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Bats of Antigua, Northern Lesser Antilles

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Introduction

No comprehensive survey of the chiropteran fauna of the Antillean island of Antigua has been undertaken in the past. Seven species of bats have been reported in the literature from the island previously, but these have appeared in scattered reports. The first report of bats from Antigua was by Allen (1890) when he reported a single specimen of *Noctilio leporinus* and two of *Artibeus jamaicensis* obtained during an ornithological survey of Antillean islands. Subsequent collections of bats on Antigua were incidental to herpetological work or paleontological surveys of Antigua's limestone cave systems. We found 138 voucher specimens from Antigua scattered in eight museums from previous collecting efforts. Before 2000, almost all extant vouchers with locality data were collected from the vicinity of "Bats Cave," situated on the southeast corner of the island near the town of English Harbour in the Parish of St. Paul. The first formal survey of Antiguan bats was performed by Matthew Morton and Kevel Lindsay in 1994. Although some mist-netting was conducted, their work focused on roost surveys, aiming to provide a resource for future work concerning sites that would benefit from local conservation efforts and further study.

The surveys conducted by parties led by Scott Pedersen in June 1998, July-August 2000, and June 2003 provide the first significant results from mist-netting bats in a variety of foraging habitats on Antigua. Because the southwestern quadrant of the island was under-represented in previous survey efforts, the primary goal of the 2000 and 2003 surveys was to focus upon this forested region and possibly provide new species records for Antigua. The secondary goal of the survey was to provide comparative data for ongoing research into the impact of natural disasters on the bat population on the adjacent island of Montserrat (Adams and Pedersen 1999; Pedersen 2001; Pedersen et al., in prep.).

Methods and Materials

Study area.–Antigua is a small neotropical island (279 km^2) located in the northern Lesser Antilles in latitude 17°05′N and longitude 61°50′W. The island measures a maximum of 21 km east to west and 16 km north to south. Boggy Peak (405 m) in the southwestern section of the island is the highest point. The mean annual temperature at St. John's is 27.8°C, with the highest monthly mean temperature in August (29.0°C) and the lowest in January (26.1°C). The mean annual rainfall for the island is 110 cm, with a dry season from January to April and a wet season from August to November. The island does lie in the hurricane zone and received damage from Hurricane Jose and Hurricane Lenny in October 1999. Antigua is divided into three natural physiographic regions–a volcanic region in the southwest, a central plain, and a limestone region occupying the northeastern third of the island (Loveless 1960). Antigua was originally covered with low forest or scrub, which was over time completely removed for sugarcane plantations, pastures, or fuel. By the end of the 18th century, nearly 142 km² were under cultivation, but by 1960, only 101 km² were under cultivation leaving about 178 km² covered by secondary types of vegetation that is maintained by clearing, shifting cultivation, and the grazing of goats. Loveless (1960) suggested that there were originally a few areas of closed-canopy, Evergreen Seasonal forest on Antigua. There are remnants of this vegetation in protected mesic valleys on Boggy Peak, Rock Peak, Sugar Loaf Mountain, and Wallings Hill. Antigua has no permanent rivers, but it does have more than 10 "seasonal" watercourses, locally called ghauts. The most important of these is the semi-permanent Bendals River located in the central plain (Loveless 1960).

Mist netting.–Mist-netting for bats was conducted in a variety of habitats, including fruit plantations, ponds, reservoirs, and access roads on four separate occasions: 18 December - 2 February 1994; 27 June 1998; 29 July - 6 August 2000; and 7-10 June 2003. The latter two surveys were the most consistent in terms of netting effort with five to seven mist-nets being erected at each site and monitored for 4-6 h depending on activity and weather. Covered flyways were netted wherever possible. At the end of each evening, bats were measured and examined (weight, forearm, reproductive status, tooth wear, presence of scars, and external parasites). Together, the four mist-netting surveys included 78 net-nights and yielded 157 captures of seven species of bat–*Noctilio leporinus, Monophyllus plethodon, Artibeus jamaicensis, Brachyphylla cavernarum, Natalus stramineus, Tadarida brasiliensis,* and *Molossus molossus*. Sixty-four *Artibeus* and nine *Brachyphylla* were wing-banded. During this time period, an additional 56 bats, representing the seven species of bat reported from Antigua, were captured by hand in a variety of bat roosts, including Bats Cave, two rock overhangs on the west coast, and several buildings.

Limited radio-tracking of *Brachyphylla* was performed using 0.63 g BD-2 transmitters (Holohil Systems Ltd.) and TRX-48S Receivers (Wildlife Materials Inc.).

Voucher specimens.–All voucher specimens from the 2000 and 2003 survey were deposited in the research collections at the University of Nebraska State Museum (UNSM) and the Museum of Texas Tech University (TTU). Other museum specimens were examined at the following institutions: AMNH, American Museum of Natural History, New York, NY; BMNH, British Museum (Natural History), London, UK; FMNH, Field Museum of Natural History, Chicago, IL; KU, Natural History Museum, University of Kansas, Lawrence, KS; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MSU, Museum of Michigan State University, East Lansing, MI; NMNH, National Museum of Natural History, Washington, DC; UF, Florida Museum of Natural History, University of Florida, Gainesville, FL.

RESULTS

Capture Rates.–Fruit bat captures per net-night (BNN) range from 0.65 to 6.65 in the Neotropics (Findley and Wilson 1983; Fenton et al. 1992; Pedersen, unpublished data). However, phyllostomid captures on Antigua were toward the low end of this scale at 1.45 BNN. It seems that Antigua's flat terrain, abundant desert scrub, and anthropogenic disturbance provide neither the altitudinal gradient to generate rainfall, nor heavily forested valleys whose native fruits might provide year-around support for additional species of fruit bats as they do on the adjacent islands of Montserrat and Guadeloupe. Indeed, only fragmentary secondary growth forest covers the flanks of the Shekerley Mountains and Boggy Peak (405 m) in the southwestern quarter of the island. These patches of forest were specifically targeted during the 2000 survey without significantly different results (Fig. 1).

Animal Health.–Fruit bats on the adjacent island of Montserrat have contended with the deposition of volcanic ash on leaves, fruits, and flowers since the

