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Authors: Pedersen, Scott C., Genoways, Hugh H., Morton, Mathew N., Johnson, James W., and Courts, Siân E.

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Bats of Nevis, northern Lesser Antilles

SCOTT C. PEDERSEN[1], HUGH H. GENOWAYS[2], MATHEW N. MORTON[3], JAMES W. JOHNSON[4], and SIÂN E. COURTS[5]

[1]*South Dakota State University*, *Brookings*, *South Dakota 57007*, *USA*; *E-mail*: *scott_pedersen@sdstate.edu*
[2]*University of Nebraska State Museum*, *University of Nebraska-Lincoln*, *Lincoln*, *Nebraska 68588*, *USA*
[3]*c/o 22 Kensal Avenue*, *Bedminster*, *Bristol*, *BS3 4QY*, *United Kingdom*
[4]*Whitehall*, *Parish of St. James*, *Nevis*, *Eastern Caribbean*
[5]*Durrell Wildlife Conservation Trust*, *Trinity*, *Jersey*, *JE3 5BP*, *United Kingdom*

Only one species of bat, *Molossus molossus*, previously has been documented as occurring on the northern Lesser Antillean island of Nevis. Field research and reviews of existing museum collections have provided documentation based on voucher specimens for an additional seven species occurring on the island — *Noctilio leporinus*, *Brachyphylla cavernarum*, *Monophyllus plethodon*, *Ardops nichollsi*, *Artibeus jamaicensis*, *Natalus stramineus*, and *Tadarida brasiliensis*. The biological diversity of the chiropteran fauna on Nevis is similar to that found on other islands in the northern Lesser Antilles. Ecologically, this is a simple chiropteran fauna, including one piscivore (*N. leporinus*), one omnivore (*B. cavernarum*), one pollenivore/nectivore (*M. plethodon*), two frugivores (*A. nichollsi*, *A. jamaicensis*), and three insectivorous species (*N. stramineus*, *T. brasiliensis*, *M. molossus*). Species-area and species-elevation analyses for the chiropteran fauna of the Greater and Lesser Antillean islands gave r^2-values of 0.74 and 0.33, respectively. In the species-area analysis the bat fauna of Nevis falls above the regression line and in the species-elevation analysis it falls almost on the line. The chiropteran fauna of Nevis lies outside the Lesser Antillean Faunal Core and would be best characterized as a generalized Lesser Antillean fauna that appears to be characteristic of the northern Lesser Antilles.

Key words: Chiroptera, biogeography, ecology, systematics, island, Nevis, West Indies

INTRODUCTION

Bats are the only native mammals known to occur on Nevis. The first and only published report of a bat from the island of Nevis was by Miller (1913) when he reported *Molossus molossus*. This record was noted in the description of *Molossus debilis*, with a type locality of St. Kitts and other records from Antigua and Montserrat. The name *Molossus molossus molossus* with the type locality restricted to Martinique currently is the accepted scientific name for this taxon (Dolan, 1989).

Islands of similar size and topography to Nevis in the northern Lesser Antilles typically support six to 10 species of bats. With only one species of bat documented in the scientific literature for Nevis, it appeared at the beginning of our study that either the island possesses a depauperate fauna or this is a simple case of under-sampling. To examine this question, two field surveys of the bats of Nevis were performed and visits

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were made to the major research collections in order to examine voucher specimens collected from throughout the region for comparative purposes. Although some mist-netting was performed during the first survey by M.M., S.C., and J.J. in 1999**,** that effort focused primarily on roost surveys, aiming to provide a resource for future work concerning sites that would benefit from local conservation efforts and indicated that further study would be necessary. The survey conducted by S.P. and J.J. in July 2001 provides the first results from mist netting of bats in a wide variety of foraging habitats on Nevis.

The survey of museum holdings revealed that some unreported earlier work on Nevis had produced voucher specimens. In 1937 Chester Roys visited Nevis and collected 18 individuals of *M. molossus* in Charleston on June 12. These specimens were subsequently deposited in the Field Museum of Natural History in Chicago. David W. Nellis also collected bats when he visited Nevis between April 4 to 7, 1980. He collected at three sites and obtained individuals representing four species that were subsequently deposited in the in American Museum of Natural History in New York. We have combined the results of our field surveys with the data from these earlier efforts to provide a description of the chiropteran fauna of Nevis.

Materials and Methods

Study Area

Nevis is a small island located at 17°10'N, 62°35'W in the northern Lesser Antilles. Nevis is joined politically with the island of St. Kitts in the nation of St. Kitts and Nevis. Even by the standards of the Lesser Antilles, Nevis is quite small with an area of 93 km^2 (Fig. 1). Nevis is nearly round with an average diameter of 12 km and is dominated by a steep volcanic cone reaching 985 m. The adjacent island of St. Kitts lies across a shallow 3.5 km wide channel to the northwest of Nevis. Nevis has a mild tropical climate with high temperatures ranging to 30.5°C in August and September and low temperatures ranging to 22.2°C in February.

The majority of Nevis is relatively low volcanic country, which is under cultivation or is covered with secondary scrub and thorn-bush, known in the West Indies as ruinate vegetation (Beard, 1949). The dominant vegetation in these low-lying areas include birch gum (*Bursera simaruba*), loblolly (*Pisonia subcordata* and *P. fragrans*), dogwood (*Lonchocarpus latifolius*), and white cedar (*Tabebuia pallida*). The slopes of the mountain are so steep and exposed in most places that the low secondary forest adjacent to the cultivated fields is quickly replaced by palm

