MISCELLANEOUS PUBLICATIONS MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 165

Systematics and Zoogeography of the Bats of the Chaco Boreal

by

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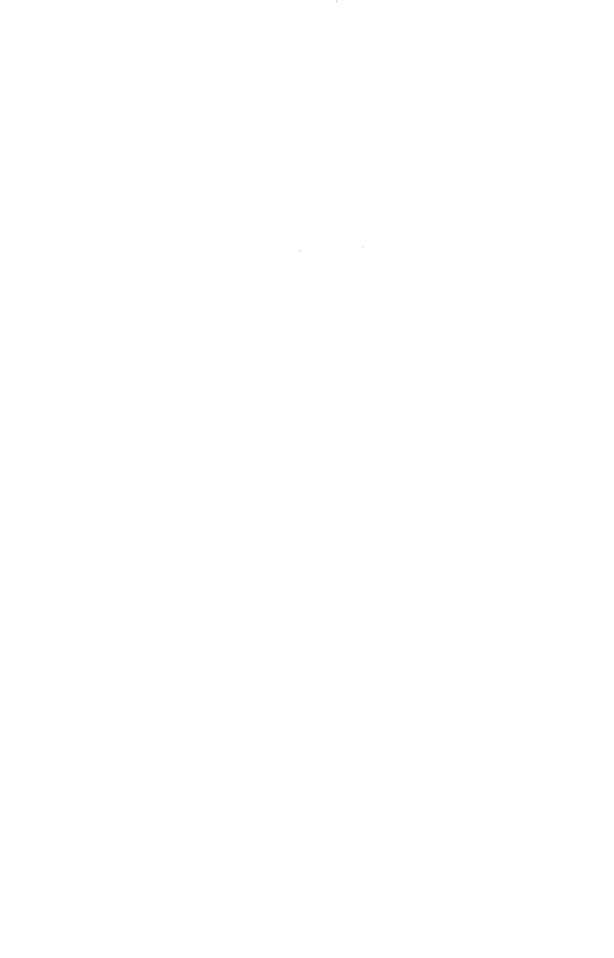
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INTRODUCTION

The Chaco, a vast alluvial plain lying east of the Andes in central South America, has been the focus of several recent analyses of the distribution of terrestrial vertebrates (e.g., Short, 1975; Gallardo, 1979; Fitzpatrick, 1980; Myers, in press). Little, however, has been published about the chiropteran fauna. In part this has been due to the lack of collecting in the Chaco, and in part to confusion over the systematics of some groups of bats.

In this paper we provide an annotated list of the Chiroptera of the northern Chaco (Chaco Boreal), and a discussion of the systematics, zoo-geography, and geographic variation of populations within and surrounding this region. We document a startling concordance in the patterns of geographic variation of body size, and we provide information on general ecological attributes and reproductive patterns for some species.

THE CHACOAN HABITAT

The Chaco is an extensive plain formed by material eroded from the Andes. It rises gradually to the west, with most elevations below 500m. The Chaco Boreal is defined by Gorham (1973a) to include the land north of the Río Bermejo, west of the Río Paraguay, east of the Andean foothills, and south of the Serranías of San José and Santiago (Fig. 1). This paper focuses on the Paraguayan and Bolivian Chaco (north of the Río Pilcomayo).

Descriptions of Chacoan habitats can be found in Grubb (1911), Wetmore (1926), Laubmann (1930), Kerr (1950), Lüders (1961), Morello and Adamoli (1968 and 1974), Villa-R, B. and M. Villa Cornejo (1969), Cabrera (1970), Ragonese and Castiglioni (1970), Adamoli et al. (1972), Gorham (1973b), Eiten (1974), Short (1975), Bucher (1980), Mares et al. (1981a) and Myers (in press). The geology is discussed by Eckle (1959). Briefly, the Chaco (including both the northern Chaco Boreal and the southern Chaco Austral) can be divided into eastern, central, and western parts. The Eastern Chaco (Chaco Oriental) of Bucher, 1980; Chaco de esteros, cañadas, y selvas de ribera of Morello and Adamoli (1968), is a land of low marshes and palm savannas (pantanal of Short, 1975), with dense riparian forests and occasional "islands" of thorny forest wherever soils are slightly elevated above the savanna. The savannas are characterized by stands of palms (Copernicia alba). Areas of saline soils are also common and support extensive stands of thorny shrubs and trees, among which legumes (especially Prosopis) are conspicuous. Annual rainfall averages 900-1300mm, but with considerable variation from year to year in amount and timing (Fariña Sanchez, 1973; Bucher, 1980). Drainage is poor and extensive flooding often results. The winter dry season lasts about two months (July-August), and during this period large areas of grassland are burned by ranchers. The Central Chaco (Chaco Central of Bucher, 1980; Chaco de parques y sabanas secos of Morello and Adamoli, 1968) is an ecotonal area, differing from the eastern Chaco primarily in its lesser rainfall (700900mm annually), more extensive dry season (4–5 months, May–September), and more xerophilic vegetation (Fariña Sanchez, 1973; Short, 1975; Bucher, 1980). In this region palm savannas and marshlands give way to thornforest (algarrobo-quebracho-Palo Santo woodlands of Short, 1975). The Western Chaco (*Chaco occidental* of Bucher, 1980; *Chaco leñoso* of Morello and Adamoli, 1968) has less rainfall (450–700mm), the vegetation tends to be scrubbier and thornier, and in some areas low rolling hills, natural grasslands, and even sand dunes break the monotony of the plains.

METHODS

This analysis is based on extensive, recent field work, primarily in Paraguay, where approximately 2500 bats representing 41 species were collected. Most bats were captured in mist nets set over small lakes, streams, or artificial ponds in thorn forest or thorn scrub. Nets set across trails or at the edge of forest were also sometimes productive. Specimens were also captured in roosts or by shooting. Because water is in short supply during part of the year, use of mist nets placed over ponds or streams often produced large numbers of bats, including high-flying and rarely collected species of molossids and vespertilionids. Detailed habitat information is given in the species accounts that follow only when the site or method of capture was in some way unusual or differed from the general descriptions given above for each region of the Chaco.

Our collecting sites tended to be concentrated near the Trans Chaco Highway, which runs from Villa Hayes, on the Río Paraguay, to Fortín Garay, on the Bolivian border. This highway crosses the three major zones of the Chaco described above, and we believe it provides an excellent transect of Chacoan habitats. Ponds created to drain the road surface extend far into the central Chaco and often provide the only free-standing water available to bats for many miles; nets set across their surfaces were highly productive. In fact, it is possible that these ponds, and ponds dug by cattle ranchers to provide water for livestock, have allowed the recent invasion of arid habitats by some species of bats.

The following measurements were taken with dial calipers to the nearest 0.1mm, and are given for each species. Only adults were measured; wing measurements were taken only from dried skins:

- FA Length of forearm (measured with wing folded, includes carpals).
- MC3 Length of third metacarpal (includes carpals).
- GLS Greatest length of skull, from anterior face of incisors to posterior limit of skull.
- CB Condylobasal length (from anterior surface of base of incisors to posterior surface of occipital condyles).
- ZB Greatest breadth across zygoma.
- IOC Least interorbital constriction.
- MW Greatest breadth across mastoid processes.
- MM Breadth of palate and molars, measured from the labial surface of the left maxillary toothrow to the labial surface of the right.
- CC Breadth across the labial cingula of the canines.
- Max Length of maxillary toothrow, from posterior end of last upper molar to anterior face of canine.
- Total Total length.
- Tail Length of tail.
- HF Length of hind foot from heel to end of claw.
- Ear Length of pinna from bottom of notch to tip of pinna.

The last four measurements were taken by collectors in the field and often display considerable variation due to differences in technique between collectors. Therefore, we include in our analyses only those measurements taken by ourselves or under our supervision.

The average skin and skull measurements presented under each species are calculated based on specimens from the Chaco Boreal only. No measurements are given for species reported in the literature but not examined by us, although the locality records are given. Most species for which adequate samples are available show sexual dimorphism in one or more dimension; therefore, sexes are usually described separately. Analysis of variance is used to test for sexual and geographic variation. Variation is reported as statistically significant when the probability of equality of population means is less than 0.05.

The section entitled "Literature Records" includes citations only for localities in the Chaco. "Specimens Examined" includes records of all specimens examined, regardless of locality. Field notes and dissections of animals preserved in fluid have provided some information concerning reproduction, which is summarized in Table 13. Finally, a field key to the bats of the Chaco Boreal, based primarily on characters discernable in intact animals, is presented in the appendix. The key includes a number of species so far unknown in the Chaco, but known to occur in neighboring areas, especially eastern Paraguay. Because of the proximity of the regions we believe that most eastern Paraguayan species will ultimately be taken, either as residents or transients, in the eastern Chaco.

Specimens were examined from the following collections: American Museum of Natural History (AMNH), University of Connecticut, Storrs (CONN), Field Museum of Natural History (FMNH), Louisiana State University Museum of Zoology (LSUMZ), Philadelphia Academy of Natural Sciences (PANS), University of California Museum of Vertebrate Zoology (MVZ), University of Michigan Museum of Zoology (UMMZ), and U.S. National Museum of Natural History (USNM).

Capitalized color terms are from Ridgway (1912).

COLLECTING LOCALITIES

The locality numbers in Figure 1 correspond to the numbers given below. Localities too close to one another to distinguish easily on the map share a number and appear as a single point.

PARAGUAYAN CHACO

- 1. Presidente Hayes: Chaco-í.
- 2. Presidente Hayes: Villa Hayes.
- 3. Presidente Hayes: 24km WNW Villa Hayes.
- 4. Presidente Hayes: Puerto Cooper.
- 5. Presidente Hayes: Puerto Piñasco.
- 6. Alto Paraguay: Puerto Casado.
- 7. Alto Paraguay: Puerto Sastre.
- 8. Alto Paraguay: Fuerte Olimpo.
- 9. Presidente Hayes: 107km by rd NW Villa Hayes.
- Presidente Hayes: Waikthlatingmangyalwa; 2km SE of Misión Inglesa.
- 11. Presidente Hayes: Monte Lindo.

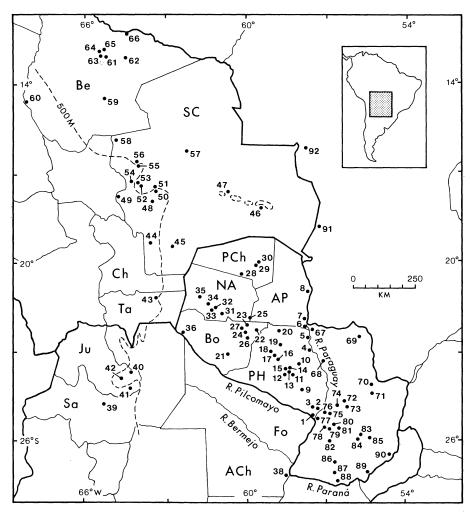


FIG. 1. Map of collecting localities in the Chaco Boreal and surrounding areas. See text for explanation. ACh = Prov. Chaco (Argentina); AP = Dept. Alto Paraguay (Paraguay); Be = Dept. Beni (Bolivia); Bo = Dept. Boquerón (Paraguay); Ch = Dept. Chuquisaca (Bolivia); Fo = Prov. Formosa (Argentina); Ju = Prov. Jujuy (Argentina); NA = Dept. Nueva Asunción (Paraguay); PCh = Dept. Chaco (Paraguay); PH = Dept. Presidente Hayes (Paraguay); Sa = Prov. Salta (Argentina); SC = Dept. Santa Cruz (Bolivia); Ta = Dept. Tarija (Bolivia).

- 12. Presidente Hayes: Retiro Mandeyú, 20km SW Km 205, Trans Chaco Hwy.
- 13. Presidente Hayes: 211km by rd NW Villa Hayes; 213km by rd NW Villa Hayes; 220km by rd NW Villa Hayes; 226km by rd NW Villa Hayes.
- 14. Presidente Hayes: 230km by rd NW Villa Hayes.
- 15. Presidente Hayes: Fortín Orihuela; Pozo Colorado.
- 16. Presidente Hayes: Rincón Charrúa, 275km by rd NW Villa Hayes.

- 17. Presidente Hayes: 300km by rd NW Villa Hayes; vic. line camp, Juan de Zalazar; Juan de Zalazar, 2km N Río Verde; 295km by rd NW Villa Hayes; 290km by rd NW Villa Hayes; 3km S Line Camp, Juan de Zalazar.
- 18. Presidente Hayes: 8km NE Juan de Zalazar; Juan de Zalazar, approx. 4km E Trans Chaco Hwy. bridge; 320km by rd NW Villa Hayes [= Juan de Zalazar].
- 19. Presidente Hayes: 50km E of Km 320, Trans Chaco Hwy.
- 20. Presidente Hayes: 80km W Puerto Piñasco; 85km E Loma Plata.
- 21. Boquerón: Estancia Pirazal, 80km SW Neuland.
- 22. Boquerón: 35km by rd E Filadelfia.
- 23. Boquerón: Estancia Iparoma, 19km N Filadelfia.
- 24. Boquerón: Orloff; 10km by rd S Filadelfia.
- 25. Nueva Asunción: 49.6km by rd N Filadelfia.
- 26. Boquerón: 417km by rd NW Villa Hayes; 419km by rd NW Villa Hayes; 420km by rd NW Villa Hayes.
- 27. Nueva Asunción: 460km by rd NW Villa Hayes.
- 28. Chaco: 50km WNW Fortín Madrejón.
- 29. Chaco: 67km by rd N Fortín Madrejón; 65km by rd N Fortín Madrejón.
- 30. Chaco: 170km W Bahía Negra, Agua Dulce.
- 31. Nueva Asunción: Teniente Ochoa.
- 32. Nueva Asunción: 2.5km S of Km 579, Trans Chaco Hwy. (COPAGRO); Trans Chaco Hwy., Km 589.
- 33. Nueva Asunción: 19km by rd WSW Km 588, Trans Chaco Hwy.
- 34. Nueva Asunción: 3km SW Km 620, Trans Chaco Hwy.
- 35. Nueva Asunción: Teniente Enciso.
- 36. Boquerón: Fortín Guachalla, Río Pilcomayo [= Guachalla]; Pedro P. Peña.

ARGENTINA

- 38. Chaco: Barranqueras.
- 39. Salta: Cerillos.
- 40. Jujuy: Yuto.
- 41. Jujuy: Santa Bárbara.
- 42. Jujuy: Ledesima.

BOLIVIA

- 43. Tarija: Caiza, or Villa Ingavi, 600m [= Caixa or Cajixa]; 8km S and 10km E Villa Montés, E bank of Río Pilcomayo.
- 44. Santa Cruz: 10km E Gutierrez, Laguna Caucaya.
- 45. Santa Cruz: Tamachindi, near Izozog.
- 46. Santa Cruz: Santiago.
- 47. Santa Cruz: San José de Chiquitos.
- 48. Santa Cruz: Ing. Mora; 10km by rd E Ing. Mora; 15km E Ing. Mora, 600m; Lostra, Ibos, 2km N, 7km E Ing. Mora.

- 49. Santa Cruz: 25km by rd W Comarapa, 2800m.
- 50. Santa Cruz: Santa Cruz, 416m.
- 51. Santa Cruz: Warnes, 350m.
- 52. Santa Cruz: Río Surutu, 400m.
- 53. Santa Cruz: Buenavista, 400m.
- 54. Santa Cruz: 25km W Buenavista, W bank of Río Yapacani.
- 55. Santa Cruz: 7km N Santa Rosa, Provincia Sara, 800m.
- 56. Santa Cruz: Río Palometilla, 400m.
- 57. Santa Cruz: Concepción.
- 58. Santa Cruz: Río Yapacani, 600m.
- 59. Beni: Trinidad.
- 60. Beni: Rurrenebaque.
- 61. Beni: San Ramón.
- 62. Beni: Magdalena.
- 63. Beni: Estancia Yutiole.
- 64. Beni: Azunta.
- 65. Beni: San Joaquín.
- 66. Beni: Itenez.

EASTERN PARAGUAY

- 67. Concepción: 24km by rd E San Lázaro, Cantero 54; 1km by rd NE San Lázaro, Cantero Italo.
- 68. Concepción: 8km by rd E Concepción.
- 69. Amambay: 4km SW Cerro Corá; Parque Nacional Cerro Corá; 20km SW Pedro Juan Caballero.
- 70. Canendiyu: Igatimí.
- 71. Canendiyu: Curuguaty; 6.3km by rd NE Curuguaty; 13.3km by rd N Curuguaty.
- 72. San Pedro: Juan de Mena.
- 73. Caaguazu: 24km NNW Carayaó.
- 74. Cordillera: 20km by rd N Altos.
- 75. Cordillera: 12km by rd N Tobatí; 2km by rd S Tobatí; 1.6km by rd S
- 76. Central: 17km by rd E Luque; 20km by rd E Luque.
- 77. Central: 5km E Asunción; 4km ESE Asunción; Asunción.
- 78. Paraguarí: Yaguarón.
- 79. Paraguarí: Paraguarí; 3km E Paraguarí, Cerro Santo Tomas.
- 80. Paraguarí: Salto de Piraretá, 10km S Piribebuy; 17km by rd SW Piribebuy.
- 81. Paraguarí: Sapucay.
- 82. Paraguarí: Parque Nacional Ybycuí.
- 83. Guiará: Villarica.
- 84. Guiará: Itapé.
- 85. Guiará: Tacuaral [= Estación Tacuaral].
- 86. Misiones: 2.7km by rd N San Antonio.
- 87. Misiones: 41km S San Ignacio.

88. Misiones: 5km ENE Ayolas.

89. Itapúa: 22km by rd NNE Encarnación; Encarnación.

90. Itapúa: vic. San Rafael.

BRAZIL

91. Mato Grosso: Urucúm.

92. Mato Grosso: Descalvados, Río Paraguay.

NOT LOCATED

We were unable to locate the following localities, which were taken from specimen labels:

PARAGUAY: Alto Paraguay: Laguna Chamacoco, 33 leagues W Fuerte Olimpo.

PARAGUAY: Caaguazu: Sommerfeld, Colony #11.

