

STUDIES ON THE FAUNA OF CURAÇAO AND OTHER  
CARIBBEAN ISLANDS: No. 121.

COMMENTS ON SYSTEMATICS AND  
ZOOGEOGRAPHY OF BATS  
IN THE LESSER ANTILLES

by

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The Lesser Antilles, extending some 500 miles from Anguilla on the north to Grenada on the south, form an archipelago connecting the Greater Antilles with Trinidad and the South American mainland.<sup>1)</sup> Bats comprise the major segment of the extant mammalian fauna of the Lesser Antillean islands and the distribution and variation of chiropterans in this area long has interested systematists and zoogeographers. A revival of this interest in the past decade has resulted in a number of published contributions – KOOPMAN (1958, 1959, 1968), HUSSON (1960), DE LA TORRE (1966), DE LA TORRE & SCHWARTZ (1966), JONES & SCHWARTZ (1967), SCHWARTZ & JONES (1967). Still, much remains to be learned.

Nineteen species of bats are on record from the Lesser Antilles. For purposes of discussion, these can be divided roughly into three groups or zoogeographic components: 1) species that have invaded the southern part of the archipelago relatively recently from South America; 2) species that represent endemic (and presumably fairly old) Antillean genera; and 3) species or species groups that are widely distributed in the Antillean region and elsewhere in the American

<sup>1)</sup> ED. – Attention may be drawn to the fact that – in these “*Studies*” – the terms “Lesser Antilles”, “Leeward Islands”, and “Windward Islands” are generally used in a different meaning (cf. Vols. II, p. 24; IV, p. 2; IX, p. 5; XIII, p. 22; XIV, p. 42; XXI, p. 115; XXIV, p. 159; XXV, p. 34, and XXVI, p. 132) as follows: Lesser Antilles = Virgin Islands to Trinidad and Aruba. Windward Group = Virgin Islands to Grenada. Leeward Group = Los Testigos to Aruba and Los Monges. Leeward Islands = [British usage] Anguilla to Guadeloupe. Windward Islands = [British usage] Dominica to Grenada.

tropics. It is convenient to discuss the Lesser Antillean fauna under these three groupings, and we have done so beyond.

Some geographers and zoologists include the Dutch and Venezuelan islands off the northern coast of South America in the Lesser Antilles, but KOOPMAN (1959) has pointed out the continental nature of their avian and mammalian faunas and we therefore have not here considered them. The major islands of the Lesser Antilles proper are shown on Figure 173 and listed in Table 14. Of note, but not indicated on the figure, is the fact that the northern islands in the Lessers (south to Guadeloupe) frequently are called the Leeward Islands, whereas those from Dominica southward, usually including the outlying Barbados, are referred to as the Windward Islands.

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#### RECENT SOUTH AMERICAN INVADERS

Of the 10 species of bats that have reached the Antilles relatively recently from South America, five occur only on Grenada. Three of these, *Micronycteris megalotis megalotis* (Gray), *Carollia perspicillata perspicillata* (L.)\*, and *Artibeus cinereus cinereus* (Gervais) are of the same subspecies recorded for both Trinidad and Tobago as well as the northern South American mainland. One, *Peropteryx macrotis macrotis* (Wagner), is known from Tobago and South America, although another subspecies (*P. m. trinitatis*) is represented on Trinidad. The fifth, *Anoura geoffroyi*, is here reported for the first time from Grenada. Preliminary study indicates that Grenadan *Anoura* average slightly larger than specimens from Trinidad and have a somewhat more inflated braincase, but they do not differ otherwise

\* HAHN's (1907: 110) report of three specimens of *C. perspicillata* from tiny Redonda Island, between Montserrat and Nevis, almost certainly is in error as pointed out by KOOPMAN (1968: 3).

and probably represent the same subspecies (*A. g. geoffroyi* Gray). *Anoura* is unknown from Tobago.

The remaining five species classed as invaders to the Lesser Antilles from the south are irregularly distributed northward as far as St. Martin, and are discussed below.