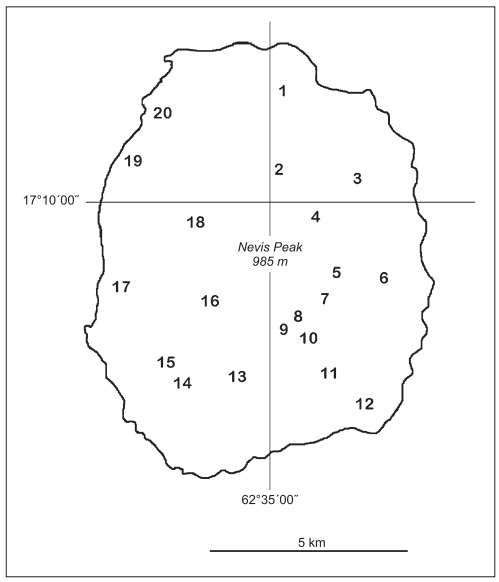

Fig. 1. Mist-netting localities and roost sites of note on Nevis. Numbers refer to locations shown in the figure: 1) Combermere School: roost within semi-abandoned school building; 2) Mt. Pleasant: tarrish pits/caves situated among ruins; 3) Butlers Government storage buildings; 4) Butlers Source: bog situated in deep ravine with moderate canopy cover; 5) New River Source: pools along river bed under dense canopy; 6) New River Estate buildings. 7) Golden Rock Estate: along trail above estate house; 8) Zetlands; 9) Herbert Heights; 10) Old Manor Estate buildings; 11) Rosehill: along Handley road; 12) Indian Castle Estate buildings; 13) Montpellier Estate buildings; 14) M'Lady Well. 15) Prospect Estate; 16) Hamilton's Estate: along gravel access roads; 17) Charlestown: collected from buildings; 18) Barnes Ghaut: flyway along gravel road above Jessup; 19) Nelson Spring. 20) Cades Estate

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brake, which continues to the summit. The vegetation in this area is primarily (50–60%) mountain cabbage (*Euterpe globosa*) and 15% tree ferns (*Cyathea arborea*), with such associated trees as blue tongue (*Marila racemosa*), pigeonberry (*Hirella triandra*), and blue box (*Ilex sideroxyloides*). Good rain forest is only present on the northwestern face of Nevis Peak above Jessop's. Two small areas of other vegetation types are dry evergreen forest along the top of a high ridge that runs to the east from the primary peak and montane thicket that is intermediate between the palm brake and the rain forest above Jessop's.

Historically, several hurricanes have hit the region, especially Hurricane Georges, which caused considerable damage on St. Kitts and Nevis when it made landfall southeast of Basseterre, St. Kitts, on September 21, 1998 (see also Rodríquez-Durán and Vázquez, 2001). In subsequent years, Hurricanes Jose and Lenny in September and November 1999, respectively, have had major impacts on the economy and forest ecology on Nevis.

Mist-netting

Mist-netting for bats was conducted in a variety of habitats, including sites associated with pools of water in rivers or bogs, flyways adjacent to fruiting mango trees, fig trees, and piper plants (*Piper dilatum*), and access roads during the two census periods. Twenty net-nights were conducted between February 6 and March 10, 1999 (6 captures), and 34 net-nights between July 2 to 8, 2001 (56 captures). Netting efforts during the latter survey involved erecting five or six mist-nets at each site and monitoring them for four to six hours depending on activity and weather. Together, the two mist-netting efforts provided 59 captures of six of the eight species of bat found on Nevis (Table 1).

Roost Surveys

An additional 141 bats (*Brachyphylla cavernarum*, *Tadarida brasiliensis*, *Molossus molossus*) were captured by hand from a dozen bat roosts, caves, and buildings during the two survey periods February 2 through March 13, 1999, and July 1 to 8, 2001.

Visual Records

Natalus stramineus was observed on numerous occasions in a cave on the Mount Pleasant Estate. One of us (J.J.) has observed greater fishing bats on at least two occasions on the west coast of Nevis.

Measurements

Voucher specimens from the 2001 survey were deposited in the research collections at the University of Nebraska State Museum. All measurements are in millimeters and body masses are given in grams. Forearms and crania were measured with digital calipers (Table 2). External measurements other than forearm are those recorded on specimen labels by collectors.

Systematic Accounts

Noctilio leporinus mastivus (Vahl, 1797)

Specimen examined (1). — St. Thomas Lowland Parish: Nelson Spring [17°11'N, 62°37'W], 1 (AMNH).

Davis (1973) reviewed geographic variation in *Noctilio leporinus*. He assigned all

Table 1. Bat captures (including the year) on northern Lesser Antillean island of Nevis

Species	Roost Captures			Habitat Captures			Total
	1937	1999	2001	1980	1999	2001	
Noctilio leporinus		visual		1			1
Monophyllus plethodon						1	1
Artibeus jamaicensis		4		21	1	27	53
Ardops nicholsi						19	19
Brachyphylla cavernarum		5	9	12	1	2	29
Natalus stramineus			1*				1
Tadarida brasiliensis		10	9	6			25
Molossus molossus	18	98	6		1	7	130
Σ							259

* Animal killed by ceiling fan, May 5, 2003

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TABLE 2. Length of forearm and cranial measurements for eight species of bats occurring on the northern Lesser Antillean island of Nevis