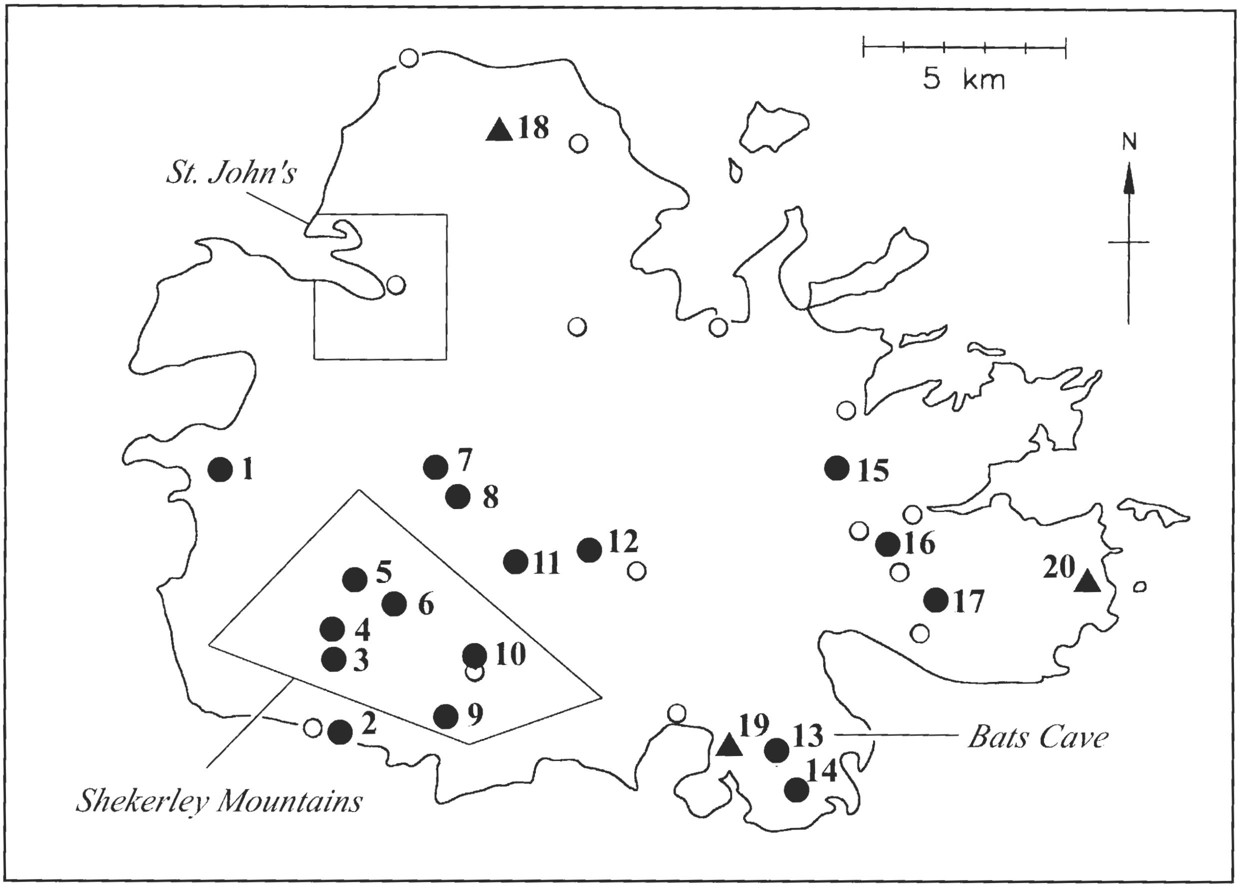

Figure 1. Map of Antigua indicating locations where bat research has been conducted. Numbers refer to locations shown in the figure. Closed circles represent mist-netting localities and active roost sites visited during the current study. Closed triangles are locations represented solely by museum voucher specimens from other studies. Open circles indicate inactive roosts visited. 1) Flat Top Hill: roost in rock overhang near Flat Top Hill. 2) Cades Bay (Goat Head): roost located in rock outcrop. 3) Cades Bay Plantation: flyways located among mango trees at center of banana plantation at upper end of valley, 2.2 km ENE Urlings, 50 m in elevation. 4) Boggy Peak Road: flyway along densely covered access-road to radio installation on top of Boggy Peak, 3.0 km NE Urlings, 350 m. 5) Christian Valley Agricultural Station: access road located among banana trees, 2.1 km S Jennings, 50 m. 6) Christian Valley Agricultural Station: roost located in rock outcrop, northeastern slope of Christian Valley. 7) Green Castle Agricultural Station: flyway along water-works and unnamed stream leading towards Fiennes Well Water Station, Emanuel, 30 m. 8) Emmanuel: roost in derelict building southeast of the Green Castle Agricultural Station. 9) Claremont Plantation: flyways located among mango trees at center of banana plantation, 1.0 km NE Old Road, 20 m. 10) Wallings Reservoir: flyway along densely covered track leading up steep hillside south of reservoir and around reservoir margin, 1 km SSE John Hughes, 150 m. 11) Swetes Dam: flyway along densely covered access-road into Swetes Dam and across the top of the concrete dam itself, 1.5 km WNW Swetes, 50 m. 12) Garden in All Saints: garden at private residence in the town of All Saints, 50 m. 13) Bats Cave: large roost in limestone cave. 14) Shirley Heights: trail along crest of ridge. 15) Collins Reservoir: roost in derelict Mill. 16) Newfield: roost in derelict out-building behind Moravian Church. 17) Montpellier: natural limestone tunnel adjacent to the Montpellier sugar factory. 18) Santa Maria Hill. 19) English Harbour Town. 20) Mill Reef.

Soufriere Hills volcano began to erupt in 1995. Although Antigua has received occasional wind-blown ash from Montserrat during many of the larger eruptive events (1997-2003), none of the fruit bats captured on Antigua in 2000 or 2003 exhibit any of the sub-lethal pathologies associated with the ingestion of ash noted on Montserrat (alopecia, dental attrition; Adams and Pedersen 1999; Pedersen 2001; Pedersen et al., in prep.). In Bats Cave on Antigua, random hand-captured male, female, and juvenile *Brachyphylla* exhibited similar loads of external parasites (2-3 streblid flies, *Trichobius*; and numerous wing-mites), but exhibited neither the extreme loads (15+ streblids), nor the extensive hair-loss noted on *Brachyphylla* on Montserrat during this period (Pedersen et al., in prep.). Lactating females often exhibit alopecia; however, *Brachyphylla* on Montserrat have exhibited advanced alopecia since 1997-2000 whether they are lactating or not (Adams and Pedersen 1999; Pedersen, unpublished data). Although *Brachyphylla* on Antigua have encountered volcanic ash, lactating females were fully furred in 2000 and 2003. This suggests that the levels of alopecia noted in *Brachyphylla* on Montserrat are due to excessive grooming and physiological stress rather than the stress imposed by lactation alone.

Bats Cave.–This large limestone cave is located on the southeast corner of the island near the town of English Harbour. The surrounding habitat is desert scrub, consisting mostly of *Acacia*. This cave is situated 1 km from the ocean, however, there is no permanent source of fresh water within a 3 km radius of the cave entrance. Beyond that distance, there are numerous swimming pools located at resorts and private residences. The main elements of this cave consist of at least eight large domed chambers arranged in a somewhat linear fashion averaging 6-7 m in diameter extending nearly 60 m into the hillside. There are numerous side chambers (possibly extensive given the geology) most of which were inaccessible to adult humans without excavation. The deepest portion of the cave that was easily accessible by walking and crawling was approximately 15-20 m below ground level. During the 2000 survey, the cave climate was 29.5° C with 81% relative humidity recorded in the distal chamber. In 2000, guano deposits were between 15 and 45 cm in depth and supported a host of beetles, roaches, and flies. There was no evidence of ground water, although small catchments of urine and liquefied guano were common. During the 1994, 1998, and 2000 surveys, only two species of bat were observed in the cave–*Brachyphylla cavernarum* and *Natalus stramineus*. In 2003, two species of bats also were encountered, but they were *Brachyphylla cavernarum* and *Monophyllus plethodon*. No *Natalus stramineus* were observed despite the excavation and exploration of several side tunnels. This cave has a well-documented history of utilization by both bats and humans (Nicholson 1992). Indeed, this cave was outfitted with lights and developed as a tourist attraction in the 1970s, and the bat population was large enough that guano mining operations are reported back to 1897 (Nicholson 1992). Given the ease of access and the apparent tolerance of the species to moderate disturbance, Bats Cave presents an extraordinary opportunity for further work on these taxa. During their 1994 survey of Antigua and Barbuda, Morton and Lindsay found that 91.3% of all identified caves (11 on Antigua and 12 on Barbuda) were in use as bat roosts. This, combined with the fact that the largest populations of bats on both islands were found in cave roosts, underlines the importance of these roosting habitats to bats. As such, Bats Cave is in great need of protection, and will clearly benefit from conservation efforts by local authorities.

