

ECOLOGY, REPRODUCTIVE BIOLOGY, AND SYSTEMATICS OF *NEOPLATYMOPS MATTOGROSSENSIS* (CHIROPTERA: MOLOSSIDAE)

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ABSTRACT.—*Neoplatymops mattogrossensis*, the South American flat-headed bat, is a ground crevice-dwelling microhabitat specialist. Small holometabolous insects are the predominant prey that it consumed in the Caatingas of Northeast Brazil. Its external morphology results in aerodynamic attributes that are unlike those of many molossidids and that are similar to those of vespertilionid bats. The species is sexually dimorphic for most morphometric characters, but the magnitude of the dimorphism is slight, probably moderated by the constraints of crevice dwelling. Significant geographic variability characterizes the species, but is neither consistent nor of sufficient magnitude to designate recognizable subspecies. Low gene flow and a mosaic genetic structure probably characterize the species.

The biology of *Neoplatymops mattogrossensis*, like that of many other South American molossidids, is poorly known. The original description of the species by Cunha Viera (1942) and the revision of flat-headed bats by Peterson (1965) represent significant contributions to our knowledge of this species; however, these works are primarily taxonomic in nature. Sufficient distributional records have recently accumulated in the literature (Handley, 1976; Mares et al., 1981; Sazima and Taddei, 1976) to enable Koopman (1982) to approximate the distributional status of the species to include a broad range in the Amazon basin and the eastern Brazilian highlands. Additionally, Willig (1982) provided basic ecological information and showed that a population of *N. mattogrossensis* from the Caatingas of Northeast Brazil exhibited consistent sexual dimorphism. Statistically significant mean differences between males and females were determined for 13 of the 16 cranial characters examined; male sample means were larger than the sample means of females for all cranial characters. In a detailed morphometric analysis of the family Molossidae, Freeman (1981) suggested that *N. mattogrossensis* may be able to consume both hard- and soft-shelled prey because of the moderately thick jaws and well-elevated condyles above the toothrow that characterize the species. Freeman (1981) further suggested allocating this species to the genus *Molossops*; however, a consensus on this taxonomic question is not yet apparent. Nothing has been reported concerning the reproductive biology and feeding ecology of *N. mattogrossensis*. Moreover, geographic variation in the species has not been elucidated.

In this paper, I describe individual, geographic, and secondary-sexual variation in *N. mattogrossensis*. Its reproductive pattern in the Caatingas is defined, and ecological information, including microhabitat preference and diet composition, is presented.

MATERIALS AND METHODS

Field studies.—Research was restricted, for the most part, to the geographic center of the Brazilian Northeast (Fig. 1). The biogeography of the region has recently been discussed by Mares et al. (1985) and extensive descriptions of the study area appear in Mares et al. (1981) and Willig (1983, 1985). It is sufficient here to note that the Northeast is an extensive semiarid region characterized by spatial heterogeneity and climatic unpredictability. The Caatingas, the most extensive formation in the Northeast, contains xeric-adapted thorn-scrub vegetation that is characteristically deciduous during periods of water deficit. In addition, various species of Cactaceae and Euphorbiaceae are common, especially in low-lying areas. In contrast, the edaphic Cerrado formation of the Northeast is an open tree and shrub savanna woodland. The vegetation is sclerophyllous and semideciduous, with leaf loss occurring asynchronously, both within and among species (Willig, 1982, 1983). All major habitats of the Caatingas (lajeiros, serrotes, caatinga alta, caatinga baixa) in the vicinity of Exu, Pernambuco, were extensively netted on a monthly schedule from September, 1976 to May, 1978. Similarly, intensive fieldwork was conducted in edaphic Cerrado habitats on the windward side of the Chapada do Araripe in the adjacent municipality of Crato, Ceará, in the



FIG. 1.—*N. mattogrossensis* is known from three major collection localities (large solid dots) in South America: Northeast Brazil (Mares et al., 1981), southeastern Venezuela (Handley, 1976), and southwestern Guyana (Peterson, 1965). The type locality in Central Brazil (open circle) and a minor collection site where a juvenile specimen was obtained (small solid dot) complete the known distribution of the species.

Floresta Nacional Araripe-Apodí. Supplemental collections were made from culverts, caves, and rock piles in order to assess potential microhabitat utilization.