Sampling localities given in the tables that follow are made up of the following collecting sites: Eastern Chaco, localities 1–10; Central Chaco, localities 11–20; Western Chaco, localities 21–36; Northern Chaco, localities 28–30; Eastern Paraguay, localities 67–90. The Eastern, Central, and Western Chaco are described above. Sites 28–30 and 46–47 lie in or near unusual, isolated rocky outcrops (Cerro León, Serranias of Santiago and San José). The vegetation at the sites in Paraguay (28–30) is typical of the Central Chaco. Most sites in Eastern Paraguay are in subtropical forest within the Paraguay River valley or in the central plateau area (Myers, in press). Localities 39 through 66 lie at the base of the Andes or in subtropical flatlands in Bolivia and Argentina.

SPECIES ACCOUNTS

Peropteryx macrotis (Wagner)

SPECIMENS EXAMINED.—BRAZIL: MATO GROSSO: Urucúm mines (3,FMNH). PARAGUAY: ALTO PARAGUAY: Fuerte Olimpo (1,AMNH). CONCEPCIÓN: 24km E San Lázaro by rd., Cantero 54 (2,UMMZ); 1km NE San Lázaro by rd., Cantero Italo (2,UMMZ).

MEASUREMENTS.—Female (n=1): FA 43.0, MC3 39.1, GLS 14.2, CB 13.4, ZB 8.6, IOC 2.9, MW 7.7, MM 6.2, CC 3.4, Max 5.5.

LITERATURE RECORDS.—The specimens from Paraguay were reported by Myers et al. (in press).

Noctilio albiventris (Desmarest)

Specimens Examined.—BOLIVIA: Beni: Itenez (30,USNM); San Joaquín (26,FMNH); San Ramón (6,FMNH); Magdalena (16,FMNH); Estancia Yutiole (6,FMNH); Santa Cruz: Buenavista, 400m (1,USNM; 5,FMNH). BRAZIL: Amazonas: Rïo Jurua (1,USNM); Itacoatiara

(1,USNM). PARAGUAY: Alto Paraguay: Fuerte Olimpo (11,AMNH). Central: 20km by rd E Luque (1,MVZ); 17km by rd E Luque (20,UMMZ). Presidente Hayes: 8km NE Juan de Zalazar (17,UMMZ); 230km by rd NW Villa Hayes (13,MVZ); .3km S of line camp, Río Verde, Juan de Zalazar (10,CONN).

MEASUREMENTS.—Males (n=10): FA 62.8 (59.6–65.5), MC3 56.7 (53.3–59.1), GLS 21.2 (20.4–22.6), CB 19.1 (18.4–20.3), ZB 15.9 (15.2–17.2), IOC 5.9 (5.3–6.3), MW 15.4 (14.4–17.0), MM 9.8 (9.4–10.5), CC 7.3 (6.9–8.1), Max 7.9 (7.2–8.2), Total 98.6 (93–104), Tail 19.4 (17–23), HF 19.2 (18–20), Ear 26.6 (25–28).

Females (n=17): FA 61.2 (57.7–63.4), MC3 55.2 (53.3–58.3), GLS 19.7 (18.9–20.6), CB 18.3 (17.5–19.0), ZB 15.0 (14.6–15.6), IOC 5.9 (5.6–6.1), MW 13.6 (13.0–14.3), MM 9.5 (9.1–9.9), CC 6.5 (6.2–7.0), Max 7.6 (7.2–8.1), Total 93.1 (84–97), Tail 18.6 (16–20), HF 17.6 (16–19), Ear 24.6 (22–27).

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: Concepción; Buenavista, 400m (Anderson et al., 1982). PARAGUAY: ALTO PARAGUAY: Fuerte Olimpo (Davis, 1976).

COMMENTS.—Most specimens were captured over lakes or large, slow streams. Two roosts were located, both in quebracho (*Schinopsis* sp.) trees. The first was in a cavity in the trunk, with an exit hole 1m above the ground at a point where the diameter of the trunk was about 30cm. The second roost was in a horizontal branch, 20cm in diameter and approximately 6m above the ground. Stomachs of three individuals examined contained hard, chitinous insect parts with no trace of fish scales.

Davis (1976) described N. a. cabrerai (type locality Fuerte Olimpo, a town in the northeastern Chaco of Paraguay) with a range including all of Paraguay and adjacent parts of Brazil, Argentina, and Bolivia. He distinguished N. a. cabrerai from geographically adjacent populations of N. a. affinis by its smaller size and lighter color. We remeasured specimens from several localities reported by Davis (1976) and forming part of his sample 9, which he assigned to N. a. affinis: Bolivia, Santa Cruz, Buena Vista (n=6); Bolivia, Beni, vicinity of San Joaquín (n=31), vicinity of Magdalena (n=25). Only adult females were included. The dimensions of these specimens, plus our new material from Paraguay, suggest a more complicated pattern of variation than was reported by Davis. Specimens from Beni on average are small (Table 1), only slightly larger than cabrerai, but with surprising differences even among geographically proximate samples from Magdalena and San Joaquín. Animals from Santa Cruz are significantly larger than Beni specimens, and similar in size to populations in the western Amazon Basin (Davis' sample 10). The populations from central and southern Paraguay are similar in size to those from Beni, and slightly larger than cabrerai, but considerably smaller than those from Santa Cruz.

The average size of *affinis* (sensu Davis 1976) appears to be the result of combining highly heterogeneous sets of populations in Beni and Santa Cruz. The differences in color between *affinis* and *cabrerai* appear minor

TABLE 1					
GEOGRAPHIC	VARIATION IN	FEMALE	Noctilio	albiventris	

	FA n	CB n	ZB n	MM n	Max n
N. a. ssp.					
Eastern Paraguay	62.2 6	18.8 14	15.3 14	9.8 14	7.9 14
	(1.46)	(0.46)	(0.44)	(0.26)	(0.21)
N. a. cabrerai					
Fuerte Olimpo,	62.2 6	18.0 6	14.5 6	9.3 6	7.7 6
Paraguay	(1.22)	(0.40)	(0.43)	(0.18)	(0.10)
N. a. ssp.					
Central Chaco,	62.3 6	18.4 11	15.2 10	9.6 10	7.6 11
Paraguay	(0.84)	(0.30)	(0.28)	(0.29)	(0.23)
N. a. affinis					
vic. Santa Cruz,	66.6 5	19.4 6	15.7 6	10.2 6	8.1 6
Bolivia	(0.53)	(0.19)	(0.38)	(0.29)	(0.19)
N. a. affinis					
vic. San Joaquín,	59.0 17	18.4 35	15.0 30	9.5 35	7.8 35
Beni, Bolivia	(2.17)	(0.44)	(0.39)	(0.27)	(0.23)
N. a. affinis					
vic. Magdalena,	58.8 7	18.6 25	15.0 20	9.8 25	7.9 25
Beni, Bolivia	(3.28)	(0.29)	(0.28)	(0.28)	(0.13)
P	0.0001	0.0001	0.0001	0.0001	0.0001

NOTES: In this table and in Tables 3–11, mean, sample size, and standard deviation (in parentheses) are given for each measurement, for each population. Localities labelled "Eastern Chaco," "Central Chaco," "Western Chaco," etc. are defined under "Collecting Localities"; measurements are defined under "Methods." Significance levels for geographic variation (ANOVA) in each variable are given in the bottom row.

and are difficult to evaluate. Suitable habitat for *N. albiventris* in the central part of South America is often distributed patchily (we found these bats only in the vicinity of water), and semi-isolated populations may often be composed of relatively few individuals. Under such conditions considerable between-sample variation is to be expected. In searching for geographic variation it seems advisable to rely heavily on samples from single populations whenever possible, rather than combining samples from large geographic areas.

Bats from the type locality of *cabrerai* are the smallest *albiventris* examined in this study, but they are only slightly smaller than some *affinis* from Beni. Bats from southern Paraguay, part of the range suggested for *cabrerai* by Davis, are indistinguishable, at least in size, from *affinis* from Beni. Yet their geographic proximity to the northwestern Chaco suggests a probably closer phyletic relationship to *cabrerai* than to *affinis*. Members of a single population from the central Chaco are intermediate in size, suggesting that, at least in the southern range of *albiventris*, changes in body size take place gradually with no sharp boundaries to define the subspecies. If

cabrerai deserves taxonomic recognition then so would the equally distinctive populations to the south and northwest of its type locality (eastern Paraguay and Santa Cruz). Until patterns of variation in *N. albiventris* are better understood, however, we prefer to avoid further proliferation of subspecific names.

Noctilio leporinus (Linnaeus)

Specimens Examined.—PARAGUAY: Boquerón: 420km by rd NW Villa Hayes (1,MVZ); 460km by rd NW Villa Hayes (5,MVZ); 3km S Line Camp, Juan de Zalazar (42,CONN). Presidente Hayes: 230km by rd NW Villa Hayes (1,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (5,MVZ); 300km by rd NW Villa Hayes (5,MVZ).

MEASUREMENTS.—Males (N=4): FA 88.8 (87.2–90.3), MC3 82.3 (81.9–83.0), GLS 27.2 (25.8–28.4), CB 24.9 (24.2–25.4), ZB 20.4 (19.9–20.7), IOC 7.2 (6.9–7.4), MW 18.9 (18.2–19.7), MM 12.6 (12.5–12.8), CC 8.6 (8.1–9.2), Max 9.9 (9.6–10.2), Total 119.8 (114–129), Tail 28.0 (25–30), HF 32.3 (32–33), Ear 33.5 (31–36).

Females (n=11): FA 85.9 (82.4–88.5), MC3 79.4 (77.3–81.9), GLS 25.5 (24.5–28.2), CB 23.4 (22.9–24.0), ZB 18.6 (18.0–19.2), IOC 6.9 (6.4–7.2), MW 16.6 (16.0–17.4), MM 12.4 (12.1–12.7), CC 8.6 (8.1–9.2), Max 9.9 (9.6–10.2), Total 116.5 (111–120), Tail 26.0 (21–29), HF 29.3 (27–31), Ear 31.1 (29–33).

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: San José de Chiquitos (Anderson et al., 1982). PARAGUAY: PRESIDENTE HAYES: Juan de Zalazar, 2km N Río Verde (Wetzel and Lovett, 1974).

COMMENTS.—These bats are very common over the slow streams and scattered temporary ponds of the lower Chaco. One individual, captured in a mist net placed over a stream, carried a partially eaten frog to the net.

Davis (1973) referred the Paraguayan populations to *N. l. rufescens* Olfers. Paraguayan specimens are somewhat smaller than *N. l. rufescens* from Bolivia and Argentina examined by Davis, but nevertheless are substantially larger than specimens of *N. l. leporinus* from the Amazon basin (Davis, 1973).

Tonatia bidens (Spix)

Specimens Examined.—PARAGUAY: Boquerón: Orloff (1,FMNH). Nueva Asunción: 19km by rd WSW Km 588 Trans Chaco Highway (1,UMMZ).

MEASUREMENTS.—Male (n=1): FA 57.1, MC3 48.3, GLS 28.2, CB 24.4, ZB 13.5, IOC 6.0, MW 13.2, MM 8.5, CC 6.1, Max 10.0, Total 99, Tail 20, HF 19, Ear 27.

Female (n=1): FA 54.9, MC3 46.5, CC 5.6, Max 9.8.

LITERATURE RECORDS.—These specimens are discussed by Myers et al. (in press).

COMMENTS.—Insect chitin and a large quantity of unidentified whitish pulp were found in the stomach of the specimen from Nueva Asunción.

Phyllostomus discolor (Wagner)

Specimens Examined.—None.

Measurements.—None.

LITERATURE RECORDS.—PARAGUAY: ALTO PARAGUAY: Laguna Chamacoco, 33 Leagues W Fte. Olimpo; Pto. Sastre (Podtiaguin, 1944).

Phyllostomus hastatus (Pallas)

Specimens Examined.—BOLIVIA: Santa Cruz: Río Yapacani, 600m (1,FMNH); Buenavista (2,FMNH).

MEASUREMENTS.—None.

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: San José de Chiquitos (Anderson et al., 1982).

COMMENTS.—This species has been taken at the western edge of the Chaco in Bolivia, and in eastern Paraguay (Baud, 1981).

Chrotopterus auritus Peters

Specimens Examined.—PARAGUAY: Caaguazu: Sommerfeld, Colony #11 (1,USNM). Canendiyu: 13.3km by rd N Curuguaty (1,UMMZ); 6.3km by rd NE Curuguaty (1,UMMZ). Chaco: 50km WNW Fortín Madrejón (1,UMMZ). Cordillera: 1.6km by rd S Tobatí (1,MVZ; 1,UMMZ). Paraguarí: 3km E Paraguarí, Cerro Santo Tomás (3,MVZ). Presidente Hayes: Fortín Orihuela (1,FMNH).

MEASUREMENTS.—Females (n=2): FA 82.4 (81.2–83.5), MC3 63.3 (61.4–65.0), GLS 36.0 (35.7–36.3), CB 31.0 (30.2–31.8), ZB 20.0 (19.5–20.4), IOC 6.4 (6.2–6.5), MW 18.1 (17.4–18.8), MM 12.3 (12.0–12.5), CC 7.6 (7.5–7.6), Max 13.1 (12.8–13.4).

LITERATURE RECORDS.—Podtiaguin (1944) reports *Chrotopterus* from the following localities along the Chacoan side of the Río Paraguay: PARAGUAY: PRESIDENTE HAYES: Chaco-í; Puerto Piñasco; Monte Lindo; Puerto Sastre.

COMMENTS.—The stomach of the specimen from Dept. Chaco contained a few feathers.

Thomas (1905) named *C. a. australis* (type locality Concepción, Paraguay) based on the more extensive white area occupying the wing tips of the type (compared to specimens from northern South America). Three individuals from Paraguay in the UMMZ collection (two from Dept. Canendiyu and one from Dept. Cordillera) are similar to Thomas's specimen in this respect. They further differ from an individual from Panamá in the UMMZ collection by their grayish (vs. brown) pelage. Nevertheless, this seems weak grounds for taxonomic recognition (Handley, 1966).

Glossophaga soricina (Pallas)

Specimens Examined.—BOLIVIA: Santa Cruz: Buenavista, 500m (3,AMNH); Sara, 7km N Sta. Rosa (2,AMNH); Lostra, Ibos, 2km N, 7km E, Ing. Mora (5,MSU). PARAGUAY: Amambay: 20km SW Pedro Juan

Caballero (1,UMMZ); Parque Nacional Cerro Corá (1,UMMZ). Central: vicinity of Asunción (2,UMMZ; 2,MVZ). Concepción: 8km by rd E Concepción (1,MVZ). Cordillera: 1.6km by rd S Tobatí (9,MVZ). Itapúa: 22km by rd NNE Encarnación (1,UMMZ). Paraguarí: 17km by rd SW Piribebuy (1,UMMZ).

MEASUREMENTS.—None.

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: Santiago (Anderson et al., 1982). PARAGUAY: PRESIDENTE HAYES: Puerto Cooper (Podtiaguin, 1944). We have taken this species on the eastern bank of the Río Paraguay. It seems likely that in the Chaco *G. soricina* is restricted to the mesic zone along the Río Paraguay.

Comments.—Miller (1913a) named G. s. microtis from eastern Paraguay (Sapucay), based on the supposedly small ears of Paraguayan specimens. We compared the length of the ear from the notch of two alcoholic specimens from eastern Paraguay (Dept. Amambay), with that of 10 alcoholic specimens from Panamá. The mean for both is 13mm. Further, our field measurements of the ears of 10 specimens from eastern Paraguay average considerably larger (16mm) than those reported by Miller (13–14mm) (Miller does not specify how his measurements were taken). Therefore we concur with Cabrera (1958) in placing microtis in synonomy under G. s. soricina.

Specimens from the eastern border of the Chaco (eastern Paraguay) average 2–4% smaller in most dimensions than specimens from the western border (Santa Cruz, Bolivia).

Carollia perspicillata (Linnaeus)

Specimens Examined.—BOLIVIA: Santa Cruz: Buenavista, 400m (7,FMNH). PARAGUAY: Amambay: 4km SW Cerro Corá (1,UMMZ); Parque Nacional Cerro Corá (1,UMMZ). Canendiyu: 13.3km by rd N Curuguaty (7,UMMZ); 6.3km by rd NE Curuguaty (4,UMMZ). Cordillera: 1.6km by rd S Tobatí (3,MVZ; 4,UMMZ). Itapúa: 22km by rd NNE Encarnación (1,MVZ). Paraguarí: 17km by rd SW Piribebuy (2,UMMZ); Parque Nacional Ybycuí (30,UMMZ).

Measurements.—None.

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: Santiago (Anderson et al., 1982). PARAGUAY: PRESIDENTE HAYES: Puerto Cooper (Podtiaguin, 1944).

COMMENTS.—*C. perspicillata* is a common forest bat in eastern Paraguay; in the Chaco it is probably restricted to the proximity of the Río Paraguay. If a subspecific epithet were used, *C. p. tricolor* would be appropriate (Pine, 1972).

Specimens from eastern Paraguay average 5–8% smaller in most dimensions than those from the western border of the Chaco.

Sturnira lilium E. Geoffroy

Specimens Examined.—BOLIVIA: Santa Cruz: 7km N Santa Rosa, Pvcia. Sara (5,AMNH); Río Palometilla, 400m (2,FMNH); Buenavista, 400m (1,FMNH). PARAGUAY: Amambay: 4km by rd SW Cerro Corá (1,UMMZ). Caaguazu: 24km NNW Carayaó (11,UMMZ). Canendiyu: 13.3km by rd N Curuguaty (15,UMMZ); 6.3km by rd NE Curuguaty (7,UMMZ). Central: vicinity of Asunción (9,MVZ; 4,UMMZ; 3,CONN). Concepción: 8km by rd E Concepción (10,MVZ). Itapúa: 22km by rd NNE Encarnación (5,UMMZ); vicinity of San Rafael (36,UMMZ). Misiones: 2.7km by rd N San Antonio (26,UMMZ); 5km ENE Ayolas (4,UMMZ). Paraguarí: Parque Nacional Ybycuí (40,UMMZ). Presidente Hayes: 24km WNW Villa Hayes (1,UMMZ).

MEASUREMENTS.—Female (n=1): FA 43.5, MC3 43.6, GLS 22.6, CB 20.3, ZB 13.6, IOC 5.9, MW 12.2, MM 8.2, CC 6.0, Max 6.6, Total 68, HF 14, Ear 18.

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: Santiago. TARIJA: 8km S and 10km E Villa Montés; Villa Ingavi, Caiza 600m (Anderson et al., 1982). PARAGUAY: Presidente Hayes: Chaco-í; Villa Hayes (Podtiaguin, 1944).

