Bats of Margarita Island, Venezuela, with Zoogeographic Comments

James Dale Smith
California State University - Fullerton

Hugh H. Genoways
University of Nebraska - Lincoln, h.h.genoways@gmail.com

Follow this and additional works at: http://digitalcommons.unl.edu/museummammalogy

Part of the Biodiversity Commons, Terrestrial and Aquatic Ecology Commons, and the Zoology Commons

http://digitalcommons.unl.edu/museummammalogy/177

This Article is brought to you for free and open access by the Museum, University of Nebraska State at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Mammalogy Papers: University of Nebraska State Museum by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.
BATS OF MARGARITA ISLAND, VENEZUELA,
WITH ZOOGEOGRAPHIC COMMENTS

JAMES DALE SMITH AND HUGH H. GENOWAYS

Reprinted from Bulletin of the Southern California Academy of Sciences
Vol. 73, No. 2, August 1974
pp. 64–79
Made in the United States of America
BATS OF MARGARITA ISLAND, VENEZUELA, WITH ZOOGEOGRAPHIC COMMENTS

JAMES DALE SMITH¹ AND HUGH H. GENOWAYS²

ABSTRACT: Sixteen species of bats are reported from Margarita Island, Nueva Esparta, Venezuela. These include two species of emballonurids, one noctilionid, two mormoopids, nine phyllostomatids, one vespertilionid, and one molossid. Accounts including natural history and taxonomic comments are given for each species. The chiropteran fauna of Margarita Island is compared with the bat faunas of the adjacent Venezuelan mainland and islands off the northern coast of South America, including Trinidad and other Antillean islands. It is concluded that the chiropteran fauna of Margarita Island represents an attenuated mainland fauna.

Margarita Island is located approximately 25 kilometers north of the Venezuelan mainland off the Araya Peninsula in northeastern Venezuela. It is the second largest island (approx. 850 square miles) of the Netherland Antilles and comprises the Venezuelan state of Nueva Esparta along with the smaller, adjacent islands of Coche and Cubaqua. These three Venezuelan islands are located on the continental shelf and probably were continuous with the mainland during Pleistocene fluctuations in sea level.

Margarita Island actually consists of two islands connected by a narrow isthmus (Fig. 1). Each island has a central mountain mass; Cerro Copey on the eastern island is approximately 957 m in elevation, whereas, Cerro Los Cedros, on the western island reaches 792 m. The majority of the island is covered by a low, xeric thorny scrub forest. A somewhat higher and denser thorny scrub forest of acacia trees and tall cacti occur in the more inland regions. On the eastern slopes of the mountains the vegetation becomes more mesic in character and limited areas of low montane rain forest occur on the tops of the mountains and in the wetter valleys. Coconut palms and tropical fruit trees are found on the eastern slope of Cerro Copey. This eastern range of mountains apparently has a rainshadow effect and results in the xeric condition of the western portion of the island. Mangrove swamps are widespread on the southeastern coast and are extensive along the isthmus connecting the two land masses. The capital city of Porlamar, located on the eastern coast at the foot of Cerro Copey, is the population center of the island.

Bats were collected and studied in northeastern Venezuela and on Margarita Island by one of us (Smith) from February 1966 to May 1967. Field investigations were supported by the University of Kansas-Universidad de Oriente Project of the Ford Foundation. The authors wish to express their thanks to Nancy Smith, Philip Montgomery, Luis Urosa, and M. Leon for their assistance in collecting and preserving material.

¹ Dept. Biological Sciences, California State University, Fullerton, California 92634.
² The Museum, Texas Tech University, Lubbock, Texas 79409.
and to Susan Payne for preparation of illustrations and typing the manuscript. We are indebted to the following institutions and persons for the loan of critical comparative material (abbreviations preceding the names of institutions are used throughout the text to identify the source of specimens): AMNH, American Museum of Natural History (Karl F. Koopman); BMNH, British Museum (Natural History) (J. E. Hill); IZT, Instituto de Zoología Tropical, Facultad de Ciencias, Universidad Central de Venezuela, Caracas (Juhani Ojasti and Edgardo Mondolfi); KU, The Museum of Natural History, The University of Kansas (J. Knox Jones, Jr.); LACM, Natural History Museum of Los Angeles County (Donald Patten); MCZ, Museum of Comparative Zoology, Harvard University (Barbara Lawrence); MLS, Museo de Historia Natural, La Salle, Caracas, Venezuela (Omar Linares); RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (A. M. Husson); TCWC, Texas A and M University, Texas Cooperative Wildlife Research Collections (W. B. Davis and Dilford C. Carter); TTU, The Museum, Texas Tech University (H. H. Genoways); and USNM, National Museum of Natural History (C. O. Handley, Jr.). We also thank Donald Patten, Natural History Museum of Los Angeles County, for identification of specimens of Artibeus. All specimens are deposited in the Museum of Natural History, The University of Kansas, unless otherwise noted.

All measurements employed in this study are defined by Smith (1972:6) and were taken with dial calipers, calibrated in twentieths of a millimeter and were recorded to the nearest tenth of a millimeter. Measurements of embryos are given as crown-rump lengths.

ACCOUNTS OF SPECIES

FAMILY EMBALLONURIDAE

Peropteryx macrotis trinitatus Miller, 1899

Specimens examined (24).—Cave SW El Vallé [Musso (1962:167) indicates this cave is surely Cueva del Piache], 1 (MCZ); no specific locality, 23 (RMNH).

Additional records.—Guatamare, near El Vallé (Hummelinck, 1940:69); Cave near La Asunción, Carretera a Porlamar; Cueva Chaure, Cerro Atagua (Musso, 1962:166).

This species apparently is one of the more common bats in the mesic regions of Margarita Island. All of the individuals reported by Musso (1962:166) were found in caves. In a cave near La Asunción, he encountered Saccopteryx leptura living with a large colony of P. m. trinitatus.

Measurements of the material examined by
us and those published by Musso (1962) agree with those given by Goodwin and Greenhall (1961:216) for four specimens of P. m. trinitatus (including the holotype) from Trinidad.

*Saccopteryx leptura* (Schreber, 1774)

*Specimens examined.—None.*

*Additional records.—Hacienda Ochenta; Cueva near La Asunción, Carretera a Poriamar (Musso, 1962:167); El Vallé (Piriot and León, 1965:369).*

Piriot and León (1965:369) reported this species as very abundant in the forest, on the higher hills of the eastern portion of the island. Individuals were found in groups of two to five living in holes in rocks and fallen trees, and between the buttresses of *Ceiba pentandra.* Musso (1962:167) found this species roosting with a large colony of *Peropteryx macrois trinitatus* in a cave near La Asunción.

---

**FAMILY NOCTILIONIDAE**

*Noctilio leporinus mastivus* (Vahl, 1797)

*Specimens examined.—1 ½ km N San Francisco de Macanao, 75 m, 1.*

A nonpregnant, lactating female, represents the first record of this large fish-eating species from Margarita Island. It was captured at dusk in a mist-net set across a small arroyo which drained into a small artificial pond. Lesser nighthawks, *Chordeiles acutipennis,* were captured at this time as they foraged over the pond. The vegetation around the pond was low, thorny scrub.

