

## COMPOSITION AND STRUCTURE OF BAT ASSEMBLAGES IN PARAGUAY: A SUBTROPICAL–TEMPERATE INTERFACE

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Little is known about geographic variation in the local composition of South American assemblages of mammals or the factors that may produce such variation. This is particularly unfortunate in Paraguay because it occurs at the interface of a number of phytogeographic regions (e.g., Cerrado, Chaco, Interior Atlantic Rainforest, and Pantanal) and is the point at which many temperate species reach their northern limits or at which tropical species reach their southern limits. Based on 2 years of intensive fieldwork, we documented the species and familial composition of bat assemblages at 25 sites throughout the country. We also estimated similarity among sites based on indices sensitive to presence or absence of species (Ochiai's index), to rank abundance of species (rank correlation index), or to relative abundance of species (Euclidean index). Geographic distance between sites accounted for little variation in composition based on presence–absence or rank abundances of species but accounted significantly for variation related to both identity and relative frequency of species. Distinct assemblages of species do not correspond to the 7 distinct biomes of the country; rather, strong differences exist between sites east (mesic) and west (xeric) of the Río Paraguay. For the most part, these differences are related to dominance by molossids (e.g., *Eumops patagonicus*, *Molossops temminckii*, and *Molossus molossus*) and vespertilionids (e.g., *Lasiurus ega*, *Myotis albescens*, and *M. nigricans*) in dry regions versus phyllostomids (e.g., *Artibeus fimbriatus*, *A. lituratus*, and *Sturnira lilium*) in mesic regions. As a consequence, classification of sites into 2 broad biogeographic regions based on bat familial composition generally is concordant with that based on plants.

Key words: biogeography, Chaco, Chiroptera, conservation, Molossidae, Paraguay, Phyllostomidae, South America, species composition, Vespertilionidae

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South American mammals have received increasing attention from systematists, ecologists, and conservation biologists in recent years. In part, this attention is a product of the high species diversity and functional complexity of tropical areas in the New World (Kaufman and Willig 1998; Lacher and Mares 1986; Pagel et al. 1991; Simpson 1964; Willig and Gannon 1997; Willig and Lyons 1998; Willig and Sandlin 1991; Willig

and Selcer 1989; Wilson 1974) and in part because diversity is being eroded by accelerating anthropogenic activity throughout South America (Gibson 1996; Johns 1997; Laurance and Bierregaard 1997; Robinson and Redford 1991). Species extinctions in tropical South America in general and in lowland Amazon rainforest in particular have become the cause celebre of conservationists and the biodiversity movement (Mann 1991). Nonetheless, some (e.g., Redford et al. 1990) have suggested that tropical rainforests

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should not hold hegemony over other areas in South America for studies of biodiversity and conservation biology. In fact, as Mares (1992) has shown for mammals, the drylands of South America harbor more endemic species, genera, and families than the Amazon Basin. Clearly, conservation of mammalian diversity requires added focus on the extensive drylands of southern South America, and by inference, on those areas where the drylands interface with biomes such as Atlantic Rainforest or Pantanal.

Paraguay, because of its central location within the climatic, geological, and biotic schema of the South American continent, is ideal for exploring a variety of biogeographic and ecological questions. This landlocked country is situated at a nexus of Cerrado, Pantanal, Atlantic Rainforest, and Wet and Dry Chaco faunas (Gorham 1973a; Hayes 1995). As a result, many mammalian species are at their distributional limits (Koopman 1982; Streilein 1982), and the assembly of those species into local communities should reflect dynamic ecological and biogeographic features (Holt 1993; Lawton et al. 1994; Myers 1982). Moreover, human land-use practices have caused appreciable habitat fragmentation and desertification throughout extensive parts of central and southern South America (Cepal-Pnuma 1983; Cozzo 1967; Soriano and Movia 1986), which in turn may have affected a substantial truncation in the distributional limits of some mammals (Roig 1991).

In general, our research focused on the taxonomic composition of chiropteran assemblages at a diversity of sites in Paraguay. Each site was associated with endangered or threatened habitats, unique biomes, or gradients of important environmental parameters (e.g., rainfall and temperature). Because many major South American biomes interdigitate in Paraguay, unique opportunities exist for studying community assembly at ecological interfaces and the response of populations to abiotic gradients and marginal environments. Our objectives

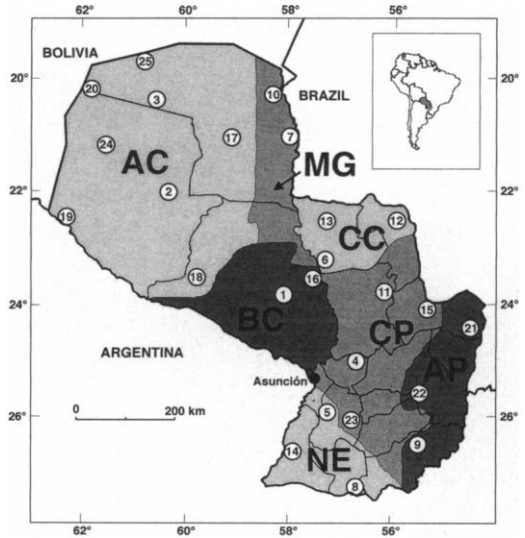


FIG. 1.—Map of the locations of the 25 collection sites (circled numbers) throughout Paraguay (see Appendix I for detailed information concerning each site). Alphabetic codes refer to each of 7 biomes: Matogrosense, MG; Alto Chaco, AC; Bajo Chaco, BC; Campos Cerrados, CC; Central Paraguay, CP; Alto Paraná, AP; Ñeembucú, NE (Table 1).

were to describe patterns in the composition of bat assemblages in Paraguay and to integrate this information with biogeographic and conservation perspectives.