COMMENTS.—Like those reported by Podtiaguin, our example was taken in forest near the Río Confuso. As with the preceding two species, *S. lilium* is probably restricted in the Chaco to riparian forests along the Río Paraguay and the lower reaches of its tributaries.

Specimens from eastern Paraguay average 3–6% smaller than those from eastern Tarija and Santa Cruz, Bolivia.

Artibeus lituratus (Olfers)

Specimens Examined.—BOLIVIA: Santa Cruz: Provincia Sara, 7km S Santa Rosa, 800m (16,AMNH). PARAGUAY: Amambay: 4km SW Cerro Corá (5,UMMZ); 20km SW Pedro Juan Caballero (1,UMMZ). Caaguazu: 24km NNW Carayaó (10,UMMZ). Canendiyu: 13.3km by rd N Curuguaty (63,UMMZ). Central: vicinity of Asunción (11,UMMZ; 9,MVZ). Presidente Hayes: Rincón Charrúa, 275km by rd NW Villa Hayes (2,MVZ).

MEASUREMENTS.—Females (n=2): FA 72.7 (71.7–73.6), MC3 69.4 (68.2–70.6), GLS 32.6 (32.3–32.9), CB 29.5 (29.5–29.5), ZB 19.4 (19.0–19.8), IOC 7.1 (6.8–7.4), MW 16.8 (16.6–17.0), MM 14.4 (14.2–14.5), CC 9.4 (9.0–9.7), Max 10.8 (10.7–10.9), Total 99 (99–99), Tail 18 (16–19), HF 26 (26–26), Ear 12 (10–13).

LITERATURE RECORDS.—PARAGUAY: PRESIDENTE HAYES: Chaco-í; Villa Hayes (Podtiaguin, 1944).

COMMENTS.—Both Chacoan specimens (first reported by Myers, 1977) were captured over the same small pond, surrounded by thornscrub, in mid August, at a time when many trees were in flower. The same pond was netted at approximately monthly intervals over most of the year, but no

further specimens were taken. The coincidence between the flowering of trees and the capture of this and the following species of bats suggests that this species may be migratory in the Chaco Boreal. Certainly, during most of the year few flowers or fruits are available to bats in the central or western Chaco. *Artibeus lituratus* is abundant in eastern Paraguay, and will probably be found in mesic areas along the Río Paraguay throughout the year.

Artibeus jamaicensis (Spix)

Specimens Examined.—PARAGUAY: Amambay: 4km SW Cerro Corá (1,UMMZ). Central: vicinity of Asunción (14,UMMZ; 14,MVZ). Presidente Hayes: Rincón Charrúa, 275km by rd NW Villa Hayes (1,MVZ).

Measurements.—None.

LITERATURE RECORDS.—The Chacoan specimen was reported by Myers and Wetzel (1979). BOLIVIA: Santa Cruz: Santiago (Anderson et al., 1982).

COMMENTS.—The Chacoan specimen, a juvenile, was captured at the same time and place as the A. lituratus described above.

Myers and Wetzel (1979) documented the presence of three species of large Artibeus in eastern Paraguay: lituratus, jamaicensis, and a third species that may represent A. fimbriatus (Gray) (C. O. Handley, Jr., pers. commun.). Anderson et al. (1982) also list three species for eastern Bolivia: lituratus, jamaicensis fuliginosus, and planirostris fallax. We compared Paraguayan material (including Chacoan specimens, which do not differ significantly from specimens from eastern Paraguay) with some of the series reported by Anderson et al. The results are summarized in Table 2. All populations of lituratus are essentially similar to a large topotypical series from Asunción, Paraguay, and are combined. Specimens of lituratus are distinguished from other species primarily by large size, clearly defined eye stripes, strongly developed orbitonasal shields (made more pronounced by the greatly constricted interorbital region), and consistent lack of an upper M³. The relationships of the other species populations are enigmatic; based on the evidence at hand no strong case can be made for regarding any trans-Chacoan pair as conspecific (other than populations of A. lituratus). On the other hand, most of the characters in Table 2 have been reported to vary within populations of large Artibeus elsewhere in South America, so that neither can a case be made for specific distinctiveness. As a result, the assignment of names for species populations other than lituratus is highly tentative, pending a much-needed revision of the large Artibeus in South America.

Vampyrops dorsalis Thomas

Specimens Examined.—None.

Measurements.—None.

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: Santiago, 700m (Anderson et al., 1982).

TABLE 2

MEASUREMENTS OF THE LARGE Artibeus OF PARAGUAY AND EASTERN BOLIVIA
(MALES AND FEMALES COMBINED)

	QUANTITATIVE CHARACTERISTICS									
	FA	n	GLS	n	ZB	n	IOC	n	Rost ¹	n
lituratus ²	70.4 (6.72)	29	31.9 (0.73)	38	19.3 (0.52)	37	8.1 (0.46)	38	6.7 (0.30)	38
cf. fimbriatus ³	65.2 (2.28)	16	31.3 (0.58)	22	18.9 (0.50)	22	8.2 (0.39)	22	7.4 (0.34)	22
jamaicensis ssp. ³	61.0 (1.67)	25	28.8 (0.49)	28	17.9 (0.38)	28	8.3 (0.37)	22	7.2 (0.28)	28
planirostris fallax ⁴	61.8 (2.36)	8	29.9 (0.52)	28	18.4 (0.56)	28	8.5 (0.36)	28	7.4 (0.25)	28
jamaicensis fuliginosus ⁵	58.5 (—)	1	27.7 (0.61)	22	16.8 (0.47)	23	7.1 (0.35)	23	6.4 (0.36)	23

QUALITATIVE CHARACTERISTICS White tips Development M^3 on dorsal Eye stripes of rostral Fur on hairs present uropatagium present shield lituratus² no dense fur extending no yes strong more than halfway from knee to ankle cf. fimbriatus³ dense fur usually no no no or moderate extending below weak to weak knee, but not halfway to ankle jamaicensis dense fur not yes yes weak moderate ${\rm ssp.}^3$ extending to knee to weak planirostris dense fur not yes yes weak weak fallax4 extending to knee (some) jamaicensis yes no dense fur not no or moderate fuliginosus⁵ weak (usually) extending to knee to weak

Vampyrops lineatus (Olfers)

Specimens Examined.—None. Measurements.—None.

¹ Measured as breadth of posterior border of orbitonasal shield.

² Includes specimens from Paraguay and Bolivia.

³ PARAGUÂY: Several localities in eastern Paraguay.

⁴ BOLIVIA: LaPaz: 20km by river N Puerto Linares, 600m (17,LSUMZ). SANTA CRUZ: Provincia Sara, 7km N Santa Rosa (11,AMNH).

⁵ BOLIVIA: LaPaz: 20km by river N Puerto Linares, 600m (23,LSUMZ). Santa Cruz: Provincia Sara, 7km N Santa Rosa (3,AMNH).

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: Santiago, 700m (Anderson et al., 1982).

COMMENTS.—This species is a common resident of forests in eastern Paraguay.

Desmodus rotundus (E. Geoffroy)

Specimens Examined.—BOLIVIA: Santa Cruz: Buenavista, 400m (15,FMNH). PARAGUAY: Boquerón: 460km by rd NW Villa Hayes (2,MVZ). Canendiyu: 6.3km by rd NE Curuguaty (2,UMMZ). Central: 4km ESE Asunción (1,MVZ). Cordillera: 1.6km by rd S Tobatí (9,MVZ; 39,UMMZ). Paraguarí: Parque Nacional Ybycuí (1,UMMZ). Nueva Asunción: 19km by rd WSW Km 588, Trans Chaco Highway (1,UMMZ); Teniente Ochoa (2,CONN). Presidente Hayes: vicinity of line camp, Juan de Zalazar (9,CONN); 230km by rd NW Villa Hayes (1,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (1,MVZ); Pozo Colorado, Trans Chaco Highway Km 250 (4,AMNH).

MEASUREMENTS.—Males (n=5): FA 61.2 (59.9–63.7), MC3 56.7 (54.5–60.1), GLS 24.6 (23.5–25.4), CB 22.3 (21.2–23.5), ZB 12.6 (12.4–12.7), IOC 5.5 (5.0–5.8), MW 12.9 (12.2–13.8), MM 7.1 (6.5–7.6), CC 6.2 (5.9–6.5), Max 3.4 (3.3–3.8), Total 87.5 (87–88), HF 17.0 (16–18), Ear 23 (22–24).

Females (n=3): FA 65.8 (64.1–67.6), MC3 60.3 (59.3–61.2), GLS 24.5 (23.9–25.0), CB 21.5 (21.5–21.5), ZB 12.7 (12.0–13.1), IOC 5.5 (5.2–5.7), MW 12.9 (12.6–13.3), MM 7.0 (6.8–7.2), CC 6.2 (5.7–6.7), Max 3.5 (3.4–3.6), Total 90.5 (90–91), HF 18.5 (18–19), Ear 22.0 (21–23).

LITERATURE RECORDS.—BOLIVIA: TARIJA: Villa Ingavi [= Caixa], 600m (Anderson et al., 1982). PARAGUAY: BOQUERÓN: Teniente Ochoa (Wetzel and Lovett, 1974). Presidente Hayes: Juan de Zalazar, 2km N Río Verde (Wetzel and Lovett, 1974).

COMMENTS.—The accounts of ranchers and our own observations of bitten cattle and horses indicate these bats are common throughout the Chaco, and of considerable economic importance. We have observed them only in areas utilized by livestock.

Specimens from eastern Paraguay average 1–2% larger in wing dimensions than Chacoan specimens (Table 3). No significant differences were detected in cranial measurements. Specimens from eastern Santa Cruz, Bolivia, average about 2% smaller than the Chacoan animals also in wing, but not cranial, measurements.

Myotis albescens (E. Geoffroy)

Specimens Examined.—BOLIVIA: Santa Cruz: 10km E Gutierrez, Laguna Caucaya (1,AMNH); 7km N Santa Rosa, Pvcia. Sara, 800m (1,AMNH). PARAGUAY: BOQUERÓN: 460km by rd NW Villa Hayes (2,MVZ); Guachalla (1,FMNH). Canendiyu: Curuguaty (18,AMNH). Central: vicinity of Asunción (3,FMNH); 17km by rd E Luque (2,UMMZ). Guiará: Tacuaral (2,FMNH; 25,USNM). Nueva Asunción: Teniente

	FA	n	GLS	n	MW	n	MM	n
Eastern Paraguay	64.4 (2.50)	6	24.8 (0.44)	6	13.1 (0.39)	6	6.8 (0.38)	6
Central Chaco, Paraguay	62.5 (2.81)	7	24.6 (0.61)	8	12.9 (0.49)	8	7.02 (0.48)	4
Santa Cruz, Bolivia	60.9 (2.27)	11	24.2 (0.60)	8	12.6 (0.23)	8	6.57 (0.25)	10
P	0.039		0.13		0.16		0.11	

TABLE 3
GEOGRAPHIC VARIATION IN *Desmodus rotundus*(MALES AND FEMALES COMBINED)

Ochoa (1,CONN). Presidente Hayes: 24km WNW Villa Hayes (1,UMMZ); Retiro Mandeyu, 20km SW Km 205, Trans Chaco Highway (2,MVZ); 226km by rd NW Villa Hayes (47,MVZ); 230km by rd NW Villa Hayes (20,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (79,MVZ); 290km by rd NW Villa Hayes (10,MVZ); 320km by rd NW Villa Hayes (12,MVZ); Juan de Zalazar (8, CONN); 50km E of Km 320, Trans Chaco Highway (10,MVZ).

MEASUREMENTS.—Males and females (n=133): FA 34.6 (32.5–37.3), MC3 32.7 (30.5–34.7), GLS 13.7 (12.9–14.4), CB 12.8 (11.6–13.9), ZB 8.6 (7.9–9.1), IOC 4.0 (3.1–4.4), MW 7.4 (6.6–7.7), MM 5.3 (4.7–5.6), CC 3.6 (3.1–3.9), Max 4.9 (4.6–5.2), Total 86.4 (79–96), Tail 36.6 (27–40), HF 9.1 (8–11), Ear 15.2 (12–18).

LITERATURE RECORDS.—BOLIVIA: TARIJA: 8km S and 10km E Villa Montés (Anderson et al., 1982). PARAGUAY: Boquerón: Fortín Guachalla, Río Pilcomayo (LaVal, 1973).

COMMENTS.—The breeding biology and natural history of this species were discussed by Myers (1977). Females are significantly larger than males in several wing and cranial measurements; however, in all cases the differences are small, and sexes were combined for the analysis of geographic variation.

Most specimens came from a restricted area in the central Chaco. Nevertheless, significant geographic variation was noted in a few morphometric variables, with Chacoan specimens averaging 1–2% smaller than those from eastern Paraguay (Table 4). A single specimen was available from eastern Santa Cruz, Bolivia; it is among the largest measured.

Myotis nigricans (Schinz)

Specimens Examined.—BOLIVIA: Beni: San Joaquín (11,FMNH); Trinidad (2,MSU). Santa Cruz: Ing. Mora (1,MSU); Warnes, 350m (5,FMNH); Buenavista, 400m (3,FMNH; 3,AMNH); Río Surutu, 400m (3,AMNH); 7km N Sta. Rosa, Pvcia. Sara (5,AMNH). Tarija: 8km S, 10km

	FA	n	СВ	n	CC	n
Eastern Paraguay	34.2 (0.88)	45	13.0 (0.28)	26	3.6 (0.11)	26
Central Chaco, Paraguay	34.6 (0.81)	121	12.7 (0.37)	129	3.7 (0.14)	124
Northern Chaco, Paraguay	34.3 (1.56)	2	12.9 (0.21)	2	3.6 (0.22)	2
Santa Cruz, Bolivia	36.1 (—)	1	13.2 (—)	1	3.5 (—)	1
P	0.01		0.02		0.09	

TABLE 4
GEOGRAPHIC VARIATION IN Myotis albescens
(MALES AND FEMALES COMBINED)

E Villa Montés (1,AMNH). PARAGUAY: AMAMBAY: 20km SW Pedro Juan Caballero (2,UMMZ). CANENDIYU: Igatimí (13,AMNH); 13.3km by rd N Curuguaty (1,UMMZ). CENTRAL: vicinity of Asunción (2,USNM; 1,FMNH). CHACO: 50km WNW Fortín Madrejón (2,UMMZ); Agua Dulce, 170km W Bahía Negra (2,UMMZ; 2,AMNH); 65km by rd N Fortín Madrejón (1,UMMZ). Concepción: 8km by rd E Concepción (1,MVZ). CORDILLERA: 1.6km by rd S Tobatí (1,UMMZ; 2,MVZ). Guiará: Villarica (4,USNM). NUEVA ASUNCIÓN: 49.6km by rd N Filadelfia (5,UMMZ); Teniente Enciso (1,CONN). PARAGUARÍ: Paraguarí (7,USNM); Sapucay (5,USNM). Pres-IDENTE HAYES: 80km W Pto. Piñasco (1,USNM); 24km WNW Villa Hayes (9,UMMZ); Retiro Mandeyu, 20km SW Km 205, Trans Chaco Highway (8,MVZ); 213km by rd NW Villa Hayes (1,MVZ); 226km by rd NW Villa Hayes (32,MVZ); 230km by rd NW Villa Hayes (13,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (58,MVZ); 290km by rd NW Villa Hayes (11,MVZ); 320km by rd NW Villa Hayes (1,MVZ); 50km E Km 320, Trans Chaco Highway (2,MVZ); Line Camp, Juan de Zalazar (2,CONN).

MEASUREMENTS.—Males and females (n=110): FA 32.7 (29.8–35.8), MC3 30.8 (28.8–34.3), GLS 13.5 (13.0–14.2), CB 12.9 (12.5–13.6), ZB 8.3 (7.8–8.9), IOC 3.5 (3.3–3.8), MW 7.1 (6.7–7.5), MM 5.3 (4.9–5.7), CC 3.5 (3.2–3.7), Max 5.0 (4.7–5.3), Total 81.8 (71–91), Tail 33.7 (25–40), HF 8.1 (6–10), Ear 14.4 (11–18).

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: San José de Chiquitos. TARIJA: Villa Montés; Villa Ingavi, Caixa, 600m (Anderson et al., 1982). PARAGUAY: BOQUERÓN: Teniente Ochoa (Wetzel and Lovett, 1974).

COMMENTS.—The breeding biology and natural history of this species were discussed by Myers (1977).

As with *M. albescens*, significant sexual dimorphism is present but slight, and the sexes were combined for statistical analysis. Significant geographic variation was recorded in most dimensions (Table 5). In general the smallest bats are found in eastern Paraguay and the central Chaco. Bats from

	FA n	GLS n	MW n	CC n
Eastern Paraguay	32.8 22	13.5 29	7.0 30	3.4 30
	(0.96)	(0.26)	(0.16)	(0.10)
Eastern Chaco,	32.7 10	13.6 9	7.0 9	3.4 9
Paraguay	(0.79)	(0.20)	(0.13)	(0.11)
Central Chaco,	32.6 86	13.5 88	7.1 88	3.5 82
Paraguay	(1.13)	(0.26)	(0.14)	(0.12)
Northern Chaco,	33.2 12	13.7 12	7.1 12	3.4 12
Paraguay	(1.34)	(0.27)	(0.18)	(0.12)
Santa Cruz,	33.9 15 (0.73)	13.7 19	7.1 19	3.5 20
Bolivia		(0.22)	(0.11)	(0.09)
Beni,	33.1 11	13.4 12	6.9 10	3.4 12
Bolivia	(0.91)	(0.25)	(0.18)	(0.14)
P	0.001	0.0001	0.002	0.002

TABLE 5
GEOGRAPHIC VARIATION IN Myotis nigricans
(MALES AND FEMALES COMBINED)

Santa Cruz, Bolivia, and the northern Chaco tend to be large. Those from the northern Chaco also tend to be lighter in color and shorter haired than those from eastern Paraguay or the central Chaco.

Myotis riparius Handley

Specimens Examined.—PARAGUAY: Boquerón: Estancia Iparoma, 19km N Filadelfia (1,CONN). Caaguazu: 24km NNW Carayaó (2,UMMZ). Itapúa: vicinity of San Rafael (3,UMMZ). Paraguarí: Sapucay (6,USNM); Parque Nacional Ybycuí (7,UMMZ). Presidente Hayes: Retiro Mandeyu, 20km SW of Km 205, Trans Chaco Highway (2,MVZ); 275km by rd NW Villa Hayes (1,MVZ); Juan de Zalazar, approx. 4km E Trans Chaco Highway bridge (1,CONN).