*Pteronotus davyi* Gray. – This naked-backed bat is presently known from Grenada and three islands half-way up the Lesser Antillean chain, Guadeloupe (Marie-Galante), Dominica, and Martinique (*vide* ALBERT SCHWARTZ). Specimens from the three northern islands average slightly larger cranially than those from Trinidad but do not differ otherwise and are appropriately referred to the subspecies *P. d. davyi*. Probably this bat will be found to occur also at least on St. Lucia and St. Vincent, and possibly in the Grenadines as well. It seems doubtful that it occurs on Barbados.

*Glossophaga longirostris* Miller. – This long-tongued species is represented in the Lesser Antilles by a weakly-defined subspecies (*G. l. rostrata*, type locality Grenada) that is recorded from as far north as Dominica, but is unknown from Martinique, St. Lucia, and the outlying Barbados. The presence of this species on Dominica is based on an adult female and accompanying juvenile that were captured in Roseau in the early 1900's; extensive field work on Dominica in recent years has failed to reveal the presence there of *Glossophaga* and the earlier-reported specimens may represent an accidental occurrence. If this be true, then St. Vincent represents the northernmost island of the Windwards where a permanent population is known. It may be significant that St. Vincent is the southernmost island whence *Monophyllus plethodon*, another long-tongued species that presumably competes with *Glossophaga*, has been recorded.

*Sturnira lilium* (É. Geoffroy St.-Hilaire). – The systematics and distribution of the yellow-shouldered bat in the islands are of particular interest. Until this decade the genus was known north of Trinidad by only two specimens, which were collected on Dominica in 1906. Recently, DE LA TORRE (1966: 271) described *Sturnira an-*

