28.2 is the same as the sample from Jamaica (Genoways et al. 2001).

Table 1 presents length of forearm and seven cranial measurements of 8 males and 8 females from Anguilla. Comparing the sexes for secondary sexual variation, means for greatest length of skull, condylar length, and postorbital constriction are equal for males and females. Males average larger for zygomatic breadth (but only by 0.1 mm) and breadth across upper molars. Females averaged larger for length of forearm, mastoid breadth, but only by 0.1 mm, and length of maxillary toothrow. Breadth across upper molars was the only measurement with a significant size difference ($P \leq 0.05$) between adult males and females.

An adult female (AMNH 544822) was missing both M2s as well as the tip of the upper right canine
was broken off and the tooth apparently was infected. These dental anomalies appear to have occurred during the life of the bat.

*Natalus stramineus stramineus*

Gray 1838

Specimens examined (4).—Cave at the head of Katouche Bay, 1.5 km NE North Hill Village, 1 (NMNH); North Side Estate, 2 (AMNH); The Fountain, 1 (UNSM).

Goodwin (1959) was the first author to note the occurrence of this insectivorous bat on Anguilla when he reported the two specimens in the American Museum of Natural History without specific locality. Goodwin (1959) presented compelling evidence that Antigua should be considered the type locality for *Natalus stramineus* and thus the appropriate name for populations in the northern Lesser Antilles was *N. s. stramineus*. These data were re-examined by Handley and Gardner (1990) and Tejedor (2006) who then supported Goodwin’s conclusions. There are conflicting views on the specific relationship among populations of the large funnel-eared bats occurring in the Lesser Antilles, Greater Antilles, and mainland of Mexico and Central America (Varona 1974; Hall 1981; Koopman 1993; Arroyo-Cabrales et al. 1997).

Dávalos (2005) and Tejedor et al. (2005) presented evidence that unrecognized taxa of *Natalus* exist within currently named populations in the West Indies. 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 Anguilla. Table 1 presents measurements of three male funnel-eared bats from Anguilla.

The specimen from The Fountain was netted along with numerous individuals of *B. cavernarum* as they emerged from the small entrance to the cavern. The specimen from near Katouche Bay was shot as it flew about in a cave, probably Iguana Cave. The latter individual had testes that measured 3 in length and it weighed 6.2. All four specimens known from Anguilla are males.

*Molossus molossus molossus*

(Pallas 1766)

Specimens examined (7).—Chalvilles, 2 (UNSM); Island Harbour, 1 (NMNH); Katouche Bay, 1 (AMNH); The Valley, 2 (1 AMNH, 1 UNSM); Wattices, 1 (UNSM).

Koopman (1968) reports specimens of this species from Anguilla 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) to apply the name *M. m. molossus* to this species throughout the Lesser Antilles. We have maintained this arrangement pending analysis of morphological variation among populations of this species throughout the Antillean region. Table 1 presents length of forearm and seven cranial measurements for two males and two females from Anguilla.

The female obtained at Island Harbour was caught in a mist net as it exited the eaves of a house. The female caught at The Valley on May 20, 1987, was taken in a mist net that was set under a row of old mahogany trees, which formed a canopy at about 7 to 10 m above our nets. Only this specimen and one of *T. brasiliensis* were caught prior to heavy rain that ended collecting activities for the night. Conditions at Chavilles are described in the account for *A. jamai-icensis*. In the small village of Wattices, nets were set under a mahogany tree adjacent to a dwelling. On the opposite side of the dwelling nets were placed in a small subsistence garden that included five banana trees.

Females obtained on May 20, May 22 (2), and October 11 evinced no gross reproductive activity. The male from Wattices taken on May 21 had testes that were 4 long. The female taken on October 11 weighed 14.
**Tadarida brasiliensis antillarum**
(Miller 1902)

*Specimens examined* (2).—Chalvilles, 1 (UNSM); The Valley, 1 (UNSM).

These specimens represent the first record of the Brazilian free-tailed bat from the island of Anguilla. This species is known from other islands in the northern Lesser Antilles such as St. Martin, St. Barthélemy, St. Eustatius, and Saba (G. M. Allen 1911; Husson 1960; Koopman 1968; Genoways et al. 2007a, 2007b; Larsen et al. 2007), but was previously unknown from Anguilla. To the west, the species is recorded from the island of St. John in the American Virgin Islands (Koopman 1975). Shamel (1931) in his revision of the genus *Tadarida* considered *antillarum* as a distinct species; however, Schwartz (1955) considered *antillarum* as a subspecies of the widely distributed *T. brasiliensis*, which is the currently accepted taxonomic arrangement. 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.

Table 1 presents measurements of our male and female specimens from Anguilla. The measurements of the male from Anguilla fall at or above the range of measurements of 10 males from Dominica (type locality of *antillarum*), whereas the measurements of the female fall within the range of measurements of 10 females from Dominica (Genoways et al. 2001). As was discussed by Genoways et al. (2001), the relationships among Antillean population of *Tadarida* are in need of systematic review.

Our female specimen from The Valley along with a single individual of *M. molossus* was taken in a mist net set under a canopy formed by large mahogany trees. The male from Chalvilles was taken under conditions described in the account for *A. jamaicensis*. The female captured on May 20 was not pregnant.