Females (n=2): FA 33.9 (33.8–39.0), MC3 32.0 (31.6–32.3), GLS 13.9 (13.9–14.0), CB 13.3 (13.2–13.4), ZB 8.5 (8.4–8.5), IOC 3.6 (3.6–3.6), MW 7.5 (7.4–7.5), MM 5.6 (5.6–5.6), CC 3.7 (3.7–3.7), Max 5.2 (5.1–5.2), Total 87 (86–88), Tail 38 (38–38), HF 9 (8–9), Ear 15 (14–16).

LITERATURE RECORDS.—PARAGUAY: PRESIDENTE HAYES: Juan de Zalazar, approx. 4km E Trans Chaco Highway bridge (Wetzel and Lovett, 1974).

COMMENTS.—The Chacoan individuals are smaller than specimens from eastern Paraguay. Too few individuals were available, however, to permit statistical testing.

Paraguayan specimens of this species are very similar to Paraguayan M. nigricans. In general the characters given by LaVal (1973) for M. riparius, including shorter fur, broad rostrum, and tendency to develop a sagittal crest, separate the species; but some individuals are difficult to classify. Northern Chacoan nigricans in particular tend to resemble riparius in the length and texture of their fur, though riparius is not yet known from that area.

Myotis simus Thomas

SPECIMENS EXAMINED.—PARAGUAY: CENTRAL: 17km by rd E Luque (1,UMMZ). Presidente Hayes: 230km by rd NW Villa Hayes (4,MVZ).

MEASUREMENTS.—Females (n=4): FA 38.7 (38.4–39.1), MC3 35.2 (34.6–35.5), GLS 13.9 (13.9–14.0), IOC 3.9 (3.9–4.0), MW 8.0 (7.9–8.2), MM 5.9 (5.8–6.1), CC 4.1 (4.0–4.2), Max 5.3 (5.2–5.4), Total 97.3 (96–100), Tail 38.8 (37–41), HF 10.0 (9–11), Ear 14.3 (13–15).

LITERATURE RECORDS.—These specimens and information about their habitat were reported by Myers and Wetzel (1979). The specimen from eastern Paraguay (Dept. Central) was taken over a river in a very Chaco-like area along the Río Salado; in Paraguay this species may be restricted to the basin of the Río Paraguay and the lower Chaco.

Eptesicus furinalis (D'Orbigny)

EXAMINED.—ARGENTINA: JUJUY: Yuto (17,AMNH); SPECIMENS Ledesima (1,AMNH); Santa Bárbara (1,AMNH). BOLIVIA: SANTA CRUZ: 25km by rd W Comarapa, 2800m (1,UMMZ); 15km E Ing. Mora, 1600-2000ft (3,AMNH); Santa Cruz, 416m (1,AMNH); 10km by rd E Ing. Mora (10,MSU). PARAGUAY: AMAMBAY: Parque Nacional Cerro Corá (1,UMMZ). CANENDIYU: 6.3km by rd NE Curuguaty (2,UMMZ); 13.3km by rd N Curuguaty (1,UMMZ); Curuguaty (1,AMNH). CENTRAL: vicinity of Asunción (24,UMMZ; 43,MVZ; 2,AMNH). Concepción: 8km by rd E Concepción (2,MVZ). CHACO: 50km WNW Fortín Madrejón (1,UMMZ). CORDILLERA: 1.6km by rd S Tobatí (1,UMMZ; 1,MVZ); 12km by rd N Tobatí (1,MVZ); 20km by rd N Altos (4,MVZ). Guiará: Itapé (1,AMNH). ITAPÚA: 8km N San Rafael (3,UMMZ). NUEVA ASUNCIÓN: 49.6km by rd N Filadelfia (1,UMMZ). PARAGUARÍ: Parque Nacional Ybycuí (1,UMMZ); Sapucay (1,AMNH). Presidente Hayes: Retiro Mandeyu, 20km SW Km 205, Trans Chaco Highway (16,MVZ); 24km WNW Villa Hayes (2,UMMZ); 213km by rd NW Villa Hayes (4,MVZ); 230km by rd NW Villa Hayes (1,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (11,MVZ); 295km by rd NW Villa Hayes (10,MVZ); 3km SE line camp, Río Verde, Juan de Zalazar (3,CONN); Pozo Colorado (1,AMNH).

MEASUREMENTS.—Males (n=20): FA 38.0 (35.2–39.9), MC3 35.9 (32.1–37.6), GLS 14.7 (14.1–15.1), CB 14.0 (13.7–14.3), ZB 10.2 (9.8–10.6), IOC 3.7 (3.4–4.0), MW 8.1 (7.7–8.6), MM 6.3 (6.1–6.5), CC 4.6 (4.4–4.8), Max 5.4 (5.1–5.7), length mandible 11.4 (10.8–11.7), length mandibular toothrow 6.9 (6.5–7.1), Total 92.8 (88–96), Tail 36.8 (32–41), HF 9.4 (8–10), Ear 16.4 (13–18).

Females (n=29): FA 38.4 (36.7–40.5), MC3 36.8 (34.8–38.7), GLS 15.0 (14.3–15.7), CB 14.3 (13.5–15.5), ZB 10.3 (9.9–10.7), IOC 3.9 (3.6–4.2), MW 8.3 (8.0–8.7), MM 6.4 (6.1–6.8), CC 4.6 (4.4–5.0), Max 5.4 (5.2–5.8), Length mandible 11.6 (11.0–12.2), Length mandibular toothrow 6.9 (6.7–7.4), Total 97.0 (86–106), Tail 38.6 (29–45), HF 9.7 (8–11), Ear 16.2 (14–18).

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: Tamachindi, near Izozog (Davis, 1966 and Anderson et al., 1982). TARIJA: Villa Montés; Villa Ingavi, Caixa, 600m (Anderson et al., 1982). PARAGUAY: PRESIDENTE HAYES: vicinity of line camp, Río Verde, Juan de Zalazar (Wetzel and Lovett, 1974; Williams, 1978).

Comments.—The reproductive pattern and natural history of *E. furinalis* were discussed by Myers (1977). The small *Eptesicus* of South America have been reviewed recently by Davis (1966) and Williams (1978). Davis (1966) included a large part of the Chaco in the range of *E. brasiliensis argentinus*, and Massoia (1976) reported this species from the Chaco Austral (Argentina, Prov. Chaco); it probably also occurs in the Paraguayan Chaco. Wetzel and Lovett (1974) report "*E. cf. fidelis*" from the Paraguayan Chaco near Juan de Zalazar; however, Williams (1978) reexamined this specimen and referred it to *E. furinalis*. *E. diminutus* (=*E. fidelis*, Williams, 1978) is known from the rainforest of southeastern Paraguay (Myers et al., in press) but so far has not been taken in the Chaco although both Davis (1966) and Williams (1978) include part or all of the Chaco within its range.

Williams (1978) recognized the populations of furinalis in the eastern Andean foothills, from Tucumán province north to Salta and Jujuy provinces, as subspecifically distinct (E. f. findleyi Williams, 1978). According to Williams, these bats differ from adjacent E. f. furinalis in their larger size and lighter coloration. We compared a series of 17 furinalis from Jujuy province (referred to findleyi by Williams, who also noted that these specimens tend to be smaller and darker than members of the type series) with large numbers of furinalis from eastern and western Paraguay (referred to the subspecies furinalis by Williams). Bats from eastern Paraguay tend to be blackish in dorsal coloration, and large (Table 6). The dorsal hairs are unbanded. Those from the central Chaco are lighter but highly variable in dorsal color (from Bone Brown to Sanford's Brown), and the dorsal hairs are distinctly banded with prominent light tips. These bats are slightly smaller in size than those from eastern Paraguay (Table 6). The specimens from Jujuy are lighter dorsally (Mummy Brown) than eastern Paraguayan specimens, and fall roughly in the middle of the Chacoan series in color. They also have strongly banded hairs. In size the Jujuy bats resemble most closely the eastern Paraguayan furinalis, but all groups overlap considerably. We see no justification for recognizing the Jujuy specimens as distinct from central Chacoan ones.

We also examined specimens from the vicinity of Santa Cruz city, Dept. Santa Cruz, Bolivia (4–600m) and from near Comarapa, Santa Cruz (2800m). The former are similar in color to central Chacoan specimens, but slightly larger (Table 6). The latter, a single specimen, is almost black and very large (Table 6).

TABLE 6							
GEOGRAPHIC	VARIATION IN	Eptesicus .	furinalis				

	FA r	1	GLS	n	Max	n	ZB	n
	Males							
Eastern Paraguay	37.4 15 (1.11)	<u> </u>	15.0 (0.36)	17	5.5 (0.09)	18	10.4 (0.33)	16
Central Chaco, Paraguay	37.9 13 (1.14)	3	14.7 (0.28)	14	5.4 (0.16)	14	10.2 (0.19)	13
Western Chaco, Paraguay	36.7 (—)	l	14.3 (—)	1	5.3 ()	1	10.0	1
Northern Chaco, Paraguay	38.6	l	14.6 (—)	1	5.7 (—)	1	10.2 (—)	l
Jujuy, Argentina	38.7 8 (1.41)	3	15.0 (0.33)	11	5.6 (0.14)	11	10.1 (0.26)	11
Tucumán, Argentina ^l	39.3	1	15.5 (—)	1	5.7 ()	1	10.4 (—)	1
Santa Cruz, Bolivia	38.0 2 (0.28)	2	15.2 (0.17)	3	5.6 (0.06)	3	10.7 (0.07)	2
P	0.32		0.04		0.004		0.03	
				FEN	MALES			
Eastern Paraguay	38.3 33 (0.63)	3	15.1 (0.40)	31	5.6 (0.16)	34	10.3 (0.27)	33
Central Chaco, Paraguay	38.3 26 (0.88)	5	15.0 (0.32)	27	5.4 (0.18)	28	10.3 (0.20)	23
Jujuy, Argentina	39.6 (2.36)	1	14.8 (0.39)	4	5.6 (0.06)	4	9.9 (0.28)	2
Tucumán, Argentina ^l	40.5 (0.92)	2	16.7 (0.35)	2	6.1 (0.07)	2	11.4 (0.07)	2
Santa Cruz, Bolivia	40.1	l	15.2 (0.39)	6	5.6 (0.17)	6	10.3 (0.35)	5
Comarapa, Santa Cruz, Bolivia	42.7 (<u> </u>	l	15.7 (—)	1	5.8 (—)	1	10.6	1
P	0.009		0.09		0.06		0.03	

¹ Measurements from Williams (1978).

Eastern Paraguayan specimens are clearly referable to *E. f. furinalis* (Williams, 1978), and the specimen from Comarapa agrees well in size with the description of *E. f. chapmani*, although it is darker. The Chacoan specimens, those from the vicinity of Santa Cruz city, and those from Prov. Jujuy, are at most only weakly differentiated from eastern Paraguayan *E. f. furinalis*. If the specimens from Jujuy are excluded from *findleyi*, the subspecies becomes known from only the type series (four specimens) and one

additional animal from Salta province. Clearly, additional material from the Argentine Chaco and the Andean piedmont is required for an assessment of the status of *findleyi*, as well as evaluation of patterns of geographic variation in more southern populations of *furinalis*.

Lasiurus borealis (Muller)

Specimens Examined.—ARGENTINA: Jujuy: Yuto (7,AMNH). PARAGUAY: Caaguazu: 24km NNW Carayaó (1,UMMZ). Canendiyu: 13.3km by rd N Curuguaty (1,UMMZ). Central: vicinity of Asunción (4,UMMZ; 16,MVZ; 1,AMNH). Chaco: 50km WNW Fortín Madrejón (1,AMNH). Cordillera: 20km by rd N Altos (1,MVZ); 12km by rd N Tobatí (1,MVZ). Guiará: Villarica (8,AMNH; 1,USNM). Itapúa: 8km N San Rafael (1,UMMZ). Paraguarí: Parque Nacional Ybycuí (2,UMMZ). Presidente Hayes: Rincón Charrúa, 275km by rd NW Villa Hayes (1,MVZ).

MEASUREMENTS.—Male (n=1): FA 36.6, MC3 42.0, GLS 12.0, CB 11.7, ZB 8.5, IOC 7.3, MW 7.3, MM 5.3, CC 4.3, Max 3.9.

Female (n=1): FA 40.7, MC3 44.5, GLS 11.6, ZB 9.1, IOC 4.2, MW 7.7, MM 5.7, CC 4.7, Max 4.0, Total 108, Tail 50, HF 10, Ear 9.

LITERATURE RECORDS.—BOLIVIA: TARIJA: Villa Ingavi, Caixa 600m (Anderson et al., 1982).

COMMENTS.—Cabrera (1958) assigned Paraguayan populations to the subspecies *blossevilli* Lesson and Garnot.

Lasiurus cinereus Beauvois

Specimens Examined.—PARAGUAY: Boquerón: 417km by rd NW Villa Hayes (1,AMNH). Chaco: 50km WNW Fortín Madrejón (3,UMMZ; 1,AMNH); 67km by rd N Fortín Madrejón (1,AMNH).

MEASUREMENTS.—Males (n=3): FA 51.2 (50.8–51.7), MC3 59.3 (58.3–60.1), GLS 15.5 (15.4–15.7), CB 15.5 (15.4–15.7), ZB 11.4 (11.2–11.6), IOC 5.4 (5.3–5.6), MW 9.7 (9.6–9.8), MM 7.7 (7.6–7.8), CC 6.5 (6.4–6.6), Max 5.5 (5.5–5.6), Total 130.3 (129–132), Tail 55.3 (50–63), HF 11.3 (10–12), Ear 15.7 (15–16).

LITERATURE RECORDS.—BOLIVIA: TARIJA: Villa Montés (Anderson et al., 1982).

COMMENTS.—Cabrera (1958) assigned Paraguayan populations to the subspecies *villosissimus* (Geoffroy).

Lasiurus ega (Gervais)

Specimens Examined.—ARGENTINA: Jujuy: Yuto (1,AMNH). BOLIVIA: Santa Cruz: Buenavista, 400m (1,FMNH). Tarija: Villa Montés (1,FMNH); Caixa (1,USNM). PARAGUAY: Boquerón: 419km by rd NW Villa Hayes (2,AMNH). Central: vicinity of Asunción (15,UMMZ; 29,MVZ). Concepción: 8km by rd E Concepción (2,MVZ). Cordillera: 20km by rd N Altos (5,MVZ); 12km by rd N Tobatí (1,MVZ). Itapúa: 8km

N San Rafael (1,UMMZ). MISIONES: 2km by rd N San Antonio (1,UMMZ). NUEVA ASUNCIÓN: 49.6km by rd N Filadelfia (1,UMMZ); Teniente Ochoa (1,CONN). PARAGUARÍ: Salto de Piraretá, 10km S Piribebuy (3,MVZ). PRESIDENTE HAYES: Retiro Mandeyu, 20km SW of Km 205, Trans Chaco Highway (5,MVZ); 107km by rd NW Villa Hayes (4,MVZ); 211km by rd NW Villa Hayes (1,MVZ); 213km by rd NW Villa Hayes (4,MVZ); 230km by rd NW Villa Hayes (4,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (50,MVZ); 295km by rd NW Villa Hayes (1,MVZ); 300km by rd NW Villa Hayes (1,MVZ); 8km NE Juan de Zalazar (4,UMMZ); vicinity of Line Camp, Juan de Zalazar (1,CONN).

MEASUREMENTS.—Males (n=31): FA 45.1 (42.9–46.9), MC3 53.2 (51.2–55.1), GLS 15.0 (14.1–15.8), CB 14.5 (13.5–15.5), ZB 10.9 (10.2–11.5), IOC 4.5 (4.1–4.9), MW 8.8 (8.2–9.6), MM 7.0 (6.5–7.5), CC 5.9 (5.4–6.2), Max 5.1 (4.7–5.7), Total 118.3 (111–126), Tail 50.1 (42–58), HF 9.8 (8–11), Ear 18.7 (16–20).

Females (n=32): FA 47.6 (46.3–48.9), MC3 55.6 (51.2–59.1), GLS 15.5 (14.6–16.3), CB 15.0 (13.6–15.9), ZB 11.3 (10.1–12.0), IOC 4.5 (4.2–4.8), MW 9.1 (8.5–9.7), MM 7.4 (6.8–8.0), CC 6.3 (5.7–6.6), Max 5.5 (5.0–6.0), Total 126.1 (117–132), Tail 51.7 (45–55), HF 10.5 (9–13), Ear 19.0 (17–21).

LITERATURE RECORDS.—BOLIVIA: TARIJA: Cajixa [=Caixa] (Handley, 1960). PARAGUAY: PRESIDENTE HAYES: Villa Montés (Handley, 1960; at present Villa Montés is within the boundaries of Dept. Tarija, Bolivia). NUEVA ASUNCIÓN: Teniente Ochoa (Wetzel and Lovett, 1974).

COMMENTS.—Reproductive patterns and natural history were discussed by Myers (1977). Specimens from the Chaco tend to be smaller than those from eastern Paraguay, or from the eastern edge of the Andes (Caixa; Table 7). Paraguayan populations were assigned to the subspecies *argentatus* Thomas by Cabrera (1958).

TABLE 7

GEOGRAPHIC VARIATION IN Lasiurus ega
(FEMALES)

	MC3 n	GLS n	ZB n	Max n
Eastern Paraguay	56.1 15	15.8 24	11.5 24	5.6 24
	(1.26)	(0.34)	(0.23)	(0.21)
Central Chaco,	56.0 10	15.4 29	11.3 29	5.4 29
Paraguay	(1.57)	(0.39)	(0.42)	(0.21)
Western Chaco,	51.2 l	15.6 1	11.7 1	5.7 1
Paraguay	(—)	(—)	(—)	(—)
Tarija,	56.7 I	16.1 2	11.8 2	5.9 2
Bolivia		(0.07)	(0.01)	(0.00)
P	0.02	0.002	0.01	0.01

Molossops abrasus (Temminck)

Specimens Examined.—PARAGUAY: Central: vicinity of Asunción (11,UMMZ; 2,MVZ). Concepción: 8km by rd E Concepción (4,MVZ). Presidente Hayes: 230km by rd NW Villa Hayes (1,MVZ); 24km WNW Villa Hayes (4,UMMZ); .3km S line camp, Juan de Zalazar (1,CONN).