Koopman (1968:2) discussed the subspecific status of *Noctilio leporinus* with particular reference to *N. l. mastivus,* and Davis (1973) has recently reviewed the species *leporinus.* The selected external and cranial measurements given
in table 1 clearly show that the Antillean bats are much larger in size than those from Surinam, which is the type locality of *N. l. leporinus* as restricted by Thomas, 1911:131. Both Koopman (1968) and Davis (1973) proposed that the antillean population should be referred to the race *N. l. mastivus*. In comparing cranial and external measurements of our specimen from Margarita Island and several from the adjacent mainland, we found them to agree more closely in size with the Antillean bats than those from Surinam. Therefore, we concur with Davis (1973) in applying the name *N. l. mastivus* to the populations of large fish-eating bats from northeastern Venezuela.

Specimens used for comparison are as follows.—BRAZIL: Cruzeiro do Sur, Acre, 1 (LACM). CUBA: Km. 7, between San Juan de Las Lajas and La Ruda, Habana, 2 (TCWC). DOMINICA: Clarke Hall Estate, 100 ft, St. Joseph Parish, 1 (KU); Mouth of Layou River, sea level, St. Joseph Parish, 3 (KU); no specific locality, 2 (1 BMNH, 1 USNM). TRINIDAD: Fyzabad, 4 (3 KU, 1 TCWC); Peral, 4 (TCWC). VENEZUELA: 1½ km NW El Pilar, Sucre, 6 (KU).

**FAMILY MORMOOPIDAE**

*Pteronotus parrnellii fuscus* J. A. Allen, 1911

*Specimens examined* (31).—Cueva Atagua, Cerro Atagua, 5 (MLS); Cerro Matasiete, 2 km N, 2 km E La Asunción, 305 m, 1 (USNM); El Vallé, 50 m, 2; Cueva Honda del Piache, SE El Vallé, 2 (RMNH); La Aguada, 3 km S La Asunción, 53 m, 12 (USNM); Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 9.

Parnell's mustached bat appears to be rather common on Margarita Island. The ecological limits of this species are not well known. It was encountered in both xeric and mesic habitats on the island.

At Cueva El Convento, near San Francisco de Macanao, *P. p. fuscus* was collected in close association with *Leptonycteris curasoeae*. It is not known whether individuals of *P. parrnellii* were roosting singly or as a segregated cluster within the colony of *Leptonycteris* as both species were obtained with a single discharge of a shotgun. The bats were roosting in a dome-like depression in the ceiling, about ten feet above the floor of the dry, guano-filled cave. One wall of the roosting chamber was open to the outside by way of a vertical passageway and, as a result, the room was dimly lighted. The accumulation of guano indicated a long and continual use of the cave by bats. Two mandibles of *P. parrnellii* were found among the skeletal remains of weathered owl pellets removed from the cave floor.

One female, captured on 16 July, was pregnant with one embryo that measured 27. Two females, taken on 12 November, showed no signs of reproductive activity.

In analyzing the geographic variation of *P. parrnellii*, Smith (1972:77) assigned specimens from Margarita Island and the Caribbean versant of Venezuela to the subspecies *P. p. fuscus*. Although individuals of *P. parrnellii* from Margarita fall well within the range of variation of mainland populations of *P. p. fuscus*, they show a slight reduction in overall size. Populations of *P. p. rubiginosus* from the Amazon Basin are considerably larger in cranial and external size (Smith, 1972). Specimens of *parrnellii* from Trinidad appear to more closely resemble *P. p. rubiginosus* than *P. p. fuscus*.

**Mormoops megalophylla tumidiceps** Miller, 1902

*Specimens examined* (4).—Cueva Honda del Piache, SE El Vallé, 3 (RMNH); Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 1.

*Additional record.*—El Vallé (Priet and León, 1965:369).

The ghost-faced bat does not appear to be an abundant species on Margarita Island and is common only locally on the Venezuelan mainland. One of our specimens is a right mandible found in the owl pellet material from Cueva El Convento. The geographic variation of this species is discussed by Smith (1972).

Selected external and cranial measurements of two males from Cueva Honda del Piache are as follows: length of forearm, 55.6, 55.2; condylobasal length, 14.4, 14.1; zygomatic breadth, 9.8, 9.6; rostral breadth, 5.5, 5.4; length of maxillary toothrow, 8.1, 7.8.

**FAMILY PHYLLOSTOMATIDAE**

*Micronycteris megalotis megalotis* Gray, 1842

*Specimens examined* (3).—El Vallé, 2 (MCZ); Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 1.

*Additional records.*—all from Museo (1962:168).
According to Musso (1962:168), this species is widely distributed on the island. Selected external and cranial measurements of one male and one female, respectively, from El Valle are as follows: length of forearm, 32.8, 33.7; zygomatic breadth, 8.7, 8.6; rostral breadth, 4.8, 4.8; length of maxillary toothrow, 6.7, 6.9; condylobasal length, —, 15.7. These measurements agree with those given by Sanborn (1949) and Husson (1962) for the subspecies *M. m. megalotis.*

At Cueva El Convento, this species was represented by a right lower jaw found in the weathered remains of owl pellets.

**Phyllostomus discolor discolor** Wagner, 1843

*Specimens examined* (6).—EI Valle, 50 m, 6.

Pirlot and León (1965:369), first reported this bat on Margarita Island. Their material also was from El Valle, the only locality on the island from which this species has been recorded. The ecological preferences of *P. discolor* seem to be for mesic habitats and for this reason the species may be restricted to the northeastern portion of the island.

Of five females mist-netted on July 15 and 16, one contained one embryo measuring 17. Two others were not pregnant but were lactating. A male taken at the same time had testes measuring 5 mm in length. These bats were captured as they foraged in a peach and mango grove.

Valdez (1970), after studying the geographic variation of *Phyllostomus discolor*, employed the name *P. d. discolor* for populations east of the Andes. Power and Tamsitt (1973) have questioned the validity of the recognition of intra-specific names in this species. In the absence of an extensive study of geographic variation in northern South America, we have assigned our material to *P. d. discolor*.

Selected external and cranial measurements of the four females (average with extremes in parentheses) and two males, respectively, from El Valle are as follows: length of forearm, 61.3 (60.1–62.2), 62.0, 63.3; condylobasal length, 26.4 (25.3–26.6), 25.8, 26.9; zygomatic breadth, 15.4 (15.0–16.0), 15.4, 15.6. These measurements agree with those given by Sanborn (1936:98) for specimens from Brazil, Venezuela, and French Guiana, and by Goodwin and Greenhall (1961:238) for material from Trinidad.

**Glossophaga longirostris longirostris** Miller, 1898

*Specimens examined* (26).—El Vallé, 50 m, 24 (3 MCZ); 1½ km N San Francisco de Macanao, 75 m, 2.

