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ABSTRACT

The bats of the Virgin Islands (including Vieques and Culebra) are discussed in relation to distribution, feeding, and roosting habits. The bat fauna of these islands is compared with those of the northern Lesser Antilles and Puerto Rico and it is concluded that the Virgin Island bat

fauna is a depauperate derivative of that of Puerto Rico. Of the eight passages of bat species here discussed between the Greater and Lesser Antilles, four probably went from west to east, three from east to west, and one is indeterminate.

INTRODUCTION

The present paper represents, to some extent, an extension of my earlier paper (Koopman, 1968), in which the bats of the Lesser Antilles were considered in relation to those of the South American mainland and those of the Greater Antilles. In this paper I examine in greater detail the nature of the relationship between the Greater Antillean (particularly Puerto Rican) bat fauna and that of the northern Lesser Antilles. The Virgin Islands, lying between these two areas, are important in understanding this relationship. As the number of bat species in the Virgin Islands is only six, I would like to summarize this limited fauna, based on collections I made over a 10-year period and other specimens largely unreported. This includes the Puerto Rican islands of Vieques and Culebra and the Virgin Islands proper.

My field work in the Virgin Islands was aided by many people and I am indebted to them. Of the personnel of the Virgin Islands National Park I am especially indebted to Messrs. Stephen Edwards, Hugh Muller, Edward Rothfuss, and Dr. Alan Robinson. I have also been given much assistance by Dr. G. A. Seaman of the Fish and Wildlife Service in St. Croix, Virgin Islands. Thanks are due Drs. Arthur E. Dammann and O. Marcus Buchanan, both formerly of the Virgin Islands Ecological Research Station. Finally I express appreciation to my sister, Miss Elinor Koopman, for assistance in the frequently frustrating business of setting up mist nets for catching bats. Dr. J. Knox Jones, Jr., gave me access to the specimens and field notes of Mr. James Bee at the Museum of Natural History, University of Kansas, for which I am grateful.

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THE VIRGIN ISLAND BAT FAUNA

Noctilio leporinus: This large widespread fish- and insect-eating species is known from St. Thomas (Dobson, 1878; Goodwin, 1928); St. John (Hall and Bee, 1960; also two specimens in the American Museum of Natural History collected by me); and St. Croix (Vahl, 1797, the original description of *mastivus*, now considered a subspecies of *N. leporinus*; also four specimens in the American Museum of Natural History collected by Harry Beatty). Goodwin (1928, p. 106) gave a sight record from Vieques. I have little information about roosting sites for this species. Beatty collected his specimens from an unused chimney. Elsewhere in the West Indies, specimens have been obtained from hollow trees and from a small sea cave. The fish-catching abilities of *N. leporinus* are well known and I have witnessed this at Caneel Bay on St. John. The stomachs of Goodwin's specimens, however, contained only insects. I have caught two specimens: one in a net set across a small salt pond near Cruz Bay, St. John, where the individual might have come to fish; the other also near Cruz Bay, but in a net set across the bed of a small stream (locally called a "gut") which contained water only after heavy rains. Bee's specimen was also netted.

Artibeus jamaicensis: This widespread fruit-eating bat is known from Vieques (specimens in the American Museum of Natural History collected by G. G. Goodwin); Culebra (Heatwole et al., 1963; also specimens in the American Museum of Natural History collected by G. G. Goodwin); St. Thomas (specimens in the American Museum of Natural History collected by G. G. Goodwin); St. John (Hall and Bee, 1960; also specimens in the American Museum of Natural History collected by G. G. Goodwin, O. Marcus Buchanan, and me); Tortola (specimens in the American Museum of Natural History collected by Harry Beatty); Virgin Gorda (J. A. Allen, 1890; G. M. Allen, 1911); Anegada (J. A. Allen, 1890; La Bastille and Richmond, 1973); St. Croix (specimens in the American Museum of Natural History collected by G. G. Goodwin and by me, also specimens in the United States National Museum in Washington). There are 10 specimens at the University of Kansas collected

by James Bee on Lovango Cay, a small island just north of the western end of St. John. This species is very labile in its roosting requirements. I have collected it from an abandoned house on St. John and from a small shed on St. Croix. Bee obtained a number of specimens from small caves, both on St. John and Lovango, often in cliffs at the edge of the sea. Elsewhere in the West Indies it is well known from both large and small caves. *Artibeus jamaicensis* is probably the species in the Virgin Islands most frequently netted, as Bee and I have found on St. John and St. Croix, and La Bastille on Anegada.