Age (juvenile or adult), sex, and reproductive condition (males: testes descended or not; females: pregnant, lactating, or nulliparous) were recorded for each individual collected. Specimens were either processed as standard museum skins and skulls, or preserved in formalin. Reproductive and alimentary tracts were preserved in FAA (formalin, ethyl alcohol, and acetic acid). Stomach contents were examined under a Zeiss stereoscopic microscope and identified to the lowest taxonomic level (usually familial) possible. The abundance of a dietary constituent was estimated as the percent of all non-empty stomachs that contained at least one item from a specified insect order. A variety of morphological characters that are related to the aerodynamic properties of wings were evaluated from recently sacrificed specimens. Surface area was estimated using a compensating polar planimeter to measure the area of wing and body tracings, as suggested by Farney and Fleharty (1969). Wing span was measured as the distance between wing tips. A variety of additional aerodynamic characteristics (Findley et al., 1972; Vaughn, 1966) were computed: (1) tip index (length of digit three/forearm length), (2) aspect ratio index (combined length of digit three and forearm/length of digit five), (3) aspect ratio ($\text{wing span}^2/2 \times \text{area}$), and (4) wing loading (weight/surface area). Half of the collection is deposited at the Carnegie Museum of Natural History, Section of Mammals (Pittsburgh, PA) and half is at the Museu de Zoologia da Universidade de São Paulo, Seção de Mamíferos (São Paulo, Estado de São Paulo, Brazil).

Museum studies.—Specimens of *N. mattogrossensis* were examined from all major collection localities (48 specimens from Northeast Brazil; 40 specimens from southwestern Guyana; 23 specimens from southeastern Venezuela; 4 specimens, including the holotype, from Central Brazil; Fig. 1). A series of 5 external and 15 cranial measurements were obtained for each specimen; a detailed description of the character suite is published elsewhere (Willig, 1983). External measurements were obtained from skin tags (if recorded);

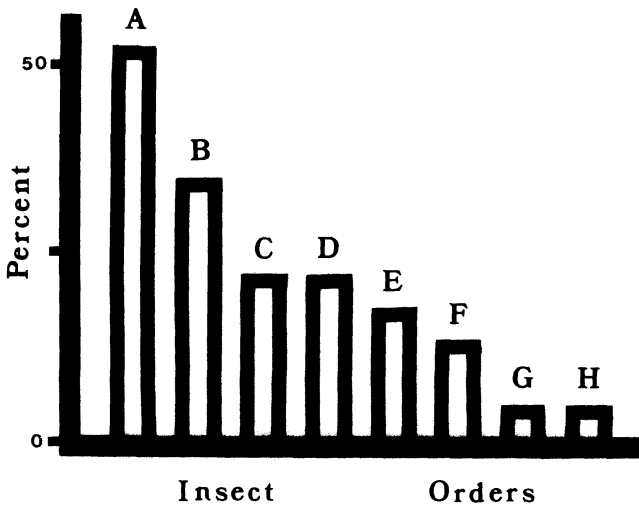


FIG. 2.—Diet composition of *N. mattogrossensis* from Northeast Brazil; percent indicates the number of non-empty stomachs containing at least one food item of the specified taxa divided by the total number of non-empty stomachs (23). (A = Coleoptera; B = Diptera; C = Hemiptera; D = Lepidoptera; E = Homoptera; F = Hymenoptera; G = Orthoptera; and H = Blattodea).

cranial measurements were obtained using Helios knife blade dial calipers and were recorded to the nearest 0.1 mm. Multivariable statistical analyses were performed using either SPSS (Nie et al., 1975) or BMDP (Dixon and Brown, 1979) package programs.

RESULTS AND DISCUSSION

Ecology.—The local distribution of *N. mattogrossensis* in the Brazilian Northeast was restricted to areas in the Caatingas associated with lajeiros or serrotes. Narrow horizontal spaces (1 to 3 cm) beneath the exfoliations of granitic boulders in lajeiros or serrotes represented preferred roosting sites, although narrow vertical cracks between boulders occasionally harbored individuals also. Roosting sites varied in height from less than 0.5 m to 5 m. Three or four individuals were sometimes found roosting under the same granitic exfoliation; nevertheless, the individuals were hyperdispersed and never formed close roosting associations. Two lizards, *Platynotus semitaeniatus* and *Phyllopezus pollicaris*, and a scorpion, *Rhopalurus roche*, were commonly found inhabiting the same microhabitat as *N. mattogrossensis*. *Peropteryx macrotis* inhabited the same outcrops as *N. mattogrossensis*; however, it roosted in openings inside rock piles, and thereby occupied a different microhabitat. *Molossops temminckii* is similar in size and shape to *N. mattogrossensis* (Freeman, 1981; Willig, 1983) and both species were frequently captured in the same nets. *Molossops temminckii* is, however, reported to roost in decaying logs (Allen, 1916). Records associated with specimens from other collection sites in Guyana and Venezuela similarly indicated that *N. mattogrossensis* was a ground-crevice microhabitat specialist. Adaptations to this peculiar roosting habit appear to be convergent with those of *Sauromys* and *Platymops* from Africa (Peterson, 1965.)

Alimentary tracts from 40 specimens were examined: 23 contained insect remains and 17 were empty. Because of the high degree of mastication achieved by molossids, food items were frequently only identifiable to the ordinal level. Nine insect orders composed the diet of *N. mattogrossensis* (Fig. 2). Coleopterans were most common, including species of Scarabaeidae, Hydrophilidae, or Dytiscidae. Within the Diptera, nematocerans were the most abundant food items, although members of the Calliphoridae also were present. Other taxa found in lesser quantities were Hemiptera (Lygaeidae, Coreidae, Pentatomidae); Lepidoptera; Homoptera

(Cicadellidae, and other species in the Fulgoroides); Hymenoptera (Formicidae); Diptera (Caliphoridae); Orthoptera; Blattodea (Blattidae). Almost all eaten insects were small (≤ 5 mm) holometabolous taxa. These data support Freeman's (1981) contention that *Neoplatymops* consumes both hard- and soft-shelled prey.