#### MATERIALS AND METHODS

*Study site.*—Paraguay is a small country (406,752 km<sup>2</sup>) that is transected by the Tropic of Capricorn (Fig. 1). It occurs at the interface of subtropical and temperate regions; is relatively flat and low lying, especially in the west; and experiences hot summers and mild to cold winters (Bertoni and Gorham 1973; Fariña Sánchez 1973; Gorham 1973b). Based on floral and geographic features (Hayes 1995), the country includes 7 phytogeographic regions or biomes (Table 1). Much of the country, especially east of the Río Paraguay, has experienced extensive deforestation and fragmentation in the last 2 decades (Unruh 1973) and is dominated by agricultural landscapes (Universidad Nacional de Asunción 1994).

We follow the phytogeographic classification of Hayes (1995) and divide Paraguay into 7 bi-

TABLE 1.—Ecological characteristics of the 7 biomes (Fig. 1) that occur in Paraguay (Hayes 1995); east and west designate locations of biomes with respect to the Río Paraguay.

Biome	Topography	Vegetation	Precipitation	Inundation	Humidity
West					
Matogrosense (MG)	Flat	Forest	Medium	Seasonal	Subhumid
Alto Chaco (AC)	Flat	Forest	Low	None	Semiarid
Bajo Chaco (BC)	Flat	Palm	Medium	Seasonal	Semihumid
East					
Campos Cerrados (CC)	Hills	Forest	High	None	Semihumid
Central Paraguay (CP)	Hills	Forest	High	None	Humid
Alto Paraná (AP)	Hills	Forest	Very high	None	Humid
Ñeembucú (NE)	Hills	Grassland	High	Seasonal	Semihumid

omes and 2 broad regions, east and west of the Río Paraguay. Three biomes compose the Chaco of western Paraguay (Fig. 1). The Matogrosense biome is characterized by medium height (10–20 m) trees and subhumid forests with dense undergrowth (e.g., bromeliads). It is often inundated, not only by local rainfall, but more generally as a consequence of rains in the Brazilian Pantanal, which is drained by the Río Paraguay. The Alto Chaco biome constitutes more than one-half of western Paraguay and despite its flat topography is seldom inundated because rainfall is low and edaphic features facilitate water percolation; in contrast to the Matogrosense, constituent rivers do not drain the Pantanal. It is semiarid and dominated by relatively short (5–10 m), dense, xerophytic thorn-scrub forest with a well-developed understory (terrestrial bromeliads and arborescent cacti). The Bajo Chaco biome comprises extensive palm savannas interdigitating with medium-height (8–15 m), xerophytic, scrub forest on slightly elevated terrain. Corridors of tall (10–20 m) subhumid riparian forest parallel a series of meandering rivers and intermittent streams that flow slowly eastward to the Río Paraguay. Extensive marshlands dominate areas adjacent to the riparian zones, and the entire area is inundated seasonally for many months.

Eastern Paraguay comprises 4 biomes (Fig. 1) that are the most topographically heterogeneous and humid regions of the country. The Campos Cerrados biome is a savanna formation characterized by a mosaic of dense forests, xerophytic woodlands (8–20 m), and grasslands. The topography is gently rolling, with the highlands supporting subhumid forests (20–50 m) and areas to the west containing patches of xerophytic

forest, subhumid forests, and palm savannas reminiscent of adjacent Chaco formations. The Central Paraguay biome is the most ecologically variable biome in Paraguay. In the west, along the Río Paraguay, it contains marshes, palm savannas, and patches of low humid deciduous forest, with more hilly terrain to the east supporting taller humid forest that is now fragmented as a consequence of timber management. Rivers in this biome are sluggish, bordered by marshes, and drain to the Río Paraguay. The Alto Paraná biome is characterized by rolling hills that are cut deeply by fast-flowing tributaries of the Río Paraná. Although historically dominated by tall (>25 m), humid, deciduous forests, the region has been subject to severe deforestation and extensive flooding as a result of large and permanent impoundments (e.g., Represa de Itaipú). Nonetheless, several areas have been protected and are relatively undisturbed. The Ñeembucú biome is dominated by extensive seasonally inundated wetlands associated with the confluence of the Río Paraguay and Río Paraná and vast grasslands in flat, low terrain with slow-moving rivers. Palm savannas typical of the Chaco and patches of low (8–15 m), subhumid, Chaco-like forest are interspersed with formations more typical of eastern Paraguay. This biome represents a transition between the Chaco to the west and the taller humid forests of the eastern biomes (Hueck 1972).

*Field methods.*—Bats were surveyed at 25 sites (Appendix I), representing all major biomes, including many protected areas, and spanning gradients of moisture and temperature in Paraguay (Fig. 1). Because of the potential importance of the Río Paraguay as a biogeographic barrier (Myers 1982), about one-half of the sites

were to the east or west of the river. In general, mist nets were erected in all obvious habitats at a site and were monitored for captures from dusk until 0100 h (July 1995–May 1997). Much of the time, mist nets were monitored until dawn. Rates of capture for bats in the field depend on a variety of factors, including net characteristics (e.g., mesh size, length, condition, placement, and configuration), temporal factors (e.g., length of time, particular hours of the night, and period in the lunar cycle), local weather conditions (especially with respect to precipitation), and history (i.e., number of consecutive nights at a site). Consequently, we did not adjust capture numbers or species richness based on a quantification of hours of effort or length of nets. Captured bats were sacrificed and prepared as standard museum specimens. Specific identification was initiated in the field but verified after comparison with systematic reference materials. In general, we followed the systematic recommendations of Koopman (1993) for bat taxa in Paraguay, except we recognized *Artibeus jamaicensis* (Handley 1987) rather than *A. planirostris*, *Lasiurus blossevillii* (Baker et al. 1988) rather than *L. borealis*, and *Eumops patagonicus* (Barquez et al. 1999) rather than *E. bonariensis beckeri* (but in addition to *E. bonariensis bonariensis*). Ectoparasites were collected from virtually all specimens, and karyotypes and frozen tissues were collected from many of them. One-half of the bat collection will be deposited at the Museum of Texas Tech University (TTU), and one-half will be deposited at the Museo Nacional de Historia Natural del Paraguay (MNHNP).