Stenoderma rufum: This rare fruit-eating bat is known only from St. Thomas (Hall and Tamsitt, 1968) and St. John (Hall and Bee, 1960; Hall and Tamsitt, 1968). I have had no field experience with this bat and my only information on roosting sites is from O. Marcus Buchanan who obtained three from a hollow silk-cotton tree at Mandahl Gut west of Lameshur, St. John (oral commun.). These bats were released after being banded. Bee obtained his specimens from nets.

Brachyphylla cavernarum: This Puerto Rican and Lesser Antillean fruit and nectar-feeding bat is known from St. Thomas (specimens in the American Museum of Natural History collected by G. G. Goodwin); St. John (Hall and Bee, 1960; also specimens in the American Museum of Natural History collected by G. G. Goodwin and by me); and St. Croix (Bond and Seaman, 1958; also specimens in the American Museum of Natural History collected by G. G. Goodwin and me). The American Museum of Natural History also has specimens from three much smaller islands. These include a series I collected on Norman Island, just to the east of St. John. Single specimens have also been collected by William Rainey from two small islands to the north of the eastern end of St. Thomas (Thatch Cay and Grass Cay). Bee and I each collected specimens from caves (at Lameshur on St. John and on Norman Island) in cliffs opening directly on the sea. Neither cave was large, but both were deep enough so that the bats were roosting in complete darkness. A similar situation obtained in an underground unused sugar house at Sion Hill, St. Croix. As far as I am aware, *Brachyphylla cavernarum* has never been found roosting

in either trees or wooden structures and it is probable that a combination of complete or nearly complete darkness and a rough stony place to hang is necessary for this species. Although not netted as frequently as *Artibeus*, I have caught *Brachyphylla* a number of times in the above-mentioned net across the "gut" at Cruz Bay, St. John.

Tadarida brasiliensis: To my knowledge, the only record of this widespread insectivorous species from the Virgin Islands is Bee's collection (Hall and Bee, 1960) from Lameshur on St. John. Bee netted his specimens, and as far as I am aware there are no data on roosting sites in the Virgin Islands. Elsewhere in the West Indies, this species is found in both caves and houses.

Molossus molossus: This widespread insectivorous bat is known from Culebra (Heatwole et al., 1963; also specimens in the American Museum of Natural History collected by G. G. Goodwin); St. Thomas (Dobson, 1878, p. 413; also specimens in the American Museum of Natural History collected by Harry Beatty); St. John (Hall and Bee, 1960; also specimens in the American Museum of Natural History collected by G. G. Goodwin, O. Marcus Buchanan, and me); Tortola (specimens in the American Museum collected by Harry Beatty); Virgin Gorda (J. A. Allen, 1890); St. Croix (specimens in the American Museum of Natural History collected by G. G. Goodwin and by G. A. Seaman). I have collected this species only from roosts, usually corrugated iron roofs, but also once from a crevice above a doorway. These roosting sites would certainly be usual throughout the West Indies. Bee picked a bat of this species off a wall at Annaberg on St. John. I have never caught any in nets but Bee obtained most of his specimens in this fashion. I have often seen what is probably this species flying at dusk on St. John and have caught a few (definitely this species) that blundered into enclosed spaces and could not escape.