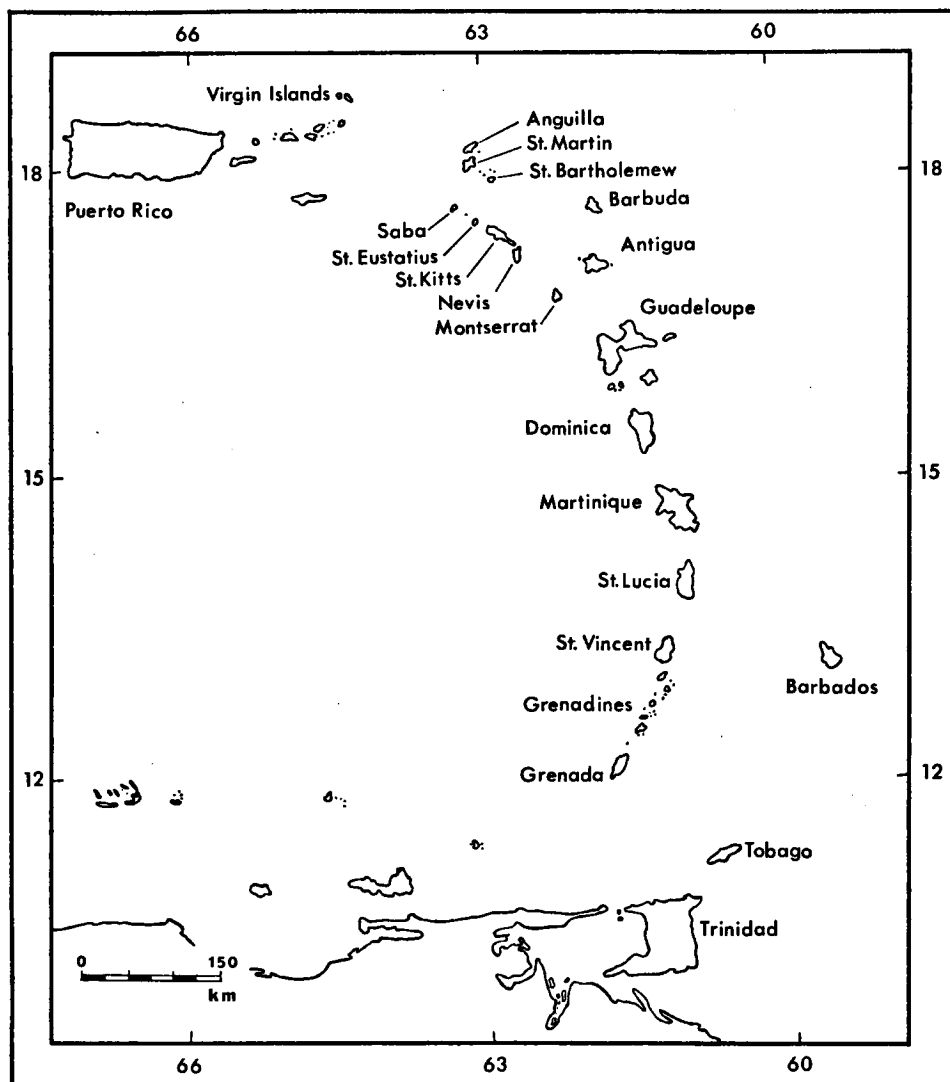


Fig. 173. Sketch-map of the Lesser Antilles, showing their relationship to Puerto Rico and the Virgin Islands on the north and to Trinidad, Tobago, and the South American mainland to the south.

*geli* from Dominica, assigning to it also a specimen from Martinique, and DE LA TORRE & SCHWARTZ (1966: 299, 301) named *S. thomasi* from Guadeloupe and *S. paulsoni* from St. Vincent, each based on a single specimen. Differences in the size and position of certain features of the molars, and, in *thomasi*, the absence of the third lower molar, were given as the principle characters separating the Antillian populations from *Sturnira lilium* of Trinidad and the South American mainland.

Subsequent to the description of *angeli*, *paulsoni*, and *thomasi*, the Museum of Natural History of The University of Kansas has acquired series of *Sturnira* from St. Vincent, St. Lucia (where the genus previously was unknown), and Dominica, and The American Museum of Natural History has obtained a series of specimens from Martinique. Detailed study of this material presently is underway. Preliminary findings indicate that although the skull generally is more elongate, the braincase less inflated, and the rostrum somewhat larger and broader in Antillean populations than in bats from Trinidad and northern South America, the dental characters vary from island to island. Bats from Dominica and Martinique resemble each other in characteristics of upper and lower molars to a greater degree than either resembles bats from St. Lucia and St. Vincent, but populations from all four islands appear to be distinct at the subspecific level. However, differences between the populations on the four islands mentioned and those on Trinidad and the mainland are variable and relatively slight, and all may be referable to a single species – *Sturnira lilium*.

The relationships of *S. thomasi* of Guadeloupe, known only by the holotype, which we have not had an opportunity to examine, are somewhat more obscure. According to its describers, *thomasi* is much larger both externally (forearm, 48.1) and cranially (greatest length of skull, 26.2; length of maxillary toothrow, 7.7) than other *Sturnira* in the Lesser Antilles; possibly it represents a distinct species dating from an earlier invasion of the islands by *lilium*-related bats from South America. The absence of third lower molars in *thomasi* does not appear to be a particularly significant feature, because some specimens from Dominica and Martinique also lack this tooth on one or both sides. KOOPMAN (1968: 4) was “. . . inclined

to regard *paulsoni*, *angeli*, and even *thomasi* as successive modifications of *lilium* out of contact with other species of *Sturnira*."

The apparent absence of *Sturnira lilium* on Grenada is of note, because that island is geographically situated as a potential "stepping stone" for northward dispersal in the Antilles.

*Artibeus lituratus* (Olfers). – This large fruit-eating species is known only from Grenada and St. Vincent and appears to be less abundant than the related *A. jamaicensis* on both islands. Antillean specimens have been assigned to *A. l. palmarum*, which occurs also on Trinidad, Tobago, and the adjacent mainland.