**Quantitative analyses.**—Based on the collection of bats and associated field notes (some individuals were released at a number of sites, depending on their representation in previous collections), we were able to ascertain presence or absence, and to estimate rank abundance and proportional abundance (ratio of number of individuals in a particular species to number of individuals in all species), of each species at each site. Those data were then used to calculate indices of similarity between all pairs of sites. For binary data (presence–absence), we used the Ochiai index; for rank abundance data, we used the rank correlation index; and for relative frequency data, we used the Euclidean distance index (Krebs 1989; Ludwig and Reynolds 1988). For each type of index, we produced a similarity

matrix of all pairwise combinations of sites and generated a dendrogram of taxonomic distance based on unweighted pair–group arithmetic averaging (UPGMA) algorithms for clustering (Sneath and Sokal 1973) in “Procedure CLUSTER” (SPSS, Inc. 1990). In addition, we produced a distance matrix for all pairs of sites based on geographic straight-line distances as estimated from an equal-area projection map of the country (Dirección del Servicio Geográfico Militar, 11th edition, 1993). The degree to which each matrix of taxonomic distance was correlated with the matrix of geographic distance was determined using Mantel analysis (Fortin and Gurevitch 1993; Manly 1994; Pacheco and Patterson 1992; Sokal and Rohlf 1995). In the same fashion, correlations between matrices of taxonomic similarity based on different indices were estimated by Mantel analyses. Differences in the familial composition of bat assemblages among sites within biomes and among biomes in Paraguay were evaluated using a hierarchical heterogeneity *G*-test (Sokal and Rohlf 1995). The proportional abundance of each family at a site was equal to the ratio of number of individuals in that family to the total number of individuals of all families at the site. Comparison-wise error rate was constant at 0.05 in correlative analyses, whereas experiment-wise error rate was held at 0.05 in the *G*-test.

## RESULTS

In total, 3,989 bats (53% in the west and 47% in the east) were collected during the study, representing 5 families, 22 genera, and 44 species (Table 2). Based on total captures, phyllostomids (79.6%), followed by molossids (12.6%) and vespertilionids (5.8%), were most abundant in the east, whereas a reversal in numerical dominance occurred in the west, with molossids (76.6%) more abundant than either vespertilionids (15.3%) or phyllostomids (2.0%). Noctilionids and natalids were rare generally, although the former were locally abundant, especially in the Ñeembucú and Matogrosense biomes. The most common species in eastern Paraguay were *Sturnira lilium* and *Artibeus lituratus* (26.6% and 25.6% of captures, respectively). In contrast, the most common species in western

TABLE 2.—Species composition of bat assemblages in the 7 biomes of Paraguay. Proportional abundances (as percentages) of each species within each biome are provided based on the total number of captured specimens; nomenclature generally follows Koopman (1993; for exceptions, see text).

Taxon	Biomes						
	West			East			
	Matogro- sense	Alto Chaco	Bajo Chaco	Campos Cerrados	Central Paraguay	Alto Paraná	Ñeembucú
Family Noctilionidae							
<i>Noctilio albiventris</i>	3.37		9.25	0.34			12.18
<i>Noctilio leporinus</i>		1.42	0.84	0.85			
Family Phyllostomidae							
<i>Artibeus fimbriatus</i>				0.68	2.66	1.55	3.59
<i>Artibeus jamaicensis</i>				6.32	1.64		
<i>Artibeus lituratus</i>				13.33	36.17	37.12	5.38
<i>Artibeus</i> sp.				0.18			
<i>Carollia perspicillata</i>				2.56	3.55	1.95	
<i>Chiroderma doriae</i>					0.53		
<i>Chrotopterus auritus</i>					0.53		
<i>Desmodus rotundus</i>	4.44	0.74		1.26	4.96		1.35
<i>Diaemus youngi</i>	0.37		4.18				
<i>Glossophaga soricina</i>				11.97	4.96		2.70
<i>Platyrrhinus lineatus</i>			0.84	14.36	2.13	0.23	0.90
<i>Pygoderma bilabiatum</i>				1.37	6.28	2.23	0.45
<i>Sturnira lilium</i>		0.62		21.54	3.14	31.85	19.28
<i>Tonatia bidens</i>		0.19					
<i>Tonatia brasiliense</i>			0.42				
Family Natalidae							
<i>Natalus stramineus</i>				0.18			
Family Vespertilionidae							
<i>Eptesicus brasiliensis</i>		0.19		0.51			
<i>Eptesicus diminutus</i>		0.12					
<i>Eptesicus furinalis</i>		1.18	4.63	4.44	1.64	0.23	4.48
<i>Histiotus macrotus</i>		0.37					
<i>Lasiurus blossevillii</i>		0.12	0.84	0.51	0.53	0.23	0.45
<i>Lasiurus cinereus</i>						0.46	0.45
<i>Lasiurus ega</i>	1.48	1.98	12.55	0.34			1.35
<i>Myotis albescens</i>	21.48	1.18	12.98				3.14
<i>Myotis nigricans</i>	7.47	2.23	21.34	1.79	1.64	0.46	4.48
<i>Myotis riparius</i>				0.85	0.79	0.23	0.45
<i>Myotis simus</i>							0.45
Family Molossididae							
<i>Eumops auripendulus</i>		0.62					
<i>Eumops bonariensis</i>			0.84	0.18		0.46	
<i>Eumops dabbenei</i>		0.19					0.45
<i>Eumops glaucinus</i>		1.86		1.79		3.45	
<i>Eumops patagonicus</i>	9.26	6.50	9.25	3.59	0.35		14.80
<i>Eumops perotis</i>		0.12					

TABLE 2.—Continued.