Species Accounts.–The following species accounts are drawn from census efforts by Morton and Lindsay in 1994, Pedersen and Adams in 1998, Pedersen, Appino, and Swier in 2000, and Pedersen, Genoways, and Larsen in 2003. Detailed descriptions of mist-netting habitats are provided in the legend accompanying Figure 1. All length measurements are in millimeters and mass is reported in grams.

Noctilio leporinus mastivus (Vahl 1797)

Specimen examined (1).–Parish Unknown: no specific locality, 1 (FMNH).

Specimens captured/released (4).–St. Mary Parish: Cades Bay Plantation, 1; Flat Top Hill, 1; Wallings Reservoir, 1. St. Paul Parish: Swetes Dam, 1 (Fig. 1).

Allen (1890) and Davis (1973) have reported this species previously from Antigua. Davis (1973), in his study of geographic variation in *Noctilio leporinus*, assigned the one male that he examined from Antigua to the subspecies *mastivus*, with its type locality on

St. Croix, Virgin Islands. The skull of our one specimen examined (FMNH 15083) is badly broken so that only the following measurements could be taken: length of forearm, 84.6; postorbital constriction, 7.4; length of maxillary toothrow, 10.6; breadth across upper molars, 12.9.

Fishing bats were commonly observed along water courses on Antigua. Visual counts of *Noctilio* foraging over Swetes Dam and Wallings Reservoir in 2000 demonstrate that mist-netting captures underestimate the *Noctilio* population at these sites by at least a factor of three. The 13 million gallon Wallings Reservoir was constructed in 1890 and is surrounded by a mixed evergreen deciduous forest that was planted in 1915. Predominant tree species include locust (*Hymenaea courbaril*), ironwood (*Exostema caribaeum*), mahoe (*Daphnosis caribaea*), black loblolly (*Pisonia fragrans*), mango (*Mangifera indica*), white cedar (*Tabebuia pallida*), mahogany (*Swietenia mohogani*), and Spanish oak (*Inga laurina*). The Wallings Reservoir and Cades Bay Plantation mist-net captures in 1998 and 2000, respectively, were along densely wooded pathways averaging a meter in width and several hundred meters away from the open water of the reservoir or the coastline. In all likelihood, these bats were commuting from unidentified roosts to their foraging habitat. Neither of the animals captured during July 2000 (female: Cades Bay, male: Swetes Dam) evinced reproductive activity. In 2003, several fishing bats were observed foraging across the Wallings Reservoir but none were captured and one bounced off a mist net set across the south end of the reservoir. The forearm lengths and body masses for the two males (Swetes Dam and Wallings Reservoir) were 89.0 and 86.0, and 71.1 and 68.5, respectively, whereas the length of forearm and body mass for the female from Cades Bay was 87.0 and 58.5.

In 1994, a non-reproductive male was extracted from a shallow fissure located under a rock overhang near Flat Top Hill during daylight hours by Morton and Lindsay. They observed *Noctilio* roosting with the body pressed flat against rock surfaces. These bats had been seen returning to Flat Top Hill to roost after dark. During a search of the adjacent cliff face, they observed *Noctilio* in large holes and fissures extending upward into rock overhangs, although *Noctilio* was never observed wedged into narrow cracks.

Monophyllus plethodon luciae Miller 1902

Specimens examined (4).–St. Mary Parish: Christian Valley, 2.1 km S Jennings, 32 m, 17°03′33″N, 61°51′44″W, 1 (TTU). St. Paul Parish: Bats Cave, 1.5 km E English Harbour Town, 23 m, 17°00′52″N, 61°45′01″W, 2 (TTU). Parish Unknown: no specific locality, 1 (MCZ).

Specimens captured/released (4).–St. Mary Parish: Cades Bay Plantation, 1; Christian Valley Agricultural Stations, 1; Claremont Plantation, 1. St. Paul Parish: Bats Cave, 1 (Fig. 1).

Schwartz and Jones (1967) first published on *Monophyllus plethodon* from Antigua based on four specimens deposited in the British Museum (Natural History) and Museum of Comparative Zoology, Harvard University. In their revision of the genus, they assigned these specimens to *M. p. luciae*, with its type locality on St. Lucia. Later, Koopman (1968) also described the specimen from Museum of Comparative Zoology and provided selected measurements. Table 1 presents measurements for three males from Antigua. These measurements fall within the range of those of samples from Guadeloupe and Dominica (Baker et al. 1978; Genoways et al. 2001), except for breadth across the upper molars, which is broader in the specimens from Antigua.

Average length of forearm and body mass for the three males that were captured and released was 40.6 (40.0–42.0) and 16.7 (16.0-17.6), respectively. Considering the number of nights spent mist-netting in fruit orchards across a range of elevations (20-250 m), we were surprised at the relatively small number of *Monophyllus* netted on Antigua in 2000 (4% of phyllostomid bat captures) in comparison to collections at similar sites on neighboring Montserrat in July 2000 (14% of phyllostomid bat captures).

In 2003, three males were captured–two in Bats Cave (June 8) and one netted in fruit orchards in Christian Valley (June 9). The *Monophyllus* taken in Bats Cave were found in a small side tunnel that opened in the floor of the right-hand chamber where no other species were found. This small descending tunnel was approximately 1 m wide and 1.5 m high, at least 30 m long, and may have had a separate opening to the outside as evidenced by a slight breeze in that tunnel. At least 20 individual *Monophyllus* were observed in this small space. Three captured males had testes lengths of 5, 4, and 3 and weighed 15.5, 13.6, and 15.4, respectively.

Brachyphylla cavernarum cavernarum
Gray 1834

Specimens examined (114).–St. Paul Parish: Bats Cave, 1.5 km E English Harbour Town, 23 m, 17°00′52″N, 61°45′01″W, 20 (16 TTU, 4 UNSM); Bats Cave, 2 mi. E Falmouth, 5 (2 FMNH, 3 UF); near Bats Cave, English Harbor [= Harbour], 12 (NMNH); 1 mi. E English Harbor [=Harbour], 3 (1 KU, 2 MSU). Parish Unknown: no specific locality, 74 (1 BMNH, 73 NMNH).

Specimens captured/released (105).–St. Mary Parish: Boggy Peak Road, 1; Cades Bay Plantation, 6; Christian Valley Agriculture Station, 1; Wallings Reservoir, 2. St. Paul Parish: Bats Cave, 95 (Fig. 1).

Miller (1913a; see also Koopman 1968) was the first author to report *Brachyphylla cavernarum* from Antigua. Swanepoel and Genoways (1978) examined 20 specimens from the island as part of their systematic review of the genus. Swanepoel and Genoways (1978) assigned the material from Antigua to the nominate subspecies, which has a type locality of St. Vincent. Table 1 presents the length of forearm and seven cranial measurements for 12 males and 9 females from Antigua. The only measurement in which there was a significant difference between the sexes was mastoid breadth, with males being larger ($P \leq 0.05$). In general, males were larger in all other cranial measurements except postorbital constriction in which the sexes were similar. Females had longer forearms. The measurements of our sample from Antigua match closely those samples of *B. c. cavernarum* presented by Swanepoel and Genoways (1978).

Sex ratio data for *Brachyphylla* hand-captured in 2000 in Bats Cave suggest near male-female parity (48 males: 44 females). This male-female balance was mirrored by a 5:4 male-female capture ratio while mist netting in several foraging habitats located many kilometers away from the cave. On 3 August 2000, we observed a mixed male/female maternity colony of *Brachyphylla cavernarum* numbering well over 20,000 animals in Bats Cave (independent estimates by three observers). In contrast to the *Brachyphylla* maternity colony on the neighboring island of Montserrat, the *Brachyphylla* colony on Antigua was not separated into male/female caves, nor was there any obvious evidence of male-female territoriality. Animals were observed in clusters ranging in size from 10 to 200 individuals. The clusters of animals occupied numerous pockets in the domed roof of each chamber of the cave. Neonates and juvenile animals appeared to be randomly located throughout the cave, giving no indication of a "crèche." Numerous mid-air collisions between individual *Brachyphylla* were observed, several resulting in the grounding of both animals. Due to the apparent difficulty in taking flight from the soft substrate (guano), most grounded bats climbed up onto an adjacent rock surface before taking off. Of note, the exposed upper surfaces of most rocks in lower half of the cave were highly burnished, no doubt in response to animal contact.