Catalog numbers, statistics, and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
			Noctilio leporinus mastivus					
AMNH 246993, ♀	83.8	26.6	23.3	18.5	7.0	17.1	9.9	12.0
			Brachyphylla cavernarum cavernarum					
UNSM 27649, ♂	64.4	31.8	28.1	17.6	6.5	15.1	10.8	11.8
UNSM 27663, ♂	65.0	31.8	28.5	17.2	6.7	14.7	11.1	11.4
UNSM 27665, ♂	64.4	32.4	28.8	17.3	6.6	15.3	11.2	11.6
UNSM 27667, ♂	64.7	32.2	28.6	17.8	6.6	15.2	10.9	11.6
			Monophyllus plethodon luciae					
UNSM 27670, ♂	39.6	23.1	21.4	10.2	4.6	9.8	7.9	5.6
			Ardops nichollsi montserratensis					
UNSM 27653, ♂	50.1	22.5	19.6	14.9	5.8	12.2	7.5	9.8
UNSM 27654, ♀	50.0	24.3	21.4	15.8	7.1	12.9	8.0	10.6
			Artibeus jamaicensis jamaicensis					
♂♂ *n*	6	6	6	6	6	6	6	6
$\bar{x}$ ± SE	59.4 ± 0.56	28.2 ± 0.25	25.1 ± 0.21	16.9 ± 0.10	7.3 ± 0.08	14.8 ± 0.09	9.9 ± 0.14	12.6 ± 0.19
(Range)	(57.9–61.4)	(27.5–29.2)	(24.6–25.9)	(16.5–17.2)	(7.1–7.6)	(14.4–15.0)	(9.6–10.4)	(12.0–13.2)
♀♀ *n*	4	4	4	4	4	4	4	4
$\bar{x}$ ± SE	60.5 ± 0.4	027.9 ± 0.27	24.9 ± 0.25	16.8 ± 0.04	7.1 ± 0.06	14.6 ± 0.05	9.8 ± 0.08	12.3 ± 0.14
(Range)	(59.8–61.6)	(27.2–28.4)	(24.2–25.3)	(16.7–16.9)	(6.9–7.2)	(14.4–14.6)	(9.6–9.9)	(11.9–12.5)
			Natalus stramineus stramineus					
UNSM 28159, ♂	39.5	17.0	15.6	8.7	3.3	7.6	7.4	5.7
			Tadarida brasiliensis antillularum					
UNSM 27675, ♂	37.7	15.9	14.8	9.5	3.7	9.1	5.6	6.5
AMNH 247029, ♂	37.1	15.7	14.7	9.4	3.6	8.9	5.5	6.7
AMNH 247030, ♂	37.9	15.8	14.8	9.7	3.7	9.0	5.5	6.7
AMNH 247031, ♂	37.4	15.8	14.6	9.2	3.7	8.7	5.4	6.5
UNSM 27674, ♀	38.9	15.2	14.7	9.5	3.7	9.0	5.5	6.2
AMNH 247032, ♀	37.9	15.6	14.3	9.0	3.6	8.5	5.5	6.5

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TABLE 2. Continued

Catalog numbers, statistics, and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
			Molossus molossus molossus					
UNSM 27671, ♂	38.6	16.4	14.6	10.4	3.4	9.8	5.4	7.4
UNSM 27672, ♂	38.9	16.8	14.8	10.0	3.3	9.7	5.8	7.3
UNSM 27650, ♀	38.2	16.0	14.1	9.9	3.2	9.3	5.8	7.2
UNSM 27651, ♀	38.8	16.0	14.1	10.0	3.1	9.7	6.0	7.3

specimens from the Antillean islands and circum-Caribbean mainland to the subspecies *N. l. mastivus*, which he recognized based on it large-size for the species (Table 2).The specimen of fishing bat that we examined was taken on the night of April 7, 1980, by D. W. Nellis at Nelson Spring in northwestern Nevis. It is a non-pregnant adult female. Nelson Spring is a small brackish water lagoon located on the leeward (western) side of Nevis. This lagoon is fed by a small spring, surrounded by marshy ground and dense sedges, and occasionally opens into the sea. The depth is about 0.5 to 1 m with a clay bottom. Small fish, shrimp, and crabs come into the area and stay. Fish species observed in the spring included juvenile mangrove snapper, small barracuda, young gars (needlefish), and tilapia (introduced).

One of us (J.J.) has observed greater fishing bat (*Noctilio leporinus*) on at least two occasions on the island. A deep recess located at Cades Point, St. Thomas Lowland Parish, contained three *N. leporinus* when visited on one occasion in the early 1990's. Unfortunately the building of a resort (Cliffdwellers) on the overlying bluff in 1994, disturbed the bats sufficiently that they vacated this shelter soon thereafter. When this Cades Point site was visited in 1999 by M.M. and S.C., and again during the summer of 2001 (S.P. and Nikki Johnson), the recess appeared to have collapsed and there was neither visual nor olfactory evidence of *Noctilio*. On numerous occasions, J.J. has observed several fishing bats foraging on the calm water adjacent to the dock at the Four Seasons Resort [2.0 km N Charleston, St. Thomas Lowland Parish] in the late evening (10:45 and 11:00 P.M.). Several of the bats were observed catching small fish of an unknown species, although large numbers of needlefish (14–16 mm in length) were observed to be schooling nearby.

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There is some question in the museum records about the location of Nelson Spring, which in part can be attributed to confusion about the name of country — St. Kitts and Nevis — and the name of the island — Nevis. According to the U. S. Board on Geographic Names gazetteer number 7 (British West Indies and Bermuda) there is only one Nelson Spring in the former British possessions in the Lesser Antilles. This place is located at 17°11'N, 62°37'W, which places it in the northwestern part of the island of Nevis near the village of Cotton Ground. Nelson Spring does appear on the 1984 United Kingdom topographic map of the island.

Brachyphylla cavernarum cavernarum
Gray, 1834

Specimens examined (22). — St. James Windward Parish: New River Source, 0.6 km N, 0.8 km W Zion, 180 m, 1 (UNSM); Mt. Pleasant Upper Cave, 0.8 km S, 0.8 km E Mt. Lily Estate, 9 (UNSM). St. John Figtree Parish: Prospect Estate [17°08'N, 62°36'W], 12 (AMNH).

Specimens captured/released (7). — St. John Figtree Parish: Hamilton's Estate, 3.5 km E Charlestown, 1; M'Lady Well, 0.5 km S Prospect Estate, 3. St. George Gingerland Parish: Herbert Heights, 0.5 km N Old Manor Estate, 1. St. James Windward Parish: Mt. Pleasant Cave, 0.8 km S, 0.8 km E Mt. Lily Estate, 2.

Swanepoel and Genoways (1978) reviewed the systematic relationships of members of the genus *Brachyphylla*. They recognized a single species — *B. cavernarum* — in the Lesser Antilles, ranging from Puerto Rico in the Greater Antilles in the north to Barbados in the south. Their analyses of the geographic variation in this species lead to the assignment of specimens from St. Croix to St. Vincent to the nominate subspecies, with its type locality on St. Vincent. This subspecies was distinguished by its large size. Our specimens from Nevis support this decision because they match closely the mean and range of samples from Montserrat and St. Martin (Swanepoel and Genoways, 1978).