Taxon	Biomes						
	West			East			
	Matogro- sense	Alto Chaco	Bajo Chaco	Campos Cerrados	Central Paraguay	Alto Paraná	Ñeembucú
Family Molossidae							
<i>Molossops abrasus</i>				0.85			3.59
<i>Molossops planirostris</i>		0.40		0.34			2.24
<i>Molossops temminckii</i>	0.75	7.49	4.18	2.74	1.77	1.42	1.79
<i>Molossus ater</i>	1.75	1.70	7.11	0.18	1.64		14.80
<i>Molossus bondae</i>	13.74						
<i>Molossus molossus</i>		14.61	1.88	7.18	0.53	0.23	0.90
<i>Nyctinomops laticaudatus</i>		2.91					
<i>Promops centralis</i>		0.62		0.18	0.18	0.23	0.45
<i>Promops nasutus</i>		0.50					
No. of individuals	270	1,615	239	585	564	493	223

Paraguay were *Eumops patagonicus* and *Molossus molossus* (48.2% and 12.3%, respectively). Although eastern and western Paraguay harbored about equal numbers of species (34 versus 30, respectively), biomes differed appreciably in species richness (Matogrosense, 10; Alto Chaco, 24; Bajo Chaco, 15; Campos Cerrados, 28; Central Paraguay, 20; Alto Paraná, 16; and Ñeembucú, 24).

*Species-level analyses.*—Dendrograms based on similarity matrices are schematic representations of the pattern of faunal composition among sites (Willig and Mares 1989). Regardless of index (Ochiai, rank correlation, or Euclidean), 2 general ecological features of the dendrograms for Paraguay were important (Fig. 2): Eastern and western regions generally represented distinct clusters of sites, and sites within particular biomes did not form distinct clusters. The only exceptions regarding homogeneity and distinctiveness of eastern and western sites appeared based on relative frequency data, in which 3 eastern sites (CC-06, NE-14, and NE-08) clustered more closely with western sites than with other eastern sites, and 1 western site (AC-03) appeared as an outlier. The high relative abundance of *Molossops temminckii* at Cerro León (AC-03) resulted in this site having a faunal com-

position unlike the other sites in the west. Faunal relationships among sites were similar (Mantel analysis,  $P < 0.001$ ) regardless of whether indices were derived from binary (Fig. 2A) or rank abundance (Fig. 2B) data. Nonetheless, the pattern among sites (Fig. 2C) based on the Euclidean distance index (relative frequency data) was uncorrelated with that produced by either of the other 2 indices (Mantel analysis,  $P > 0.99$ ).

Results of Mantel analyses assessing the degree to which differences between sites was a consequence of geographic separation differed depending on the type of similarity index. A significant positive correlation ( $P < 0.001$ ) existed between matrices based on geographic distance and Euclidean distance (i.e., as geographic distance increased, so did Euclidean distance), whereas matrices based on binary data or rank abundances (Ochiai or rank correlation) were correlated significantly with the matrix based on geographic distance ( $P > 0.99$ ).

*Family-level analyses.*—Quantitative comparisons of the familial composition of bat assemblages in Paraguay provided a complementary assessment of biogeographic patterns (Fig. 3) to that obtained at the specific level. Proportional abundances of bat families differed significantly among

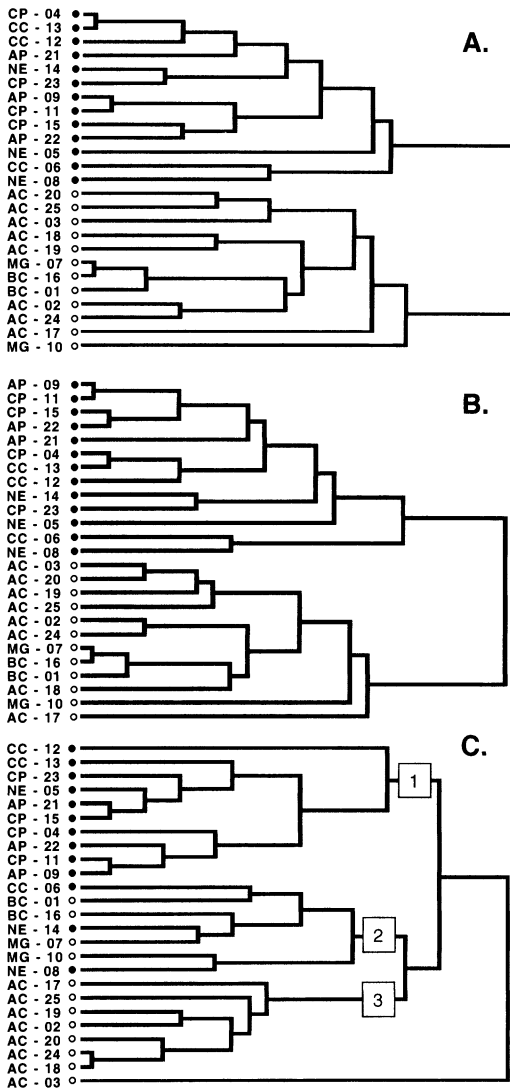


FIG. 2.—Dendrograms based on cluster analyses (UPGMA) of sites using each of 3 similarity coefficients. A) Ochiai index,  $r = 0.764$ ; B) rank correlation index,  $r = 0.711$ ; C) Euclidean distance index,  $r = 0.808$ . Alphabetic codes refer to biomes (Table 1), and numeric codes refer to sites (Appendix I; Fig. 1). Sites east or west of the Río Paraguay are designated by closed or open circles, respectively. Clusters C1, C2, and C3 represent eastern highland, seasonally flooded, and dry Chaco sites, respectively.