Bats Cave was visited on 8 June 2003, when the majority of the females in the colony were carrying pups. The females were located in the deeper, hotter, more humid portions of the cave. Many of the males were congregated near the entrance and in the outermost chambers where the temperature was considerably lower and ambient light made the bats clearly visible. Five of the six females obtained in 2003 were lactating and were collected along with their infants. The sixth female was non-reproductive. The testes length of six adult males collected at this time averaged 6.3 (4-9). The length of forearm and weight of three male and one female infant were 56.6, 51.6, 51.8, and 52.2 and 25.6, 21.8, 20.6, and 20.7, respectively. A male captured on 25 June 1958, had testes that were 5.0 long. Of 10 females collected and preserved from Bats Cave on 29 April 1959, nine were pregnant. Some of the embryos had been removed for other studies, but the crown-rump length of remaining four embryos was 34, 36, 37, and 39. All 21 females collected on 1 May 1958 were pregnant, with one of the embryos measuring 37 in crown-rump length. None of the nine females taken on 2 and 7 August 1903, the 3 females taken on 7 November 1903, or the 5 females from 20 November 1903 were pregnant. These combined reproductive data suggest that a monestrus reproductive pattern with synchronous breeding (Wilson 1979) occurs in *Brachyphylla* on Antigua.

Average length of forearm and body mass (1994 and 2000 capture/release) for 12 adult males was 66.2 (64.6-69.0) and 49.5 (41.8-56.0), and the same for six adult females was 66.2 (64.0-68.0) and 46.4 (41.1-49.4), respectively. Five lactating females captured in early June 2003 weighed an average of 42.7 (38.6-46.3), whereas a non-reproductive adult female weighed 36.5. Six adult males taken at this time weighed an average of 43.4 (39.0-48.5).

Morton and Lindsay recorded roost emergence behavior for *Brachyphylla* from Bats Cave in February 1994. They observed that a small number of bats began to exit the cave to forage around 1845 h, whereas the majority of the colony waited until after dark (1915 h) to exit the cave. The emergence continued sporadically through 1945 h.

Radio-tracking data for two male *Brachyphylla* indicate that these robust bats travel nightly up to 22 km away from Bats Cave to forage in the moist, higher altitude valleys and farm lands on the southwestern side of the island. In addition, one of the wing-banded *Brachyphylla* was recaptured at 14.3 and 15.4 km from the roost on consecutive evenings (minimum-commuting distance of 60 km over two nights).

Artibeus jamaicensis jamaicensis
Leach 1821

Specimens examined (28).–St. John Parish: Santa Maria Hill, 2+ mi. NE St. Johns, 4 (NMNH). St. Mary Parish: Christian Valley, 2.1 km S Jennings, 32 m, 17°03′33″N, 61°51′44″W, 6 (TTU); Wallings Reservoir, Wallings, 166 m, 17°02′04″N, 61°49′30″W, 6 (TTU). St. Paul Parish: English Harbor [= Harbour], 10 (1 MCZ, 9 NMNH). Parish Unknown: no specific locality, 2 (1 FMNH, 1 MCZ).

Specimens captured/released (80).–St. John Parish: Green Castle Agricultural Station, 7. St. Mary Parish: Boggy Peak Road, 9; Cades Bay Plantation, 6; Christian Valley Agriculture Station, 10; Claremont Plantation, 11; Wallings Reservoir, 12. St. Paul Parish: All Saints, 4; Swetes Dam, 16. St. Philip Parish: Collins, 1; Montpellier, 4 (Fig. 1; Table 1).

J. A. Allen (1890, see also G. M. Allen 1911) first reported this species from Antigua based on an adult male captured on 30 December 1889, and an adult female captured on 23 April 1890. Genoways et al. (2001) reviewed Antillean populations of the Jamaican fruit bat based upon morphometrics and presence/absence of M3/m3 and Phillips et al. (1989) and Pumo et al. (1996) presented genetic data for these populations. These studies support the use of the subspecific name *A. j. jamaicensis* for Antiguan populations. Table 1 presents length of forearm and seven cranial measurements for four male and five female *A. jamaicensis* from Antigua. The sexes differed significantly only in postorbital constriction in which females were larger on average. Females were larger on average than males in all other measurements as well except length of the maxillary toothrow in which the sexes had the same mean.

Eighteen of the 29 males (62%) captured and released in July 2000 exhibited scrotal testes. Of the 35 females captured and released in July 2000, five were pregnant and 11 were lactating or post-lactation (45% of the females were reproductively active). Six adult males collected between 7-9 June 2003, had testes that averaged 9 (6-11) in length. Of six females taken during this same time period, three evinced no reproductive activity, two were lactating, and one carried an embryo that was 20 mm in crown-rump length. Two females taken at Santa Maria Hill on 14-15 August 1980 were lactating.

For individuals that were captured and released, the average length of forearm and body mass for 12 adult males were 59.5 (57.0-63.0) and 40.9 (36.3-50.6), respectively, and the same for 26 adult non-pregnant females were 60.4 (57.0-62.0) and 42.5 (34.7-50.4), respectively. The weights of three non-pregnant females taken in early June 2003 were 34.7, 36.9, and 36.9, whereas two lactating females weighed 39.7 and 39.9. Six adult males, also taken in early June 2003, weighed an average of 38.9 (35.5-43.2).

Although W. R. Forrest recorded in his field notes that *Artibeus* was present in "Bats Cave" in 1918, *Artibeus* was not observed there in 1994, 1998, 2000, or 2003. However, *Artibeus* was commonly observed in abandoned buildings and was collected at all mist-netting localities in 1994, 1998, 2000, and 2003. These animals were observed hanging pendant from foliage and from the ceilings/rafters of unused buildings, either individually or in very tight clusters. The individuals

Table 1.–Length of forearm and cranial measurements of six species of bats occurring on the West Indian island of Antigua.