Reproductive data are sparse for *B. cavernarum* on Nevis. Four of eight males taken on April 6, 1980, had testes lengths of 6.5, 7, 9, and 10. Two of the four females taken on this date carried embryos, measuring 7.5 and 22 in crown-rump length. During February of 1999, one male and three females were non-reproductive, and a single female was clearly a juvenile with unfused phalangeal epiphyses. In 2001, 10 males were found to be non-reproductive and the single female captured at Hamilton's Estate was lactating (July 5, 2001). The male from near Zion taken on July 4 had a testis length of 6.5 and those of three individuals from Mt. Pleasant Upper Cave taken on July 7 were 6, 7, and 8. The male from near Zion weighed 53.1 g when taken on July 4, whereas the nine males from Mt. Pleasant Upper Cave collected on July 7 had a mean body mass of 50.1 g (47.9–51.4).

Brachyphylla has only been found in cave-like roosts on Nevis, however, in recent years, such places have become increasingly scarce owing to the practice of filling in these large tunnels and pits for public safety reasons. We have heard several reports that some of these chambers had housed large numbers of bats; one notable example being a tunnel running several hundred meters east from Gingerland Methodist Church.

M'lady Well is a large vertical shaft thought to have been a mine for either sulfur or mercury. It is located on the southeast corner of the island and serves as a large permanent roost for *Brachyphylla*. The 22 m deep shaft is reinforced with cut stone and is and approximately 7 m in diameter

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and is surrounded by lowland desert scrub and acacia. The sheer, vertical walls of this defunct mine were covered with active *B. cavernarum* during July of 2001. M.M. and S.C. estimated that this colony included 1,000 individuals in 1999 and no attempt at a census was made in 2001. Due to the ease of access to the area surrounding the entrance to this well by humans and livestock — a potential safety hazard — this roost is in great need of protection by the local conservation authorities.

Each of the three 'caves' at the Mount Pleasant site is a tarrish pit — a crude, pit mine for fine volcanic gravel used in the manufacture of concrete. The upper cave is the largest (10 m in diameter, 7 m in dome height), sitting 75 m uphill from the ruins, while the middle and lower caves skirt the lower portions of the ruins. The middle and lower caves were smaller, cooler, and more humid than the upper cave. The middle cave is composed of two chambers, the larger of the two was more or less spherical but did not exhibit a complete roof. The smaller chamber (4–5 m in height) was more enclosed and was occupied by numerous *Brachyphylla*, which were located along the walls of the cave within easy reach from the cave floor. The lower cave at the Mt. Pleasant site has a more tubular enclosed shape and was the most humid of the three caves. *Brachyphylla* were noted in the upper and middle caves, whereas only *Natalus* was noted in the lower cave. The area surrounding the ruins at Mt. Pleasant is strewn with rocky outcrops, and is predominantly covered by highland dry forest intermingled with larger trees in the deeper ghauts.

The *B. cavernarum* cave roosts at Mount Pleasant are not continuously occupied, suggesting a frequent movement of bats between the caves at Mount Pleasant, to the large *B. cavernarum* roost at M'Lady Well on the opposite side of the island (6.5 km southwest), or to other unknown roosts. These movements may be related to the formation of breeding aggregations, the availability of food, roost disturbance by humans or livestock, or a complex balance of the these factors. A conservative estimate of the number of *B. cavernarum* at the Mt. Pleasant roost complex on July 8, 2001, was 6,000 animals located in the middle cave. Of note, bat guano is periodically collected by local agriculturists from the upper cave at Mount Pleasant.

During periods of drought, hurricane, or heavy ash fall, *Brachyphylla* may resort to foraging on alternate forage such as legumes (pigeon peas; Pedersen *et al.*, 1996) or possibly the flowers, leaves, and young pods of false tamarind (*Leucaena leucocephala*). The use of alternate forage by *Brachyphylla* is not unprecedented because these bats have been observed by one of us (J.J.) crawling out from sour orange fruits (*Citrus aurantium*) during times of hard drought on Nevis. Bats are suspected of eating cocoa pods on Nevis in the Green Ghaut above Fountain Village. As these soft pods ripen, bats can gain access to the jellied inner mass. Monkeys tear off the pods and eat them whole, rats chew the stem where they attach to the trees, but it appears that bats are perforating and eating them from the soft distal end while they are still attached to the tree. The liquid guano that accumulates under the pods does not exhibit white uric acid that characterizes the guano of fruit-fed birds.

There is some question in the museum records about the location of Prospect Estate. According to the U. S. Board on Geographic Names gazetteer number 7 (British West Indies and Bermuda) there is only one Prospect Estate in the former British possessions in the Lesser Antilles. This place is located at 17°08'N, 62°36'W, which places it in the southwestern part of the island of

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Nevis and the 1984 United Kingdom topographic map of the island shows 'Prospect Estate' at this location.

Monophyllus plethodon luciae
Miller, 1902

Specimen examined (1). — St. James Windward Parish: Butler's Source, 0.75 km S, 2.3 km W Butlers, 360 m, 1 (UNSM).

Schwartz and Jones (1967) reviewed the systematic relationships of members of the genus *Monophyllus*. They recognized a single species in the Lesser Antilles, being represented on the islands of Anguilla, Barbuda, Antigua, Dominica, and St. Lucia by the subspecies *M. plethodon luciae*. Subsequently, Baker *et al*. (1978) and Genoways *et al*. (2001) have published measurements of series of this taxon from Guadeloupe and Dominica, respectively. The measurements of our single male specimen fall at the lower end of the range of measurements of both of these samples in cranial measurements. The length of forearm for the specimen from Nevis is the shortest of all of these bats. Clearly, additional material will be needed to fully assess the meaning of these differences. External measurements of our single male were as follows: total length, 75; length of tail, 12; length of hind foot, 12; length of ear, 13 (for cranial measurements see Table 2). This individual taken on July 7 weighed 15.9 g and had testes that measured 3 mm in length.