*Additional records.*—La Estancia, 2 km W Paraguachi; Salamanca; Cueva del Piache; Hacienda Ochenta; San Francisco de Macanao (Musso, 1962:169); El Vallé (Pirlot and León, 1965:369).

G. M. Allen (1902:96) reported on three specimens from a large cave near El Vallé which he referred to the species *Glossophaga soricina.* One was an adult male, another a young (sex unknown) individual with deciduous teeth, and the third specimen was an adult female. He noted that the latter seemed distinct from the other two and thought that it might represent an undescribed species. We have examined Allen's three specimens and found that only the female is an adult. We concur with Koopman (1958:437) who assigned all three bats to *Glossophaga longirostris.*

Pirlot and León (1965:369) report two male *G. soricina* from El Vallé. We have not examined these specimens, but suspect that these, too, are but immature individuals of *G. longirostris.* Adult *G. longirostris* are easily distinguished from *G. soricina* on the basis of greater length of forearm. In addition, the upper incisors of longirostris are nearly equal in size and are equally procumbent. The outer incisors of soricina are smaller than the inner pair and somewhat less procumbent.

Eight of fourteen females mist-netted in a peach and mango grove at El Vallé on 15 July, carried one embryo which averaged 17.0 (12.0–20.0) crown-rump length. The remaining six females showed no sign of reproductive activity.

Table 2 shows the means and extremes of several selected external and cranial measurements of *G. longirostris* from selected localities. Our material from Margarita Island is well within the range of variation of the mainland *G. l. longirostris.* These measurements also widely overlap those given for the Antillean race *G. l. rostrata.* Whether or not this indicates a close relationship between these populations is not clear at this time. However, this may indicate that the source for the Antillean populations may have been directly from the mainland rather than from the mainland by way of Trinidad and Tobago. Until
TABLE 2. Selected cranial and external measurements of *Glossophaga longirostris* from the Antilles and north-eastern South America. Superscript numbers indicate a sample size that differs from those given in the left-hand column.

<table>
<thead>
<tr>
<th>Number</th>
<th>Forearm</th>
<th>Condylobasal length</th>
<th>Breadth of braincase</th>
<th>Mastoid breadth</th>
<th>Breadth of rostrum at canines</th>
<th>Length of maxillary toothrow</th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>37.3</td>
<td>22.5</td>
<td>8.7</td>
<td>—</td>
<td>—</td>
<td>8.1*</td>
</tr>
<tr>
<td></td>
<td>(35.6–39.0)</td>
<td>(21.8–23.2)</td>
<td>(8.4–9.0)</td>
<td></td>
<td>(8.0–8.4)</td>
<td></td>
</tr>
<tr>
<td><em>Glossophaga longirostris elongata</em>, Curacao (Miller, 1913:429)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>37.8</td>
<td>21.2</td>
<td>8.8</td>
<td>9.2</td>
<td>4.0</td>
<td>7.9</td>
</tr>
<tr>
<td></td>
<td>(36.4–29.6)</td>
<td>(21.0–21.6)</td>
<td>(8.5–8.9)</td>
<td>(8.8–9.5)</td>
<td>(3.7–4.3)</td>
<td>(7.7–8.2)</td>
</tr>
<tr>
<td><em>Glossophaga longirostris longirostris</em>, Margarita Island, Venezuela</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>37.4</td>
<td>21.2</td>
<td>8.8</td>
<td>9.4</td>
<td>4.1</td>
<td>7.8*</td>
</tr>
<tr>
<td></td>
<td>(36.2–39.4)</td>
<td>(20.4–22.0)</td>
<td>(8.5–8.9)</td>
<td>(9.1–9.6)</td>
<td>(3.9–4.2)</td>
<td>(7.5–8.0)</td>
</tr>
<tr>
<td><em>Glossophaga longirostris longirostris</em>, Estados Sucre, Venezuela</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>37.2</td>
<td>21.7</td>
<td>9.1</td>
<td>—</td>
<td>—</td>
<td>8.1*</td>
</tr>
<tr>
<td></td>
<td>(35.4–38.6)</td>
<td>(21.0–22.4)</td>
<td>(8.8–9.4)</td>
<td></td>
<td>(7.8–8.8)</td>
<td></td>
</tr>
<tr>
<td><em>Glossophaga longirostris major</em>, Trinidad</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>40.2*</td>
<td>21.5</td>
<td>10.1*</td>
<td>9.1*</td>
<td>4.2</td>
<td>8.1</td>
</tr>
<tr>
<td></td>
<td>(39.8–41.0)</td>
<td>(20.8–22.2)</td>
<td>(10.0–10.3)</td>
<td>(9.0–9.2)</td>
<td>(4.1–4.3)</td>
<td>(7.9–8.4)</td>
</tr>
<tr>
<td><em>Glossophaga longirostris rostrata</em>, Grenada</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>37.7</td>
<td>21.5</td>
<td>8.8</td>
<td>9.4</td>
<td>4.1</td>
<td>7.9</td>
</tr>
<tr>
<td></td>
<td>(37.1–38.5)</td>
<td>(20.8–22.0)</td>
<td>(8.6–9.0)</td>
<td>(9.2–9.7)</td>
<td>(3.8–4.4)</td>
<td>(7.8–8.0)</td>
</tr>
<tr>
<td><em>Glossophaga longirostris rostrata</em>, St. Vincent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>37.4</td>
<td>21.1</td>
<td>—</td>
<td>9.4</td>
<td>4.0</td>
<td>7.7</td>
</tr>
<tr>
<td></td>
<td>(36.4–38.8)</td>
<td>(20.6–21.9)</td>
<td></td>
<td>(9.3–9.6)</td>
<td>(3.9–4.2)</td>
<td>(7.5–7.9)</td>
</tr>
</tbody>
</table>

this relationship is better understood we tentatively assign our material to *G. l. longirostris*.

*Leptonycteris eurasoae* Miller, 1900

Specimens examined (88).—El Valle, 50 m, 5; Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 81; 1½ km N San Francisco de Macanao, 75 m, 2.

Additional record.—The holotype and type series of *L. c. tarsosti* from El Valle (Pirlot, 1965:6–7).

Individuals of this apparently widespread and common species were captured in mist-nets and shot in caves. The majority of our material resulted from two visits (July and November) to Cueva El Convento, near San Francisco de Macanao. The cave is described in the account of *Pteronotus pamelius fuseus*, a species found living in direct association with this colony of *Leptonycteris*.

When first discovered in July the colony was composed of approximately 4000 females nursing nearly full-grown young. The young bats had unfused phalangeal epiphyses and were covered with sparse greyish, juvenile pelage. In addition, these young were in varying stages of losing the upper deciduous canines and lower incisors, the third upper molars and the permanent lower incisors were nearly completely erupted, and all cranial sutures were unfused. The forearms of 15 young bats averaged 53.3 (52.0–55.2) in comparison with 53.4 (51.3–55.8) of 61 adult females. No adult males were captured on the July visit.