Statistics or catalogue number and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
				Monophyllus plethodon luciae				
TTU 6061, Male	43.1	23.5	22.1	10.7	4.8	10.0	8.4	6.0
TTU 6062, Male	41.3	23.4	21.9	10.3	4.9	10.1	8.1	6.1
MCZ 17468, Male	41.0	23.6	22.1	10.7	4.7	10.3	7.9	5.9
				Brachyphylla cavernarum cavernarum				
Males								
N	12	12	12	12	12	11	12	12
Mean	65.5	31.6	28.5	17.3	6.4	14.8	11.1	11.8
Range	(62.3-69.3)	(31.1-32.1)	(28.1-29.3)	(16.9-18.0)	(6.2-6.7)	(14.3-15.2)	(10.9-11.4)	(11.5-12.2)
± SE	±0.52	±0.07	±0.10	±0.10	±0.05	±0.07	±0.05	±0.07
Females								
N	9	9	9	9	9	9	9	9
Mean	65.9	31.5	28.2	16.9	6.4	14.5	11.0	11.6
Range	(63.7-68.4)	(30.5-32.1)	(27.5-28.7)	(16.1-17.5)	(6.2-6.6)	(14.1-15.3)	(10.6-11.2)	(10.9-12.0)
± SE	±0.61	±0.17	±0.17	±0.18	±0.06	±0.12	±0.08	±0.13
				Artibeus jamaicensis jamaicensis				
Males								
N	4	4	4	4	4	4	4	4
Mean	59.8	28.3	24.8	17.0	6.9	14.7	9.9	12.5
Range	(59.4-60.5)	(27.2-29.2)	(24.1-25.8)	(16.5-17.9)	(6.7-7.1)	(14.2-14.9)	(9.4-10.3)	(12.2-13.1)
± SE	±0.25	±0.41	±0.41	±0.32	±0.09	±0.17	±0.19	±0.20
Females								
N	5	5	5	5	5	5	5	5
Mean	61.4	28.4	25.2	17.2	7.2	15.0	9.9	12.9
Range	(59.5-63.7)	(28.1-29.3)	(24.4-26.3)	(16.7-17.5)	(6.9-7.5)	(14.6-15.4)	(9.8-10.2)	(12.6-13.3)
± SE	±0.69	±0.23	±0.33	±0.13	±0.12	±0.14	±0.08	±0.13
				Natalus stramineus stramineus				
MCZ 17469, Male	39.1	16.8	15.6	8.6	3.1	7.5	7.4	5.6
MCZ 17470, Male	38.9	16.8	15.7	8.6	3.2	7.6	7.4	5.7
TTU 6080, Male	39.0	17.0	15.5	8.7	3.2	7.9	7.4	5.7
MCZ 17472, Female	37.2	ó	ó	8.4	3.1	ó	7.2	5.5
TTU 6079, Female	38.2	16.4	15.3	8.5	3.1	7.3	7.2	5.7
UNSM 27900, Female	38.4	16.8	15.6	8.5	3.1	7.4	7.2	5.5

Table 1 (cont.)

Statistics or catalogue number and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
				Molossus molossus molossus				
Males								
N	5	5	5	5	5	5	5	5
Mean	37.5	16.4	14.7	10.2	3.2	9.7	5.7	7.2
Range	(36.5-38.0)	(15.9-17.0)	(14.1-15.2)	(10.0-10.4)	(3.2-3.3)	(9.3-10.0)	(5.4-5.9)	(7.1-7.3)
± SE	±0.31	±0.18	±0.19	±0.08	±0.02	±0.12	±0.09	±0.05
Females								
N	5	5	5	5	5	5	5	5
Mean	37.2	15.8	14.1	9.9	3.2	9.4	5.6	7.2
Range	(36.5-37.6)	(15.7-15.9)	(13.9-14.3)	(9.6-10.1)	(3.1-3.3)	(9.1-9.6)	(5.4-5.7)	(7.0-7.4)
± SE	±0.21	±0.04	±0.07	±0.12	±0.04	±0.09	±0.06	±0.08
				Tadarida brasiliensis antillularum				
Males								
N	5	5	5	5	5	5	5	5
Mean	37.4	16.1	14.9	9.2	3.7	8.9	5.6	6.6
Range	(36.5-38.4)	(15.7-16.3)	(14.8-15.2)	(8.8-9.5)	(3.6-3.9)	(8.7-9.1)	(5.5-5.7)	(6.2-6.9)
± SE	±0.31	±0.12	±0.08	±0.12	±0.07	±0.07	±0.04	±0.13
Females								
N	5	5	5	5	5	5	5	5
Mean	39.2	15.9	14.7	9.3	3.6	8.8	5.6	6.6
Range	(38.4-40.3)	(15.6-16.2)	(14.5-15.0)	(9.2-9.6)	(3.5-3.8)	(8.7-9.1)	(5.5-5.7)	(6.5-6.6)
± SE	±0.33	±0.11	±0.09	±0.07	±0.05	±0.07	±0.04	±0.02

captured at Santa Maria Hill were taken from a limestone overhang. In direct contrast to the raucous nature of *Brachyphylla* roosts, *Artibeus* roosts typically remain quiet unless the animals are disturbed by attempts to capture them.

Of the eight individuals examined, seven were missing both upper third molars and possessed both lower third molars. The eighth individual was missing both third upper molars as well as the lower left third molar. The lower right molar was minute. On Antigua, heavy tooth wear was noted only on a single female *Artibeus* in 2000 (1% of captures) that was clearly a very old animal.

Natalus stramineus stramineus Gray 1834

Specimens examined (8).–St. Paul Parish: Bats Cave, 1.5 km English Harbour Town, 23 m, 17°00′52″N, 61°45′01″W, 1 (UNSM); English Harbor [= Harbour], 2 (MCZ). St. Philip Parish: Montpelier Cave, 1.2 km E, 0.2 km S, 78 m, 17°02′36″N, 61°425′2″W, 3 (TTU). Parish Unknown: no specific locality, 2 (MCZ).

Specimens captured/released (9).–St. Mary Parish: Christian Valley, 2. St. Paul Parish: Bats Cave, 7.

Goodwin (1959), in his revision of members of the subgenus *Natalus*, restricted the type locality of *Natalus stramineus* to Antigua rather than Lagoa Santa, Minas Gerais, Brazil, as was done by earlier authors. With this decision, which later was reconfirmed by Handley and Gardner (1990), the nominate subspecies *N. s. stramineus* becomes the appropriate name to apply to the population on Antigua. Goodwin (1959) gives measurements for two males from Antigua in the British Museum (Natural History) as follows: length of forearm, 38.0, 38.8; greatest length of skull, 16.6, 16.6; condylobasal length, 15.5, 15.7; zygomatic breadth, 8.7, 8.8; breadth of braincase, 8.1, 8.0; interorbital breadth, 3.4, 3.5; breadth across upper molars, 5.9, 5.9; length of maxillary toothrow, 7.4, 7.5. Table 1 presents the length of forearm and seven cranial measurements for three males and three females from Antigua. The range of measurements of these topotypic individuals fall within the range of a larger sample from Dominica (Genoways et al. 2001).

Seven specimens were hand-collected in Bats Cave, while two others were hand-collected in a large rock crevice between very large boulders in Christian Valley in 1994 (1600 h) (Fig. 1). In 2000, numerous *Natalus* (n = 90+) were observed in Bats Cave, but no young were observed. As is typical of the species, each bat hung fully pendant a short distance (15-20 cm) from neighboring bats across the ceiling of Bats Cave. In 2000, *Natalus* was again observed to utilize height restricted portions of the cave ceiling along large fissures that diverge laterally from the main chamber. The apparent preference for these smaller side passages along the middle and at the back of the cave may be due to a variety of reasons including: (1) the slightly higher relative humidity in these microclimates (85% humidity), and (2) a desire to avoid the much larger *Brachyphylla*. Indeed, we witnessed a mid-air collision between *Natalus* and *Brachyphylla* that fractured the right humerus of the smaller bat (UNSM 27900). When funnel-eared bats began emerging around 1840 h, they were flying low to the ground, but did not appear to have made use of the main exit hole. The facultative use of secondary exits may avoid collisions with *Brachyphylla* that also began to exit around this time. No *Natalus* were observed in Bats Cave on 8 June 2003.

During the 1998 and 2003 surveys, a limestone cave 600 m east of the disused Montpellier sugar factory east of St. Philips was visited. This tunnel ran for nearly 120 m with a relatively constant diameter of 1.5 to 2.0 m. At least five *Natalus* were observed in this cave in 1998 and 12 to 15 animals were observed in 2003. The northeastern half of Antigua is dominated by xeric habitats like those surrounding the Montpellier Cave and Bats Cave. These caves are very important from a management perspective as they provide critical humid microenvironments that *Natalus* must have across this xeric part of the island.