Although 10 to 15 individuals of *M. plethodon* were observed feeding on piper fruit (*Piper dilatum*) at Butler's Source, capture success was severely hampered by difficulties in placing mist-nets along the steep hillsides at this location. This deep ravine was filled with large fruiting trees and a small stream. Indeed, the ground was covered with the fruits of pitch apples (*Clausia major*) and hogplums (*Spondia mombin*) that had been knocked down by bats (probably *Artibeus* and *Ardops*) foraging in the canopy.

Ardops nichollsi montserratensis
(Thomas, 1894)

Specimens examined (3). — St. James Windward Parish: New River Source, 0.6 km N, 0.8 km W Zion, 180 m, 2 (UNSM); Butlers Source, 0.75 km S, 2.3 km W Butlers, 360 m, 1 (UNSM).

Specimens captured/released (16). — St. George Gingerland Parish: Golden Rock Estate, 1. St. James Windward Parish: New River Source, 0.6 km N, 0.8 km W Zion, 180 m, 4; Butlers Source, 0.75 km S, 2.3 km W Butlers, 360 m, 11.

Jones and Schwartz (1967) reviewed the genus *Ardops*, recognizing a single species — *A. nichollsi* — which is confined to the Lesser Antilles. Determining the subspecific status of our specimens from Nevis is problematic, however. Plotting the Nevis specimens on to figure 1 of Jones and Schwartz (1967), places the male from Nevis close to *A. n. annectens* with a type locality of Guadeloupe, whereas the female from Nevis falls with specimens of *A. n. montserratensis*. We tentatively assign our specimens to the latter taxon on geographic grounds because Nevis lies between Montserrat and St. Eustatius where *A. n. montserratensis* was reported by Jones and Schwartz (1967). However, we believe the subspecific variation of this species should be re-investigated because far more material is now available than that studied by Jones and Schwartz (1967). External measurements of a female from near Zion were as follows: total length, 82; length of hind foot, 15; length of ear, 15. A single male from this same locality weighed 23.7 g and the pregnant female taken on July 4 weighed 34.3 g. (Table 2).

The reproductive status of the 19 *A. n. montserratensis* captured during July 2001

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can be summarized as follows: four scrotal and nine non-scrotal males; three pregnant, two lactating, and one non-reproductive female. The male captured on July 4 near Zion had a testis length of 5. The female from there taken on the same date was pregnant with a near-term embryo, measuring 32 in crown-rump length. The male captured on July 7 from near Butlers was a subadult judging by its unfused phalangeal epiphyses. The length of forearm for the latter specimen was 49.4, which approached the size of the adult male, but its weight at 18.5 was slightly less than 80% of that of the adult male. All *Ardops* captures were along rivers or in very boggy areas adjacent to trees in fruit and thickets of piper plants (*P. dilatum*). Individuals of *Ardops* were noted feeding upon a variety of both small and large figs, pitch apples (*C. major*), and hogplums (*S. mombin*).

Artibeus jamaicensis jamaicensis Leach, 1821

Specimens examined (26). — St. James Windward Parish: New River sugar mill ruins [New River Estate, 17°09'N, 62°33'W], 6 (AMNH); New River Source, 0.6 km N, 0.8 km W Zion, 180 m, 5 (UNSM). St. John Figtree Parish: Prospect Estate [17°08'N, 62°36'W], 1 (AMNH). St. Thomas Lowland Parish: Nelson Spring [17°11'N, 62°37'W], 14 (AMNH).

Specimens captured/released (27). — St. Thomas Lowland Parish: 1.5 km W Jessup, 2. St. George Gingerland Parish: Golden Rock Estate, 2. St. James Windward Parish: New River Source, 0.6 km N, 0.8 km W Zion, 7; Zetlands, 1; Rosehill, 4. St. John Figtree Parish: Hamilton's Estate, 3.5 km E Charlestown, 6. St. James Windward Parish: Butlers Source, 0.75 km S, 2.3 km W Butlers, 360 m, 5.

Genoways *et al*. (1998, 2001) have presented morphometric analyses, and Phillips *et al*. (1989) and Pumo *et al*. (1996) have presented mtDNA analyses of the relationships among Antillean populations of the Jamaican fruit bat. Specimens from Cuba and the Bahamas to which the subspecific name *parvipes* is applicable, are smaller, both externally and cranially, than are those from Jamaica south to Dominica and beyond. A comparison of specimens in external or cranial dimensions from Jamaica southward to Dominica revealed no significant differences among the populations. Thus, the specimens from Nevis, which fit within this pattern of variation, are appropriately referred to the nominate subspecies.

The six males and four females did not reveal significant secondary sexual variation in any of the eight measurements (Table 2). Males did average larger than females in all measurements except length of forearm. In the latter measurement, females averaged a millimeter longer than the males. Two males taken on July 4 weighed 41.7 and 42.0 g, whereas a pregnant female taken on that date weighed 42.3 g.

We hand-netted one of the clusters of *A. jamaicensis* in a disused house at Rosehill, and found one adult male and three adult females. This is typical of the small harems formed by males of this species (Handley *et al*., 1991) — this type of cluster was commonly noted at other sites during roost survey work in 1999. All roosts of *A. jamaicensis* located during these surveys were assumed to be temporary due to the lack of accumulated guano at each site.