MEASUREMENTS.—Males (n=1): FA 48.1, MC3 50.6, GLS 20.8, CB 20.1, ZB 15.2, IOC 5.2, MW 15.5, MM 10.2, CC 6.6, Max 8.3, Total 116, Tail 40, HF 13. Ear 23.

Females (n=1): GLS 20.4, CB 20.0, ZB 14.0, IOC 5.1, MW 13.7, MM 9.8, CC 5.6, Max 7.8, Total 129, Tail 40, HF 12, Ear 19.

LITERATURE RECORDS.—PARAGUAY: CHACO: (Bertoni, 1939).

COMMENTS.—Chacoan specimens agree well with the description given by Thomas (1901a) for *M. cerastes*. Recognition of subspecies, however, awaits revision of the species.

Molossops planirostris (Peters)

Specimens Examined.—BOLIVIA: Beni: San Joaquín (1,FMNH). Santa Cruz: 10km by rd E Ing. Mora (5,MSU); SE end of airport, Santa Cruz (1,MSU). BRAZIL: Mato Grosso: Urucúm (1,FMNH). PARAGUAY: Alto Paraguay: Fuerte Olimpo (5,AMNH); Puerto Casado (1,FMNH). Central: 5km E Asunción (1,MVZ). Chaco: Agua Dulce, 170km W Bahía Negra (1,UMMZ); 67km by rd N Fortín Madrejón (1,UMMZ). Presidente Hayes: 213km by rd NW Villa Hayes (1,MVZ); Retiro Mandeyu, 20km SW of Km 205, Trans Chaco Highway (1,MVZ); .3km S line camp, Río Verde, Juan de Zalazar (2,CONN).

Measurements.—Males (n=4): FA 31.9 (31.5–32.3), MC3 31.8 (24.2–34.5), GLS 15.8 (15.2–16.4), CB 15.2 (15.0–15.3), ZB 10.5 (9.6–10.6), IOC 4.2 (4.0–4.2), MW 10.3 (9.6–10.6), Max 7.4 (7.1–7.5), CC 4.7 (4.4–4.8), Max 6.2, Total 87, Tail 26, HF 7, Ear 15.

Females (n=5): FA 30.8 (30.2–31.4), MC3 32.9 (32.2–33.7), GLS 15.0 (14.2–15.7), CB 14.6 (14.0–15.1), ZB 10.3 (10.1–10.7), IOC 4.2 (4.0–4.3), MW 9.9 (9.7–10.0), MM 7.2 (7.1–7.2), CC 4.1 (4.0–4.2), Max 5.8 (5.4–6.2), Total 78, Tail 23, HF 8, Ear 15.

LITERATURE RECORDS.—None.

COMMENTS.—These specimens are lighter in color and smaller than *M. p. paranus* from Pará, Brazil (measurements in Thomas, 1901b). As in the case of the preceeding species, we prefer to delay assignment of a subspecific epithet until a more comprehensive study of geographic variation is made.

Molossops temminckii (Burmeister)

SPECIMENS EXAMINED.—ARGENTINA: JUJUY: Yuto (16,AMNH); Ledesima (1,AMNH). BOLIVIA: Beni: San Joaquín (2,AMNH; 6,FMNH). SANTA CRUZ: 25km by rd W Buenavista, W bank Río Yapacani (1,UMMZ).

TARIJA: 8km S, 10km E Villa Montés, E bank of Río Pilcomayo (1,AMNH). PARAGUAY: BOQUERÓN: Orloff (3,FMNH); Pedro Peña (1,CONN); 460km by rd NW Villa Hayes (1,MVZ). CANENDIYU: 6.3km by rd NE Curuguaty (1,UMMZ). CENTRAL: vicinity of Asunción (2,MVZ; 2,UMMZ). CHACO: 50km WNW Fortín Madrejón (5,UMMZ); Agua Dulce, 170km W Bahía Negra (1,UMMZ; 2,AMNH; 2,CONN; 2 uncatalogued); 67km by rd N Fortín Madrejón (2,AMNH); 65km by rd N Fortín Madrejón (1,UMMZ). Concepción: 8km by rd E Concepción (2,MVZ). Cordillera: 20km by rd N Altos (1,MVZ). MISIONES: 41km S San Ignacio (3,AMNH). NUEVA ASUN-CIÓN: Teniente Ochoa (1,CONN); 2.5km S of Km 579, Trans Chaco Highway (COPAGRO) (2,CONN). PARAGUARÍ: Parque Nacional Ybycuí (5,UMMZ); Sapucay (2,AMNH; 10,USNM). Presidente Hayes: 24km WNW Villa Hayes (2,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (1,MVZ); 290km by rd NW Villa Hayes (6,CONN); 295km by rd NW Villa Hayes (14,MVZ); vicinity of Río Verde line camp, Juan de Zalazar (33,CONN); Pozo Colorado (1,AMNH). SAN PEDRO: Juan de Mena (1,UMMZ).

Measurements.—Males (n=48): FA 30.0 (27.8–32.8), MC3 32.1 (28.7–33.7), GLS 13.3 (12.0–14.0), CB 12.9 (12.3–13.2), ZB 9.0 (8.2–9.9), IOC 3.7 (3.3–4.1), MW 8.5 (7.8–9.4), MM 6.5 (5.8–7.1), CC 3.9 (3.3–4.2), Max 5.3 (4.7–5.8), Total 73.8 (66–79), Tail 26.0 (20–33), HF 7.6 (5–9), Ear 13.0 (10–15).

Females (n=50): FA 29.7 (28.5–31.0), MC3 31.4 (30.1–33.1), GLS 12.9 (12.1–13.6), CB 12.5 (12.1–13.0), ZB 8.6 (8.1–9.4), IOC 3.6 (3.2–4.1), MW 8.1 (7.7–9.0), MM 6.2 (5.8–6.8), CC 3.6 (3.3–3.9), Max 5.1 (4.6–5.9), Total 72.3 (61–85), Tail 22.9 (14–29), HF 7.5 (6–9), Ear 13.1 (10–15).

LITERATURE RECORDS.—BOLIVIA: TARIJA: 8km S and 10km E of Villa Montés, 467m. (Anderson et al., 1982). PARAGUAY: NUEVA ASUNCIÓN: Teniente Ochoa (Wetzel and Lovett, 1974). PRESIDENTE HAYES: Juan de Zalazar (Wetzel and Lovett, 1974).

COMMENTS.—Most individuals were caught in nets placed over ponds in thorn scrub, or at the edge of clearings in thorn scrub. Many were discovered roosting in roofs made of overlapping, split palm logs, which they shared with *Myotis albescens*, *Myotis nigricans*, and *Eumops bonariensis*.

Geographic variation is striking. Individuals from localities in the north-western Chaco are light brown (Prout's Brown) dorsally, tan ventrally, and small (Table 8). Specimens from the eastern Chaco and eastern Paraguay are blackish dorsally and ventrally, and average 10% larger. Samples from geographically intermediate localities appear intermediate in size and color. Body size increases at the base of the Andes, with individuals from Beni, Santa Cruz, and Jujuy equalling or exceeding eastern Paraguayan specimens in size.

Thomas (1901a) compared specimens of *M. temminckii* from eastern Paraguay with those from the type locality (Lagoa Santa, Brazil), and could find no differences. *M. t. sylvia* Thomas was described from Corrientes, Argentina (Thomas, 1924). It resembles the Chacoan populations in being

lighter than true temminckii, but it is larger in size than M. t. temminckii. The northern subspecies M. t. griseiventer (Sanborn, 1941) also is larger than M. t. temminckii, as is the recently described M. neglectus (Williams and

TABLE 8
GEOGRAPHIC VARIATION IN Molossops temminchii

	FA n	GLS n	ZB n	Max n			
	MALES						
Eastern Paraguay	30.9 10	13.8 10	9.3 9	5.4 11			
	(0.75)	(0.28)	(0.22)	(0.17)			
Central Chaco,	30.2 31	13.6 27	9.1 29	5.4 31			
Paraguay	(0.92)	(0.28)	(0.30)	(0.19)			
Western Chaco,	30.0 8 (0.47)	13.2 8	8.9 4	5.4 8			
Paraguay		(0.31)	(0.21)	(0.09)			
Northern Chaco,	29.5 7	12.7 8	8.5 7	4.9 8			
Paraguay	(0.99)	(0.38)	(0.24)	(0.18)			
Jujuy,	31.3 6 (0.67)	13.4 6	9.1 4	5.3 6			
Argentina		(0.32)	(0.36)	(0.19)			
Santa Cruz,	_ 0	13.7 1	_ 0	5.4 l			
Bolivia	(_)	(—)	(_)	(—)			
Beni,	30.4 4 (0.24)	13.9 4	9.6 2	5.4 4			
Bolivia		(0.28)	(0.28)	(0.08)			
Mato Grosso, Brazil	30.3 3 (0.58)	13.6 4 (0.13)	8.8 4 (0.13)	5.2 4 (0.10)			
P	0.002	0.0001	0.0001	0.0001			
		Fем	ALES				
Eastern Paraguay	29.81 9	13.3 9	8.9 8	5.2 11			
	(0.77)	(0.21)	(0.25)	(0.15)			
Central Chaco,	29.8 31	13.1 27	8.7 29	5.2 29			
Paraguay	(0.61)	(0.30)	(0.19)	(0.14)			
Western Chaco,	29.6 10	12.7 9	8.5 8	5.0 9			
Paraguay	(0.42)	(0.32)	(0.27)	(0.37)			
Northern Chaco,	29.6 8 (0.56)	12.5 10	8.3 8	4.8 10			
Paraguay		(0.18)	(0.20)	(0.12)			
Jujuy, Argentina	31.3 3 (0.61)	13.1 4 (0.22)	8.6 3 (0.17)	5.2 4 (0.08)			
Santa Cruz,	30.6 1	13.2 1	8.6 1	5.2 1			
Bolivia	(—)	(—)	(—)	(—)			
Beni,	30.2 4	13.7 3 (0.35)	9.1 3	5.4 3			
Bolivia	(0.98)		(0.06)	(0.21)			
Mato Grosso,	30.5 3 (1.01)	13.2 3	8.7 3	5.2 3			
Brazil		(0.26)	(0.47)	(0.11)			
P	0.005	0.0001	0.0001	0.0001			

Genoways, 1980). *M. aequatorianus* Cabrera is apparently highly distinctive and has recently been elevated to a new genus, *Cabreramops* (Ibáñez, 1980).

Based on these comparisons, we assign our specimens from eastern Paraguay to the nominate subspecies. Specimens from the northern Chaco are strongly differentiated, but appear to grade into true *temminckii* in the Central Chaco, with no clear breakpoint in morphology separating the populations. Therefore we do not recommend formal taxonomic recognition of the western Chacoan populations.

Sexual dimorphism is striking, with females about 5% smaller than males. Dimorphism affects skull measurements more than wing measurements, and is greater for measures of cranial breadth than cranial length.

Eumops auripendulus (Shaw)

Specimens Examined.—BOLIVIA: Beni: Azunta (2,FMNH); San Joaquín (4,FMNH). Santa Cruz: 10km by rd E Ing. Mora (8,MSU). PARAGUAY: Central: vicinity of Asunción (2,MVZ). Concepción: 8km by rd E Concepción (1,MVZ).

Measurements.—None.

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: 10km by rd E Ing. Mora (Anderson et al., 1982). PARAGUAY: CENTRAL: Asunción, Recoleta (Eger, 1977).

COMMENTS.—Specimens from both sides of the Chaco (eastern Paraguay along the Río Paraguay and the base of the Andes in Santa Cruz, Bolivia) were examined, although so far no specimens have actually been captured in the Chaco. Those from Santa Cruz are smaller than those from eastern Paraguay, although samples are too small to permit statistical testing. The western populations agree with the measurements given for *E. a. auripendulus* by Eger (1977), while the eastern specimens are *E. a. major*.

Eumops bonariensis (Peters)

SPECIMENS EXAMINED.—BOLIVIA: BENI: San Joaquín (10,FMNH); Itenez, Magdalena (6,USNM). PARAGUAY: ALTO PARAGUAY: Fuerte Olimpo (19,AMNH). Boquerón: 35km by rd E Filadelfia (1,AMNH); 10km by rd S Filadelfia (2,AMNH); Estancia Pirazal, 80km SW Neuland (1,CONN); Pedro P. Peña (1,CONN). CANENDIYU: Curuguaty (1,AMNH). CENTRAL: vicinity of Asunción (3,AMNH; 12,MVZ; 4,UMMZ). CHACO: Agua Dulce, 170km W Bahía Negra (5,UMMZ); 65km by rd N Fortín Madrejón (14,UMMZ; 7,AMNH). Concepción: 8km by rd E Concepción (4,MVZ). GUIARÁ: Villarica (1,AMNH). ITAPÚA: Encarnación (1,MVZ). NUEVA ASUNCIÓN: 49.6km by rd N Filadelfia (23,UMMZ); Trans Chaco Highway, Km 589 (6,UMMZ); 3km SW Km 620 Trans Chaco Highway (2,uncatalogued); 19km by rd SW Km 588, Trans Chaco Highway (45,uncatalogued); Teniente Ochoa (79,CONN). Presidente Hayes: Pozo Colorado (2,AMNH); 24km WNW Villa Hayes (1,UMMZ); Retiro Mandeyu, 20km SW Km 205, Trans Chaco Highway (1,MVZ); 230km by rd NW Villa Hayes (3,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (12,MVZ); Juan de Zalazar (1,CONN); 85km E Loma Plata (1,CONN).

MEASUREMENTS.—Males (n=27): FA 44.2 (41.9–46.2), MC3 46.0 (43.6–48.6), GLS 17.5 (16.9–19.0), CB 16.5 (15.9–18.0), ZB 10.9 (10.6–11.6), IOC 4.1 (3.7–4.4), MW 10.3 (9.8–11.2), MM 7.7 (7.4–8.2), CC 4.3 (4.1–4.7), Max 6.8 (6.5–7.3), Total 101.0 (92–114), Tail 35.2 (30–40), HF 9.7 (8–11), Ear 19.9 (18–23).

Females (n=40): FA 43.6 (40.2–45.7), MC3 45.3 (42.2–48.4), GLS 17.1 (16.3–17.7), CB 16.1 (15.3–16.6), ZB 10.7 (10.2–11.2), IOC 4.1 (2.9–4.4), MW 10.1 (9.6–10.6), MM 7.6 (7.2–8.0), CC 4.1 (3.8–4.5), Max 6.7 (6.4–7.1), Total 99.0 (92–110), Tail 33.8 (27–39), HF 9.3 (7–10), Ear 19.2 (18–21).

LITERATURE RECORDS.—PARAGUAY: BOQUERÓN: Teniente Ochoa (Wetzel and Lovett, 1974). Presidente Hayes: 275km by rd NW Villa Hayes; 230 km by rd NW Villa Hayes (Eger, 1977); Waikthlatingmangyalwa (Thomas, 1901a).

COMMENTS.—These are common house bats in the Chaco, where they usually inhabit roofs made of overlapping split palm logs along with several other species (see account of *Molossops temminckii*). Large numbers of these bats were also captured in nets set over ponds.

Color varies geographically, with dorsal coloration tending to be lighter (Mummy Brown) in the northwest Chaco, and darker (nearly black) in the eastern Chaco and in eastern Paraguay. A few cranial measurements also showed slight geographic variation (Table 9), with animals from eastern Paraguay and the central Chaco tending to be larger than those from the northwestern Chaco.

Eger (1977) assigned populations from the Chaco Boreal to the subspecies beckeri Sanborn.

FA MM Max n 7.7 Eastern Paraguay 43.1 9 6.9 9 (0.92)(0.15)(0.10)7.5 Eastern Chaco, 43.7 6.6 (1.23)(0.19)(0.14)Paraguay Central Chaco, 42.810 7.6 10 6.7 10 Paraguay (1.48)(0.18)(0.17)44.2 11 Western Chaco, 7.7 11 6.7-11 Paraguay (0.88)(0.19)(0.15)43.7 9 7.6 11 6.611 Northern Chaco, (0.23)(0.13)Paraguay (1.06)Beni, 44.3 7.7 10 6.7 10 Bolivia (0.93)(0.18)(0.20)P 0.040.05 0.04

TABLE 9
GEOGRAPHIC VARIATION IN Eumops bonariensis

Eumops dabbenei Thomas

SPECIMENS EXAMINED.—COLOMBIA: Magdalena: Magdalena River (1,PANS). PARAGUAY: PRESIDENTE HAYES: .3km S line camp, Río Verde, Juan de Zalazar (1,CONN); 24km WNW Villa Hayes (8,UMMZ). VENEZUELA: Yaraguy: 10km NW of Urama, Río Yaraguy (1,USNM).

MEASUREMENTS.—Males (n=3): FA 78.1 (78.0–78.1), MC3 79.2 (79.2–79.2), GLS 32.1 (31.8–32.4), CB 31.6 (31.3–31.9), ZB 20.1 (19.9–20.3), IOC 6.3 (6.1–6.6), MW 17.1 (17.1–17.2), MM 13.7 (13.5–14.0), CC 8.7 (8.6–8.8), Max 13.5 (13.4–13.6), Total 189.7 (188–192), Tail 63.3 (62–66), HF 18.0 (18–18), Ear 31.7 (31–32).

Females (n=3): FA 78.1 (78.1–78.1), MC3 80.5 (80.5–80.5), GLS 30.9 (29.7–31.9), CB 30.0 (28.4–30.9), ZB 19.7 (19.7–19.7), IOC 6.0 (5.8–6.2), MW 16.8 (16.7–16.9), MM 13.4 (13.1–13.6), CC 8.3 (8.2–8.4), Max 13.0 (12.5–13.3), Total 187.5 (184–191), Tail 62.5 (59–66), HF 18.0 (18–18), Ear 29.0 (28–30).

LITERATURE RECORDS.—PARAGUAY: PRESIDENTE HAYES: 2km SE of Misión Inglesa (Harrison et al., 1979).

COMMENTS.—The specimens from near Villa Hayes were captured as they emerged from the top of a hollow, dead tree, approximately 5m above the ground. The interior of the trunk was laced with interconnecting narrow cracks, in which the bats apparently roosted. The tree stood along a dirt road near a small artificial lake, surrounded by thorn forest and palm savanna. When handled the bats emitted piercing shrieks, which we also heard as bats foraged overhead. The males possessed greatly enlarged gular glands, the secretions of which stained and matted the fur of the neck.