Length of forearm and body mass for two females captured/released in 1994 and 2000 were 39.0 and 40.0 and 5.2 and 6.5, respectively. A female and two males taken on 9 June 2003, weighed 4.4, 4.8, and 5.0, respectively. The female evinced no gross reproductive activity and the males had testes lengths of 1.0 and 2.0.

Molossus molossus molossus (Pallas 1766)

Specimens examined (20).–St. Mary Parish: Christian Valley, 2.1 km S Jennings, 32 m, 17°03′33″N, 61°51′44″W, 8 (TTU); Wallings Reservoir, Wallings, 166 m, 17°02′04″N, 61°49′30″W, 9 (TTU). St. Paul Parish: English Harbor [= Harbour], 1 (NMNH). St. Philip Parish: Mill Reef, 1 (AMNH). Parish Unknown: no specific locality, 1 (NMNH).

Specimens captured/released (8).–St. Mary Parish: Cades Bay Plantation, 3; Claremont Plantation, 1; Wallings Reservoir, 1. St. Paul Parish: Swetes Dam, 2. St. Philip Parish: outbuilding adjacent to Newfield Moravian Church, 1 (Fig. 1; Table 1).

Miller (1913b; see also Miller 1924: 89) included the first specimens of this species reported from Antigua in the material that he described under the species name *Molossus debilis* and Koopman (1968) listed two specimens from Antigua obtained by Clayton E. Ray in 1963. The name *M. debilis* and a number of others have been applied to this bat in the Antillean islands. It is now believed that the most appropriate name to apply to these bats is *Molossus molossus*, which is a widespread Neotropical species. Husson (1962) restricted the type locality of *M. molossus* to the island of Martinique, which lead Dolan (1989) to apply the name *M. m. molossus* to this species in the Lesser Antilles. Table 1 presents the length of forearm and seven cranial measurements of five males and five females from Antigua. Males were significantly larger than females at the $P \leq 0.01$ level for greatest length of skull and at the $P \leq 0.05$ level for condylobasal length and mastoid breadth. Males were larger than females on average for length of forearm and zygomatic breadth, whereas the sexes had the same mean values for postorbital constriction, length of maxillary toothrow, and breadth across upper molars.

Between 29 July and 1 August 2001, three pregnant females and one lactating female were captured and released. Eight of 11 females netted 7-9 June 2003, were pregnant carrying single embryos, with the following crown-rump lengths: 6, 7, 7, 8, 9, 10, 10, and 16. Four males captured at this time had testes lengths of 3, 4, 4, and 6.

During the period 28 July - 2 August 2000, the length of forearm and body mass for a single adult male captured/released were 38.0 and 14.0, whereas the average length of forearm and body mass for three adult females were 35.3 (34.0-36.0) and 10.0 (9.6-10.8); three pregnant females, 36.0 and 13.8 (12.6-14.8); and a single lactating female 37.0 and 11.9, respectively. The three non-pregnant females obtained in early June 2003 had weights of 9.1, 10.1, and 10.2, whereas the eight pregnant females weighed an average of 11.0 (10.0-12.2). Five males collected at this time weighed an average of 11.4 (10.6-13.1).

Tadarida brasiliensis antillularum
(Miller 1902)

Specimens examined (28).–St. Mary Parish: Wallings Reservoir, Wallings, 166 m, 17°02′04″N, 61°49′30″W, 16 (TTU). St. Paul Parish: English Harbor [= Harbour], 12 (NMNH).

Specimens captured/released (17).–St. Mary Parish: Flat Top Hill, 9. St. Philip Parish: Newfield, 8.

Shamel (1931) reported 21 specimens of this species from Antigua under the name *Tadarida antillularum*. Miller (1902) had described this taxon with a type locality at Roseau, Dominica. Schwartz (1955) reduced this taxon to a subspecies in the widespread *Tadarida brasiliensis*, with a geographic range extending from Puerto Rico to St. Vincent (Genoways et al. 2001). Table 1 presents the length of forearm and seven cranial measurements for five males and five females from Antigua. Female *Tadarida* were found to have a significantly longer forearm than males at the $P \leq 0.01$ level, whereas males had a significantly longer condylobasal length than females at the $P \leq 0.05$ level. The genders did not differ significantly in any of the other measurements, but males were somewhat larger on average for greatest length of skull, postorbital constriction, and mastoid breadth, and females were larger on average for zygomatic breadth. The sexes averaged the same for length of maxillary toothrow and breadth across upper molars.

During 1994, Morton and Lindsay examined seventeen specimens that had been hand-collected during daylight hours. Eight specimens of *Tadarida* were collected from under the roofing of a derelict outbuilding at the Moravian Church in the town of Newfield (6 males, 2 females; 1830 h) on 2 February. Nine other animals were extracted from tiny crevices in a rock overhang near Flat Top Hill (3 males, 6 females; 1915 h) (Fig. 1) on 16 January. On the night of 6 June 2003, five male and four female *Tadarida* were netted over water in the Wallings Reservoir and on 9 June two males and five females were taken in the same place. In 2003, the water behind the dam was greatly reduced, but the pool was still at least 20 m wide and 50 m long. The specimens collected in 1918 by W. K. Fisher from English Harbour were all females.

Of the nine females netted in early June 2003, seven evinced no gross reproductive activity, one was lactating, and one carried a single embryo measuring 5.0 in crown-rump length. Seven males taken during this time had testes that averaged 3.9 (3-5) in length.

Average length of forearm (mm) and body mass for nine males captured and released in 1994 were 38.6 (37.0-40.0) and 9.4 (8.7-10.5), respectively, whereas eight females were 38.7 (38.0-40.0) and 9.2 (7.9-11.1). Seven nonpregnant females captured in June 2003 weighed an average of 9.6 (8.8-10.4), a lactating female weighed 9.1, and a pregnant female weighed 9.5. Seven males taken at this time weighed an average of 9.0 (7.9-9.8).

Discussion

In theory, the number of species found on islands along an archipelago is correlated with the size (area) of each island, but this effect is ameliorated by distance from a source area such as a continent. The number of species occurring on an island also is dependent on the diversity of habitats available, which in most cases is directly affected by elevation of the island. Increased elevation usually results in increased rainfall and a more diverse vegetation (MacArthur 1972). For example, Morgan and Woods (1986) studying the whole West Indian mammalian fauna found that 69% of the variance in species diversity could be explained by area of the islands alone. They concluded that "The remaining 31% of the variance must be dependent upon other variables such as habitat diversity and distance from source areas."

Following models that have been applied to amphibians and reptiles (Preston 1962a, 1962b), birds (Hamilton et al. 1964), and West Indian bats or mammalian fauna (Morgan and Woods 1986; Griffiths and Klingener 1988), we constructed a species-area curve for the bat fauna throughout the Antilles (Fig. 2). Under this general model, several islands including Antigua fall below the regression-line relative to other islands of their size. These deviations amount to the "absence" of species from their respective chiropteran faunas. These particular islands may simply be under-sampled (Saba) or perhaps these islands may not provide sufficient habitats to support bat diversity, despite their size (Antigua, St. Eustatius).

Antigua is situated at the northern end of what Genoways et al. (1998, 2001) termed the Lesser Antillean Faunal Core. However, the paucity of chiropteran taxa on Antigua (notably the absence of *Ardops nichollsi, Chiroderma improvisum, Sturnira thomasi, Eptesicus guadeloupensis*, and *Myotis dominicensis*) distinguishes Antigua from neighboring Guadeloupe (Genoways and Baker 1975; Genoways and Jones 1975; Jones and Genoways 1975; Jones and Phillips 1976). Neither species of insectivorous bat (*Eptesicus guadeloupensis* and *Myotis dominicensis*) has been reported from Antigua, or from neighboring Montserrat despite extensive efforts that span 20 years on those islands (Adams and Pedersen 1999; Jones and Baker 1979; Morton and Lindsay 1994; Morton and Fawcett 1996; Pedersen et al. 1996; Pierson and Warner 1990). However, it should be remembered that for most islands, *Myotis* is known only from a single specimen or from a small series. Following an extensive earlier survey (Baker et al. 1978), the genus *Myotis* was first reported from Guadeloupe based on only two specimens in 1992 (Masson and Breuil 1992). The other insectivorous species missing from both Antigua and Montserrat is *Eptesicus guadeloupensis*, which is currently known only from Guadeloupe.