Two males taken on April 4 had testes measurements of 6 and 10 and those of four males taken on April 7 were 7.5, 8, 9, and 10. Nine female Jamaican fruit-eating bats from early April were examined for reproductive activity with the following results: April 4, two pregnant, with crown-rump length of embryos being 6 and 7; April 6, one non-reproductive; April 7, two pregnant, with embryo crown-rump lengths of

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11 and 12, three lactating, and one non-reproductive. Together, the reproductive status of the 27 *A. jamaicensis* captured during July 2001 can be summarized as follows: one juvenile, nine scrotal, and three non-scrotal males; one juvenile, nine pregnant, one lactating, and three non-reproductive females; one animal was released before reproductive data could be registered. Of the three males and two females taken as vouchers on July 4, 2001, testes lengths of the two scrotal males were 5.5 and 8, the third male was non-reproductive; one female was non-reproductive while the second female was lactating.

Three females collected at Nelson Spring in 1980, show varying degrees of alopecia. One individual (AMNH 247020) was naked on its cheeks and showed thinning of the hair on its chin and upper chest. Another individual (AMNH 247026) was naked on its chin and upper chest, while the third (AMNH 247025) was naked on the crown of its head, chin, chest, and upper abdomen. None of these individuals was noted as lactating.

Of the 10 specimens examined, all lacked both M3 and all possessed both m3. Two other specimens did exhibit dental anomalies. A female (AMNH 247012) from Prospect Estate had mal-aligned lower teeth with both of the m3 displaced lingually. The other individual was a male from Nelson Spring (AMNH 247014) that exhibited heavily worn teeth. This specimen had part of the crown of m2 and all of the crown of m3 missing on both sides of the lower jaws. Right i1 and i2 and left i1 were missing. Left I1 and I2 were missing, but the root of I2 was visible. All of the dental changes in this male appeared to have occurred during its life. The exact location of 'New River sugar mill ruins' (AMNH specimens) is not known for certain, but in all likelihood refers to the mill ruins associated with New River Estate, St. James Windward Parish, rather than with the nearby village of New River, St. George Gingerland Parish.

Natalus stramineus stramineus Gray, 1838

Specimen examined (1). — St. Thomas Lowland Parish: Cades Estate, 15 m, 1 (UNSM).

The appropriate scientific name for specimens of this species coming from the island of Nevis is *N. stramineus stramineus* based on the work of Goodwin (1959) and Arroyo-Cabrales *et al*. (1997). Goodwin (1959) provided evidence that the type locality of *N. stramineus* was not Lagoa Santa, Minas Gerais, Brazil, and fixed the type locality as Antigua in the Lesser Antilles. He assigned specimens from Anguilla and Dominica in addition to those from the type locality from Antigua to the nominate form. Handley and Gardner (1990) made a more detailed investigation of this situation, but ultimately they agreed with Goodwin's (1959) decision. Arroyo-Cabrales *et al*. (1997) used genetic data to study the relationship among island and mainland populations of *Natalus*. They concluded that the allozymic data supported the presence of a single species in the Antillean islands to which the name *N. stramineus* would apply. Forearm and cranial measurements of our specimen from Nevis (Table 2) fall within the range of a sample of nine males from Dominica (Genoways *et al*., 2001), but are noticeably larger than the measurements of a female reported from Guadeloupe (Baker *et al*., 1978).

Our specimen was obtained on May 5, 2003, by a 6-year old boy, Shaun Brear. The bat was found after it had collided with a ceiling fan and was brought to one of the authors (J.J.) for identification. Testes of the adult male measured 1.5 in length. In addition, three *N. stramineus* were observed on July 8, 2001, in a cave on the Mount

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Pleasant Estate [1.25 km northeast from the village of Fountain]. Although we were not able to capture any of these bats with mist-nets or by hand, their proximity and characteristic external features left no doubt as to their identification. Their occupation of the smallest, most protected cave at Mount Pleasant Estate (lower cave has a distinctly tubular enclosed shape and was the coolest and most humid of the three caves at the Mt. Pleasant site; 3 m wide, 6 m dome height) is not surprising given their predilection for humid microenvironments. One of us (J.J.) has observed these bats on several occasions in this lower cave during daylight hours throughout 2001 and 2002, but their occupation of this roost has been inconsistent, often with the animals being present or absent for several weeks at a time.

Tadarida brasiliensis antillularum
(Miller, 1902)

Specimens examined (9). — St. James Windward Parish: Combermere School [abandoned], Scarborough, 30 m, 3; New River sugar mill ruins [New River Estate, 17°09'N, 62°33'W], 6 (AMNH).

Specimens captured/released (16). — St. James Windward Parish: Combermere School [abandoned], Scarborough, 30 m, 16.

Miller (1902) described *Nyctinomus antillularum* from Roseau, Dominica, and assigned specimens from Montserrat, St. Kitts, St. Lucia, and Tobago to the new taxon. Miller (1902) distinguished the new species based on its size being smaller than populations in the Greater Antilles. Shamel (1931) in his revision of the genus *Tadarida* treated this species under the name *T. antillularum*. Shamel (1931) added material from Guadeloupe, Antigua, and Puerto Rico to the monotypic species and continued to distinguish the taxon based on its small size. Finally, Schwartz (1955) reduced this monotypic species to subspecific rank within the widespread mainland species *Tadarida brasiliensis*, which is the arrangement that we have followed.

External and cranial measurements of four males and two females (Table 2) agree closely with those presented for bats from Guadeloupe (Baker *et al*., 1978) and Dominica (Genoways *et al*., 2001). The male from Scarborough weighed 9.0 and the pregnant female from there taken on July 8 weighed 11.7. In the March 1999 survey, six of the 10 captured animals were non-reproductive males, two were post-lactating and two were non-reproductive females. Two males taken on April 5, 1999, had testes lengths of 1.5 and 2 and the female from this date evinced no reproductive activity. In July 2002, four of the nine captured bats were non-reproductive males, three were pregnant, and two were non-reproductive females. The male taken on July 8, 2002, had testes measuring 3.5 in length. Both females taken on this date were pregnant each with single embryos measuring 11.5 and 13 crown-rump length.