Summing up the distributional pattern, we now know that Vieques has *Artibeus jamaicensis*, and perhaps *Noctilio leporinus*; Culebra has *Artibeus jamaicensis* and *Molossus molossus*; St. Thomas has all the Virgin Island species except *Tadarida brasiliensis*; St. John has all six species; Tortola has *Artibeus jamaicensis* and *Molossus molossus*; Virgin Gorda the same two species;

Anegada only *Artibeus jamaicensis*; and St. Croix has *Noctilio leporinus*, *Artibeus jamaicensis*, *Brachyphylla cavernarum*, and *Molossus molossus*. It is possible that the low dry islands of Vieques, Culebra, and Anegada do indeed support only *Artibeus* and *Molossus*, although Goodwin, 1928, p. 106, gave a sight record of *Noctilio* for Vieques. Tortola and Virgin Gorda, however, are, like St. Thomas and St. John, higher (and therefore wetter) islands. It therefore seems very likely that *Noctilio*, *Brachyphylla*, and even *Stenoderma* occur on, but are not known from, Tortola and Virgin Gorda because they have been less adequately collected than St. Thomas or St. John.

TAXONOMY OF THE VIRGIN ISLAND BATS

Noctilio leporinus: Davis (1973) has shown that *mastivus* is not only the subspecies found throughout the West Indian range but also has a circum-Caribbean distribution.

Artibeus jamaicensis: The nominate subspecies occurs over most of the West Indies including the entire area under consideration. A number of synonyms are listed by Hall and Kelson (1959, p. 137). La Bastille and Richmond (1973, p. 96) seemed to imply that J. A. Allen's (1890, pp. 170-173) Anegada specimens were different in color from the specimens they collected in 1970. In part this resulted from their misinterpretation of Allen's "the pelage below the surface nearly pure white" to mean that the pelage on the ventral side was white, whereas examination of one of Allen's specimens (AMNH 3073/2382) shows that Allen was referring to the bases of the hairs being white. It is true that this specimen has "facial stripes two, grayish, very inconspicuous." Most Virgin Island *Artibeus* lack these stripes altogether, but a few such as AMNH 214229 from St. John do show them as clearly as does the above-mentioned Anegada specimen.

Stenoderma rufum: Two subspecies have been described recently, *S. r. anthonyi* (Choate and Birney, 1968) based on a Pleistocene population from west-central Puerto Rico and *S. r. darioi* (Hall and Tamsitt, 1968) for living populations in the northeastern part of the island. Hall and Tamsitt restricted the type locality of *S. r. rufum*

to the Virgin Islands. Although there is little doubt that *S. r. anthonyi* can be distinguished from the other two subspecies, I believe that the distinction of these two from each other is much less clear. This is based entirely on the shade of color, which in my experience is a most unreliable character in bats, certainly without extensive series of skins of both forms taken at various times of the year.

Brachyphylla cavernarum: The nominate subspecies occurs throughout the area under consideration. See Koopman (1968) for reasons for considering *minor* of Barbados a subspecies of *B. cavernarum*.

Tadarida brasiliensis: *T. b. antillarum* is the subspecies throughout the area discussed here (Shamel, 1931; Schwartz, 1955).

Molossus molossus: In recent years, two species of this genus, *M. fortis* of Puerto Rico and *M. debilis* of the northern Lesser Antilles have been recognized. I have previously shown (Koopman, 1968) that *debilis* is at most a subspecies of *M. molossus*. I am now inclined to follow Varona (1974) in regarding *fortis* as another subspecies of *M. molossus*. Specimens from Culebra, St. Thomas, St. John, Tortola, and Virgin Gorda are all referable to the Puerto Rican *M. m. fortis*. Those from St. Croix, however, are better allocated to the Lesser Antillean *M. m. debilis*, although showing intergradation with *fortis*.

ZOOGEOGRAPHICAL RELATIONSHIPS BETWEEN LESSER AND GREATER ANTILLEAN BAT FAUNAS

Both Jones and Phillips (1970) and I (Koopman, 1968) have discussed the bats of the northern Lesser Antilles (north of Guadeloupe but not including the Virgin Islands). Excluding the dubious record of *Carollia perspicillata* from Redonda, there are nine species: *Noctilio leporinus*, *Monophyllus plethodon*, *Artibeus jamaicensis*, *Ardops nichollsi*, *Brachyphylla cavernarum*, *Natalus stramineus*, *Myotis nigricans* (although judged from La Val, 1973, this may not be the correct name for the northern Lesser Antillean populations), *Tadarida brasiliensis*, and *Molossus molossus*. Five (all except *Monophyllus*, *Ardops*, *Natalus*, and *Myotis*) have been recorded from the Virgin Islands. *Monophyllus plethodon* is known (as a fossil) from Puerto