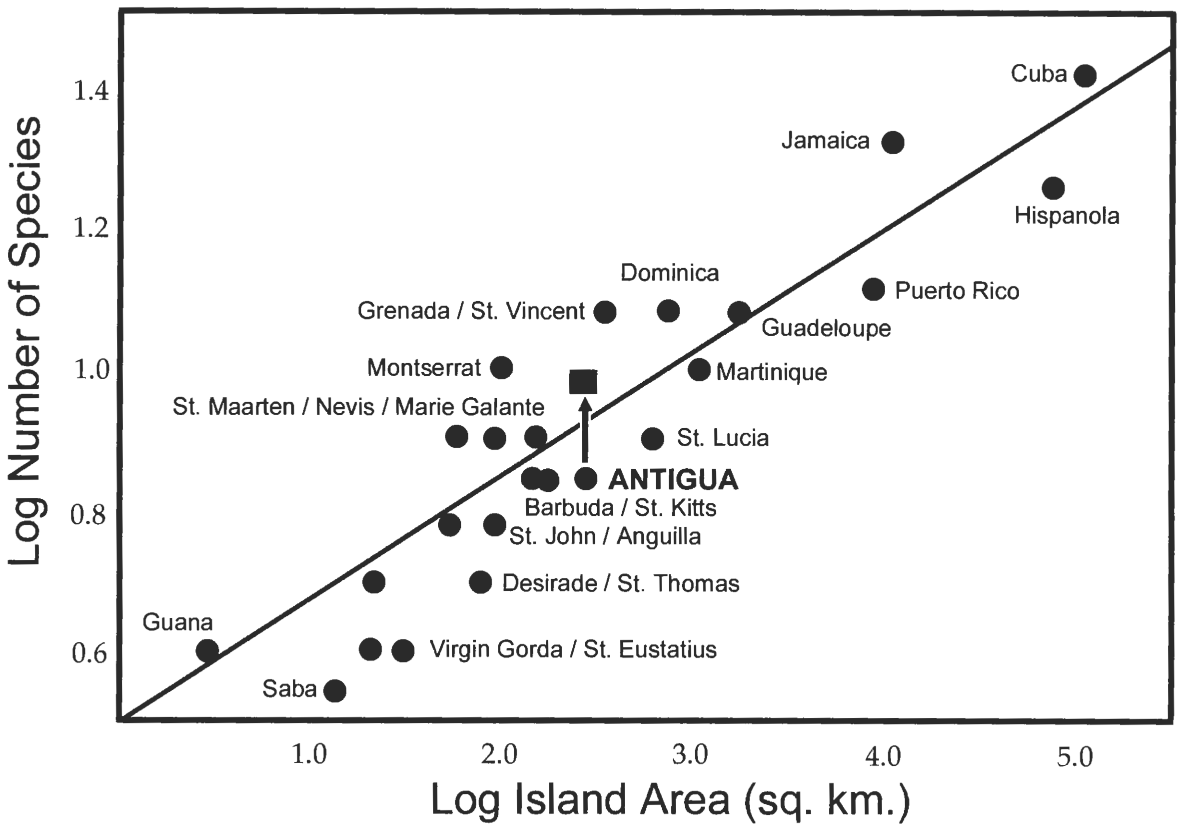

Figure 2. Species/area curve for the chiropteran fauna in the Antilles. Data are from Genoways et al. (2001) with minor modification. Linear regression of log-transformed data: y = 0.17x + .49 (R-squared = 0.81). For argument (see text), Antigua has been represented twice with the extant compliment of seven species of bats (closed circle) and with it's compliment increased by three additional species (Arrow: Square).

Conversely, three species of fruit bat–*Ardops nichollsi*, *Sturnira thomasi* (Genoways 1998; Pedersen et al. 1996), and *Chiroderma improvisum* (Jones and Baker 1979; Pierson and Warner 1990)–have been reported from both of Antigua's neighbors, Montserrat (50 km WSW) and Guadeloupe (75 km SSE; Baker et al. 1978; de la Torre and Schwartz 1966), but have not been found on Antigua. Most notable by its absence is *Ardops nichollsi*, a common tree-roosting fruit bat found throughout the Lesser Antilles that is quite common on the smaller nearby islands of Montserrat (approximately 15% of frugivore captures; Pedersen et al. 1996) and Nevis (Pedersen et al. 2003). Despite efforts to sample nearly identical habitats on Montserrat and Antigua in 2000, no *Ardops* have been observed nor collected on Antigua.

Part of the explanation for the differences in the chiropteran fauna of Antigua as compared to those of Guadeloupe and Montserrat may lie in the elevations of the islands–Guadeloupe, area 1779 km^2, maximum elevation 1465 m; Antigua, 279 km^2, 405 m; Montserrat, 102 km^2, 910 m. The much lower average elevation of Antigua would have resulted in less diversity of the vegetation of the island. As Loveless (1960) stated, the island originally may have been forested, but this would have been a low scrub forest with limited areas of Evergreen Seasonal forest. This forest type probably would not provide a source of fruit for the fruit-eating bats throughout the year, thus their absence may be attributed to the lack of diversity in the flora of the island. The apparent absence of several insectivorous species of bats also may relate to this same issue. Again with the reduced diversity of flora on the island there should be a resulting reduction in the diversity of the insect fauna, which consequently may not support a diversity of insectivorous bats.

The missing species of bats on Antigua also may lie in the fossil record of the island. Steadman et al. (1984) and Pregill et al. (1988) reported on three species of bats in the fossil record of Antigua that no longer occur on the island–*Pteronotus parnellii*, *Mormoops blainvillii*, and *Phyllonycteris major*–from deposits that range from 4300 years B.P. at the bottom to 2560 years B.P. at the top. They also reported four species in the fossil record that still live on Antigua–*Brachyphylla cavernarum, Natalus stramineus, Tadarida brasiliensis*, and *Molossus molossus*. Finally, they described a mandible from a glossophagine bat, possibly *Glossophaga* or *Monophyllus*, the latter being more likely as it is still extant on Antigua.

Only recently has *Pteronotus parnellii* been discovered in a living chiropteran fauna on a Lesser Antillean island–St. Vincent (Vaughan and Hill 1996). Historically, *P. parnellii* could have reached Antigua either from the south or from the northwest, but Vaughan and Hill concluded that the population on St. Vincent was more closely related to South American mainland populations than to those that occur in the Greater Antilles (Smith 1972), a conclusion that has been subsequently supported by Lewis-Oritt et al. (2001) who used molecular data to show that all populations of *P. parnellii* in the Antilles would have originated in northeastern South America.

Mormoops blainvillii has occupied a broader geographic range in the past than at the present time, with fossil records from Abaco, Exuma, and New Providence in the Bahamas and Anguilla and Barbuda in the Lesser Antilles (Koopman 1951; Morgan 2001). Antigua is far removed from the present geographic ranges of *Mormoops blainvillii* and the fossil species *Phyllonycteris major* whose eastern-most locality is Puerto Rico.