sites within each of the 7 biomes (Fig. 3B). With 1 exception (Central Paraguay and Alto Paraná), all biomes were statistically distinct from all other biomes at the family

level (Fig. 3A) despite significant heterogeneity among sites within biomes. Central Paraguay and Alto Paraná biomes were dominated greatly by phyllostomids (>92% in both cases) and had equivalent familial compositions (Fig. 4). The Campos Cerrados biome was dominated by phyllostomids (73%) but had appreciable molossid (17%) and vespertilionid (8%) components. The Alto Chaco was dominated by molossids (90%). The Bajo Chaco was dominated by vespertilionids (53%), followed by molossids (32%) and noctilionids (10%). The Matogrosense was codominated by molossids (34%), noctilionids (30%), and vespertilionids (30%). Ñeembucú, the transitional biome, was codominated by molossids (39%) and phyllostomids (34%), the dominant taxa in the west and east, respectively, and had appreciable numbers of vespertilionids (15%) and noctilionids (12%).

## DISCUSSION

*Species boundaries and distributions.*—Our faunal surveys identified 5 species of bat that represent new records for Paraguay, 4 (*Chiroderma doriae*, *Tonatia brasiliense*, *Histiotus macrotus*, and *Natalus stramineus*) reported by López-González et al. (1998) and 1 reported here for the 1st time, *Molossus bondae* (27 specimens at Estancia Doña Julia, site code 10 in Fig. 1, Appendix I). We also captured 38 of 49 species of bats previously known from the country (Baud and Menu 1993; Gamarra de Fox and Martin 1996; López-González et al. 1998; Myers 1981; Myers and Wetzel 1979, 1983; Myers et al. 1983; Podtiaguin 1944; Thomas 1916; Wilson and Gamarra de Fox 1991). Of the remaining 11 species (*Peropteryx macrotis*, *Anoura caudifer*, *Macrophyllum macrophyllum*, *Phyllostomus discolor*, *P. hastatus*, *Tonatia sylvicola*, *Vampyressa pusilla*, *Myotis ruber*, *Histiotus velatus*, *Nyctinomops macrotis*, and *Tadarida brasiliensis*), all but *N. macrotis* are at the edge of their geographic range (Koopman 1982) and likely occur at low densities (for

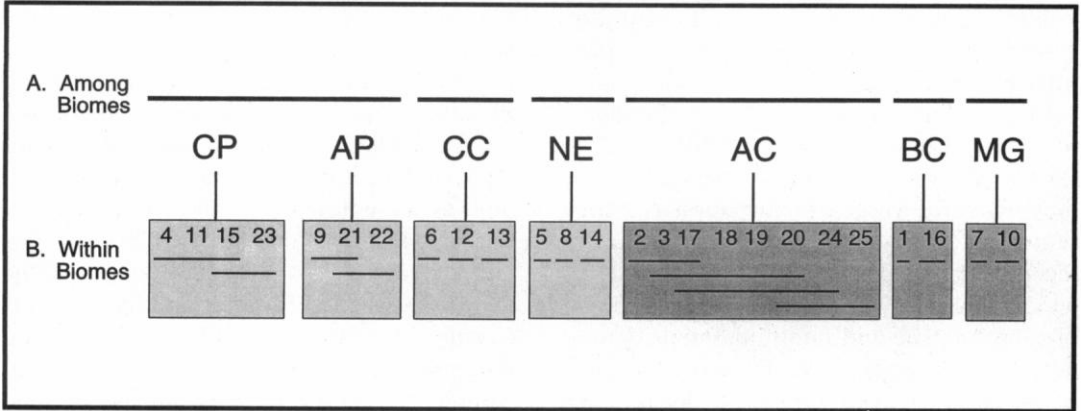


FIG. 3.—Results of a hierarchical heterogeneity *G*-test (Sokal and Rohlf 1995) assessing differences in the proportional abundance of families of bats among biomes A) within Paraguay or B) among sites within biomes. Alphabetic codes (Table 1) representing biomes that are below the same horizontal line have statistically indistinguishable familial compositions. Numeric codes (Appendix I; Fig. 1) representing sites that are above a horizontal line had statistically indistinguishable familial compositions. Light shading indicates biomes and sites east of the Río Paraguay; dark shading indicates biomes and sites west of the Río Paraguay.

theoretical considerations, see Brown 1984; Brown et al. 1995).

Eight of the species that we did not capture are known in Paraguay from only a few

(usually  $\leq 6$ ) specimens or localities (*P. macrootis*, 6 specimens, 3 localities; *A. caudifer*, 4 specimens, 3 localities; *M. macrophyllum*, 18 specimens, 2 localities; *P. dis-*