Tadarida and *Molossus* roosted in small clusters (5 to 100 animals) throughout the unused Combermere Primary School centered within the small community of Scarborough. The building is surrounded by a large, gravel, playing field. The nearest tree was located 50 meters from the building. The numerous species-specific clusters noted within the building were typically separated from each other by a distance of at least one meter and were most often associated with rafters or wedged into crevices in the suspended ceiling. Despite windows or doors that were ajar, the bats left through narrow cracks in the masonry located at three of the four corners of the building.

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Molossus molossus molossus
(Pallas, 1766)

Specimens examined (23). — St. James Windward Parish: New River Source, 0.6 km N, 0.8 km W Zion, 180 m, 3; Combermere School [abandon], Scarborough, 30 m, 2. St. Paul Charlestown Parish: Charlestown, 18 (FMNH).

Specimens captured/released (107). — St. George Gingerland Parish: Hotel, Montpellier Estate, 1; Indian Castle Estate, 33. St. James Windward Parish: Combermere School [abandoned], Scarborough, 30 m, 17; Government storage buildings, Butlers, 52; Butlers Source, 0.75 km S, 2.3 km W Butlers, 360 m, 1. St. Thomas Lowland Parish: Barnes Ghaut, 3.

The previous record of *Molossus* from Nevis was noted in the description of *Molossus debilis*, with a type locality of St. Kitts and other records from Antigua and Montserrat (Miller, 1913). This name and a number of others have been applied to this species in the Antillean islands. It now is 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 throughout the Lesser Antilles**.** Two males were collected in the Combermere Primary School in Scarborough and two females were collected near Zion. The males taken on July 8 weighed 15.3 and 12.2 and the females, both pregnant, taken on July 4 weighed 13.6 and 14.3 (Table 2).

The 18 individuals obtained by Chester Roys in Charleston on June 12, 1937, included five males and 13 females. The males had testes length of 4, 4.5, 4.5. 5, and 5. All five of the females examined for reproductive activity were pregnant with embryos having crown-rump lengths of 10, 10, 10.5, 10.5, and 12.5. Of the 99 *M. molossus* captured in February and March of 1999, each of the 45 males was non-reproductive. There were five pregnant females, eight were post-lactation, 32 were non-reproductive, and nine were juveniles. Of the 13 *M. molossus* captured in July 2001, four were non-reproductive males, one was a non-reproductive female, and the remaining eight were pregnant. The two males from Scarborough in 2001 had testes lengths of 3 and 4. The three females captured in 2001 near Zion were pregnant each containing a single embryo measuring 16, 16, and 18 in crown-rump length.

Discussion

Data presented here provide new and previously unpublished records of seven species of bats for the island of Nevis: *N. leporinus*, *B. cavernarum*, *M. plethodon*, *A. nichollsi*, *A. jamaicensis*, *N. stramineus*, and *T. brasiliensis*. This clearly answers our initial question about the number of species of bats occurring on the island and indicates that the initial low number was a sampling artifact. The biological diversity of the chiropteran fauna on Nevis is similar to that found on other island in the Lesser Antilles to the north of Guadeloupe (Baker and Genoways, 1978; Jones, 1989). Ecologically, this is a simple chiropteran fauna of eight species including one piscivore (*N. leporinus*), one omnivore (*B. cavernarum*), one pollenivore/nectarivore (*M. plethodon*), two frugivores (*A. nichollsi*, *A. jamaicensis*), and three insectivorous species (*N. stramineus*, *T. brasiliensis*, *M. molossus*), representing four families — Noctilionidae, Phyllostomidae, Natalidae, and Molossidae.

In theory, the number of species found on an island is correlated with the size (area) of the island, but this effect is influenced by other factors, including for example distance from a source area such

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as a continental mainland. 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). Species-area curve models have been used in biogeographic studies of insular amphibians and reptiles (Preston, 1962*a*, 1962*b*), birds (Hamilton *et al*., 1964), and mammals (Morgan and Woods, 1986; Griffiths and Klingener, 1988). 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: "The remaining 31% of the variance must be dependent upon other variables such as habitat diversity and distance from source areas." (Morgan and Woods, 1986).

We provide a species-area curve for the chiropteran fauna of the Greater and Lesser Antilles (Fig. 2), which includes data culled from the literature (Pinchon, 1967; Jones, 1989; Masson *et al*., 1990; McCarthy and Henderson, 1992; Genoways *et al*., 2001; Timm and Genoways, 2003) and data presented here. Under this general model, the island of Nevis falls above the regression line relative to other islands in the region. With the inclusion of new species records reported herein, the position of the island relative to the empirically derived curve has been altered (former position indicated by arrow) in a predictable manner, but it is now understood that the former position on the graph was simply because of under-sampling. The r^2-value for the analysis using the current Nevis data is 0.74, indicating that for the islands included in Fig. 2, size of the islands explains 74% of the species diversity. The new position above the regression line for the bat fauna of Nevis indicates that there are more species of bats on the island than its size alone would predict.

Because the remaining variation in species diversity in part may be attributed to the elevation of the island and its resulting floral diversity, we compared the number of species on the same islands to the elevation