*Myotis nigricans* (Schinz). – This small insectivorous bat is known from six widely scattered islands in the Lesser Antilles (see Table 14), but remains unreported from a number of islands where it undoubtedly occurs. Three different subspecific names have been applied to Antillean populations – *M. n. nigricans* (from Grenada), *M. n. dominicensis* (type locality Dominica), and *M. n. nesopolus* (from St. Martin) – and, additionally, an undescribed subspecies occurs on Barbados. HUSSON'S (1960: 156) assignment of material from St. Martin (northernmost point of distribution in the Lessers) to *nesopolus* is geographically improbable (KOOPMAN, 1968: 7). Beyond this, little can be said concerning taxonomy of this species until series of specimens are available from throughout the region.

#### ANTILLEAN ENDEMICIS

Three species of bats endemic to the Antilles occur in the island chain under consideration. These include a monotypic genus limited to the Lesser Antilles (*Ardops*), and two species of polytypic Antillean genera – *Monophyllus plethodon* and *Brachyphylla cavernarum* – that are known also from Puerto Rico.

*Monophyllus plethodon* Miller. – This species occurs on a number of the Leeward and Windward islands, from Barbados and St. Vincent northward at least to Barbuda (SCHWARTZ & JONES, 1967). The species is known also from fossil cave deposits on Puerto Rico

TABLE 14

DISTRIBUTION OF BATS ON MAJOR ISLANDS IN THE LESSER ANTILLES

based on records from the literature and specimens examined. Puerto Rico and Trinidad-Tobago are included for reference.

Species	Islands (and number of species)																			
<i>Pteropteryx macrotis</i>																				
<i>Noctilio leporinus</i>	X		X																	
<i>Microonycteris megalotis</i>																				
<i>Pteronotus davyi</i>																				
<i>Glossophaga longirostris</i>																				
<i>Monophyllus plethodon</i>	X		X																	
<i>Anoura geoffroyi</i>																				
<i>Carollia perspicillata</i>																				
<i>Sturmia litum</i>																				
<i>Brachyphylla cavernarum</i>	X		X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Artibeus cinereus</i>																				
<i>Artibeus jamaicensis</i>	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Artibeus lituratus</i>																				
<i>Artibeus nichollsi</i>																				
<i>Natalus stramineus</i>			X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Myotis nigricans</i>				X																
<i>Eptesicus fuscus</i>	X																			
<i>Tadarida brasiliensis</i>	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Molossus molossus</i>	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

\* Known by a single specimen from Tobago, but not known from Trinidad or the adjacent South American mainland.

along with *Monophyllus redmani*, the species of the Greater Antilles. The recognized subspecies are *M. p. plethodon* of Barbados, *M. p. luciae*, from elsewhere in the Lesser Antilles, and *M. p. frater* of Puerto Rico.

*Brachyphylla cavernarum* Gray. – This fruit-eating bat is widely distributed in the Lesser Antilles, having been reported from all but three of the major islands south to Barbados and St. Vincent (see Table 14). The species occurs also on Puerto Rico; related species are known from the Greater Antillean islands of Cuba (*B. nana*) and Hispanola (*B. pumila*). Two races of *B. cavernarum* are recognized, the nominate subspecies from Puerto Rico southward to St. Vincent (type locality), and *B. c. minor* of Barbados. The latter was regarded as a distinct species from the time of its description (MILLER, 1913: 32) until KOOPMAN (1968: 4–5) reduced it to subspecific status under the earlier-named *cavernarum*. Our independent assessment of the situation is in accord with KOOPMAN'S.

*Ardops nichollsi* (Thomas). – The genus *Ardops* is endemic to the Lesser Antilles and is monotypic. Related genera occur in the Greater Antillean region. This fruit-eating bat is known by five subspecies (JONES & SCHWARTZ, 1967) as follows: *A. n. montserratensis* (St. Eustatius and Montserrat), *A. n. annectens* (Guadeloupe), *A. n. nichollsi* (Dominica), *A. n. koopmani* (Martinique), and *A. n. luciae* (St. Lucia and St. Vincent). Taking into account that males are smaller than females, a gradient in size can be demonstrated among the subspecies, which do not differ otherwise; the size gradient, however, is not geographically clinal.

#### WIDELY DISTRIBUTED SPECIES

Six bats that occur in the Lesser Antilles are widely distributed elsewhere in the American tropics (and in two cases also in temperate North America). The routes by which most of these species reached the Lessers are unknown or not certainly known. In at least one instance (*Artibeus jamaicensis*), a double invasion probably was involved.