In general, molossids are considered to be rapid and enduring flyers—mammalian analogues of swifts and swallows (Vaughan, 1966, 1970). Because of their long narrow wings, members of the Molossidae frequently roost in elevated structures from which they can attain sufficient speed when taking-off to provide the necessary lift to overcome wingloading problems. Most data on aerodynamic attributes of the Molossidae are derived from studies on larger species (Findley et al., 1972; Lawlor, 1973; Pirlot, 1977; Vaughan, 1966, 1970), which clearly conform to the aforementioned trends. In contrast, Freeman (1981) examined almost every molossid species (approximately 80 taxa) and found that appreciable variation in wing shape characterized the family. Because of its small size (Freeman, 1981; Willig, 1983) and unusual roosting habits (Mares et al., 1981; Willig, 1983), *N. mattogrossensis* may exhibit aerodynamic characteristics that diverge from most other species in the family.

Four aerodynamic characters (surface area, wing span, aspect ratio, and wing loading) exhibited statistically indistinguishable mean values for males and females; males had larger tip indexes than females, and the difference was highly significant (Table 1). In comparison with other molossids, *N. mattogrossensis* had a remarkably lower average wing loading, lower average aspect ratio index and similar tip index (Table 1). In short, *N. mattogrossensis* has narrow-tipped wings like most molossids; is more like the Miniopterinae (2.47) and Lasiurini (2.33) of the family Vespertilionidae than the Molossidae (2.87) when considering aspect ratio index; and has wing loading both an order of magnitude less than published values for the Molossidae (0.20) and similar to those of the Vespertilionidae (0.07–0.11). This substantiates Freeman's (1981) suggestion that *N. mattogrossensis* is more maneuverable than most larger molossid species. According to the formula provided by Findley et al. (1972), this flat-headed bat may attain maximum flight speeds around 20.4 mph. Low flight speed, combined with the metabolic requirement of small bats to forage frequently to maintain extended energy demanding activities, probably result in small cruising ranges for *N. mattogrossensis*. However, its small size allows *N. mattogrossensis* to roost in areas inaccessible to other fast-flying insectivores, while additionally conferring flight adaptations consistent with ground roosting and maneuverability within the forest understory. *Molossops temminckii* is similar externally to *N. mattogrossensis* and probably is endowed with parallel flight characteristics (Freeman, 1981; Willig, 1983). Rather than an adaptation to ground-crevice dwelling, the aerodynamic properties of *M. temminckii* are hypothesized as adaptations to the reported ground log-dwelling habits of the species (Allen, 1916). An investigation of the aerodynamic characteristics of *Sauromys* and *Platymops* is planned in order to evaluate if other ground crevice-dwelling species of molossids exhibit similar flight adaptations. Interestingly, Smith and Starrett (1979) found *Sauromys* to be among the aerodynamically least specialized molossids. Moreover, *Tadarida (Mormopterus) loriae*, a small molossid whose forearm length is equal to that of *N. mattogrossensis*, was "misclassified" as a vespertilionid in their discriminant analysis of aerodynamic variables. Other generalized (= small?) species of *Tadarida* also were oriented close to the vespertilionid dispersion. Freeman (1981) indicated that all of the New World molossids that possess broad wing tips are small species. Hence, small or primitive species of the Molossidae may, in terms of flight, more closely resemble other insectivores than they do the larger species in the family.

Reproductive patterns.—Although samples of females were small ($n = 27$), the data were sufficiently consistent to suggest that *N. mattogrossensis* exhibited seasonal monestry (Fig. 3) in the Caatingas. Pregnant females appeared for the first time in the middle of the dry season (August). Parturition occurred during the transition from the dry to wet season (November to December) and lactation persisted during the wet season from December to April. Complete reproductive synchrony characterized the Caatingas population.

Individual variation.—Means, standard deviations, and coefficients of variation were used to

TABLE 1.—*Descriptive statistics* (n = sample size; \bar{Y} = sample mean; SE = standard error of the mean) for the aerodynamic characters of male and female *N. mattogrossensis* from northeastern Brazil. One-way ANOVAs (Model I) with replication evaluate the existence of mean differences between the sexes for each character; statistical significance is indicated by 'P' values ≤ 0.05 . Levene's Test indicated statistical homoscedasticity for all characters. Data for the Molossidae are obtained from Findley et al. (1972).