In November, the composition of the colony had changed. There were no young individuals with unfused wing bones, and adult males in breeding condition (testes 6–8 mm in length) were present. Of the 34 females captured in November seven were pregnant; each with one small embryo which averaged 6.3 (3.1–11.3). The smallest embryos had the limb buds only slightly differentiated, whereas these structures were relatively well developed in the largest embryos. Skeletal elements and complete skulls
of *Leptonycteris* also were encountered in the owl-pellet material from the floor of the cave.

Hyperdontia in the genus *Leptonycteris* was encountered only in the species *L. sanborni* by Phillips (1971:76). In our series of *L. curasoae* from Margarita Island, we found one adult female (KU 118206) with a unilateral duplication of the upper right canine (Fig. 2). Another adult female (KU 118193) exhibited a persistent left upper deciduous canine in the space between the permanent canine and first premolar; all teeth were fully erupted and partially worn. Our sample also indicates that incisors are apparently lost frequently during life. In two individuals upper premolars had been lost and in another the second right upper molar was lost.

Pirlot (1965:607) evidently was unable to compare his material from Margarita Island with specimens from Aruba, Curacao, or Bonaire when he described *L. c. tarlosti*. Table 3 shows selected external and cranial measurements (average with extremes in parentheses) of specimens of *L. curasoae* from Margarita, Aruba, Curacao, and Bonaire islands. As can be seen, there is a great deal of overlap, especially between individuals from Margarita and Aruba. Although individuals from the oceanic islands Curacao and Bonaire appear to have somewhat narrower crania, a meaningful interpretation of any geographic trend is difficult with so few specimens. There appears to be little evidence to support the recognition of the population from Margarita Island as a distinct race. The species is widespread along the coastal lowlands of northern Colombia and Venezuela (Marinkelle and Cadena, 1972:53; Matson and Brown, 1974) and we believe that an analysis of geographic variation will show that mainland and insular populations are undifferentiated. We therefore consider *Leptonycteris curasoae* to be monotypic.

**Table 3.** Selected cranial and external measurements of *Leptonycteris curasoae*. Superscript numbers indicate a sample size that differs from those given in the left-hand column.

<table>
<thead>
<tr>
<th>Number</th>
<th>Length of Forearm</th>
<th>Zygomatic breadth</th>
<th>Breadth of braincase</th>
<th>Breadth across canines</th>
<th>Length of maxillary toothrow</th>
<th>Condylar length</th>
<th>Length mandibular toothrow</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Margarita Island, Venezuela</td>
<td>Aruba Island</td>
<td>Curacao Island</td>
<td>Bonaire Island</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>53.4 (51.3–55.2)</td>
<td>11.1^a (10.7–11.4)</td>
<td>10.1^a (9.9–10.4)</td>
<td>4.9^a (4.8–5.0)</td>
<td>9.4 (9.0–9.7)</td>
<td>26.4 (25.4–26.9)</td>
<td>10.2 (9.9–10.6)</td>
</tr>
<tr>
<td>2</td>
<td>54.4^a (53.7–54.7)</td>
<td>11.4, 11.6</td>
<td>10.2, 10.5</td>
<td>5.1, 5.1</td>
<td>9.6, 9.7</td>
<td>27.0, 27.6</td>
<td>10.7, 10.6</td>
</tr>
<tr>
<td>5</td>
<td>54.3 (51.4–55.7)</td>
<td>10.9^a (10.7–11.3)</td>
<td>10.1^a (9.8–10.2)</td>
<td>4.9</td>
<td>9.4 (9.2–9.6)</td>
<td>26.6^a (26.0–27.2)</td>
<td>10.4 (10.2–10.8)</td>
</tr>
<tr>
<td>1</td>
<td>52.5</td>
<td>–</td>
<td>10.2</td>
<td>5.1</td>
<td>9.5</td>
<td>26.8</td>
<td>10.6</td>
</tr>
</tbody>
</table>
Table 4. Selected external and cranial measurements of *Artibeus planirostris* from northeastern Venezuela and Trinidad. Superscript numbers indicate a sample size that differs from those given in the left-hand column.

<table>
<thead>
<tr>
<th>Number</th>
<th>Forearm length</th>
<th>Condylobasal breadth</th>
<th>Zygomatic breadth</th>
<th>Mastoid breadth</th>
<th>Breadth of rostrum at canines</th>
<th>Length of maxillary toothrow</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>55.9</td>
<td>24.0</td>
<td>16.6</td>
<td>14.7</td>
<td>7.3</td>
<td>9.7</td>
</tr>
<tr>
<td></td>
<td>(52.6-57.4)</td>
<td>(23.7-24.4)</td>
<td>(16.2-17.0)</td>
<td>(14.4-14.9)</td>
<td>(7.1-7.6)</td>
<td>(9.4-10.0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>58.6</td>
<td>24.2</td>
<td>17.2$^{2s}$</td>
<td>15.2</td>
<td>7.6</td>
<td>9.7</td>
</tr>
<tr>
<td></td>
<td>(55.7-61.0)</td>
<td>(23.7-25.1)</td>
<td>(16.4-17.9)</td>
<td>(14.8-15.6)</td>
<td>(7.2-8.2)</td>
<td>(9.4-10.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>59.6</td>
<td>24.6</td>
<td>17.4</td>
<td>15.2</td>
<td>7.8</td>
<td>10.5</td>
</tr>
<tr>
<td></td>
<td>(56.3-62.9)</td>
<td>(23.8-25.4)</td>
<td>(16.6-18.1)</td>
<td>(14.6-15.8)</td>
<td>(7.5-8.1)</td>
<td>(9.6-10.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>59.8$^{2s}$</td>
<td>24.6</td>
<td>17.4</td>
<td>15.2</td>
<td>7.9</td>
<td>10.0</td>
</tr>
<tr>
<td></td>
<td>(57.1-62.9)</td>
<td>(24.0-25.4)</td>
<td>(16.7-18.2)</td>
<td>(14.6-15.7)</td>
<td>(7.4-8.5)</td>
<td>(9.7-10.5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>57.1$^{s}$</td>
<td>24.3$^{s}$</td>
<td>17.2</td>
<td>14.8$^{s}$</td>
<td>7.7</td>
<td>9.9$^{s}$</td>
</tr>
<tr>
<td></td>
<td>(54.8-58.9)</td>
<td>(23.6-25.1)</td>
<td>(16.7-17.9)</td>
<td>(14.4-15.6)</td>
<td>(7.5-7.9)</td>
<td>(9.6-10.2)</td>
</tr>
</tbody>
</table>

*Carollia perspicillata perspicillata* (Linnaeus, 1758)

Specimens examined (2).—Las Piedras, 2.

Additional records.—La Estancia, 2 km W Paraguachi (Musso, 1962:170).

Two males were captured in a mist-net as they foraged along a dry arroyo bordered by tall broad-leaved gallery forest composed primarily of the fig tree, *Ficus yoponensis*. Musso (1962:170) collected this species from under the roof of an old abandoned house. Only two other species of bats, *Artibeus planirostris* and *A. lituratus*, were netted at this locality.