Cabrera (1958) synonomized dabbenei with Eumops perotis. This was contradicted by Eger (1977), who recognized dabbenei as a valid species, though expressing some doubt. Her phenetic analysis of the genus *Eumops* (1977) alternately linked dabbenei with perotis or underwoodi, or placed it as an outlier to a group variously composed of several species of *Eumops*. Massoia (1976) described E. underwoodi mederai, with type locality near the type of dabbenei. He did not compare the new subspecies with dabbenei, suggesting he was not aware of that species. We concur with Ibáñez (1979) in considering E. u. mederai a junior synonym of E. dabbenei, and with Massoia (1976) and Ibáñez (1979) in stressing the relationship between dabbenei (=mederai) and underwoodi. The following features distinguish dabbenei and underwoodi from perotis: (1) short, broad palate (vs. long and narrow); (2) shallow basisphenoid pits (vs. deep); (3) lambdoidal crest very well developed (vs. moderate); (4) nostrils not tubular (vs. nasals raised in center, giving nasal aperature a tubular appearance); (5) anterior upper premolar crowded to the side of the toothrow (vs. included within the toothrow and not crowded); (6) posterior loph of M3 weakly developed or absent (corresponding to character states four or five of character C66, Freeman, 1981) (vs. character state three moderately developed); (7) incisors extremely proodont (vs. moderately proodont); (8) molars broad due to a well-developed hypocone (vs. molars less broad); (9) baculum present (vs. absent; Ibáñez, 1979); (10) posteriorly directed bristles (vibrissae) project from rump over uropatagium (vs. rump vibrissae absent); (11) ears large (vs. ears extremely large).

Molossid systematics are unsettled (Freeman, 1981) and choice of outgroups to determine the polarity of these characters is difficult. Based on the states of these characters in the genera *Molossus*, *Promops*, and *Molossops* (including *Cynomops*) we estimate that characters 3, 5, 7, and 8 represent synapomorphies, while the remaining similarities probably either are plesiomorphic or their polarity cannot be determined at present.

Characters 3, 5, 7, and 8 suggest that underwoodi and dabbenei shared a common ancestor more recently than either did with perotis. The resemblance between the former two is strong, with the primary difference being size. Do both merit specific recognition? E. underwoodi is known only from Mexico and Central America, south to Honduras (Eger, 1977). E. dabbenei is known from the Chaco, and from localities in northern South America (one specimen from Colombia, four from Venezuela, Eger, 1977; Ibáñez, 1979). No specimens have been taken in the intervening part of Central America. Northern underwoodi (E. u. sonoriensis) are small, approximately 90% the size of E. dabbenei, while southern populations (E. u. underwoodi) tend to be larger, approaching 95% the size of dabbenei (measurements of E. u. underwoodi from Eger, 1977). On the other hand, a trend toward increasing size in the northern populations of dabbenei was suggested by Ibáñez (1979) and is a reinforced by our measurements. Nevertheless, based on the high degree of morphological similarity between dabbenei and underwoodi, we predict that populations intermediate in size will be discovered in Panama and Costa Rica, and that underwoodi will be considered at best a subspecies of *dabbenei*. At this time, however, the evidence available is not sufficient to justify a formal taxonomic recommendation.

Eumops glaucinus (Wagner)

Specimens Examined.—BOLIVIA: Santa Cruz: 10km by rd E Ing. Mora (4,MSU). PARAGUAY: Presidente Hayes: Rincón Charrúa, 275km by rd NW Villa Hayes (5,MVZ).

Females (n=2): FA 60.1 (59.8–60.4), MC3 62.5 (62.2–62.7), GLS 23.2 (23.1–23.3), CB 22.7 (22.5–22.9), ZB 14.8 (14.8–14.8), IOC 5.3 (5.2–5.4), MW 13.2 (13.0–13.3), MM 10.3 (10.2–10.4), CC 6.0 (6.0–6.1), Max 9.9 (9.9–9.9), Total 144.0 (142–146), Tail 51.0 (50–52), HF 13.5 (13–14), Ear 27.0 (26–28).

LITERATURE RECORDS.—BOLIVIA: SANTA CRUZ: 10km by rd E Ing. Mora (Anderson et al., 1982). PARAGUAY: PRESIDENTE HAYES: 275km by rd NW Villa Hayes (Eger, 1977).

COMMENTS.—Specimens from the lower Chaco are similar in size and color to those from Santa Cruz, Bolivia.

Eger (1977) assigned populations from the Chaco Boreal to the nominate subspecies.

Eumops perotis (Schinz)

Specimens Examined.—ARGENTINA: Jujuy: Yuto (1,AMNH). BOLIVIA: Beni: San Joaquín (15,FMNH). PARAGUAY: Chaco: Agua Dulce, 170km W Bahía Negra (1,UMMZ; 2,AMNH); 67km by rd N Fortín Madrejón (1,UMMZ). San Pedro: Juan de Mena (1,UMMZ).

MEASUREMENTS.—Males (n=3): FA 81.6 (80.5–83.2), MC3 83.0 (82.5–83.3), GLS 32.2 (31.5–32.8), CB 31.1 (31.0–31.3), ZB 19.3 (19.1–19.6), IOC 5.4 (5.3–5.5), MW 15.9 (15.7–16.2), MM 13.2 (12.7–13.4), CC 8.8 (8.7–8.9), Max 13.2 (13.0–13.3), Total 178.0 (171–185), Tail 59.5 (59–60), HF 17.0 (16–18).

Females (n=1): FA 79.8, MC3 80.2, GLS 31.2, CB 30.1, ZB 18.7, IOC 5.3, MW 15.2, MM 13.3, CC 8.8, Max 13.2.

LITERATURE RECORDS.—PARAGUAY: BOQUERÓN: Filadelfia (Eger, 1977). COMMENTS.—Paraguayan individuals of this species average approximately 10% larger than individuals of *E. p. californicus* from North and Central America (see measurements in Eger, 1977), paralleling the variation seen in *E. dabbenei/E. underwoodi*. In general the northern Chacoan specimens were slightly larger than those from Beni, but small samples precluded statistical comparison.

Eger (1977) assigned populations from the Chaco Boreal to the nominate subspecies.

Tadarida brasiliensis (Geoffroy)

Specimens Examined.—ARGENTINA: Chaco: Barranqueras (1,ROM). Jujuy: Yuto (3,AMNH). Salta: Cerillos (1,ROM). Tucumán: Monteagudo (2,ROM). PARAGUAY: Central: Asunción (1,UMMZ). Guiará: Villarica (1,AMNH). Itapúa: Encarnación (3,MVZ).

Measurements.—None.

LITERATURE RECORDS.—None.

COMMENTS.—*T. brasiliensis* almost certainly occurs in the Paraguayan or Bolivian Chaco, though we know of no records. Specimens are available from Asunción (on the east bank of the Río Paraguay), from the Chaco Central immediately south of the Río Pilcomayo in Prov. Formosa, Argentina (Barquez and Ojeda, 1975), and from the western border of the Chaco at Yuto, Prov. Jujuy, Argentina.

Tadarida laticaudata (Geoffroy)

Specimens Examined.—BOLIVIA: Beni: Magdalena (13,AMNH). Tarija: 8km S, 10km E Villa Montés, E bank of Río Pilcomayo, 467m (1,AMNH). PARAGUAY: Central: vicinity of Asunción (20,AMNH; 2,ROM). Chaco: 50km WNW Fortín Madrejón (5,UMMZ; 2,AMNH). Cordillera: 1.6km by rd S Tobatí (13,UMMZ); 2km by rd S Tobatí (4,MVZ). Paraguarí: Parque Nacional Ybycuí (1,UMMZ).

MEASUREMENTS.—Males (n=4): FA 45.1 (44.8–45.4), MC3 45.1 (44.1–46.1), GLS 18.0 (17.7–18.3), CB 16.8 (16.5–17.0), ZB 10.3 (10.0–10.4), IOC 3.6 (3.5–3.6), MW 10.0 (9.8–10.0), MM 7.5 (7.2–7.6), CC 4.1 (3.9–4.1), Max 6.8 (6.5–7.0), Total 106.5 (102–113), Tail 39.3 (37–42), HF 9.5 (9–10), Ear 19.8 (19–21).

Females (n=1): FA 45.1, MC3 45.2, GLS 17.5, CB 16.4, ZB 9.9, IOC 3.6, MW 9.9, MM 7.2, CC 3.7, Max 6.6, Total 100, Tail 35, HF 10, Ear 20.

LITERATURE RECORDS.—BOLIVIA: TARIJA: 8km S and 10km E Villa Montés (Anderson et al., 1982).

COMMENTS.—Chacoan specimens are strikingly smaller and lighter than those from eastern Paraguay, but slightly larger than specimens from Beni (Table 10). Males average 2–4% larger than females in most dimensions.

TABLE 10
GEOGRAPHIC VARIATION IN Tadarida laticaudata

	FA	n	GLS n	ZB n	Max n
			MA	ALES	
Eastern Paraguay	46.7 (1.15)	8	18.5 17 (0.28)	10.5 16 (0.26)	7.0 17 (0.19)
Northern Chaco, Paraguay	45.1 (0.26)	4	18.0 4 (0.25)	10.3 4 (0.17)	6.8 4 (0.21)
Tarija, Bolivia	46.7 (—)	1	18.2 1 (—)	10.2 1 (—)	7.0 1 (—)
Beni, Bolivia	— (—)	0	17.0 5 (0.38)	9.9 7 (0.05)	6.4 9 (0.31)
P	0.05		0.0001	0.0001	0.0001
			FEM	IALES	
Eastern Paraguay	45.4 (1.15)	5	18.1 17 (0.35)	10.4 16 (0.13)	6.9 18 (0.17)
Northern Chaco, Paraguay	45.1 (—)	1	17.5 l (—)	9.9 1 (—)	6.6 1 ()
Beni, Bolivia	_ (_)	0	16.4 1 (—)	9.8 2 (0.07)	6.4 3 (0.15)
P	0.84		0.0005	0.0001	0.001

Specimens from eastern Paraguay may be referred to the nominate subspecies, while the small northern Chacoan populations are probably *T. l. europs* (Allen) (Silva-Taboada and Koopman, 1964).

Tadarida macrotis (Gray)

Specimens Examined.—PARAGUAY: Alto Paraguay: Fuerte Olimpo (1,AMNH).

Measurements.—None.

LITERATURE RECORDS.—None.

COMMENTS.—A single specimen, a juvenile with a partially disarticulated skull, is known from the Chaco.

Promops centralis Thomas

Specimens Examined.—PARAGUAY: Central: vicinity of Asunción (6,UMMZ; 4,MVZ). Concepción: 8km by rd E Concepción (1,MVZ). Cordillera: 20km by rd N Altos (2,MVZ). Guiará: Villarica (1,USNM). Paraguarí: Sapucay (3,USNM). Presidente Hayes: Rincón Charrúa, 275km by rd NW Villa Hayes (1,MVZ).

MEASUREMENTS.—Female (n=1): FA 51.7, MC3 54.9, GLS 19.1, CB 18.2, ZB 12.5, IOC 4.1, MW 11.7, MM 8.9, CC 5.1, Max 7.4, Total 124, Tail 47, HF 11, Ear 18.

LITERATURE RECORDS.—None.

COMMENTS.—Thomas (1915) named *P. occultus* from eastern Paraguay. We follow Handley (1960) in referring *occultus* to subspecific status under *centralis*. The Chacoan specimen is indistinguishable from those from eastern Paraguay.

Promops nasutus (Spix)

Specimens Examined.—ARGENTINA: Jujuy: Yuto (4,AMNH). PARAGUAY: Chaco: Agua Dulce, 170km W Bahía Negra (1,UMMZ). Guiará: Itapé (3,USNM); Villarica (3,USNM). Nueva Asunción: 49.6km by rd N Filadelfia (1,UMMZ); Teniente Ochoa (1,CONN; 1,USNM); 19km by rd WSW Km 588, Trans Chaco Highway (1,UMMZ). Paraguarí: Sapucay (9,USNM).

Measurements.—Male (n=1): GLS 17.3, CB 16.0, ZB 11.2, IOC 3.9, MW 10.6, MM 7.9, CC 4.2, Max 6.7.

Females (n=2): FA 49.3 (49.2–49.3), MC3 52.2 (52.0–52.4), GLS 17.6 (17.4–17.8), CB 16.4 (16.1–16.6), ZB 11.0 (10.9–11.1), IOC 4.1 (3.9–4.2), MW 11.1 (10.7–11.4), MM 7.8 (7.7–7.9), CC 4.2 (4.1–4.3), Max 6.7 (6.6–6.7), Total 124.0 (122–126), Tail 45.0 (41–49), HF 9.5 (9–10), Ear 13.5 (13–14).

LITERATURE RECORDS.—PARAGUAY: BOQUERÓN: (now Nueva Asunción): Teniente Ochoa (Wetzel and Lovett, 1974). "Chaco" (Bertoni, 1939).

COMMENTS.—Thomas (1901a) described a small species, *P. fosteri*, from Villa Rica, eastern Paraguay, and later (1915) named a larger species, *P.*

occultus, from the same locality. In 1915 he also named P. ancilla, a small species (slightly smaller than P. fosteri) from Prov. Salta, in the Argentine Chaco. He distinguished P. ancilla from P. fosteri by its size, lighter color and less inflated braincase. Are Chacoan P. ancilla and eastern Paraguayan P. fosteri conspecific? The size and color differences described by Thomas (1901a, 1915), and confirmed by our comparison of Chacoan and eastern Paraguayan material, parallel changes occurring among eastern and Chacoan species of other molossid bats reported above, and indeed seem to be less extreme (judging by the measurements given by Thomas) than those among populations of, for example, Molossops temminckii. It is difficult to assess the systematic importance of the degree of swelling of the braincase. Certainly, within a series of *P. centralis occultus* from eastern Paraguay considerable variation in swelling appears to be present. We strongly suspect that eastern Paraguayan populations of P. fosteri will prove conspecific with P. ancilla, which is usually regarded as representing a subspecies of P. nasutus (e.g., Genoways and Williams, 1979). With further study ancilla and fosteri both may prove to be junior synonyms of P. n. nasutus (type locality Río São Francisco, eastern Brazil).

Molossus ater E. Geoffroy

Specimens Examined.—BOLIVIA: Beni: San Joaquín (8,FMNH). Santa Cruz: Buenavista (1,FMNH). BRAZIL: Mato Grosso: Descalvados, Río Paraguay (1,USNM; 5,FMNH); 284km by rd N Xavantina (18,USNM). Minas Gerais: 3mi NE Viscosa (10,USNM). PARAGUAY: Alto Paraguay: Fuerte Olimpo (2,AMNH). Central: vicinity of Asunción (28,UMMZ; 1,MVZ; 1,CONN). Concepción: 8km by rd E Concepción (6,MVZ). Cordillera: 20km by rd N Altos (1,MVZ). Guiará: Villarica (2,USNM). Misiones: 2.7km by rd N San Antonio (1,UMMZ). Paraguarí: Sapucay (8,USNM); Salto de Piraretá, 10km S Piribebuy (3,MVZ). Presidente Hayes: Retiro Mandeyu, 20km SW of Km 205 on Trans Chaco Highway (2,MVZ); 230km by rd NW Villa Hayes (3,MVZ); 320km by rd NW Villa Hayes (1,MVZ); .3km S line camp, Río Verde, Juan de Zalazar (5,CONN).

Females (n=3): FA 47.8 (45.2–50.0), MC3 49.5 (46.6–51.3), GLS 20.7 (19.9–21.3), CB 19.0 (18.3–19.7), ZB 13.4 (12.9–14.0), IOC 4.3 (4.2–4.3), MW 12.9 (12.1–13.4), MM 9.5 (9.2–9.9), CC 5.6 (5.2–6.0), Max 8.0 (7.8–8.2), Total 123.5 (121–126), Tail 40.5 (39–42), HF 12.0 (11–13), Ear 19.0 (18–20).

LITERATURE RECORDS.—PARAGUAY: PARAGUARÍ: Sapucay. GUIARÁ: Villarica (Miller, 1913b).

COMMENTS.—Roosts were discovered in the space between corrugated iron roofing and its wooden backing, and in cracks and small hollows in trees.

No evidence of differentiation of Chacoan populations compared to populations in the eastern region was noted, but few specimens from the Chaco were available. Paraguayan specimens are considerably larger than those from Beni. They agree well in size with animals from Mato Grosso and Minas Gerais, but tend to be dark brown in contrast to black (Minas Gerais) or brownish black or black (northern Mato Grosso). Sexual dimorphism is pronounced, with females about 6% smaller than males in most dimensions. The systematics of large *Molossus* in South America are poorly understood; we follow Goodwin (1960), Husson (1962), and Koopman (1978) in applying the specific name *ater* to this bat.

Molossus molossus (Pallas)

EXAMINED.—ARGENTINA: Jujuy: Yuto (2,AMNH). BOLIVIA: Beni: San Joaquín (10,FMNH); Itenez, Magdalena (28,USNM); Tumapasa (2,USNM); Huachi (1,USNM); Vacadias, Riberalta (1,USNM); Rurrenebaque (1,USNM). SANTA CRUZ: Buenavista (12,FMNH); 10km E Ing. Mora (20, MSU). BRAZIL: MATO GROSSO: 264km by rd N Xavantina (1,USNM). MINAS GERAIS: 3mi ESE Sete Lagoas (5,USNM). PARAGUAY: ALTO PARAGUAY: Fuerte Olimpo (2,AMNH). BOQUERÓN: 419km by rd NW Villa Hayes (6,AMNH); Pedro P. Peña (4,CONN). CANENDIYU: Igatimí (2,AMNH); 13.3km by rd N Curuguaty (4,UMMZ). CENTRAL: vicinity of Asunción (1,USNM; 7,UMMZ; 2,MVZ). CHACO: Agua Dulce, 170km W Bahía Negra (13,UMMZ; 6,AMNH); 50km WNW Fortín Madrejón (1,UMMZ); 65km by rd N Fortín Madrejón (3,UMMZ); 67km by rd N Fortín Madrejón (10,UMMZ); 49.6km by rd N Filadelfia (17,UMMZ). Guiara: Tacuaral (9,USNM); Villarica (4,USNM; 2,AMNH). Paraguarí: Yaguarón (1,AMNH). Presidente Hayes: 220km by rd NW Villa Hayes (1,MVZ); 230km by rd NW Villa Hayes (1,MVZ); Rincón Charrúa, 275km by rd NW Villa Hayes (7,MVZ); 290km by rd NW Villa Hayes (10,CONN); .3km S line camp, Río Verde, Juan de Zalazar (1,CONN); Orloff (1,FMNH); Pozo Colorado, Trans Chaco Highway Km 250 (9,AMNH).