| Aerodynamic character | Molossidae | | | Male | | Females | | | ANOVA | | |
|-----------------------------------|------------|------|----|-----------|-------|---------|-----------|-------|-------|------------|--------------|
| | \bar{Y} | SE | n | \bar{Y} | SE | n | \bar{Y} | SE | MS | $F_{1,34}$ | Significance |
| Surface area (cm ²) | 167 | 32 | 13 | 34.2 | 0.96 | 23 | 32.6 | 0.61 | 19.80 | 2.02 | $P = 0.165$ |
| Wing span (cm) | — | — | 13 | 21.7 | 0.15 | 23 | 21.3 | 0.15 | 1.08 | 2.43 | $P = 0.128$ |
| Aspect ratio (—) | — | — | 13 | 7.0 | 0.20 | 23 | 7.0 | 0.15 | 0.06 | 0.11 | $P = 0.746$ |
| Aspect ratio index (—) | 2.87 | 0.03 | 13 | 2.54 | 0.05 | 23 | 2.6 | 0.03 | 0.24* | 0.11 | $P = 0.739$ |
| Tip index (—) | 1.87 | 0.04 | 13 | 1.9 | 0.01 | 23 | 1.8 | 0.01 | 0.03 | 10.70 | $P = 0.003$ |
| Wing loading (g/cm ²) | 0.20 | 0.02 | 13 | 9.3* | 0.30* | 23 | 8.6* | 0.30* | 0.04* | 1.59 | $P = 0.216$ |

* Values in table represent true value $\times 100$.

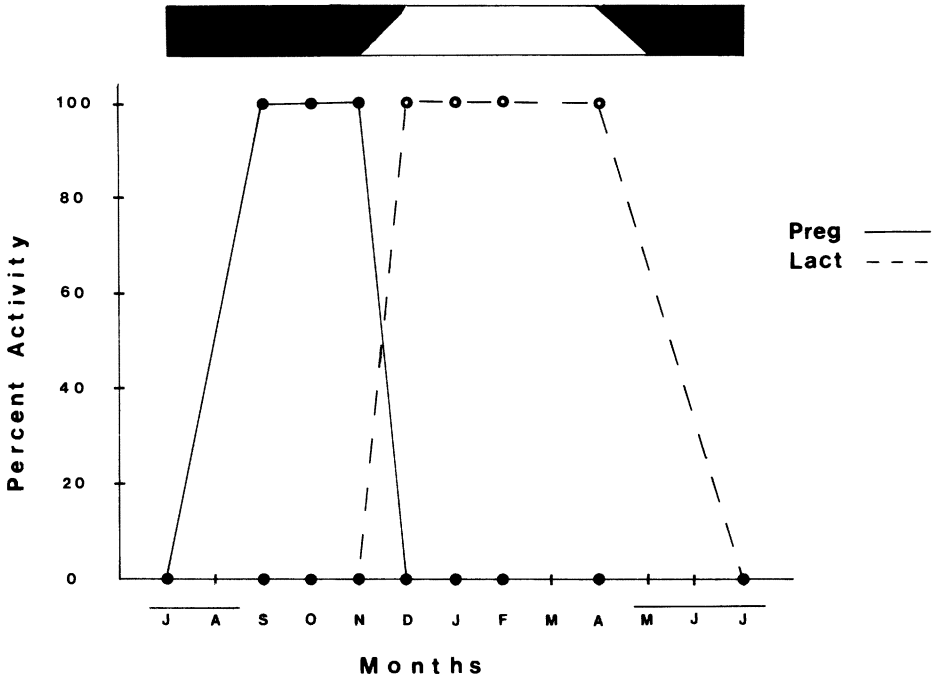


FIG. 3.—Reproductive activity in *N. mattogrossensis* from Northeast Brazil. The shaded portion of the bar at the top of the graph indicates periods of water deficit, whereas the open portion represents times of water surplus (see Streilein, 1982). The solid line above months indicates times when males appear reproductively active based upon testis size.

estimate individual variation for males and females from Northeast Brazil, southeastern Guyana, and southwestern Venezuela (Table 2). Variances were homoscedastic for one external and nine cranial characters (Table 3), including forearm length, greatest length of skull, condylobasal length, zygomatic breadth, postorbital constriction, breadth of the braincase, breadth across the upper molars, length of the maxillary toothrow, width of the widest molar, and greatest length of the mandibular toothrow, whereas the other 4 cranial and 4 external characters exhibited heteroscedastic variances (Table 3). Rostral breadth, height of braincase, length of the upper molariform toothrow, and width of the widest molar consistently exhibited high coefficients of variation, whereas greatest length of skull, condylobasal length, breadth of braincase, and breadth across the upper molars consistently exhibited low coefficients of variation. The amount of variability exhibited by populations of *N. mattogrossensis* from Northeast Brazil was usually less than that for the samples from Guyana or Venezuela. This was expected because the Brazilian sample estimates true intrademic variation, whereas the variation for both other locations is confounded by inter- and intrademic variation. Nonetheless, the amount of variability exhibited by samples of *N. mattogrossensis* is not appreciably different than that reported for other microchiropteran species (Williams and Findley, 1979; Willig, 1983). Moreover, the coefficients of variation were smaller than those considered characteristic of the Mammalia (Long, 1969).