*Noctilio leporinus* (Linnaeus). – This large fish-eating bat occurs in the American tropics northward to Mexico and has been recorded from the four islands in the Greater Antilles as well as from many of the Lesser Antillean islands (Table 14). Too few specimens are yet available to assess geographic variation in *N. leporinus* in the area here under consideration: the name *N. l. leporinus* (type locality Surinam) has been used for bats from the southern part of the Lesser Antilles, whereas *N. l. mastivus* (type locality St. Croix in the Virgin Islands) generally has been applied to those from the northern islands. KOOPMAN (1968: 2) was inclined to regard all Lesser Antillean specimens as *mastivus*.

*Artibeus jamaicensis* Leach. – KOOPMAN (1968: 6), after discussing variation in Lesser Antillean populations of this fruit-eating bat, summarized his observations as follows: "If all populations of *Artibeus* from Barbados north belong to *A. j. jamaicensis*, then derivation from Central America through the Greater Antilles is the most probable. There is another subspecies on Trinidad, Tobago, and Grenada, *A. j. trinitatis*, which differs most conspicuously from *A. j. jamaicensis* in having a third upper molar. *Artibeus j. trinitatis* is probably most closely related to *A. j. planirostris* of eastern South America. Thus in the Lesser Antilles, we have *A. j. jamaicensis* moving southward and reaching Barbados, *A. j. trinitatis* moving northward and reaching Grenada, but neither subspecies reaching St. Vincent, which is occupied only by the related *A. lituratus*." Our findings support KOOPMAN's contention that the nominate subspecies occurs southward in the islands to St. Lucia and Barbados (*eva* Cope, named from St. Martin, is a synonym, as is *praeceps* Andersen, named from Guadeloupe and incorrectly referred to the species *lituratus* by HERSHKOVITZ, 1949: 447). The occurrence of *A. j. jamaicensis* on Barbuda, based on specimens in the Rijksmuseum van Natuurlijke Historie (Leiden), is reported here for the first time.

As did KOOPMAN, we note a trend to slightly larger size, both externally and cranially, in *A. j. jamaicensis* in the southern part of its range in the Lesser Antilles. Also, we concur that bats on Grenada are clearly related to those on Trinidad and Tobago, because they approach

TABLE 15

SELECTED MEASUREMENTS (mm) AND PRESENCE OR ABSENCE OF M3  
for *Artibeus jamaicensis* from  
several of the southern islands in the Lesser Antilles and Trinidad

Sample size is indicated to the left of each mean measurement; extremes are in parentheses.  
For M3, sample size and percentage of specimens having the tooth are given.

Island		Forearm		Condylobasal length		Zygomatic breadth		Per cent M3 present
<i>Artibeus jamaicensis jamaicensis</i>								
Barbados	7	58.9 (55.6-62.1)	7	25.3 (24.9-26.1)	7	17.6 (17.2-17.9)	7	0
St. Lucia	11	60.1 (56.5-64.0)	15	26.1 (25.4-26.7)	15	17.7 (17.1-18.1)	17	0
<i>Artibeus jamaicensis</i> , new subspecies								
St. Vincent	20	64.3 (60.5-67.4)	32	27.3 (26.2-28.6)	32	19.4 (17.9-20.6)	35	12*
<i>Artibeus jamaicensis trinitatis</i>								
Grenada	23	58.1 (55.8-60.5)	15	25.0 (24.7-25.8)	15	17.5 (17.1-18.2)	18	94
Trinidad	16	57.3 (55.1-61.1)	11	24.2 (23.4-25.0)	11	17.4 (16.8-18.5)	12	100

\* Two of four specimens had but one M3, on the right side in each case.

them in size (only slightly larger) and possess the small M3 that is lacking in *A. j. jamaicensis*. KOOPMAN and others have referred to Grenadan specimens under the name *Artibeus jamaicensis trinitatis*, although the subspecific name *grenadensis* Andersen, 1906, is available for them. The slight differences in size (Table 15) between Grenadan bats and those from Trinidad do not, in our opinion, justify the recognition of *grenadensis*, especially when the degree of variation among insular populations of *A. j. jamaicensis* is considered.