**Discussion**

Data presented herein provide records of a species of bat new to the fauna of the island of Anguilla—*Tadarida brasiliensis*. This brings the known chiropteran fauna of the island to six species and we are confident that with additional work a seventh species, *Noctilio leporinus*, will be added to this fauna. Presently, this simple chiropteran fauna includes representatives of three families—Phyllostomidae, Natalidae, and Molossidae—including one omnivore (*B. cavernarum*), one pollenivore/nectarivore (*M. plethodon*), one frugivore (*A. jamaicensis*), and three insectivorous species (*N. stramineus, T. brasiliensis*, and *M. molossus*). The chiropteran fauna of Anguilla is composed of 50% aerial insectivores, which is a composition characteristic of the islands of the Greater Antilles, but only Dominica in the Lesser Antilles. However, if *Noctilio leporinus* is formally added to the fauna, the percentage of aerial insectivores will drop below 50% bringing the trophic structure of the chiropteran fauna into line with other Lesser Antillean islands where aerial insectivores typically constitute less than 50% of the total (Genoways et al. 2001, 2005).

Anguilla’s geographic location at the eastern edge of Anegada Passage presents an opportunity to examine the Passage’s potential as a zoogeographic barrier. The deep and relatively wide Anegada Passage serves as the physiographic feature that separates the Greater and Lesser Antilles, and looking at the modern chiropteran fauna of the West Indies, it appears to form a zoogeographic barrier as well; however, as the fossil evidence is considered, it appears to be less of a barrier. Some genera of bats are limited to islands to the west of the Passage, including *Ariteus, Erophylla, Eumops, Lasiurus, Macrotus, Mormoops, Phyllonycteris, Phyllops*, and *Stenoderma*, whereas *Ardops, Micronycteris, Myotis*, and *Sturnira* are limited to the east in the Lesser Antilles (Baker and Genoways 1978; Jones 1989; Koopman 1989; Breuil and Masson 1991; Genoways et al. 2001, 2005). Pregill et al. (1994) report no fossil bats on Sombrero Island but present data on two species from Anguilla based on two fossil dentaries of *Macrotus waterhousii* found in Little Bay Cave and three fossil dentaries of *Mormoops blainvillii* from “Cave I, Little Bay.” Extant populations of these two species...
are confined to the Greater Antilles, with *M. blainvillii* being found on Puerto Rico (Gannon et al. 2005) and *M. waterhousii* on Hispaniola (Klingener et al. 1978). Fossil *M. waterhousii* are known from Puerto Rico (Choate and Birney 1968) as well as St. Martin in the Lesser Antilles (Pregill et al. 1994). Fossil *M. blainvillii* also are known from Antigua in the central Lesser Antilles (Pregill et al. 1988). In addition, Pregill et al. (1988) report fossils of another species—*Phyllonycteris cf. major*—of Greater Antillean bats from Antigua in the Lesser Antilles. This reduces the number of genera limited to one side or the other of the Anegada Passages from 13 to 10.

Among these 10 remaining genera *Stenoderma*/*Ariteus*/*Phyllops*/*Ardops* are parapatric genera that form the Antillean endemic subtribe *Stenodermatina* that have evolved from a single ancestor (Baker et al. 2003). The Anegada Passage does divide members of this group with *Stenodermatina*/*Ariteus*/*Phyllops* to the west of the passage and *Ardops* to the east. They approach each other at the Passage with *Stenoderma* occurring as far east as St. Croix in the Virgin Islands (Kwiecinski and Coles 2007) and *Ardops* known from Saba, the westernmost of the northern Lesser Antilles (Genoways et al. 2007a). There is no evidence that individuals of the genus *Erophylla*, which is a member of the Antillean endemic subtribe *Phyllonycterini*, have crossed into the Lesser Antilles. The five remaining genera (*Eumops, Lasiurus, Micronycteris, Myotis*, and *Sturnira*) are mainland genera that occupy relatively small areas of the West Indies or occur in very low numbers (Breuil and Masson 1991). At the species level, we count at least eight species, besides those already discussed, that occur on both sides of the Anegada Passage—*Noctilio leporinus, Pteronotus parnellii, Monophyllus plethodon, Brachyphylla cavernarum, Artibeus jamaicensis, Eptesicus fuscus, Tadarida brasiliensis*, and *Molossus molossus*. Our conclusion is that the Anegada Passage has had only a limited impact as a zoogeographic barrier for the chiropteran fauna, particularly if a perspective of the last 10,000 years is taken.

Because the terrestrial habitats on Anguilla are so degraded, we are somewhat surprised that the chiropteran fauna of Anguilla is as diverse as that of other islands in the northern Lesser Antilles—St. Martin, 8 species (Genoways et al. 2007b); Saba, 7 (Genoways et al. 2007a); St. Kitts, 7 (Pedersen et al. 2005); Nevis, 8 (Pedersen et al. 2003); St. Barthélemy, 5 (Larsen et al. 2007); and Antigua, 7 (Pedersen et al. 2006). In our opinion, this diversity has been maintained because of the extensive cave systems present on Anguilla. Four of the six species present on Anguilla (*B. cavernarum, M. plethodon, N. stramineus*, and *T. brasiliensis*) are obligate cave or deep crevice roosting species and *Artibeus jamaicensis* is a facultative user of caves. The remaining species, *M. molossus*, at present roosts primarily under the roofs and siding of homes and other buildings. We did not take *Noctilio leporinus* during our survey, but we expect it to be present because appropriate foraging sites are available and it is a facultative cave roosting species. The other species not present on Anguilla that is found on the adjacent islands of Saba and St. Martin (Genoways et al. 2007a, 2007b) is *Ardops nichollsi* and we do not anticipate its presence on Anguilla. It is a tree-dwelling frugivore and the conditions on Anguilla are simply not favorable for it. As the island of Anguilla continues its economic development, we urge the island government to protect as many of the cave systems as possible. It will insure the conservation of the bat fauna of the island and in turn bats will insure the health of the cave ecosystems and will aid any future attempts at restoration of native vegetation.

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