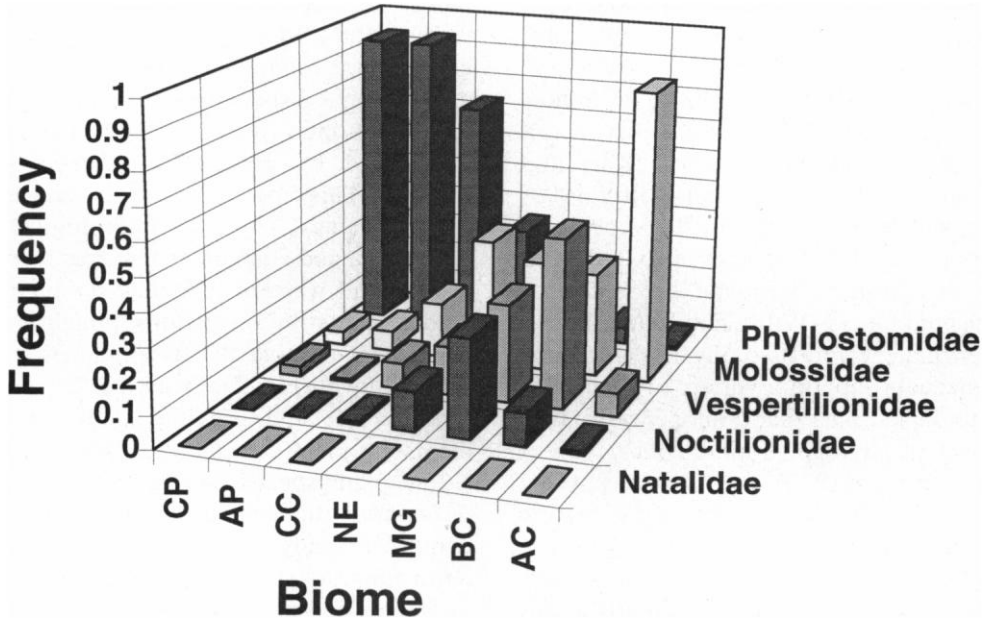


FIG. 4.—Three-dimensional histogram illustrating proportional abundances of each of 5 families of bats in 7 biomes (Central Paraguay, CP; Alto Paraná, AP; Campos Cerrados, CC; Ñeembucú, NE; Matogrosense, MG; Bajo Chaco, BC; Alto Chaco, AC) of Paraguay (Table 1).

*color*, 2 specimens, 2 localities; *P. hastatus*, 1 specimen, 1 locality; *T. sylvicola*, 8 specimens, 2 localities; *V. pusilla*, 5 specimens, 1 locality; and *H. velatus*, 2 specimens, 1 locality—López-González 1998). These taxa may no longer occur in the country or may be on the verge of extirpation as a consequence of extensive deforestation during the past 2 decades (Keel et al. 1993; Ríos and Zardini 1989). Alternatively, our choice of sampling site and sampling intensity may not have been adequate to detect presence of especially rare or stenotopic species.

*Faunal organization.*—The manner in which faunal composition of particular sites reflected phytogeographic characteristics depended on the level of taxonomic resolution. At the specific level, only the dichotomy of a dry west versus humid east was apparent in the bat fauna. Absence of distinct biome-specific assemblages of bats within each region may be a consequence of a variety of factors acting alone or in concert. Vegetational differences among biomes may not be sufficient to favor or maintain formation of distinct assemblages, movement of individuals from source to sink habitats may homogenize species compositions despite differences in inherent ecological value (Pulliam 1988), or anthropogenic and natural disturbances may result in nonequilibrium communities (Karr and Freemark 1985; Stevens and Willig 1999; Willig and McGinley 1999). In Venezuela, assemblages of bat species also failed to show concordance with the life zones of phytogeographers (Willig and Mares 1989). Rather, gallery forests along river systems in Venezuela support a variety of species of forest-adapted bats that homogenize faunas of different phytogeographic zones.

Weil et al. (1972) provided a physiographic classification of Paraguay that is different from that of Hayes (1995) in recognizing a single Chaco Boreal region, west of the Río Paraguay, and a slightly more complex subdivision of the region east of the Río Paraguay. More specifically, they expanded the Alto Paraná Biome (Paraná

Plateau) to the west and north along the border with Brazil so that it included Parque Nacional Cerro Corá (site 12) and Reserva Natural del Bosque Mbaracayú (site 15). They also distinguished the southern one-fourth of the Central Paraguay Biome as a Central Hill Belt (represented by Parque Nacional Ybycuí, site 23) and further reduced the southwestern extent of the Campos Cerrados Biome such that Estancia Cerrito (site 6) was included in the Central Paraguay Biome. Our quantitative conclusions based on analyses at the specific and familial levels were robust with regard to this alternative (physiographic) subdivision of the country. At the specific level, sites did not form clusters corresponding to the 5 eastern biomes. At the familial level, sites within each biome were heterogeneous, whereas Alto Paraná and Central Paraguay Biomes had indistinguishable compositions overall.

In a zoogeographic investigation of Paraguay, Myers (1982) considered vicariance and dispersal models to explain patterns of mammalian assemblages. Rodent and bat faunas on each side of the Río Paraguay were distinct. Myers (1982) concluded that a vicariance model was a less likely explanation than a dispersal model (i.e., dispersal of species into areas for which they were preadapted by conditions in their prior ranges). This interpretation is consistent with our study. Climatic, hydrological, topographic, and edaphic differences between eastern and western Paraguay produce disparate vegetative formations, which in turn support distinctive bat assemblages at the specific level (Fig. 2). Eastern alluvial clays retain water and provide stable environments for plant communities where at least a few plant species are in flower or fruit throughout the year. In contrast, the west comprises sandy soils that do not retain water or impermeable clays that are seasonally inundated and dry to concrete hardness, exposing the biota to highly variable and unpredictable conditions. As a consequence, tropical fruit-bearing plants are supported in

eastern Paraguay and sustain large populations of frugivorous phyllostomids, which are essentially absent from the west. In the vast areas of the Chaco that are devoid of lentic systems, at least during the dry season, man-made and natural ponds provide the only concentrations of food and water, and are few and scattered. Therefore, the long-flying molossids may be better adapted to exploit the seasonal, unpredictable Chaco compared with other guilds of bats.