Secondary sexual variation.—Two-way ANOVAs were used to identify morphometric characters displaying significant secondary-sexual variation. With the exception of length of the upper molariform toothrow, all cranial characters yielded significant *F*-ratios (Table 3), and the majority of those characters were significant at the $P < 0.001$ level. Total length was the only external character to exhibit significant dimorphism. Even in the cases where significant location

TABLE 2.—*Summary statistics for external and cranial characters (n, sample size; \bar{Y} , sample mean; s, standard deviation; CV, coefficient of variation) of Neoplatymops mattogrossensis from northeast Brazil, southwestern Guyana, and southeastern Venezuela.*

| Mensural character | Northeast Brazil | | | | Guyana | | | | Venezuela | | | |
|---|------------------|-----------|------|-------|--------|-----------|------|-------|-----------|-----------|------|-------|
| | n | \bar{Y} | s | CV | n | \bar{Y} | s | CV | n | \bar{Y} | s | CV |
| Males | | | | | | | | | | | | |
| Total length | 22 | 79.1 | 3.12 | 3.94 | 17 | 75.0 | 1.94 | 2.59 | 14 | 76.4 | 5.26 | 6.88 |
| Tail length | 22 | 25.5 | 2.84 | 11.11 | 17 | 21.9 | 1.39 | 6.35 | 14 | 23.5 | 3.53 | 15.02 |
| Hindfoot length | 22 | 5.3 | 0.55 | 10.38 | 20 | 5.7 | 1.16 | 20.35 | 14 | 7.4 | 0.84 | 11.35 |
| Forearm length | 22 | 30.0 | 0.90 | 3.00 | 20 | 29.6 | 0.75 | 2.53 | 14 | 29.1 | 1.44 | 4.95 |
| Weight | 22 | 6.1 | 0.63 | 10.33 | 0 | — | — | — | 3 | 6.2 | 2.27 | 36.61 |
| Greatest length of skull | 19 | 14.13 | 0.36 | 2.55 | 16 | 14.24 | 0.45 | 3.16 | 15 | 14.46 | 0.31 | 2.14 |
| Condylbasal length | 19 | 13.92 | 0.33 | 2.37 | 16 | 13.94 | 0.34 | 2.44 | 15 | 14.15 | 0.25 | 1.77 |
| Zygomatic breadth | 15 | 9.76 | 0.25 | 2.56 | 5 | 9.96 | 0.38 | 3.82 | 2 | 10.05 | — | — |
| Postorbital constriction | 20 | 3.37 | 0.09 | 2.67 | 20 | 3.43 | 0.12 | 3.50 | 15 | 3.58 | 0.15 | 4.19 |
| Mastoid breadth | 14 | 9.64 | 0.40 | 4.15 | 18 | 9.61 | 0.40 | 4.16 | 10 | 10.05 | 0.19 | 1.89 |
| Breadth of braincase | 19 | 7.09 | 0.28 | 3.95 | 20 | 6.94 | 0.16 | 2.31 | 15 | 6.91 | 0.15 | 2.17 |
| Rostral breadth | 20 | 4.30 | 0.17 | 3.95 | 20 | 4.26 | 0.19 | 4.46 | 16 | 4.26 | 0.34 | 7.98 |
| Height of braincase | 18 | 6.04 | 0.23 | 3.81 | 18 | 6.10 | 0.21 | 3.44 | 15 | 6.07 | 0.50 | 8.24 |
| Breadth across the upper molars | 19 | 6.55 | 0.13 | 1.98 | 20 | 6.73 | 0.17 | 2.53 | 16 | 6.74 | 0.15 | 2.23 |
| Breadth across the upper canines | 19 | 3.93 | 0.13 | 3.31 | 20 | 4.05 | 0.19 | 4.69 | 16 | 4.04 | 0.14 | 3.47 |
| Length of the maxillary toothrow | 19 | 5.57 | 0.15 | 2.69 | 20 | 5.75 | 0.18 | 3.13 | 16 | 5.81 | 0.14 | 2.41 |
| Length of the upper molariform toothrow | 19 | 4.26 | 0.13 | 3.05 | 20 | 4.51 | 0.22 | 4.88 | 16 | 4.40 | 0.27 | 6.14 |
| Width of the widest molar | 19 | 1.99 | 0.08 | 4.02 | 20 | 1.93 | 0.10 | 5.18 | 16 | 1.99 | 0.13 | 6.53 |
| Greatest length of the mandible | 20 | 10.60 | 0.28 | 2.64 | 20 | 10.94 | 0.38 | 3.47 | 15 | 10.80 | 0.29 | 2.69 |
| Length of the mandibular toothrow | 19 | 5.99 | 0.10 | 1.67 | 20 | 6.13 | 0.16 | 2.61 | 16 | 6.16 | 0.20 | 3.25 |
| Females | | | | | | | | | | | | |
| Total length | 26 | 76.8 | 4.49 | 5.85 | 10 | 73.3 | 2.95 | 3.16 | 7 | 74.7 | 0.95 | 1.27 |
| Tail length | 26 | 25.7 | 2.50 | 9.73 | 10 | 22.3 | 1.64 | 7.35 | 7 | 23.9 | 1.07 | 4.48 |
| Hindfoot length | 26 | 5.0 | 0.45 | 9.00 | 19 | 6.5 | 1.43 | 22.00 | 7 | 7.9 | 0.38 | 4.81 |
| Forearm length | 26 | 30.2 | 1.03 | 3.41 | 20 | 28.9 | 0.79 | 2.73 | 3 | 29.3 | 0.58 | 1.98 |
| Weight | 26 | 5.4 | 1.02 | 18.89 | 0 | — | — | — | 2 | 7.1 | 0.21 | 2.96 |
| Greatest length of skull | 23 | 13.46 | 0.34 | 2.53 | 20 | 13.58 | 0.27 | 1.99 | 7 | 13.90 | 0.22 | 1.58 |
| Condylbasal length | 23 | 13.24 | 0.30 | 2.27 | 19 | 13.28 | 0.28 | 2.11 | 7 | 13.61 | 0.23 | 1.69 |
| Zygomatic breadth | 12 | 9.27 | 0.27 | 2.91 | 2 | 9.15 | — | — | 2 | 9.45 | — | — |
| Postorbital constriction | 26 | 3.29 | 0.08 | 2.43 | 20 | 3.44 | 0.12 | 3.49 | 7 | 3.37 | 0.14 | 4.15 |
| Mastoid breadth | 14 | 9.06 | 0.22 | 2.43 | 20 | 8.91 | 0.23 | 2.58 | 7 | 9.33 | 0.24 | 2.57 |
| Breadth of braincase | 23 | 6.81 | 0.17 | 2.50 | 20 | 6.85 | 0.17 | 2.48 | 7 | 6.69 | 0.12 | 1.79 |
| Rostral breadth | 26 | 3.87 | 0.22 | 5.68 | 20 | 4.09 | 0.16 | 3.91 | 7 | 4.23 | 0.14 | 3.31 |
| Height of braincase | 23 | 5.94 | 0.24 | 4.04 | 20 | 5.87 | 0.21 | 3.58 | 7 | 5.58 | 0.57 | 10.22 |
| Breadth across the upper molars | 26 | 6.40 | 0.15 | 2.34 | 20 | 6.44 | 0.16 | 2.48 | 7 | 6.61 | 0.15 | 2.27 |
| Breadth across the upper canines | 25 | 3.56 | 0.15 | 4.21 | 20 | 3.69 | 0.13 | 3.52 | 7 | 3.74 | 0.16 | 4.28 |
| Length of the maxillary toothrow | 26 | 5.34 | 0.13 | 2.43 | 20 | 5.39 | 0.15 | 2.78 | 7 | 5.44 | 0.17 | 3.13 |
| Length of the upper molariform toothrow | 26 | 4.20 | 0.16 | 3.81 | 20 | 4.22 | 0.24 | 5.69 | 7 | 4.33 | 0.30 | 6.93 |