Measurements.—Males (n=24): FA 39.1 (36.2–40.1), MC3 40.9 (39.0–42.9), GLS 16.8 (16.4–17.6), CB 15.4 (15.0–16.1), ZB 10.8 (10.2–11.5), IOC 3.7 (3.5–3.9), MW 10.5 (10.0–11.2), MM 7.8 (7.6–8.2), CC 4.4 (4.2–4.6), Max 6.3 (6.2–6.5), Total 101.8 (96–110), Tail 34.7 (29–41), HF 9.3 (7–10), Ear 13.0 (11–14).

Females (n=47): FA 38.7 (34.3–42.1), MC3 40.9 (38.5–44.3), GLS 16.1 (15.2–17.5), CB 14.8 (14.1–16.0), ZB 10.3 (9.7–11.2), IOC 3.6 (3.3–3.9), MW 10.0 (9.6–10.9), MM 7.5 (6.8–8.5), CC 4.2 (3.8–5.0), Max 6.1 (5.8–6.8), Total 97.5 (90–106), Tail 35.4 (31–39), HF 9.0 (7–11), Ear 12.8 (12–14).

LITERATURE RECORDS.—BOLIVIA: TARIJA: Villa Ingavi, Caixa (Anderson et al., 1982). PARAGUAY: Guiará: Villarica; Tacuaral (Miller, 1913b). Nueva Asunción: Teniente Ochoa (Wetzel and Lovett, 1974: *M. major crassicaudatus*).

COMMENTS.—We follow Husson (1962) in use of the name *Molossus molossus* for this species.

Several roosts were discovered in the roofs of buildings, where bats occurred either solitarily or in small groups. Most individuals, however, were captured in mist nets set over small ponds.

Specimens from the northern Chaco tend to be lighter in dorsal color (Prout's Brown) than those from eastern Paraguay (Mummy Brown). Within Paraguay, geographic variation in size is slight (Table 11). Specimens from the western border of the Chaco in Santa Cruz, Bolivia, and to the north in Beni, Bolivia, tend to be 3–4% larger than those from the Paraguayan Chaco. Sexual dimorphism is pronounced, with females averaging 5% smaller than males in most dimensions.

TABLE 11
GEOGRAPHIC VARIATION IN Molossus molossus

	FA n	GLS n	ZB n	Max n
		MA	LES	
Eastern Paraguay	38.2 6	16.7 6	10.8 6	6.3 6
	(1.40)	(0.18)	(0.18)	(0.12)
Central Chaco,	39.1 10	16.9 12	10.9 12	6.3 13
Paraguay	(1.53)	(0.41)	(0.34)	(0.11)
Western Chaco, Paraguay	_ 0 (_)	16.8 5 (0.15)	10.8 5 (0.13)	6.3 5 (0.11)
Northern Chaco, Paraguay	39.1 3 (1.02)	16.7 6 (0.21)	10.7 6 (0.23)	6.3 6 (0.08)
Santa Cruz,	41.5 2 (0.64)	17.2 11	11.0 11	6.6 12
Bolivia		(0.27)	(0.32)	(0.11)
Beni,	41.7 7	17.4 24	11.2 23	6.2 24
Bolivia	(1.06)	(0.37)	(0.29)	(0.14)
<i>P</i>	0.001	0.0001	0.0004	0.0001
•			ALES	
Eastern Paraguay	38.1 20	16.1 16	10.4 16	6.0 16
	(1.26)	(0.33)	(0.22)	(0.15)
Central Chaco,	38.4 14	16.1 20	10.3 20	6.1 20
Paraguay	(1.62)	(0.39)	(0.26)	(0.14)
Western Chaco, Paraguay	_ 0 (—)	16.2 5 (0.12)	10.3 5 (0.05)	6.1 5 (0.07)
Northern Chaco,	38.6 11	16.1 20	10.2 20	6.1 20
Paraguay	(0.81)	(0.34)	(0.24)	(0.14)
Santa Cruz,	41.0 9	16.5 18	10.6 18	6.4 19
Bolivia	(0.85)	(0.29)	(0.28)	(0.11)
Beni,	40.6 15	16.8 29	10.7 26	6.4 29
Bolivia	(1.40)	(0.30)	(0.21)	(0.11)
P	0.0001	0.0001	0.0001	0.0001

DISCUSSION

ZOOGEOGRAPHIC PATTERNS

Recent papers on Chacoan zoogeography outline often conflicting patterns of endemism and phyletic relationship. In the most detailed study yet published, Short (1975) emphasized the low endemicity of the Chacoan avifauna, as well as the tendency for species of birds that occur in the Chaco to be widely distributed over South America. Strongly repeated patterns of phyletic relationships of Chacoan bird species to those of other areas were generally lacking, with the weak exception of the arid Caatinga region of Brazil (Short, 1975; Fitzpatrick, 1980). In contrast, Gallardo (1979) showed substantial endemism among the amphibian fauna of the Chaco, with an often-repeated pattern of sister group relationships between species endemic to the Chaco and those occurring to the east of the Río Paraná. Gallardo (1979) discovered a similar pattern for snakes, but in contrast, he found that Chacoan lizard species generally were most closely related to species in the Andean foothills and Patagonia. Myers (in press) reported that the rodent fauna of the Paraguayan Chaco differs sharply from that of Paraguay's eastern region, and contains a substantial number of endemics. In general Chacoan rodent species appear most closely related to members of faunas in the Andes and to the south, rather than to Amazonian or eastern Paraguayan and Brazilian forms.

The Chaco Boreal lacks endemic species of bats. Further, most of its bat species have very broad distributions over South America. To document this pattern we compiled Table 12, which lists the bat species known from each of eight faunas in South America. These faunas were chosen on the basis of their representing diverse geographical and ecological regions of South America, and of the availability of published accounts of species occurring in each area. Detailed faunal comparisons are difficult to make at this time because of numerous disagreements among authorities about the nomenclature used for many groups of South American bats, and Table 12 undoubtedly is marred by duplications and omissions. Nevertheless, we believe that the general pattern presented therein probably portrays with reasonable accuracy the zoogeographic affinities of the Chaco's chiropteran fauna.

Of the 37 Chacoan species included in Table 12, six occur in each of the eight faunas listed, and 10 additional species occur in every fauna except that of Uruguay. Thus, nearly half of the Chacoan bat species have a documented range crossing the northern two-thirds of the continent. Of the remaining 21 species, two are known to occur in every fauna except that of Venezuela. In addition, based on their distributions, we believe 14 more species will prove to range widely and perhaps continuously over much of the area covered by these surveys, except probably Uruguay (Noctilio albiventris, Tonatia bidens, Phyllostomus discolor, Chrotopterus auritus, Myotis albescens, Myotis riparius, Lasiurus cinereus, Molossops abrasus, Tadarida laticaudata, Tadarida macrotis, Tadarida brasiliensis, Eumops glaucinus, Promops

TABLE 12
DISTRIBUTION RECORDS OF SOUTH AMERICAN BATS

S. 500 S.	-	Amazon	; ;	NE 1.	SE	Eastern	Chaco	
sanado	v enezuela ·	reru-	Bolivia	Brazil '	Brazil	Paraguay	Boreal	Uruguay ^o
Rhynchonycteris naso	×	×	X		×			
Saccopteryx bilineata	×	×	×	×	×			
Saccopteryx canescens	×	×						
Saccopteryx laptura	×	×	×	×				
Cormura brevirostris	×	×						
Peropteryx kappleri	×	×			×			
Peropteryx macrotis	×	×	×	×	×	×	×	
Peropteryx leucopterus	×	×						
Peropteryx trinitatus	×							
Centronycteris maximiliani	×				×			
Diclidurus albus	×	×			×			
Diclidurus ingens	×							
Diclidurus isabellus	×							
Diclidurus scutatus	×							
Noctilio albiventris	×	×	×	×		×	×	
Noctilio leporinus	×	×	×	×	×	×	×	
Chilonycteris rubiginosa	×							
Pteronotus davyi	×			×				
Pteronotus parnellii	×	×		×				
Pteronotus gymnonotus		×						
Pteronotus personatus	×			×				
Pteronotus suapurensis	×							
Mormoops megalophylla	×							
Micronycteris brachyotis	×							
Micronycteris hirsuta	×	×						
Micronycteris megalotis	×	×	×		×			
Micronycteris microtis	×							

TABLE 12 Continued

		Amazon		NE	SE	Fastern	Chaco	
Species	Venezuela ¹	Peru ²	Bolivia ³	Brazil ⁴	Brazil ⁵	Paraguay	Boreal	Uruguay ⁶
Micronycteris minuta	×	×	×	×	×			
Micronycteris nicefori	×	×						
Micronycteris schmidtorum	×							
Micronycteris sylvestris	×	×			×			
Micronycteris daviesi	×	×						
Lonchorhina aurita	×	×	×	×	×			
Lonchorhina orinocensis	×							
Macrophyllum macrophyllum	×	×	×		×			
Tonatia brasiliense	×	×		×				
Tonatia carrikeri	×	×	×					
Tonatio bidens	×	×		×	×	×	×	
Tonatia silvicola	×	×	×		×	×		
Tonatia schulzi	×							
Mimon crenulatum	×	×	×	×				
Mimon bennettii					×			
Phyllostomus discolor	×	×	×	×	×		×	
Phyllostomus elongatus	×	×	×		×			
Phyllostomus hastatus	×	×	×	×	×	×	×	
Phyllostomus latifolius	×							
Phylloderma stenops	×	×	×		×			
Trachops cirrhosus	×	×	×	×	×			
Chrotopterus auritus	×		×		×	×	×	
Vampyrum spectrum	×	×						
Glossophaga soricina	×	×	×	×	×	×	×	
Glossophaga longirostris	×							
Lonchophylla thomasi	×	×	×					
Lonchophylla robusta	×	×						
Lonchophylla mordax				×				

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Lionycteris spurrelli Anoura brevirostrum	Anoura caudifer	Anoura cultrata	Anoura geoffroyi	Choeroniscus intermedius	Choeroniscus godmani	Choeroniscus minor	Leptonycteris curasoae	Lichonycteris obscura	Lichonycteris degener	Scleronycteris ega	Carollia castanea	Carollia perspicillata	Carollia brevicauda	Rhinophylla pumilio	Rhinophylla fischeri	Sturnira erythromos	Sturnira bidens	Sturnira bogotensis	Sturnira lilium	Sturnira oporaphilum	(=ludovici)	Sturnira magna	Sturnira nana	Sturnira tildae	Uroderma bilobatum	Uroderma magnirostrum	Vampyrops aurarius	Vampyrops dorsalis	Vampyrops lineatus	Vampyrops infuscus	Vampyrops helleri	Vampyrops umbratus

TABLE 12 Continued

Vampyrops vittatus Vampyrops brachycephalus Vampyrossa melissa Vampyressa melissa Vampyressa bidens Vampyressa bidens Vampyressa bidens Chiroderma trinitatum Chiroderma alvini Chiroderma salvini Chiroderma salvini Artibeus hartii Artibeus concolor Artibeus concolor	×××	7	Bolivia ³	Brazil ⁴	3E Brazil ⁵	Paraguay	Boreal	Uruguay ⁶
Vampyrops Vampyrops brachycephalus Vampyrossa melissa Vampyressa bidens Vampyressa bidens Vampyressa brocki Chiroderma trinitatum Chiroderma salvini Chiroderma salvini Chiroderma salvini Artibeus nacconnelli Artibeus andersens Artibeus anderseni	:××		\ 					
Vampyrodes caraccioloi Vampyressa melissa Vampyressa bidens Vampyressa bidens Vampyressa brocki Chiroderma triniatum Chiroderma salvini Chiroderma salvini Artibeus hartii Artibeus concolor Artibeus cancolor	×	×	:					
Vampyressa melissa Vampyressa bidens Vampyressa bidens Vampyressa pusilla Vampyressa brocki Chiroderma triniatum Chiroderma aslvini Chiroderma villosum Ectophylla macconnelli Artibeus hartii Artibeus concolor Artibeus anderseni		: ×	×					
Vampyressa bidens Vampyressa pusilla Vampyressa brocki Chiroderma triniatum Chiroderma salvini Chiroderma sulvini Chiroderma villosum Ectophylla macconnelli Artibeus cinereus Artibeus anderseni		×						
Vampyressa pusilla Vampyressa brocki Chiroderma trinitatum Chiroderma doriae Chiroderma salvini Chiroderma villosum Ectophylla macconnelli Artibeus hartii Artibeus anderseni	×	×						
Vampyressa brocki Chiroderma trinitatum Chiroderma doriae Chiroderma salvini Chiroderma villosum Ectophylla macconnelli Artibeus hartii Artibeus caneeus Artibeus anderseni	×	×			×	×		
Chiroderma trinitatum Chiroderma doriae Chiroderma salvini Chiroderma villosum Ectophylla macconnelli Artibeus hartii Artibeus concolor Artibeus anderseni	×							
Chiroderma doriae Chiroderma salvini Chiroderma villosum Ectophylla macconnelli Artibeus cinereus Artibeus concolor Artibeus anderseni	×	×	×					
Chiroderma salvini Chiroderma villosum Ectophylla macconnelli Artibeus cinereus Artibeus concolor Artibeus anderseni					×			
Chiroderma villosum Ectophylla macconnelli Artibeus hartii Artibeus cinereus Artibeus concolor Artibeus anderseni	×		×					
Ectophylla macconnelli Artibeus hartii Artibeus cinereus Artibeus concolor Artibeus anderseni	×	×	×					
Artibeus hartii Artibeus cinereus Artibeus concolor Artibeus anderseni	×	×	×					
Artibeus cinereus Artibeus concolor Artibeus anderseni	×	×	×					
Artibeus concolor Artibeus anderseni	×	×	×	×				
Artibeus anderseni Artibaus izmaizmais	×	×		×				
Artibone immercancie		×	×					
mineus jamanensis								
(including fuliginosus,								
see Anderson et al., 1982)	×	×	×					
Artibeus jamaicensis								
(including j. planirostris of								
Viera, 1955 and others)	×			×	×	×	×	
Artibeus planirostris fallax								
(see Anderson et al., 1982)		×	×					
Artibeus cf. fimbriatus					×	×		
Artibeus lituratus	×	×	×	×	×	×	×	
Ametrida centurio	×							
Sphaeronycteris toxophyllum	×	×	×					

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Pygoderma bilabiatum Centurio senex	Desmodus rotundus Desmodus youngii Diphylia teacaudata	Natalus stramineus Natalus stramineus Furipterus horrens Thyroptera discifera Thyroptera tricolor	Myotis nigricans Myotis keaysi Myotis levis Myotis albescens Myotis nesopolus	Myotis oxyotus Myotis ruber Myotis simus Myotis riparius	Myotis surnamensis Eptesicus andinus Eptesicus brasiliensis Eptesicus diminutus (=dimidiatus, dorianus) Eptesicus furnalis	Eptesicus montosus Eptesicus melanopterus Eptesicus melanopterus Histiotus montanus Histiotus velatus Rhogeesa minutilla Rhogeesa tumida Lasiurus borealis

TABLE 12 Continued

Species	Venezuela	Amazon Peru ²	Bolivia ³	NE Brazil ⁴	SE Brazil ⁵	Eastern Paraguay	Chaco Boreal	Uruguay ⁶
Lasiurus cinereus	×	×	×		×	×	×	×
Lasiurus egregrius					×			
Lasiurus ega	×	×	×	×	×	×	×	×
Molossops abrasus								
(=brachymeles)	×	×		×	×	×	×	
Molossops greenhalli	×			×				
Molossops paranus	×							
Molossops planirostris	×	×	×	×	×	×	×	
Molossops temminckii		×	×	×	×	×	×	×
Neoplatymops mattogrossensis	×			×				
Tadarida brasiliensis	×	×	×		×	×	×	×
Tadarida gracilis	×							
Tadarida laticaudata	×		×	×	×	×	×	
Tadarida phrudus		×						
Tadarida macrotis	×	×					×	×
Tadarida aurispinosa		×			×			
Eumops amazonicus								
$(=\bar{h}ansae?)$	×							
Eumops auripendulus	×	×	×	×	×	×		
Eumops dabbenei	×						×	
Eumops glaucinus	×		×		×	×	×	
Eumops bonariensis			×		×	×	×	×
Eumops nanus	×							
Eumops perotis	×	×	×	×	×	×	×	
Eumops maurus	×			×				
Promops centralis	×	×				×	×	
Promops nasutus	×					×	×	
Molossus ater	×	×	×	×	×	×	×	

×	18 14 78%
×	37
×	42 33 89%
×	65 30 81%
×	50 25 68%
×	79 29 78%
×	107 30 81%
****	148 33 89%
Molossus aztecus Molossus bondae Molossus molossus Molossus sinaloae Molossus trinitatus	Totals No. shared with Chaco Simpson's index of faunal resemblance

¹ Includes Suriname and Guyana; data from Handley (1976), Husson (1978), Genoways and Williams (1979a,b), Williams and Genoways (1980), and Genoways et al. (1981).

² Data from Koopman (1978).

³ Data from Anderson et al. (1982).

⁵ Restricted to the coastal states from Rio de Janeiro south to Rio Grande do Sul, plus Minas Gerais; data from Viera (1955), Cabrera (1958), Peracchi ¹ Restricted to Caatinga; data from Mares et al. (1981b), supplemented by records from Viera (1955) and Cabrera (1958).

In addition, lists were supplemented by records from LaVal (1973) and Eger (1977).

and Tenorio (1971), Taddei (1976, 1979), Taddei et al. (1976), Vizotto and Taddei (1976), Taddei and Garutti (1981), and Trajano (1982).

⁶ Data from Ximenez et al. (1972).

centralis, and Promops nasutus). Only one Chacoan species (Eumops dabbenei) is restricted to a single fauna besides the Chaco; in this case, however, additional records are from Venezuela and Colombia (including both dry and moist regions), suggesting that the lack of records in intervening areas may be due to low population levels or difficulty of capture, rather than restricted geographical or ecological distribution.