Molossids typically have a patchy spatial distribution within their geographic ranges (Dolan 1989). The high local heterogeneity of bat assemblages in the Alto Chaco reflects this pattern despite the relative homogeneity of the habitat. In general, molossids are better adapted to persist in drier open areas. Indeed, abundances of many molossids are nearly always greater in drier areas, and distributions of many species are restricted to coastal deciduous forest, scrub forest, or savannas. In northeastern Brazil, Mares et al. (1981) found molossids in all xeric habitats surveyed but did not find molossids in more mesic habitats (e.g., humid forests and palm groves), with the exception of a single *Molossops greenhalli* found in remnant Atlantic Rainforest. In Bolivia, most records of molossids are from eastern savannas, subhumid forests, and Chaco (Anderson 1997). In Costa Rica, molossids were taken more commonly in pastures and dry forests than in mesic forests (Timm et al. 1989). In the southern cone of South America, molossid distributions are confined largely to the Chaco and Pampas regions (Redford and Eisenberg 1992). In contrast, Handley (1976:39) reported most species of molossids from xeric and mesic habitats in Venezuela; however, taxa reported from mesic habitats nearly always were captured "over (or near) a pond in a clearing in evergreen forest." Molossids generally do not appear to be abundant forest species but quickly take advantage of anthropogenic activities to forage in pastures and drink from cattle ponds recently formed in forested areas. Although we rec-

ognize the inherent bias associated with mist-netting at ground level, the intensity of our survey activities suggest that absence of many species of molossids from particular sites in the east is a real phenomenon, and the heterogeneity among sites in the west similarly reflects true faunal differences. Nonetheless, it is clear that in multistratal tropical forests, such as those along an elevational gradient at Manu in the Andes of southeastern Peru (Patterson et al. 1996), high-flying insectivores (molossids) are extremely difficult to capture, resulting in a potentially biased estimate of their contribution to local assemblages. As such, caution must be employed when evaluating the entire chiropteran assemblage of an area, at least until such time that it can be resolved that the absence of a species from a site known to occur within the broad geographic distribution of the taxon reflects ecological filters or artifacts related to sampling efficacy.

Analyses at the specific level that were sensitive to relative frequencies (Euclidean distance index, Fig. 2C) distinguished 3 broad clusters of sites. Seasonally flooded sites on either side of and in association with the Río Paraguay form a group (cluster 2, Fig. 2C) because they have similar relative abundances of a suite of insectivores (*Noctilio albiventris*, *Eptesicus furinalis*, *Myotis albescens*, *M. nigricans*, *E. patagonicus*, and *M. ater*). Dry Chaco sites form a group (cluster 3, Fig. 2C) as a result of the similar dominance by molossids (*E. patagonicus*, *E. glaucinus*, *Molossops temminckii*, and *M. molossus*) and to a lesser extent vespertilionids (*M. nigricans* and *L. ega*). Finally, dominance by phyllostomids (*A. fimbriatus*, *A. lituratus*, *Carollia perspicillata*, *Platyrrhinus lineatus*, *Pygoderma bilabiatum*, and *S. lilium*) with low diversity of vespertilionids and molossids characterizes eastern highland sites (cluster 1, Fig. 2C).

Paralleling results at the specific level, local heterogeneity characterizes the familial composition of bat assemblages from

each of the 7 biomes in Paraguay (Fig. 3B). This local heterogeneity may reflect historical land use (e.g., deforestation and agriculture) in eastern biomes, ephemeral unpredictable characteristics of the Chaco, and land use in the west. Despite such local heterogeneity, familial composition of bat assemblages from biomes were distinct, with the exception of Central Paraguay and Alto Paraná, whose bat faunas are dominated similarly by phyllostomids (Figs. 3A and 4).

In a study of the biogeography of birds in Paraguay, Hayes (1995) found the Central Paraguay and Alto Paraná biomes to contain the greatest numbers of species. This was attributed to the greater diversity of foraging niches, food items, and nesting sites available in taller humid forests than in relatively open savannas and scrub forests. In contrast, Central Paraguay and Alto Paraná ranked 4th and 5th, respectively, in bat species diversity, whereas Campos Cerrados contained the greatest number of bat species, and Alto Chaco and Ñeembucú were tied for 2nd. For bats, more species-rich communities in Paraguay are found in contact areas between fairly distinct phytogeographic zones; the Campos Cerrados of Paraguay occurs at the convergence of the Cerrados of Brazil and the Interior Atlantic Rainforest, and Ñeembucú at the convergence of the Chaco and Interior Atlantic Rainforest. The high species diversity found in the Alto Chaco probably is a function of greater sampling effort (8 localities and 11 expeditions) compared with any other biome (more than double that of the next most intensively sampled biome, Central Paraguay; Appendix I). Thus, in contact zones between more xeric (Cerrado and Chaco) and mesic (Interior Atlantic Rainforest) habitats, both phyllostomids, which are common in mesic forests, and molossids, which are common in xeric habitats, are more likely to be found in sympatry, increasing species richness (Fig. 4).

Short (1975) reported low endemism for Chacoan avifauna and the tendency for bird

species that occur in the Chaco to be distributed widely over South America. An investigation of the Chacoan Chiroptera (Myers and Wetzel 1983) found similar patterns, with distinct tendencies of Chacoan bats to be distributed widely compared with other South American bats. Deletions of species from neighboring faunas rather than differentiation or incorporation of new elements appear to explain the unique species composition of the Chaco (Myers and Wetzel 1983).

*Conservation.*—Eighty-five percent of eastern Paraguay (138,000 km<sup>2</sup>) was covered originally in forest. The rate of deforestation in eastern Paraguay (>1,000 km<sup>2</sup>, or 0.7% loss/year) is about twice as fast as that in the Amazon Basin (0.4% loss/year—Redford et al. 1990). By 1984, <22% (30,000 km<sup>2</sup>) of the original forest remained in Paraguay (Keel et al. 1993) compared with nearly 90% of the Amazon that remained intact in 1989. Consequently, the need to initiate and implement a conservation strategy in eastern Paraguay may be as urgent for the management of Paraguayan forests as for those of Amazonia. In addition, Paraguay occurs at a tropical-temperate interface where xeric and mesic habitats converge, giving rise to faunal and floral assemblages that, although not as species rich as their Amazonian counterparts, are distinctive in species composition. High levels of local heterogeneity in bat assemblages throughout Paraguay support the formation of a conservation program with many smaller protected areas rather than of a program with a few larger areas. Such a system currently is mandated by the Paraguayan government and the Fundación Moisés Bertoni (Gauto 1989), a private nongovernment organization. More than a dozen national parks are in different stages of establishment, including many that have been designated officially for more than a decade (e.g., Parque Nacional Cerro Corá, Parque Nacional Teniente Enciso, Parque Nacional Defensores del Chaco, Parque Nacional Serranía San Luís, and Parque Na-