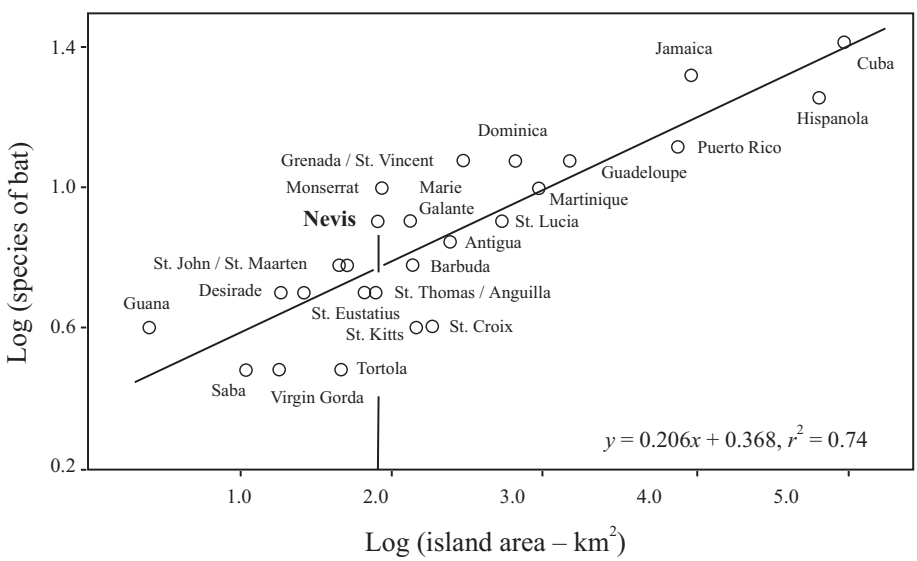

FIG. 2. Species/area curve based on the published data (August, 2001) for the chiropteran fauna in the Antilles. The vertical line indicates the shift in location of Nevis on this curve due to our report of an additional seven species of bat from this island, from the long-standing record of a single species (*M. molossus*) on Nevis

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of the island (Fig. 3). The r^2-value is only 0.33, much lower than found for species-area analysis. Nevertheless, this analysis does indicate that 33% of the bat species diversity on these islands could be explained by elevation. The fauna from Nevis falls almost on the regression line (Fig. 3). This indicates to us that the elevation of Nevis certainly is important in explaining the diversity of bats on the island and helps account in part for why it falls above the regression line in the species-area analysis. Another important fact to consider is that the interiors of mountainous islands in the West Indies, such as Nevis, were harder to access by colonists and consequently have suffered (and are suffering) less anthropogenic deforestation. Returning to the issue of 'under-sampling', the inaccessibility of these habitats also creates logistical difficulties for biologists attempting to adequately survey an island. However, it is exactly these sites that must to be sampled, as they may be functioning as refugia, maintaining the majority of the original chiropteran fauna of the island as compared to islands with lower elevations or uncomplicated terrain.

Nevis is situated just to the north of the islands that exhibit a fauna Genoways *et al.* (2001) designated as the Lesser Antillean Faunal Core. The eight species in the chiropteran fauna of Nevis can be divided in two general biogeographic units. The first is composed of five species that have widespread Neotropical distributions that extend well beyond the Antillean to the mainland of South and Central America and Mexico — *N. leporinus*, *A. jamaicensis*, *N. stramineus*, *M. molossus*, and *T. brasiliensis*. These species are not informative about biogeographic relations within the Lesser Antilles because their distribution extend so far beyond the West Indies. The second biogeographic unit is composed of three species that are Lesser Antillean regional endemics. These species are widely distributed in the Lesser Antilles and either do not extend out of the region or only extend as far as Puerto Rico — *A. nichollsi* occurs

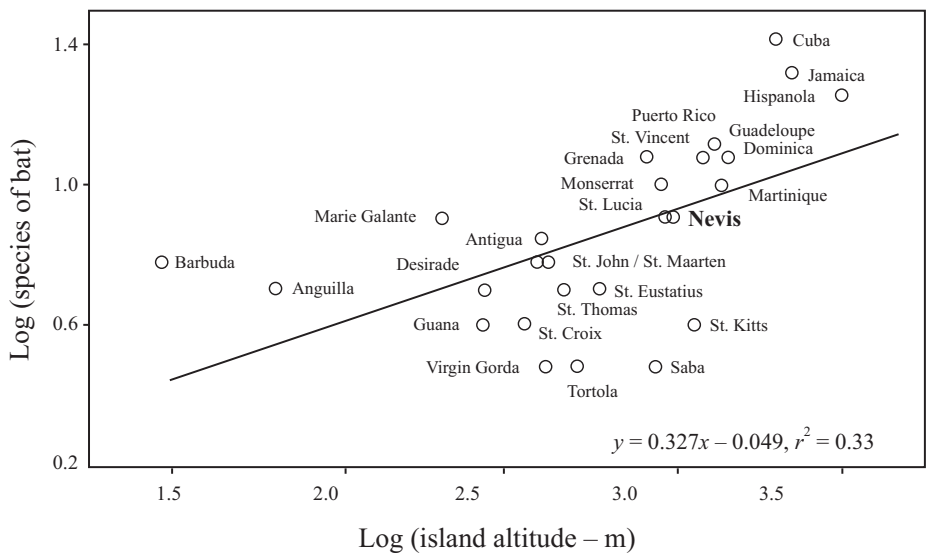

FIG. 3. Species/altitude curve based on the published data (August, 2001) for the chiropteran fauna in the Antilles

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from St. Eustatius to St. Vincent; *B. cavernarum* occurs from Puerto Rico to Barbados; *M. plethodon* occurs from Anguilla to Barbados, with a fossil representative on Puerto Rico.

One of the more interesting biogeographic characteristics of the bat fauna on Nevis relates to the species that are apparently missing from the fauna, including *Chiroderma improvisum*, *Sturnira thomasi* or *S. lilium*, *Myotis dominicensis*, *M. martiniquensis*, or *M. nigricans* (Husson, 1960), and *Eptesicus guadeloupensis* or *E. fuscus*. The Lesser Antillean endemic species *C. improvisum* and *S. thomasi* are known from Montserrat (Jones and Baker, 1979; Pedersen *et al*., 1996; Genoways, 1998) and Guadeloupe (de la Torre and Schwartz, 1966; Baker *et al*., 1978), *M. dominicensis* from Dominica (Genoways *et al*., 2001) and Guadeloupe (Masson and Breuil, 1992), and *E. guadeloupensis* from Guadeloupe (Baker *et al*., 1978). These species along with *S. lilium*, which occurs on islands from Dominica southward, are important species that define the Lesser Antillean Faunal Core. The absence of any of these species on Nevis confirms the conclusion of Genoways *et al*. (2001) that the fauna of Nevis lies outside of the Lesser Antillean Faunal Core. In summary, the chiropteran fauna of Nevis would be best characterized as a generalized Lesser Antillean fauna that appears to be characteristic of many islands located in the northern Lesser Antilles.

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