The chiropteran fauna of Antigua raises some interesting questions for island biogeographers. What is the appropriate slice of time that should be used when constructing species-area curves? Using only the data from the last 200 years, the chiropteran fauna of Antigua appears unbalanced, but if data from the last 4000-5000 years are used, the chiropteran fauna seems to fit the predicted species-area curve. How should human impact be factored into species-area curve analyses? Steadman et al. (1984) attributed the loss of the three species of bats and other vertebrates on Antigua to "human-caused environmental degradation in the past 3500 yr." However, given the accelerated rate of development and deforestation on these small islands in the last 25 years, how should conservation officers best utilize species-area curves in their management decisions? How can elevation be factored into species-area curves? Should insectivorous and frugivorous guilds be treated separately? Clearly, there needs to be a re-evaluation of how to factor-in the entire profile of an island into a biogeographical analysis.

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LITERATURE CITED

Adams, R., and S. Pedersen. 1999. The effects of natural disasters on bat populations on Montserrat, BWI: A 20-year history. American Zoologist 38(5):52A.

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

Allen, J. A. 1890. Notes on a small collection of West Indian bats, with description of an apparently new species. Bulletin of the American Museum of Natural History 3:169-173.

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

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

de la Torre, L., and A. Schwartz. 1966. New species of *Sturnira* (Chiroptera: Phyllostomidae) from the islands of Guadeloupe and Saint Vincent, Lesser Antilles. Proceedings of the Biological Society of Washington 79:297-303.

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

Fenton, M. B., L. Acharya, D. Audet, M. B. Hickey, C. Merriman, M. K. Obrist, and D. Syme. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica 24:440-446.

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

Genoways, H. H. 1998. Two new subspecies of bats of the genus *Sturnira* from the Lesser Antilles, West Indies. Occasional Papers of the Museum, Texas Tech University 176:1-7.

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

Genoways, H. H., and J. K. Jones, Jr. 1975. Additional records of the stenodermine bat, *Sturnira thomasi*, from the Lesser Antillean Island of Guadeloupe. Journal of Mammalogy 56:924-925.

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

Genoways, H. H., 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 Publication of the Museum, Texas Tech University 43:1-43.

Goodwin, G. G. 1959. Bats of the subgenus *Natalus*. American Museum Novitates 1977:1-22.

Griffiths, T. A., and D. Klingener. 1988. On the distribution of Greater Antillean bats. Biotropica 20:240-251.

Hamilton, T. H., R. H. Barth, and I. Rubinoff. 1964. The environmental control of insular variation in bird species abundance. Proceedings of the National Academy Science 52:132-140.

Handley, C. O., Jr., and A. L. Gardner. 1990. The holotype of *Natalus stramineus* Gray (Mammalia: Chiroptera: Natalidae). Proceedings of the Biological Society of Washington 103:966-972.

Husson, A. M. 1962. The bats of Suriname. Zo□logische Monographier□n, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands 2:xxxiv + 1-569.

Jones, J. K. Jr., and R. J. Baker. 1979. Notes on a collection of bats from Montserrat, Lesser Antilles. Occasional Papers of the Museum, Texas Tech University 60:1-6.

Jones, J. K., Jr., and C. J. Phillips. 1976. Bats of the genus *Sturnira* in the Lesser Antilles. Occasional Papers of the Museum, Texas Tech University 40:1-16.

Jones, J. K., Jr., and H. H. Genoways. 1975. *Sturnira thomasi*. Mammalian Species 68:1-2.

Koopman, K. F. 1951. Fossil bats from the Bahamas. Journal of Mammalogy 32:229.

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

Lewis-Oritt, N., C. A. Porter, and R. J. Baker. 2001. Molecular systematics of the Family Mormoopidae (Chiroptera) based on cytochrome b and recombination activating gene 2 sequences. Molecular Phylogenetics and Evolution 20:426-436.

Loveless, A. R. 1960. The vegetation of Antigua, West Indies. Journal of Ecology 48:495-427.

MacArthur, R. H. 1972. Geographical ecology–patterns in the distribution of species. Harper and Row, New York.

Masson, D., and M. Breuil. 1992. Un *Myotis* (Chiroptera, Vespertilionidae) en Guadeloupe (Petites Antilles). Mammalia 56:473-475.

Miller, G. S., Jr. 1902. Twenty new American bats. Proceedings of the Academy of Natural Sciences of Philadelphia 54:389-412.

Miller, G. S., Jr. 1913a. Five new mammals from tropical America. Proceedings of the Biological Society of Washington 26:31-33.

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

Miller, G. S., Jr. 1924. List of North American Recent mammals, 1923. Bulletin of the United States National Museum 128:xvi + 1-673.

Morgan, G. S. 2001. Patterns of extinction in West Indian bats. Pp. 369-407 in Biogeography of the West Indies: Patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, FL.

Morgan, G. S., and C. A. Woods. 1986. Extinction and the zoogeography of West Indian land mammals. Biological Journal of the Linnean Society 28: 167-203.

Morton, M., and D. Fawcett. 1996. A short survey of the bats of Montserrat, July 1995-September 1995. Uncirculated report to Fauna & Flora International.

Morton, M., and K. Lindsay. 1994. A short survey of the bats of Antigua and Barbuda, December 1963-February 1994. Uncirculated report to the Island Resources Foundation, St. Thomas, USVI.

Nicholson, D. V. 1992. Heritage landmarks of Antigua and Barbuda. Brochure published by the Museum of Antigua and Barbuda.

Pedersen, S. C. 2001. The impact of volcanic eruptions on the bat populations of Montserrat, BWI. American Zoologist 40:1167A.

Pedersen, S. C., H. H. Genoways, and P. W. Freeman. 1996. Notes on the bats from Montserrat (Lesser Antilles), with comments concerning the effects of Hurricane Hugo. Caribbean Journal of Science 32:206-213.

Pedersen, S. C., 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., M. Morton, G. Kwiecinski, R. Adams, H. Genoways, K. Hadley, and V. Swier. (in prep). Impact of catastrophic hurricanes and volcanoes on Caribbean bat populations. In preparation for submission to Biotropica.

Phillips, C. J., D. E. Pumo, H. H. Genoways, and P. E. Ray. 1989. Caribbean island zoogeography: A new approach using mitochondrial DNA to study Neotropical bats. Pp. 661-684 in Biogeography of the West Indies (C. A. Woods, ed.). Sandhill Crane Press, Gainesville, Florida.

Pierson, E. D., and R. M. Warner. 1990. Chapter: Bats. Pp. 91-96 in The Wildlife of Montserrat (J. R. Blankenship, ed.). Publication of the Montserrat National Trust, Montserrat, West Indies.

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.

Preston, F. W. 1962a. The canonical distribution of commonness and rarity: Part I. Ecology 43:185-215.

Preston, F. W. 1962b. The canonical distribution of commonness and rarity: Part II. Ecology 43:410-432.

Pumo, D. E., I. Kim, J. Remsen, C. J. Phillips, and H. H. Genoways. 1996. Molecular systematics of the fruit bat, *Artibeus jamaicensis*: Origin of an unusual island population. Journal of Mammalogy 77:491-503.

Schwartz, A. 1955. The status of the species of the *brasiliensis* group of the genus *Tadarida*. Journal of Mammalogy 36:106-109.

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.

Shamel, H. H. 1931. Notes on the American bats of the genus *Tadarida*. Proceedings of the United States National Museum 78(19):1-27.

Smith, J. D. 1972. Systematics of the chiropteran family Mormoopidae. Miscellaneous Publications of the Museum of Natural History, University of Kansas 56:1-132.

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 USA 81:4448-4451.

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.

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

Wilson, D. E. 1979. Reproductive patterns. 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 Publication of the Museum, Texas Tech University 16:1-441.

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