TABLE 2.—Continued.

| Mensural character | Northeast Brazil | | | | Guyana | | | | Venezuela | | | |
|-----------------------------------|------------------|-----------|------|------|--------|-----------|------|------|-----------|-----------|------|------|
| | n | \bar{Y} | s | CV | n | \bar{Y} | s | CV | n | \bar{Y} | s | CV |
| Width of the widest molar | 26 | 1.96 | 0.08 | 4.08 | 20 | 1.89 | 0.11 | 5.82 | 7 | 1.96 | 0.10 | 5.10 |
| Greatest length of the mandible | 23 | 10.25 | 0.29 | 2.83 | 20 | 10.36 | 0.33 | 3.19 | 7 | 10.66 | 0.33 | 3.10 |
| Length of the mandibular toothrow | 25 | 5.69 | 0.13 | 2.28 | 20 | 5.80 | 0.20 | 3.45 | 7 | 5.94 | 0.16 | 2.69 |

by sex interactions were detected in the ANOVA (postorbital constriction, rostral breadth, length of the upper molariform toothrow, greatest length of the mandible), the direction of the dimorphism was consistent, with males larger than females. The significant interactions can be most easily considered reflections of varying degrees of dimorphism in different populations. Regardless of geographic location, *N. mattogrossensis* is dimorphic for size. Nonetheless, the magnitude of dimorphism, estimated by the mean ratios of males to females, is small, varying from approximately 1.00 to 1.11 in each population. This reduced dimorphism for *N. mattogrossensis* is quite similar in magnitude to the observed values for neotropical vespertilionid bats in which females are larger than males (Myers, 1978; Ralls, 1976; Williams and Findley, 1976). The selective agents affecting the low magnitude of dimorphism in *N. mattogrossensis* are, however, different than those for the Vespertilionidae. Sexual selection (Darwin, 1859; Trivers, 1972), in which males compete for access to females, is the most parsimonious explanation for size dimorphism in *N. mattogrossensis* (see Willig, 1983 for a critique of the Differential Niche Hypothesis). That the size differences are small (unlike many molossid species) is probably affected by the roosting habits of the species. It should not be surprising that roost environment plays such an important role in moderating sexual selection (Kunz, 1982), because these bats spend well over half of their life beneath granitic exfoliations. The constraints of occupying narrow crevices may well limit the amount of variability realized in this species. Indeed, height of braincase, probably the most critical adaptation to crevice dwelling, is the only cranial character that does not exhibit significant geographic variation.