The forearms of the two males captured 15 July measured 42.2 and 40.5. We follow Goodwin and Greenhall (1961), Husson (1962), and Pine (1972) in assigning our specimens to *Carollia perspicillata perspicillata*.

*Artibeus planirostris trinitatis* Andersen, 1906

Specimens examined (18).—Las Piedras, 8; El Vallé, 50 m, 10.

Additional records.—Hacienda Ochenta (Musso, 1962:170); El Vallé (Pirlot and León, 1965:369).

This bat is one of the most common species in the wetter portions of the island and the adjacent mainland. At Las Piedras, the fruits of the native fig (*Ficus yoponensis*) were found in the nets along with both *Artibeus planirostris* and *A. lituratus*. Some flying individuals also were observed carrying a single fruit of this fig.

Two of five females caught at Las Piedras on 15 July each carried one embryo measuring 22.3 and 28.8, respectively. Two other females were lactating and a third showed no signs of reproductive activity. In addition, two females collected at El Vallé on 15 July were pregnant with embryos that measured 27 and 28.

We follow Patten (1974) in applying the specific name *planirostris* to these specimens of *Artibeus* from Margarita. Although our material of this species from Margarita averages slightly smaller in external and cranial size than specimens from the adjacent Venezuelan mainland and Trinidad (Table 4), we do not feel justified in recognizing this population as a distinct geographic race. We therefore assign our material to *Artibeus planirostris trinitatis*.

*Artibeus lituratus palmarum* J. A. Allen and Chapman, 1897

Specimens examined (6).—Las Piedras, 1; El Vallé, 50 m, 5.

Additional records.—Salamanca (Musso, 1962:170); El Vallé (Pirlot and León, 1965:369).

This large *Artibeus* does not appear to be common on Margarita Island. Musso (1962) first
reported the species on the island on the basis of one adult male. Pirlot and León (1965) reported 17 specimens of *lituratus* in their collection from Margarita. One of our specimens was captured in a mist-net set across a dry boulder-filled arroyo bordered by fig trees. *Artibeus planirostris* also was captured at this site. At El Vallé, *A. lituratus* was netted in a peach, mango, and coconut grove. External and cranial measurements of our material agree with those given by Goodwin and Greenhall (1961: 261) for specimens from Trinidad.

One of two females captured on 15 July at El Vallé carried a single embryo measuring 25. The testes of three males obtained the same night at El Vallé measured 5, 6, and 7.

*Desmodus rotundus (E. Geoffroy-St. Hilaire, 1810)*

*Specimens examined* (1).—1½ km N San Francisco de Macanao, 75 m, 1.

*Additional records.*—El Vallé (Pirlot and León, 1965:360).

Although this species is abundant on the Venezuelan mainland, its presence on Margarita Island was not reported until relatively recently by Pirlot and León (1965). Our specimen, an adult male, was caught in a mist-net set over a dry wash. The specimens reported by Pirlot and León (1965) were captured in a peach, mango, and coconut grove near El Valle.

In July 1966, the Food and Agriculture Organization of the United Nations reported several cases of paralytic rabies in cattle from the areas of San Antonio and "Ochenta." Cave fumigation was employed by the Venezuelan Ministerio de Agricultura e Cria in an effort to eradicate bats on the island early in 1967.

Selected external and cranial measurements of the individual from near San Francisco de Macanao followed by those (average with extremes in parentheses) of four males from the adjacent mainland (Cumaná and vicinity) are as follows: length of forearm, 59.1, 55.4 (54.1-57.6); condylobasal length, 19.9, 20.4 (20.0-20.7); zygomatic breadth, 11.6, 11.6 (11.2-12.0); length of maxillary toothrow, 3.3, 3.3 (3.2-3.5). These measurements agree with those given by Goodwin and Greenhall (1961) and Husson (1962) for the nominal subspecies *rotundus*.

*Diaemus youngi youngi* (Jentink, 1893)

*Specimen examined* (1).—El Vallé, 50 m, 1.

*Additional records.*—Sierra del Copey; Cueva del Pache (Musso, 1962:171); El Vallé (Pirlot and León, 1965:6).

The avian vampire was first reported from Margarita Island by Musso (1962:171). In the region around Cerro Copey, Musso noted that *Diaemus* was common throughout the forest and that flying individuals were easily identified by their large white wing tips [*A. planirostris* and *A. lituratus* also possess white wing tips]. Seven individuals of *D. youngi* reported by Musso were from a large colony which he encountered in a hollow tree trunk.

Goodwin and Greenhall (1961:271) described the peculiar oral glands of *Diaemus* which are located in the corners of the mouth. These glands were observed on the specimen from Margarita as well as several individuals from the adjacent mainland. When disturbed, the bat opens its mouth and the two glands evert, nearly filling the oral cavity. Each gland is bulbous in shape and measures about 2-3 mm in diameter when fully everted. The mouth glands of our July-taken specimen appeared to be quiescent because the odor described by Goodwin and Greenhall (1961:271) was not noted. Several February-taken males from the mainland had very active glands that squirted a fine stream of liquid, which had a "mustelid-like" odor, when these individuals were disturbed.

Selected external and cranial measurements of our specimen from Margarita Island, those of three males (average with extremes in parentheses) and one female from the adjacent mainland, and the holotype of *D. youngi* (taken from Husson, 1962:199) are respectively: length of forearm, 52.2, 52.1 (51.1-53.3), 52.3, 50.9; condylobasal length, 21.3, 21.4 (21.2-21.8), 21.4, 21.1; zygomatic breadth, 13.9, 14.0 (13.9-14.1), 13.3, 13.3; breadth of the braincase, 12.5, 13.0 (12.9-13.1), 12.9, 13.0; length of maxillary toothrow, 3.2, 3.6 (3.5-3.6), 3.5, 3.0. Thomas (1928:288-289) proposed the recognition of a separate race, *D. y. cypselinus*, from Pecas, Peru, based on one female specimen. Later, Sanborn (1949:282-283) reported an additional specimen identified as *cypselinus* from Yarinacocha, Peru. Comparison of the above-listed measurements with those given by Thomas (1928) and Sanborn (1949) suggests to us that the Peruvian subspecies is only slightly larger than *youngi*. In view of the paucity of material, we tentatively retain the name *D. y. cypselinus* as a weakly defined
race. The specimens from northeastern Venezuela and Margarita Island are referred to *Diaemus youngi youngi*.

Other Venezuelan specimens of *Diaemus* that we examined in this study include: Tacal, 11 km SSW Cumani, Sucre (KU) 1; Chara Santa Rita, 3 km SE Cumani, Sucre (KU) 1; 2 km S Cachipo, Monagas (KU) 2.

**FAMILY VESPERTILIONIDAE**

*Rhogeessa minutilla* Miller, 1897

Specimens examined (2).—El Valle, 1 (USNM); unspecified locality, 1 (USNM).

Additional record.—Laguna de las Marites (Musso, 1962:171).