KOOPMAN (1968: 6) noted the apparent absence of *Artibeus jamaicensis* on St. Vincent. In the summer of 1967, we collected a series of 39 specimens of *jamaicensis* on St. Vincent that average considerably larger than individuals from any other Antillean population and that apparently represent an unnamed subspecies that is distinct both from *A. j. jamaicensis* to the north and *A. j. trinitatis* to the south. The bats from St. Vincent also average larger than a specimen of *Artibeus lituratus palmarum* taken by us on the same island. The

species *jamaicensis* and *lituratus* are most easily separated on the basis of the structure of the orbital region of the skull and in that *lituratus* has brownish hairs on the ventral surface, whereas the ventral pelage of *jamaicensis* is composed of grayish-tipped hairs. Nevertheless, the two species are closely related and so similar in external appearance that we feel certain some specimens previously referred to *lituratus* from St. Vincent actually represent *jamaicensis* – particularly so because throughout much of the broadly sympatric distributions of the two species, *lituratus*, not *jamaicensis*, is the larger bat.

The large size of the undescribed race on St. Vincent is best illustrated by comparison with samples of *A. j. jamaicensis* from nearby Barbados and St. Lucia, and with individuals of *A. j. trinitatis* to the south (see Table 15). Four of our St. Vincent bats possess the small upper M3, two on the right side only and two on both sides, possibly indicating at least some genetic influence from the south.

*Natalus stramineus* Gray. – The funnel-eared bat has been reported from five scattered islands in the Lesser Antilles (Anguilla, Saba, Antigua, Montserrat, and Dominica); certainly additional zoological exploration will reveal its presence on other islands as well. According to GOODWIN (1959), *N. s. stramineus* (type locality restricted to Antigua) is the subspecies occurring throughout the area. The species *stramineus* is unknown from the Greater Antilles (although it occurs on the Middle American mainland), and is unknown also from Trinidad, Tobago, and adjacent areas in coastal South America (although it occurs elsewhere on that continent). Other species of *Natalus* occur in parts of the Greater Antilles as well as on Trinidad and evidently the adjacent South American mainland. GOODWIN's review of the subgenus *Natalus* provides a useful starting point for additional study of this interesting group. KOOPMAN's (1968: 7) hypothesis that *stramineus* has reached the Lesser Antilles from the south probably is correct, although the peculiar distributional picture outlined above stresses our current ignorance of the exact origin of the Antillean populations.

*Eptesicus fuscus* (Palisot de Beauvois). – The one report of the big brown bat from the Lesser Antilles, DOBSON's (1878: 194) mention

of a specimen from Barbados, likely resulted from an error in labeling or represents an accidental occurrence (Koopman, 1968: 8). In any event, *E. fuscus* occurs throughout much of North and Middle America, in the Greater Antilles, and in northern South America.

*Tadarida brasiliensis* (I. Geoffroy St.-Hilaire). – Several closely related subspecies of this widely distributed free-tailed bat occur in the Antillean region. The race of the Lesser Antilles and Puerto Rico is *T. b. antillularum* (type locality Dominica), which is known from most of the islands south to St. Lucia (see Table 14), but is unreported from Barbados, St. Vincent, the Grenadines, and Grenada. A single specimen has been reported from Tobago (Goodwin & Greenhall, 1961: 285), possibly representing an accidental occurrence because the species evidently is absent from Trinidad and the adjacent South American mainland. The subspecies *antillularum* is a small, brownish, sedentary bat as contrasted with, say, *T. b. mexicana* of the North American mainland, which is a larger, grayish-colored bat, and is migratory. Owing to (1) the apparent absence of bats of the species *brasiliensis* from Trinidad and the north coast of South America, and apparently also the southern Windward Islands, and (2) the morphological and behavioral features that set Antillean populations apart from at least some on the North and Middle American mainland, the specific status of *Tadarida* in the Antilles is in need of critical re-evaluation. Two alternative possibilities are: (1) *antillularum* and other insular Antillean populations represent a distinct species, or (2) they are related specifically to some population on the North American mainland, possibly *cynocephala* of the southeastern United States, but not to others.