Geographic variation.—Two-way ANOVAs were used as preliminary indicators of geographic variation in *N. mattogrossensis* (Table 3). All but one character, height of braincase, exhibited statistical significance. Multiple comparison tests, although less powerful than ANOVA, are designed to facilitate pair-wise comparisons and were used to identify statistically distinguishable geographic localities. The Games and Howell Method (Sokal and Rohlf, 1981) was used to compare particular means when the variances were judged unequal based upon the results of Levene's Test of variance homogeneity (Dixon and Brown, 1979). When variances were homoscedastic, the Tukey-Kramer Method for unequal sample sizes (Sokal and Rohlf, 1981) was used to evaluate mean differences between locations. All multiple comparisons of geographic variation were analyzed separately for males and females because sexual dimorphism is consistently significant in this molossid (Willig, 1983; Table 3). Multiple comparisons were possible for all mensural characters except weight, zygomatic breadth, and height of the braincase. The Brazilian sample was usually distinguishable from at least one of the other two samples. Samples from Guyana and Venezuela, on the other hand, were usually indistinguishable from each other (Table 3).

Multivariate statistical analyses were performed on males and females separately, using a restricted cranial character suite. Zygomatic breadth and mastoid breadth were excluded from consideration because they involved broken structures for an appreciable proportion of the individuals and would appear as missing values in the statistical analyses.

Principal Component Analysis (PCA) was performed using BMD-P4M (Dixon and Brown, 1979). Eight factors were extracted for the males ($n = 49$) before at least 90% of the total variance was accounted for in the analysis; 9 factors were required to meet this same criterion

TABLE 3.—Two-way Analysis of Variance with replication (Model I) for external and cranial characters. When variances are homoscedastic (Levine's Test), the Tukey-Kramer multiple comparison method for unequal sample sizes is used to compare geographic localities (B = Brazil, G = Guyana, V = Venezuela). The Games and Howell Method is used to compare locations when variances are heteroscedastic. Locations are statistically indistinguishable if they share a common numeric superscript.

| Mensural character | Analysis of variance | | | | Multiple comparisons | | | | | |
|---|----------------------|-----|--------------|---------------|----------------------|------------------|----------------|----------------|------------------|----------------|
| | Location | Sex | Inter-action | Levine's test | Males | | | Females | | |
| | | | | | | | | | | |
| Total length | *** | * | NS | ** | G ¹ | V ^{1,2} | B ² | G ¹ | V ¹ | B ¹ |
| Tail length | *** | NS | NS | ** | G ¹ | V ^{1,2} | B ² | G ¹ | V ^{1,2} | B ² |
| Hindfoot length | *** | NS | * | *** | V ¹ | G ^{1,2} | B ² | G ¹ | V ^{1,2} | B ² |
| Forearm length | *** | NS | NS | NS | V ¹ | G ¹ | B ¹ | G ¹ | V ^{1,2} | B ² |
| Weight | — | — | — | *** | — | — | — | — | — | — |
| Greatest length of skull | *** | *** | NS | NS | B ¹ | G ¹ | V ¹ | B ¹ | G ^{1,2} | V ² |
| Condylbasal length | ** | *** | NS | NS | B ¹ | G ¹ | V ¹ | B ¹ | G ^{1,2} | V ² |
| Zygomatic breadth | — | — | — | NS | — | — | — | — | — | — |
| Postorbital constriction | *** | *** | ** | NS | B ¹ | G ¹ | V ² | B ¹ | V ^{1,2} | G ² |
| Mastoid breadth | *** | *** | NS | ** | G ¹ | B ¹ | V ¹ | G ¹ | B ^{1,2} | V ² |
| Breadth of braincase | * | *** | NS | NS | V ¹ | G ² | B ³ | V ¹ | B ¹ | G ¹ |
| Rostral breadth | ** | *** | *** | ** | G ¹ | V ¹ | B ¹ | B ¹ | G ² | V ³ |
| Height of braincase | NS | * | NS | *** | — | — | — | — | — | — |
| Breadth across the upper molars | *** | *** | NS | NS | B ¹ | G ² | V ² | B ¹ | G ^{1,2} | V ² |
| Breadth across the upper canines | *** | *** | NS | NS | B ¹ | V ¹ | G ¹ | B ¹ | G ¹ | V ¹ |
| Length of the maxillary toothrow | *** | ** | NS | NS | B ¹ | G ² | V ² | B ¹ | G ¹ | V ¹ |
| Length of the upper molariform toothrow | ** | NS | * | *** | B ¹ | V ^{1,2} | G ² | B ¹ | G ¹ | V ¹ |
| Width of the widest molar | ** | *** | NS | NS | V ¹ | B ¹ | G ¹ | V ¹ | B ¹ | G ¹ |
| Greatest length of the mandible | *** | *** | * | NS | B ¹ | V ^{1,2} | G ² | B ¹ | G ^{1,2} | V ² |
| Length of the mandibular toothrow | *** | *** | NS | NS | B ¹ | G ¹ | V ¹ | B ¹ | G ^{1,2} | V ² |

* 0.05 \geq P > 0.01, significant.