The three specimens listed above are the only examples of *Rhogeessa minutilla* from Margarita Island, the type locality. The individual reported by Musso (1962:171) was captured in a mangrove swamp.

Miller (1897:139) described the first specimen from the island as a full species, which it remained until Goodwin (1958:7) relegated it a subspecies of *R. parvula*. Along with the material from Margarita Island, Goodwin assigned specimens from Trinidad, northern Venezuela, and eastern Colombia to this race. LaVal (1973) has recognized *Rhogeessa minutilla* as a distinct species and assigned to it specimens from Margarita Island, northeastern Venezuela, and adjacent Colombia. Tentatively, we follow LaVal's arrangement with some reservations. We believe that when the relationships of these bats in northern South America are fully understood, *minutilla* will prove to be, at most, a geographic race of *R. tumida*.

**FAMILY MOLOSSIDAE**

*Molossus molossus molossus* (Pallas, 1766)

Specimens examined (2).—El Valle, 2 (MCZ).

Additional records.—Guatamare, near El Valle (Hummelinck, 1940:72); Juan Griego Salamanca (Musso, 1962:172).

This species is probably much more common than available specimens indicate. Musso (1962:172) reported collecting his material (all males) from a bell tower of a church. One of us (Smith) observed this species at dusk as they emerged from under the eaves or out of the rain spouts of houses in Porlamar.

We follow Husson (1962:251) in applying the specific name *molossus* to our specimens of this species which were reported earlier by G. M. Allen (1902:91) under the name *obscura*; Hummelinck (1940:72) and Musso (1962:172) reported their specimens under the species *major*. Examination of material from the Lesser Antilles, mainland South America, Central America, and México leads us to believe that enough inter-population variation exists to warrant the use of the trinomial at this time, although the species is still badly in need of a thorough review.

The specimens from Margarita Island closely resemble typical material of *M. m. molossus* from St. Lucia, Grenada, St. Vincent (all in MCZ), Trinidad (TTU), and a large series from Dominica (KU). Also material from adjacent parts of the mainland (Josepin, Monagas, and San Antonio del Golfo, Sucre) seem to be assignable to this subspecies (Table 5). A series of specimens from Maripa, Bolívar, are somewhat smaller in size than typical *molossus* but this may be simply a result of local variation (Jones, Smith, and Turner, 1971:23-24). Further delineation of the range of *M. m. molossus* on the mainland and the relationship of the Maripa specimens will have to wait until more material is available; however, it is sufficient at present to say that *M. m. molossus* occurs on the mainland of northeastern South America.

**ZOOGEOGRAPHIC COMMENTS**

Koopman (1958) has discussed the zoogeography and distribution of bats on islands off the northern coast of South America. We take this opportunity to update Koopman's data based on recent publications and re-examine his conclusions in light of this new information. The islands in the following list are those considered by Koopman (the first number, in parentheses, represents species reported by Koopman, 1958; the second number refers to species presently known from the island followed by the references upon which this number is based): Aruba, (3) 4 (Hussan, 1960); Curacao, (6) 8 (Husson, 1960); Bonaire (3) 6 (Husson, 1960); Margarita, (7) 16 (this paper); Trinidad, (44) 63 (Goodwin and Greenhall, 1961, 1962, 1964; Genoways, Baker, and Loregnard, 1973); Tobago, (16) 17 (Goodwin and Greenhall, 1961); Grenada, (11) 12 (Jones and Phillips, 1970). We estimate the bat fauna of northern Venezuela...
TABLE 5. Selected external and cranial measurements of *Molossus molossus* from the Antilles and northeastern South America. Superscript numbers indicate a sample size that differs from those given in the left-hand column.

<table>
<thead>
<tr>
<th>Number and sex</th>
<th>Forearm</th>
<th>Zygomatic breadth</th>
<th>Breadth of braincase</th>
<th>Condylar-basal length</th>
<th>Length of maxillary toothrow</th>
<th>Breadth of rostrum at canines</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7  $\delta$</td>
<td>38.3</td>
<td>10.5$^{a}$</td>
<td>8.5$^{a}$</td>
<td>14.8</td>
<td>5.9</td>
<td>4.3</td>
</tr>
<tr>
<td>(37.2-39.2)</td>
<td>(10.3-10.9)</td>
<td>(8.4-8.7)</td>
<td>(14.5-15.3)</td>
<td>(5.7-6.0)</td>
<td>(4.1-4.4)</td>
<td></td>
</tr>
<tr>
<td>8  $\Omega$</td>
<td>37.8</td>
<td>10.0</td>
<td>8.3</td>
<td>14.1</td>
<td>5.6</td>
<td>4.0</td>
</tr>
<tr>
<td>(36.2-39.0)</td>
<td>(9.8-10.1)</td>
<td>(8.0-8.6)</td>
<td>(13.8-14.6)</td>
<td>(5.5-5.7)</td>
<td>(3.9-4.1)</td>
<td></td>
</tr>
<tr>
<td>St. Vincent</td>
<td>10.2</td>
<td>8.7</td>
<td>14.6</td>
<td>5.7</td>
<td>4.2</td>
<td></td>
</tr>
<tr>
<td>2  $\Omega$</td>
<td>9.8, 9.9</td>
<td>8.8, 8.8, 8.8</td>
<td>13.8, 14.4, 13.8, 14.4</td>
<td>5.5, 5.7, 5.7</td>
<td>4.0, 4.0</td>
<td></td>
</tr>
<tr>
<td>Grenada</td>
<td>9.7, 10.2</td>
<td>8.3, 8.6</td>
<td>13.7, 14.3</td>
<td>5.2, 5.7, 5.2</td>
<td>3.8, 4.1</td>
<td></td>
</tr>
<tr>
<td>Trinidad</td>
<td>10  $\delta$</td>
<td>38.1</td>
<td>10.8</td>
<td>8.9</td>
<td>15.1</td>
<td>6.1</td>
</tr>
<tr>
<td></td>
<td>(37.0-39.2)</td>
<td>(10.4-11.1)</td>
<td>(8.7-9.2)</td>
<td>(14.7-15.4)</td>
<td>(5.9-6.2)</td>
<td>(4.2-4.6)</td>
</tr>
<tr>
<td></td>
<td>10  $\Omega$</td>
<td>37.6</td>
<td>10.1</td>
<td>8.4</td>
<td>14.3</td>
<td>5.8</td>
</tr>
<tr>
<td></td>
<td>(35.5-39.2)</td>
<td>(9.9-10.5)</td>
<td>(8.0-8.7)</td>
<td>(13.8-14.7)</td>
<td>(5.4-6.2)</td>
<td>(4.0-4.4)</td>
</tr>
<tr>
<td>Margarita Island, Nueva Esparta, Venezuela</td>
<td>10  $\delta$</td>
<td>36.9</td>
<td>11.0</td>
<td>9.1</td>
<td>15.5</td>
<td>6.0</td>
</tr>
<tr>
<td>San Antonio del Gulfo, Sucre, Venezuela</td>
<td>10  $\Omega$</td>
<td>35.2</td>
<td>8.8</td>
<td>14.3</td>
<td>5.7</td>
<td>4.2</td>
</tr>
<tr>
<td>Jusepin, Monagas, Venezuela</td>
<td>5  $\delta$</td>
<td>38.9</td>
<td>10.4</td>
<td>8.5</td>
<td>15.1</td>
<td>6.1</td>
</tr>
<tr>
<td></td>
<td>(37.3-39.9)</td>
<td>(10.2-10.5)</td>
<td>(8.4-8.6)</td>
<td>(14.8-15.4)</td>
<td>(6.0-6.3)</td>
<td>(4.1-4.6)</td>
</tr>
<tr>
<td></td>
<td>5  $\Omega$</td>
<td>38.4</td>
<td>10.1</td>
<td>8.4</td>
<td>14.5</td>
<td>5.9</td>
</tr>
<tr>
<td></td>
<td>(37.3-39.5)</td>
<td>(9.8-10.4)</td>
<td>(8.3-8.7)</td>
<td>(14.3-14.7)</td>
<td>(5.8-6.0)</td>
<td>(4.0-4.3)</td>
</tr>
<tr>
<td>Maripa, Bolivar, Venezuela</td>
<td>5  $\Omega$</td>
<td>33.8</td>
<td>10.0$^{a}$</td>
<td>8.4</td>
<td>13.7</td>
<td>5.6</td>
</tr>
<tr>
<td></td>
<td>(32.7-34.9)</td>
<td>(9.8-10.1)</td>
<td>(8.2-8.6)</td>
<td>(13.5-13.9)</td>
<td>(5.4-5.7)</td>
<td>(3.8-4.0)</td>
</tr>
</tbody>
</table>