*Molossus molossus* (Kerr). – “This common house bat probably occurs on virtually every Lesser Antillean island,” according to Koopman (1968: 9). It has been recorded from all major islands save St. Barthélemy (= St. Bartholemew), Saba, and the Grenadines (see Table 14). This species, and indeed the entire genus *Molossus*, is in need of critical systematic study. Preliminary examination of Antillean populations leads us to believe that all are referable to a single species recognized by its small size and white-based hairs,

which occurs also in much of South America and northward in Middle America as far as Tamaulipas, Mexico. The oldest specific name for this group is *Molossus molossus* (Kerr, 1792), based on material from Martinique.

As many as seven names have been applied in recent years to insular populations of *M. molossus* in the Antillean region. Three of these names were associated with specimens from the Lesser Antilles (see HALL & KELSON, 1959: 216–217, map 165), but the number recently has been reduced to two – *Molossus molossus debilis* (type locality St. Kitts) from the islands north of Guadeloupe and *M. m. molossus* from Guadeloupe southward onto the South American mainland (HUSSON, 1962; KOOPMAN, 1968).

#### DISCUSSION

As pointed out in the preceding comments, much remains to be learned, both from distributional and taxonomic points of view, about bats in the Lesser Antilles. Recent field work in the islands and the subsequent study of several groups (*Artibeus*, *Ardops*, *Monophyllus*, and *Sturnira*) in detail has resulted in considerable alteration of previously held concepts concerning their distributional patterns and systematics. The 19 species presently known from the area fall fairly well into three zoogeographic groupings, and yet the mosaic distributional pattern of many suggests the need for detailed studies of conditions on individual islands and of the biology of individual species, indeed, populations, of bats.

Presently, little can be written concerning the relationships between island size and biological diversity relative to kinds of bats, because few of the Lesser Antillean islands have been studied intensively. Dominica probably is the best known in this regard; there, 12 species (one perhaps an accidental) occupy a land mass of 305 square miles, or one species per 25.4 square miles. On the other hand, Montserrat, a mountainous island like Dominica but much smaller, has eight known species on 32.3 square miles (one per slightly more than four square miles). DARLINGTON (1957: 482) stated that "the effect of limitation of area on the number and kind of animals on islands is profound," but also noted (p. 483) that "the effect is very

complex and is modified by many factors." MACARTHUR & WILSON (1967: 8) have pointed out that area in itself does not have a direct effect on whether or not a given species occurs on an island but that, instead, area is related to diversity of habitats. In the Lesser Antilles, and on other islands as well, elevation also is an important factor in determining floristic diversity. The data given for number of species of bats per square mile for Dominica and Montserrat indicate, therefore, that biological diversity of individual islands, as it influences such factors as food and roosting sites, is more immediately important than size alone in determining the number of resident chiropteran species on Lesser Antillean islands. It should be noted that all the islands under consideration are essentially "small," especially when compared with the Greater Antilles.

The factors discussed in the foregoing commentary must be balanced, of course, against dispersal patterns of the bats themselves, and the influence of prevailing winds, effectiveness of water barriers, and other non-biologic considerations. "Accidental" occurrence of bats on islands in the Antillean region is instructive in this regard. Several such occurrences are mentioned in the foregoing accounts and when all the Antillean islands are considered the number is noteworthy. When one considers the relatively few biologists that have been on hand in the past century to preserve such bats, the number of those that have been recorded is impressive and suggests that inter-island movement of at least some species may be a fairly regular occurrence. In other words, the potential for active colonization of islands and genetic exchange between populations of the same species on at least adjacent islands may be considerably greater than ordinarily supposed. Another factor, which must be considered when studying the distribution of bats on islands, is that in insular situations established (breeding) populations are by no means permanent.

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