Rico (Schwartz and Jones, 1967) and must have occurred, if it does not now occur, somewhere in the Virgin Islands. *Ardops* is closely related to and may be said to be represented by *Stenoderma* of Puerto Rico and the Virgin Islands. In fact Varona (1974) considers them to be congeneric. *Natalus major* of Hispaniola, Jamaica, and Cuba is closely related to and possibly conspecific with *Natalus stramineus*. Thus only *Myotis* can be said to be unrepresented in or beyond the Virgin Islands.

Sixteen species are now known to occur or to have occurred in Puerto Rico (Starrett, 1962; Starrett and Rolle, 1963; Choate and Birney, 1968). The species are as follows: *Noctilio leporinus*, *Pteronotus fuliginosus*, *P. parnellii*, *Mormoops blainvillii*, *Macrotus waterhousii* (extinct), *Monophyllus plethodon* (extinct), *M. redmani*, *Artibeus jamaicensis*, *Stenoderma rufum*, *Brachyphylla cavernarum*, *Erophylla bombifrons*, *Phyllonycteris major* (extinct), *Eptesicus fuscus*, *Lasiurus borealis*, *Tadarida brasiliensis*, *Molossus molossus*. Five (*Noctilio*, *Artibeus*, *Brachyphylla*, *Tadarida*, *Molossus*) occur, as we have seen, both in the Virgin Islands and in the northern Lesser Antilles. *Stenoderma* occurs in the Virgin Islands and has a representative (*Ardops*) in the Lesser Antilles. Only *Monophyllus plethodon* occurred on Puerto Rico and still occurs in the northern Lesser Antilles, but is not known to occur on the Virgin Islands. Of course, since no Pleistocene fossil remains of bats are known from the Virgin Islands, there is no reason to assume that the species did not occur there. It may since have become extinct there as it has on Puerto Rico. The remaining nine species are not known to occur east of Puerto Rico in the West Indies.

The subgenus *Natalus* poses a special problem. *Natalus stramineus* is known from several Lesser Antillean islands. The closely related *N. major* (Varona, 1974, considered them to be conspecific) is known from Hispaniola, Jamaica, and Cuba, the Hispaniolan *N. m. major* being the smallest and therefore most like *N. stramineus*. There is a considerable gap between the ranges of *N. stramineus* and *N. major* (nothing between Anguilla and Saba on the east and Hispaniola on the west). It is indeed odd that no *Natalus* is known on Puerto Rico. There is, of course, always the possibility that it does or did occur.

These bats are never abundant and are usually found in small numbers far back in large caves. The chance of fossilization is also poor as the *Natalus* skull is unusually delicately built and therefore quite fragile.

In short, there are nine Greater Antillean species that reach (or reached) Puerto Rico, but are not known farther eastward. Of these only *Phyllonycteris major* was endemic to Puerto Rico. Five species extend from Puerto Rico through the Virgin Islands to the Lesser Antilles and of these, only *Brachyphylla cavernarum* does not occur on islands west of Puerto Rico. Even here, there is a close relative, *B. nana* (including *B. pumila*, both considered to be subspecies of *B. cavernarum* by Varona, 1974). One species, *Monophyllus plethodon*, occurred both on Puerto Rico (but not on islands west of Puerto Rico) and in the Lesser Antilles, but is not known from the Virgin Islands. *Stenoderma rufum* is endemic to Puerto Rico and the Virgin Islands, but has a representative in the Lesser Antilles (*Ardops*) and others on islands west of Puerto Rico (*Phyllops*, *Artibeus*). One species group (probably at most a superspecies), *Natalus stramineus-major* occurs in the Lesser Antilles and the islands west of Puerto Rico, but not from the islands between. Finally, a member of the *Myotis nigricans* group occurs in the northern Lesser Antilles, but has no representative in the Virgin Islands, Puerto Rico, or any islands farther west. Thus, whereas a majority of Puerto Rican bats are Greater Antillean forms that do not reach the Lesser Antilles, the northern Lesser Antilles are dominated by species that also occur in Puerto Rico, the Virgin Islands, or the more western Greater Antilles. This might imply that the Greater Antilles rather than the Lesser Antilles was the main source for species going "around the corner" of the Antilles.