cional Ybycúf). These national parks represent all biomes recognized by Hayes (1995), except for the Matogrosense (Ríos and Zardini 1989). Some private reserves and protected areas, administered to varying degrees by the Fundación Moises Bertoni, also are being established throughout eastern Paraguay (including the Reserva Natural del Bosque Mbaracayú) and the Bajo Chaco. These reserves, parks, and protected areas cover >1.5 million hectares, more than two-thirds of which is in the Chaco, and represent a significant commitment to the preservation of biodiversity in Paraguay. However, the effectiveness of these areas remains uncertain. A lack of financial and political support has left many government reserves protected poorly. The formation of some private reserves were attempts to prevent an increasing number of squatters (i.e., *campesinos sin tierra*) from invading private holdings. Despite expanding international markets, local economic and political stability are prerequisites for the successful establishment and administration of conservation programs.

Many species of bats reach their southern ( $n = 14$ ) or northern ( $n = 3$ ) distributional limits in Paraguay. Isolated populations at the edge of a species range may occupy marginal habitats where physiological stresses reduce the size of local populations (Andrewartha and Birch 1954; Brown et al. 1995) and enhance susceptibility to natural disturbances, thereby minimizing the likelihood of long-term persistence. Moreover, opportunities for recovery by local populations during favorable periods are diminished because of the rarity of nearby source populations (i.e., absence of mass or rescue effects, *sensu* Brown and Kodric-Brown 1977). Global climate change also may enhance the likelihood of local extinction for southern species whose ranges contract toward the poles as a consequence of global warming (Parmesan 1996). Finally, desertification in arid portions of the southern cone and increased economic development throughout Paraguay heighten concern

about the status of the bat fauna in the country. In summary, conservation strategies for Paraguay may be more complex than in many areas because its landscape represents a shifting mosaic of habitats occupied by species at the termini of their distributional ranges and is subject to increasing fragmentation as a consequence of economic development. The challenge to the future will be to prioritize conservation needs within this context and better support or expand the existing network of protected areas in the country.

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## APPENDIX I

Description of 25 sites (Fig. 1) at which bats were collected from Paraguay (July 1995–May 1997). Biome codes appear in Table 1; sampling regime includes year, season (wet, W; dry, D), and number of net nights.

Site code	Site name	Biome code	Departamento (s)	Latitude (S)	Longitude (W)	Elevation (m)	Sampling regime
1	Estancia La Victoria	BC	Presidente Hayes	23°39.03'	58°34.79'	120	95D–20
2	Estancia San Jorge	AC	Boquerón	22°02.11'	60°19.93'	160	95D–20
3	Cerro León	AC	Alto Paraguay	20°26.25'	60°19.19'	250	95D–10
4	Estancia Sombrero	CP	Cordillera	25°04.26'	56°36.08'	100	95W–37, 97W–70
5	Lago Ypoá	NE	Paraguari	25°56.71'	57°26.80'	120	95W–30
6	Estancia Cerrito	CC	Concepción	23°15.14'	57°29.57'	120	95W–36
7	Fuerte Olimpo	MG	Alto Paraguay	21°02.37'	57°52.29'	120	95W–22
8	Ayolas	NE	Misiones	27°23.42'	56°50.15'	70	96W–39
9	Parque Nacional San Rafael	AP	Itapúa	26°45.46'	55°51.67'	170	96W–43
10	Bahía Negra	MG	Alto Paraguay	20°10.98'	58°09.42'	90	96W–25
11	Yaguareté Forest	CP	San Pedro	23°48.50'	56°07.68'	250	96W–47
12	Parque Nacional Cerro Corá	CC	Amambay	22°37.90'	56°01.43'	280	96W–86
13	Parque Nacional Serranía San Luis	CC	Concepción	22°37.91'	57°21.35'	270	96D–75, 96W–137
14	Estancia Yacaré	NE	Ñeembucú	26°37.94'	58°07.46'	60	96D–107, 97W–97
15	Reserva Natural del Bosque Mbaracayú	CP	Canindeyú	24°07.69'	55°30.34'	250	96D–143, 96W–202
16	Estancia Loma Porá	BC	Presidente Hayes	23°29.92'	57°32.92'	80	96D–63, 97W–75
17	Estancia Tres Marias	AC	Alto Paraguay	21°16.72'	59°33.13'	70	96D–139, 97D–99
18	Estancia Samaklay	AC	Presidente Hayes	23°28.81'	59°48.43'	120	96D–111, 97W–87
19	Dr. Pedro P. Peña	AC	Boquerón	22°27.16'	62°20.65'	240	96D–148
20	Destacamento Militar Gabino Mendoza	AC	Alto Paraguay/Boquerón	20°05.30'	61°47.22'	390	96D–71, 97D–27
21	Estancia Rivas	AP	Canindeyú	24°30.43'	54°38.25'	300	96D–136, 97W–63
22	Estancia Golondrina	AP	Caazapá	25°32.30'	55°29.02'	300	96W–87
23	Parque Nacional Ybycuí	CP	Paraguari	26°04.64'	56°50.98'	150	96W–64
24	Parque Nacional Teniente Enciso	AC	Boquerón	21°11.40'	61°41.81'	250	97W–57
25	Palmar de las Islas	AC	Alto Paraguay	19°32.91'	60°31.64'	150	97D–108