** 0.01 \geq P > 0.001, very significant.

*** P \leq 0.001, highly significant.

NS P > 0.05, not significant.

for females ($n = 46$). The percent of the total variation accounted for among females by each of the first 9 factors, in order, was: 34.4, 11.8, 11.5, 8.5, 7.0, 5.9, 5.5, 4.8, and 3.9. Similarly, for males, the percent of total variation accounted for by each succeeding factor was: 37.5, 12.3, 9.6, 8.7, 7.8, 5.8, 4.8, and 3.8. Most of the characters had low multiple correlations with all of the other characters, and thus each exhibited appreciable unique variability. Thus, for *N. matogrossensis*, PCA was not an effective data reduction system. Moreover, the geographic designations did not appear as natural groups when all paired combinations of the first four factors were considered. Cluster Analysis (CA) of individuals (BMD-P2M) for each sex also produced equivocal results. Again, natural clusters representing each of the three geographic localities were not obtained.

Finally, Discriminant Function Analysis (DFA) was executed using SPSS Program DISCRIMINANT. The classification results for females properly identified 87% of the individuals into their correct sample locations (90% success for Brazil; 85% for Guyana; and 86% for Venezuela). Two significant canonical discriminant functions accounted for 100% of the inter-individual variation (Function I, 78%; Function II, 22%). Ninety-two percent of the males were correctly classified into the proper geographic locality (94% for Brazil; 89% for Guyana; and 93% for Venezuela). Again, 2 significant canonical discriminant factors accounted for all of the inter-individual variation (63% for Factor I, 37% for Factor II). The loadings of mensural characters on factors I and II for both males and females appear on Table 4. These results are not contradictory to those for PCA and CA. The large character suite relative to the within locality sample sizes potentially results in DFA describing sample differences rather than population differences. Nonetheless, if the populations from the three localities were distinct taxa, then the results of the DFA would be the best available indicators of the mensural characters distinguishing the taxa.

TABLE 4.—Rotated (VMAX) standardized discriminant function coefficients for DFA on male and female *N. mattogrossensis*. Mensural characters with high loadings on a particular factor are indicated by an asterisk; characters not entered into the DFA algorithm are indicated by a dash (—).

| Mensural character | Male | | Female | |
|---|----------|-----------|----------|-----------|
| | Factor I | Factor II | Factor I | Factor II |
| Greatest length of skull | — | — | — | — |
| Condylobasal length | -0.171 | 1.099* | — | — |
| Postorbital constriction | 1.205* | 0.114 | 0.345 | 0.950* |
| Breadth of braincase | -0.812* | -0.052 | -0.745* | 0.111 |
| Rostral breadth | — | — | 0.769* | 0.163 |
| Height of braincase | — | — | -0.645* | 0.091 |
| Breadth across the upper molars | 0.291 | -0.358* | 0.418 | -0.689* |
| Breadth across the upper canines | -0.708 | -0.106 | — | — |
| Length of the maxillary tooththrow | 0.549* | -0.544 | — | — |
| Length of the upper molariform tooththrow | -0.530* | -0.357 | — | — |
| Width of the widest molar | 0.326 | 0.750* | 0.173 | -0.427* |
| Greatest length of the mandible | 0.080 | -0.813* | 0.363* | 0.267 |
| Length of the mandibular tooththrow | 0.473* | 0.181 | 0.029 | 0.732* |

Although the ANOVAs and Multiple Comparison Tests do indicate some geographic differentiation in *N. mattogrossensis*, the results do not argue for the recognition of subspecific status for any population. However, chromosomal or genic divergence among these populations may have occurred that is not detectable by quantitative analysis of morphology. The failure of both PCA and CA to identify cohesive groups of individuals from the same location is the strongest argument against subspecific recognition. This result was surprising because the low vagility (for a molossid) and high degree of microhabitat specialization exhibited by *N. mattogrossensis* should contribute to the genetic isolation of these distant populations. Perhaps isolation and genetic drift do occur for particular demes, but the mosaic distribution of suitable habitat may also result in a mosaic genetic structure for the species, where random differences accumulate within isolates that preclude the evolution of recognizable forms within particular geographic areas. In addition, the constraints of ground crevice roosting may effectively minimize the degree of variation realized in any particular isolate, thereby reducing the extent or rate of divergence.

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