to comprise 50-60 species based upon field investigations by Smith and previous records; sixty species of bats were reported from Surinam by Husson (1962).

The only change in Koopman’s (1958) rank order of islands based on the number of chiropteran species inhabiting them is Margarita, which is now known to have more species than Grenada. This could have been predicted by the fact that Margarita is a much larger and higher island as well as being a continental island rather than an oceanic island.

Among the 16 species which presently comprise the chiropteran fauna of Margarita Island there are two species of emballonurids, one noctilionid, two mormoopids, nine phyllostomatids, one vespertilionid, and one molossid. Within the family Phyllostomatidae, the subfamilies are represented as follows: Phyllostomatinae, 2; Glossophaginae, 2; Carollinae, 1; Stenoderminae, 2; Desmodontinae, 2. *Rhogeessa minutilla* Miller, 1897 and *Leptonycteris curasoae tarloesi* Pirlot, 1965 were described from Margarita Island; neither is currently regarded as unique to the
### Figure 3

Composite, two-dimensional niche matrix for the 16 bat species from Margarita Island and the 39 species actually captured on the adjacent Venezuelan mainland. The trophic role values are those employed by Wilson (1973) or only slightly modified. The model values for forearm length are those used by Fleming et al., (1972). Each of the 49 cells of the matrix is divided into two parts, the upper represents species (abbreviated scientific names) and trophic role values for the Venezuelan mainland and the lower represents those for Margarita Island. At the left-hand margin appear the importance values (IV) for each trophic role in each of the two regions. The importance values are derived by dividing the total trophic values by the number of bat species in each fauna and expressed as a percentage. Crosshatching represents "niches" that are apparently not occupied by the known chiropteran fauna of these regions. Dots represent "mainland niches" that are apparently unoccupied by the chiropteran fauna of Margarita Island. The dotted cells for aerial insectivores from Margarita may represent sampling biases.

---

All of these bats are Neotropical in their affinities and all are found on the adjacent Venezuelan mainland.

Notably absent from the chiropteran fauna of Margarita Island are the three small, insectivorous families Natalidae, Thyropteridae, Furipertidae, and the frugivorous Sturnirinae (Phyllostomidae), all of which occur in the chiropteran
fauna of the adjacent mainland. In addition it should be noted that no more than two species of each major taxonomic group are known from the island. The latter observation is particularly striking when considering the wide diversity of the Phyllostomatinae and Stenodermatinae on the adjacent mainland (Fig. 3). Only in the case of Artibeus planirostris and A. lituratus is a genus represented by more than one species on Margarita Island. However, of the genera represented on the island, the following are represented on the mainland by two or more sympatric species: Saccopteryx, Peroptyerx, Noctilio, Pteronotus, Micronycteris, Phyllostomus, Glossophaga, Artibeus, Rhogeessa, and Molossus. The apparent absence of some species of vespertilionids and molossids on Margarita may be an artifact due to the fact that these bats are not readily captured in mist-nets and extensive collecting in and around their potential roost-sites such as attics of buildings, rain spouts, and elsewhere, was not conducted. With the use of other collecting techniques we would anticipate the addition of other species of these two insectivorous families to the Margarita fauna.

As noted above, all of the species which inhabit Margarita Island also occur on the mainland of northeastern Venezuela. Only 13 of the taxa from Margarita have been recorded on Trinidad; the three exceptions are Leptonycteris curasoae, Pteronotus parnellii fuscus, and Glossophaga longirostris longirostris. The latter two species are represented on Trinidad by different geographic races; P. p. rubiginosus with its affinities apparently with the Amazon Basin fauna (Smith, 1972:76) and G. l. major apparently independently differentiated on Trinidad and Tobago. Compared with the chiropteran fauna of Surinam (Husson, 1962), only six taxa occurring on Margarita Island are presently known from that country also. Four, six, and four species found on Margarita also inhabit Aruba, Curacao, and Bonaire, respectively. Seven species are shared by Margarita and Grenada islands.

From the foregoing account, it should be apparent that the chiropteran fauna of Margarita Island represents an attenuation of a fauna characteristic of northeastern South America (including Trinidad).

The representation of most major taxonomic groups of bats on Margarita Island, but in markedly reduced numbers when compared to the adjacent Venezuelan fauna, may reflect (1) the area of the island, (2) the proximity of the island to the source area, and (3) the ecological diversity of the island. These three factors have been discussed by Koopman (1958, 1968), MacArthur (1965), MacArthur and Wilson (1963, 1967), and others. More recently, McNab (1971), MacArthur, Diamond, and Karr (1972), and Fleming, Hooper, and Wilson (1972) have approached the problems of island faunas from the viewpoint of the ecological role of the individual species which comprise the fauna. Unfortunately, such studies are greatly limited by the paucity of available information on the ecological roles of many species; this is especially true of bats.

Inasmuch as the entire adaptive radiation of Neotropical bats seems to have revolved around diverse feeding habits, the availability of particular food sources and food items of particular sizes would appear to be primary parameters in the chiropteran niche. McNab (1971) also considered these two factors to be most important in the niche partitioning of tropical bat faunas.