Jones and Phillips (1970) and I (Koopman, 1968) have discussed this general problem, but I think it should be re-examined in a broader context, using any additional new data that may be available. Of the eight passages of bats here enumerated between the Greater and Lesser Antilles, I have no reason to change my earlier opinion that two (*Artibeus jamaicensis*, *Tadarida brasiliensis*) have clearly gone from the Greater to the Lesser Antilles, whereas two others (*Natalus stramineus*, *Molossus molossus*) have

gone in the opposite direction. Particularly in the light of Davis's revision (1973), I think it is impossible to say in which direction *Noctilio* went and it is perfectly possible that some population movement has gone in both directions. This leaves for further discussion the three cases involving endemic West Indian genera. The finding by Silva and Pine (1969) that *Brachyphylla* is not a stenodermine, but a member of the otherwise Greater Antillean Phyllonycterinae means that all the species of this subfamily occur in the Greater Antilles and all but one are endemic to it. To me this means that movement of *Brachyphylla cavernarum* from the Greater to the Lesser Antilles is far more probable than the reverse. Schwartz and Jones (1967) revised the genus *Monophyllus*, reducing it to two species, allopatric except for Pleistocene sympatry on Puerto Rico. It may still be considered to be more diversified on the Greater than on the Lesser Antilles, but the difference is slight. I still think *Monophyllus* was probably derived from *Glossophaga longirostris* (Varona, 1974, considered them to be congeneric) and the origins of *Monophyllus* in the Lesser Antilles and its later spread to the Greater Antilles seems most probable to me. Jones and Schwartz (1967) also revised *Ardops* and recognized a single Lesser Antillean species. However, here the Greater Antillean representation of the group to which it belongs is much richer. There are at least four good species (*haitensis* may be only a subspecies of *Phyllops falcatus*), some of them quite distinct. It seems most reasonable, therefore, to regard the *Stenoderma* complex as having originated in the Greater Antilles and the Lesser Antillean *Ardops* as being derived from it, albeit earlier than other invasions into the Lesser Antilles. My count of the eight passages stands, therefore, at four from west to east (*Artibeus*, *Ardops*, *Brachyphylla*, *Tadarida*), three from east to west (*Monophyllus*, *Natalus*, *Molossus*), and one unknown (*Noctilio*).

ZOOGEOGRAPHICAL RELATIONSHIPS OF VIRGIN ISLAND BATS

The Virgin Islands actually form two quite distinct geographical units. Vieques, Culebra, St. Thomas, St. John, Tortola, Virgin Gorda, Anegada, and most of the smaller islands are on the Puerto Rican bank, which formed a land

extension of Puerto Rico up until about 10,000 years ago (Heatwole and MacKenzie, 1967). St. Croix (together with a few small associated islands), on the other hand is on its own small bank, separated from the Puerto Rican bank by a deep channel, the Anegada Passage. St. Croix might be expected to lack some Puerto Rican elements present on the other Virgin Islands but absent in the Lesser Antilles. This is true only of *Stenoderma rufum*. All four bat species known from St. Croix are present on both Puerto Rico and the Lesser Antilles. The only indication of any special Lesser Antillean affinity on St. Croix is the fact that the St. Croix *Molossus molossus* is more like *M. m. debilis* of the Lesser Antilles than like *M. m. fortis* of other Virgin Islands and Puerto Rico. All the other Virgin Islands have, as might be expected, a depauperate Puerto Rican bat fauna (particularly depauperate on the smaller, drier islands). As is usual in border zones between distinctive faunas, there is not so much a mixing of distinctive elements as a disappearance of distinctive elements of both faunas, leaving only the widespread varicants. (See Hershkovitz, 1958, p. 589, for use of this term.) This is true of the Virgin Islands and it is also true of the northern Lesser Antilles. The "corner" of the Antilles is indeed an area that lacks most of the distinctive elements of both Greater and Lesser Antilles.

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