To further demonstrate the cosmopolitan nature of the bat fauna of the Chaco Boreal, we plotted frequency distributions of the number of bat species occurring in all eight regions, in seven regions, six, five, etc. This was done for all species in Table 12, and then separately for Chacoan species (Fig. 2). The tendency for Chacoan species to be widely distributed is striking. Finally, Simpson's indices of faunal relationship (Simpson, 1968) were calculated for the Chacoan fauna with each of the other faunas. They are given in the final row of Table 12. No strong pattern is evident; the Chacoan fauna resembles most of the others at about the same level, irrespective of geographic proximity or ecological similarity.

Thus, the chiropteran fauna of the Chaco resembles the avifauna in its low rate of endemicity, and lack of special relationships to faunas in other parts of South America. Birds and bats stand sharply in contrast to rodents, squamates, and amphibians, all of which show relatively high rates of endemicity and distinctive patterns of phyletic relationships to populations in other areas (Short, 1975; Gallardo, 1979; Fitzpatrick, 1980; Myers, in

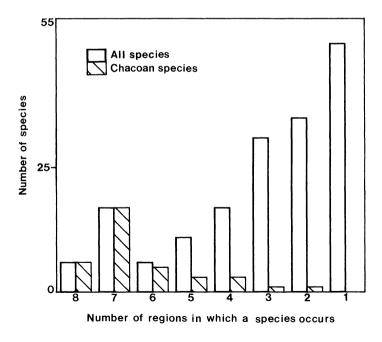


FIG. 2. Histogram of the number of bat species occurring in all eight regions of Table 12, seven regions, six, etc.

press). These general patterns may be the result of the generally increased vagility of volant, in contrast to terrestrial, vertebrates.

The unique composition of the Chacoan bat fauna appears to result from the deletion of species from neighboring faunas, rather than from the differentiation or incorporation of new elements. Why do fewer species of bats inhabit the Chaco? Myers (in press) suggested that the reason lies in an hypothesized increased seasonality in the availability to frugivores of fruiting and flowering trees in the Chaco, compared to surrounding areas. Increased seasonality results from the interaction of poor soils, a severe flooding/drying cycle, and consequent reduced diversity of plant species. It affects most strongly species that depend for their existence on a continual supply of fruiting or flowering trees. Frugivorous bats are conspicuously absent in most parts of the Chaco, with all present records either from comparatively mesic areas along the Río Paraguay, or from that time of year (late winter, August) when many trees are in flower. In contrast, resident populations of insectivorous, piscivorous, carnivorous, and sanguinivorous species probably are found throughout the Chaco Boreal.

GEOGRAPHIC VARIATION

Despite the lack of endemic species, members of the Chacoan bat fauna are often differentiated morphologically from contiguous, conspecific populations on all sides of the Chaco. Not surprisingly in an arid environment, many species are lighter in color; these include Noctilio albiventris, Myotis nigricans, Eptesicus furinalis, Molossops planirostris, Molossops temminckii, Eumops bonariensis, Tadarida laticaudata, Promops nasutus, and Molossus molossus. Bats of many species also tend to be smaller in the Chaco than in surrounding areas (Tables 1-11). We were able to compare statistically several measures of body size in Chacoan and extra-Chacoan populations of 10 species. Of these, six species clearly were smaller in the Chaco than in neighboring regions (N. albiventris, E. furinalis, Desmodus rotundus, Lasiurus ega, M. temminckii, and T. laticaudata). Populations of only one species (M. nigricans) appeared to be larger in the Chaco; Chacoan populations of three species (E. bonariensis, M. molossus, and Myotis albescens) changed very slightly or not at all. Thus, most species exhibited similar patterns of geographic variation in body size: populations from the eastern Chaco generally resembled those from eastern Paraguay, while those from the arid and western Chaco were quite small. These changes took place gradually across the Central Chaco. Average size increased over relatively lesser distances, however, in populations of bats from near the base of the Andes. Bats from the Andean piedmont also tended to be darker, often resembling eastern Paraguayan specimens in both size and color.

Why are most bat species smaller in the arid Chaco than in surrounding, more mesic, regions? McNab (1971) reviewed explanations of geographic (especially latitudinal) trends in body size. He stressed the importance to hunters of the size of food particles, and of competition by other species. For the Chaco, no information is available concerning geographic variation

in food particle size. For any bat species the number and identity of competitors for nocturnal flying insects are probably similar in the arid Chaco and surrounding mesic regions. If anything, fewer species of bats are present in the Chaco, which, according to McNab, should lead to increased, rather than decreased, body size in Chacoan bats.

MacMillen and Hinds (in press) documented an inverse relationship between body size and efficiency of water use in heteromyid rodents. They hypothesized that the pattern was due to the steeper negative slope of the curve of weight-specific metabolic water gain vs. body weight, compared to weight-specific respiratory water loss vs. body weight. Because of their different slopes the two curves intersect at some body weight, below which point metabolic water gain exceeds respiratory water loss. The smaller the animal, the greater the difference between the curves and the more water available. Those species of bats with smaller body size in the Chaco, however, are primarily insectivorous. Whether the relationship documented by MacMillen and Hinds for heteromyids applies to species that rely heavily on protein in their energy metabolism is not clear.

EFFECTIVENESS OF SAMPLING

How thorough is our sampling of the Chacoan bat fauna? The area collected most intensively within the Chaco lies between kilometers 200 and 320 on the Trans Chaco Highway, in the area referred to as Central Chaco in our analyses of geographic variation. Within this region Myers devoted over 60 nights to the collection of bats. Most collecting was by means of mist nets, and a large number of *Myotis* and many molossids were taken from roosts. Collecting took place over 18 months and included some effort in all seasons. To estimate the effectiveness of sampling we plotted the cumulative number of species captured as a function of "collecting nights" (i.e., nights during which bats were collected, by any means; Fig. 3). We made no attempt to estimate the intensity of effort for each night; our point is that over the more than 60 nights, considerable sampling was done. We also estimated the total number of species believed to occur in the Central Chaco, based on captures in the Central Chaco during and after the sampling period, and on records from surrounding parts of the Chaco.

We captured only 20 of the estimated 29 species occurring in the Central Chaco, and new species continued to be taken throughout the period (Fig. 3). The species not collected during the sampling period include Chrotopterus auritus, Tonatia bidens, Lasiurus cinereus, Eumops dabbenei, Eumops perotis, Tadarida laticaudata, Tadarida brasiliensis, Promops nasutus, and Promops occultus. Some species (Chrotopterus, Tonatia, Eumops dabbenei) were uncommon wherever found in Paraguay. The others tended to be common locally, but distributed patchily.

Because of the difficulty in obtaining relatively complete local samples, we have not attempted to compare, in detail or quantitatively, local faunas within the Chaco. The distribution records at hand suggest, however, that few differences would be found beyond the disappearance of stenoder-

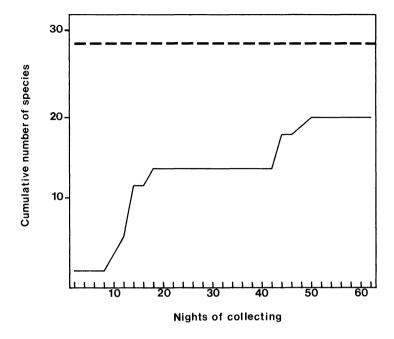


Fig. 3. Plot of the cumulative number of species of bats collected as a function of the number of nights of collecting. The dashed line indicates the total number of species believed to be present. The area sampled lies between Km 200 and Km 320 along the Trans Chaco Highway.

mine phyllostomids and noctilionids from xeric areas. Figure 3 also suggests caution in the interpretation of Table 12, particularly for those regions sampled less intensively than the Chaco. The stronger relationship between Chacoan and Venezuelan faunas than between Chacoan and northeastern Brazilian faunas, for example, is probably an artifact of incomplete sampling. Further, due to its large proportion of high-flying and agile insectivores, the Chacoan fauna may be an unusually difficult one to sample exhaustively.

REPRODUCTION

Chacoan bats do not appear to breed during the southern winter; records from early though mid-winter (July through August) indicate no reproductive activity (Table 13). By late winter (late August and early September) most species appear to commence breeding. Unfortunately, we have few records from other times of year. Myotis albescens, Myotis nigricans, Lasiurus ega, and Eptesicus furinalis were studied intensively by Myers (1977); like the bats reported here, these species begin breeding in August–September. Similarly, Ojeda and Barquez (1978) reported very little or no reproductive activity in several species of phyllostomids, molossids, and vespertilionids captured during July and August in Dept. Santa Cruz,

	Sept. Oct.		Nov. De	Dec.	Jan.	Feb. Mar.	Mar.	Apr.	Мау	June	July	Aug.
Noctilio albiventris Noctilio	11ac(1)	4(7)			ljuv							9(15)
leporinus Chrotobterus	2(2)							41ac(6)				4(4)
auritus Sturmira											0(1)	
lilium Artibeus												0(1)
jamaicensis Artibeus												ljuv
lituratus Desmodus												2(2)
rotundus Mvotis		0(1)						0(1)	0(1)			11ac(1)
riparius Myotis		1(1ac)										
simus		4(4)										
borealis Moloscops	1(1)											
abrasus		1(1)										0(4)

	0(1)	•	0(13)				0(1)		0(3)							,	0(1)				0(3)	
0(1)	0(10)		0(11)		0(1)						0(1)		0(1)				0(1)	;	0(1)			
	0(2)	`	0(20)																		0(19)	
	0(2)		0(2)																		0(14)	
			0(1)																		0(2)	
			0(1)															11ac(2)	ljuv			
					1(1)																1(1)	
2(2)	5(5)		2(2)						1(1)												0(1)	
	19(99)	(==)	1(1)				1(1)								1(1)						1(2)	
Molossops planirostris	Molossops temminckii	Eumobs	bonariensis	Eumops	auripendulus	Eumops	glaucinus	Eumops	dabbenei	Eumops	perotis	Tadarida	laticaudata	Promops	occultus	Promops	nasutus	Molossus	ater	Molossus	molossus	

active females were taken in that sample. A number by itself indicates pregnant females; thus, 4(7) reports that four females were pregnant out of seven 1 The number in parentheses indicates the number of females captured each month. Preceding it is a number indicating how many reproductively captured. Lactating individuals are shown by "lac" following the number observed; 41ac(6) indicates that four females were lactating of six examined. "Juv" indicates the capture of a juvenile.

Bolivia, at a site at the base of the Andes east of Santa Cruz de la Sierra. In contrast, Taddei (1976) reported that phyllostomids in eastern Brazil tend to concentrate reproduction from June through October-November and in February-March. At no time of year was the cessation of breeding as complete in eastern Brazil as in the Paraguayan Chaco. Taddei's study focused primarily on frugivorous species, however, which are rare or absent in the Chacoan fauna. Vizotto and Taddei (1976) and Taddei et al. (1976), working in southeastern Brazil, found that breeding by Molossops abrasus, Molossops temminckii, and Molossops planirostris began in July, also in contrast to Paraguayan populations. Mares et al. (1981a) also reported July breeding in Sturnira captured in "mesic" habitats in Salta Province, Argentina. Further, Eptesicus furinalis from Salta taken in November were reproductively quiescent; at this time in Paraguay almost 100% of the population reproduces (Myers, 1977). In contrast, Mares et al. (1981a) reported that in Salta, during November, M. temminckii, Eumops bonariensis, and Molossus molossus resembled these species in Paraguay in that they all showed evidence of breeding. Thus, breeding patterns vary substantially among Chacoan and extra-Chacoan populations of bats. At present, however, few species have been studied intensively, and in no case can we make detailed comparisons of the breeding habits of populations of one species in several habitats.

SUMMARY

- 1. Systematic and ecological notes, locality records, and measurements are provided for bats from the Chaco Boreal.
- 2. Species of bats found in the Chaco Boreal tend to have distributions covering large areas of South America. No endemic species are known. The composition of the Chacoan bat fauna appears to result from the deletion of species, especially frugivorous phyllostomids, from faunas of neighboring regions.
- 3. Chacoan bats tend to be smaller in body size and lighter in color than their conspecifics in surrounding areas. Lighter colors are probably related to the increased aridity of Chacoan habitats. The reasons for smaller body sizes, however, are not known.
- 4. Obtaining accurate lists of species present at sites in the Chaco for faunal comparisons is extremely difficult, perhaps due to the predominance of high flying and agile vespertilionids and molossids. At our most intensively sampled localities, during a sampling period of over 60 nights, only about 2/3 of the bat species believed to be present were represented in our collections.
- 5. In the Chaco, most bat species appear to cease breeding in mid winter (July-early August), and to commence breeding in late winter (late August). Much variation occurs, however, particularly in areas peripheral to the Chaco.
- 6. A key to the bats of the Chaco Boreal, based on characters that can be observed on intact animals, is given.

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APPENDIX

FIELD KEY TO THE BATS OF THE CHACO BOREAL AND SURROUNDING AREAS

This key is intended for use in the field, and is based on characteristics of bats that can easily be observed in intact animals. Note that the initial choice is among four items. The key includes species known to occur in the Chaco, as well as several we believe likely to occur there. We are especially grateful to Dr. Charles Handley for assistance in its construction.

I. Tail extending well beyond end of tail membrane
A. forearm covered with horny warts
B. forearm not covered with horny warts
1. forearm longer than 70mm
a. ears longer than 35mm, tragus broad and square Eumops perotis
b. ears shorter than 34mm; tragus small, pointed or
square Eumops dabbenei
2. forearm less than 70mm
a. size very small; forearm less than 35mm
(1). forearm usually longer than 31mm; extensive areas of pure
white on throat, chest, and sometimes belly; four lower incisors;
large square antitragus
(2). forearm usually shorter than 31mm; throat may be light, but
usually not white; underside usually dark; two lower incisors;
small, narrow, recurved antitragus
b. size larger
(1). antitragus constricted at base
(a). palate distinctly domed; upper incisors shaped like canines,
tips usually separated; base of fifth metacarpal distinctly furry
((1)). forearm longer than 50mm
((2)). forearm less than 50mm
(b). palate not domed; upper incisors triangular, tips together
forming a beak-like structure; base of fifth metacarpal much less
hairy, though some hairs present
((1)). forearm longer than 45mm
((2)). forearm shorter than 45mm
(2). antitragus not constricted at base
(a). deep grooves or folds on upper lips; tips of upper incisors
convergent
((1)). ears meeting in midline but not joined; forearm
less than 50mm
((2)). ears joined at base in midline
((a)). forearm greater than 55mm
((b)). forearm less than 50mm
(((1))). forearm usually greater than 45mm Tadarida laticaudata
(((2))). forearm usually less than 45mm
(b). deep grooves on lips lacking
((1)). large, forearm longer than 46mm
((a)). ears clearly separate
((b)). ears meet in midline
(((1))). tragus fairly well developed, truncate; dorsal color clay
or brownish
(((2))). tragus minute and pointed; dorsally very dark brown
or black
((2)). small, forearm less than 46mm

II. Tail absent or short, not reaching edge of uropatagium; noseleaf present
(fleshy, leaflike projection above nose)
A. white stripes (sometimes very faint) on face above eyes; tail absent
1. size small, forearm less than 50mm
a. white stripe down middle of back
(1). color gray or brown; eye stripes well defined; forearm usually
longer than 40mm; common in eastern Paraguay Vampyrops lineatus
(2). color black or blackish brown; eye stripes weakly defined; forearm
longer than 40mm; known only from northern
Chaco
b. no white stripe on back; forearm less than 35mm
2. size larger, forearm longer than 50mm
a. forearm usually longer than 65mm; eye stripes
pronounced
b. forearm less than 65mm; eye stripes not pronounced
(1). forearm usually longer than 62mm; eye stripes weak or absent;
2 upper molars; dorsal color dark gray or dark brown
Artibeus cf. fimbriatus
(2). forearm usually less than 62mm; eye stripes weak but usually present;
3 upper molars (the third a small peg); dorsal color medium gray
B. no eye stripes; tail absent or short
1. ears long, greater than 25mm, and when laid forward, project beyond
end of snout; tail short
a. forearm longer than 70mm
b. forearm less than 60mm but longer than 50mm
(1). ear longer than 30mm; forearm almost naked
(2). ear less than 30mm; forearm furry
2. ears less than 25mm; forearm less than 45mm
a. tail absent
(1). tail membrane mostly absent (never as wide as foot) Sturnira lilium
(2). tail membrane wide; white spots on shoulders, color brownish
or tan
b. tail present; tail membrane wider than foot
(1). forearm less than 35mm
(2). forearm longer than 35mm
(a). dorsal fur tricolored; tail short
(b). dorsal fur unicolored; tail extending nearly to edge of
uropatagium
III. Tail not extending to edge of uropatagium; no obvious noseleaf (though
nose region may appear complex and folded)
A. hind feet very large, longer than 30mm
B. hind feet less than 25mm
1. forearm longer than 55mm
a. color reddish; teeth not strongly modified
b. color grayish; central incisors and canines much enlarged;
molars reduced; tail absent
2. forearm less than 55mm
a. 2 whitish stripes on back
(1). color blackish; wing sac in male; forearm naked Saccopteryx bilineata
(2). color grayish; wing sac absent; forearm with tufts of hair
b. no dorsal stripes; forearm naked
o. no doisai surpes, forearm naked Feropieryx macrous

IV. Tail extending to edge of uropatagium, but not more than the length of one or two vertebrae beyond; no noseleaf A. ears extend much beyond nose when folded forward
b. reddish, often frosted gray (1). forearm longer than 45mm
a. two small, peg-like teeth behind canine in upper jaw (1). size large, forearm longer than 37mm
(a). fur wooly, less than 3mm long on back; color yellow-orange
(b). fur silky, 4mm or more long on back; color darker, red brown to gray brown ((1)). color redder, tips of hairs not contrasting to bases
in color
(2). size smaller, forearm less than 37mm
(a). color reddish or brownish; fur short, less than 3mm
on back; wooly
((1)). tips of hairs light, strongly contrasting
with bases, resulting in a "frosted" apearance
((2)). tips of hair either not contrasting with bases or
weakly contrasting
b. canine in contact with first molar-like tooth (1). size large, forearm longer than 42mm
(2). size smaller, forearm less than 41mm
(a). size smaller, forearm less than 36mm Eptesicus diminutus (b). size larger, forearm longer than 36mm Eptesicus furinalis

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