A consistent classification of chiropteran food habits has not been readily available in the past and in fact, the food habits of many species simply are not known. Wilson (1973) made a noteworthy attempt at such a classification. In our analysis of the chiropteran fauna of Margarita Island and the adjacent mainland we have followed his method of categorizing the various species into trophic categories. These categories are (Fig. 3): carnivores (CARN.—feeding on tetrapods); piscivores (PISC.—feeding on fish); sanguinovores (SANG.—feeding on blood); foliage gleaners (FOL. GLE.—feeding on insects on foliage or on the ground); aerial insectivores (AER. INSECT.—feeding on flying insects); frugivores (FRUG.—feeding on fruit); and nectarivores (NECT.—feeding on flowers, nectar, and/or pollen).

For comparative purposes, we have categorized the trophic habits of the species comprising the fauna of Margarita and those of 39 species actually captured by Smith on the adjacent Venezuelan mainland. We have adopted Wilson's (1973) trophic values in most cases or only deviated slightly from his assessed value. In addition, our values are placed at the specific level rather than at the generic level.

A combined, two-dimensional niche matrix for the bat fauna of Margarita Island and the Venezuelan mainland is presented in figure 3. Several interesting points can be seen in this diagram.
Table 6. Importance values for the seven trophic roles of the chiropteran faunas of northeastern South America and the Antilles. The number in parentheses represents the number of species in each of the updated faunas; see text for citations.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Aruba (4)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>2.5</td>
<td>50.0</td>
<td>7.5</td>
<td>40.0</td>
</tr>
<tr>
<td>Curacao (8)</td>
<td>0.0</td>
<td>7.5</td>
<td>0.0</td>
<td>2.5</td>
<td>55.0</td>
<td>15.0</td>
<td>20.0</td>
</tr>
<tr>
<td>Bonaire (6)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.6</td>
<td>50.0</td>
<td>21.7</td>
<td>26.7</td>
</tr>
<tr>
<td>Margarita (16)</td>
<td>0.0</td>
<td>3.8</td>
<td>11.9</td>
<td>7.5</td>
<td>43.1</td>
<td>22.5</td>
<td>10.6</td>
</tr>
<tr>
<td>Venezuela (39)</td>
<td>3.8</td>
<td>1.5</td>
<td>7.4</td>
<td>12.6</td>
<td>40.8</td>
<td>26.9</td>
<td>6.9</td>
</tr>
<tr>
<td>Surinam (61)</td>
<td>3.7</td>
<td>1.0</td>
<td>3.2</td>
<td>10.8</td>
<td>48.0</td>
<td>23.8</td>
<td>9.5</td>
</tr>
<tr>
<td>Trinidad (63)</td>
<td>3.5</td>
<td>0.9</td>
<td>3.0</td>
<td>11.3</td>
<td>48.9</td>
<td>26.8</td>
<td>5.6</td>
</tr>
<tr>
<td>Tobago (17)</td>
<td>2.3</td>
<td>3.5</td>
<td>0.0</td>
<td>7.6</td>
<td>40.6</td>
<td>40.0</td>
<td>5.9</td>
</tr>
<tr>
<td>Grenada (12)</td>
<td>0.0</td>
<td>5.0</td>
<td>0.0</td>
<td>4.2</td>
<td>45.0</td>
<td>31.6</td>
<td>14.2</td>
</tr>
<tr>
<td>Dominica (12)</td>
<td>0.0</td>
<td>5.0</td>
<td>0.0</td>
<td>2.5</td>
<td>45.0</td>
<td>29.2</td>
<td>18.3</td>
</tr>
</tbody>
</table>

1 Based on actual captures.
2 Based on Jones and Phillips (1970).

The 39 mainland species occupy 29 of the 49 cells of the matrix and the 16 bats from Margarita occupy 20 of these cells. At this time it is difficult to comment on the "unoccupied" cells in both faunas. Future studies no doubt will reveal these to be either nonexistent or to be occupied by other terrestrial vertebrates. With respect to bat faunas in general, we doubt that the six cells in the upper left-hand corner (small-sized carnivores, piscivores, and sanguinovores) exist for bat species. This is based on problems of body size versus prey size and various physiological parameters. The unoccupied cells on the right-hand side of the matrix either reflect sampling biases or do not exist for bats in northeastern South America. With the exception of the sanguinovore cells, these unoccupied cells are indeed occupied by bats in other faunal regions.

McNab (1971:354) notes that carnivorous species of bats, other than fishing species, are generally absent from island faunas. He cites species of the genus *Phyllostomus* as the only carnivorous species on Margarita and Tobago. *Phyllostomus discolor* is the species occurring on Margarita, and to our knowledge is not a carnivorous species (Fleming et al., 1972:559; Goodwin and Greenhall, 1961:238). Therefore, the carnivorous cells of Margarita Island at this time appear to be unoccupied by bats. The apparent absence of carnivorous bats on islands is further illustrated in Table 6.

As can be seen in figure 3, the bulk of the bat faunas of Margarita and the adjacent mainland occupy the aerial insectivore-frugivore cells, 67.5 and 65.6 percent, respectively. In representative chiropteran faunas from northern South America and the Antilles (Table 6) these trophic roles are also predominant with the aerial insectivore complement comprising the larger of the two.

Koopman (1958:434) points out that the ecological differences among the various islands off the northern coast of South America are rather extreme. Aruba, Curacao, and Bonaire, the most xeric of these islands, have a disproportionately large aerial insectivore and nectarivore fauna compared to that of Trinidad, Tobago, and Grenada, which are the most mesic of the islands. Margarita Island, which has both xeric and mesic conditions, is intermediate, at least with regards to the nectarivorous trophic role. The foliage gleaning trophic role appears to be reduced on all islands except Trinidad. There is a marked disharmony (MacArthur and Wilson, 1967:175-78) in the bat faunas of Aruba, Curacao, Bonaire, Grenada, and Dominica, as compared with the mainland fauna, as illustrated by the absence of carnivores and sanguinovores (Table 6). The Margarita fauna is disharmonic with the mainland in lacking carnivorous species as is Tobago in lacking sanguinovorous species. It should be pointed out that Trinidad essentially represents an extension of the mainland chiropteran fauna with all trophic roles being represented.

In conclusion, the bats of Margarita Island comprise a depauperate chiropteran fauna which is most closely allied to the adjacent Venezuelan bat fauna. Ecological diversity and the size of the island seem to be the most relevant factors influencing the composition of the Margarita fauna. The proximity to the source area, at least with regards to the islands off the north coast.
of Venezuela, does not appear to be a major limiting factor for these respective faunas. We believe that the reduced size of the Margarita bat fauna is a result of repartitioning or expansion of the mainland niches on the island. In examining increasing population density on species-poor islands MacArthur et al. (1972) note that species utilized more space (that is, wider range of altitude, or habitats, or vertical foraging strata, or any combination of these; wider range of foraging techniques; or broader utilization of food items). Although we do not have sufficient data relating to population densities of the chiropteran species from Margarita Island, we suspect that they also utilize wider niche space which might account for the reduced bat fauna of this island.

LITERATURE CITED


Accepted for publication February 14, 1974.