

COMPARATIVE COMMUNITY ECOLOGY OF BATS FROM EASTERN PARAGUAY: TAXONOMIC, ECOLOGICAL, AND BIOGEOGRAPHIC PERSPECTIVES

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Based on more than a year and a half of intensive fieldwork, we document the community structure of bats at 2 sites (Reserva Natural del Bosque Mbaracayú and Yaguareté Forests) in eastern Paraguay. Twenty-nine species from 17 genera and 3 families were documented based on more than 7,000 captures. In general, these communities share greatest affinities with either Atlantic rainforest or savanna-grassland sites of South America. Significant differences exist between these communities in terms of structure based on rank-abundance distributions and species composition. Moreover, Yaguareté exhibits significantly more species than does Mbaracayú even after removing the effects of differences due to high-flying insectivores. No significant differences existed between communities regarding other aspects of taxonomic diversity (e.g., evenness, diversity, or dominance of species) or any aspect of functional diversity. A higher degree of habitat heterogeneity at Yaguareté likely underlies these differences in community structure.

Key words: Atlantic rainforest, bat community, Chiroptera, community structure, functional diversity, Molossidae, Paraguay, Phyllostomidae, taxonomic diversity, Vespertilionidae

Chiroptera is the 2nd largest mammalian order and represents more than half of all mammalian species in many Neotropical communities (Aguirre 2002; Lim and Engstrom 2001; Voss and Emmons 1996). Moreover, bats are particularly abundant in the tropics and contribute greatly to patterns of species richness and diversity at the local level (Estrada and Coates-Estrada 2001; Findley 1993; Fleming 1973; Patterson et al. 2003). As a group, bats exhibit a high degree of ecological diversity, as evidenced in part by a wide variety of plant and animal products they are known to consume. Consequently, bats can have considerable impacts on rates of immobilization and mineralization of nutrients and energy within ecosystems, as well as contribute substantially to other ecosystem services such as seed dissemination, flower pollination, and the control of prey populations (Ascorra and Wilson 1992; Fleming 1988; Gorchoff et al. 1993; Marinho-Filho and Vasconcellos-Neto 1994; Medellín and Gaona 1999; Rainey et al. 1992; Willig and Gannon 1996).

Although ecological importance of Chiroptera is well appreciated, few broad-scale patterns have emerged regarding organization of bat communities. For example, when communities are divided into feeding guilds, they demonstrate much variation in terms of the degree to which deterministic models describe structure. While these models most often describe structure of aerial insectivore and frugivore feeding guilds (Perry 2001; Stevens and Willig 1999, 2001), general patterns regarding structure of entire communities do not emerge. In contrast, strong patterns exist with respect to effects of latitude on taxonomic diversity of New World bat communities. Latitudinal gradients in diversity of communities exist in the New World such that richness but not evenness of species increases toward the equator (Stevens and Willig 2002). Nonetheless, this general pattern is not representative of all families of bats that occur in the New World. At the community level, phyllostomids and emballonurids exhibit the classical negative relationship between species richness and latitude; mormoopids and molossids exhibit no relationship; and the number of species of vespertilionids within communities increases positively with latitude (Stevens 2004). Accordingly, vespertilionids dominate temperate communities and phyllostomids dominate tropical communities (Findley 1993; Voss and Emmons 1996). Where vespertilionid-dominated temperate

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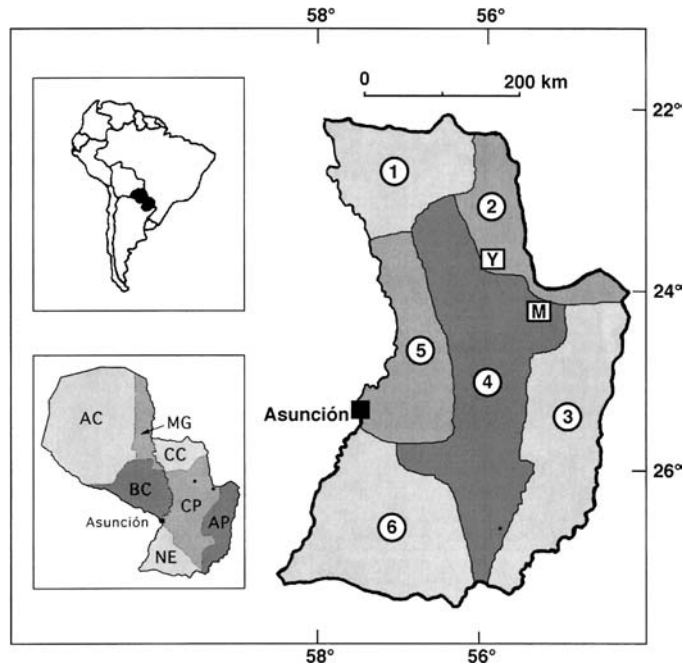


FIG. 1.—Location of Mbaracayú and Yaguareté in eastern Paraguay (right). Numbers correspond to ecoregions defined by Keel et al. (1993): (1) Aquidabán, (2) Amambay, (3) Alto Paraná, (4) Selva Central, (5) Litoral Central del Paraguay, (6) Ñeembucú. Upper left inset indicates location of Paraguay in South America. Lower left inset locates the 7 biomes used in Willig et al. (2000): Alto Chaco (AC), Matogrosense (MG), Campos Cerrados (CC), Bajo Chaco (BC), Central Paraguay (CP), Alto Paraná (AP), Ñeembucú (NE).

communities intergrade into phyllostomid-dominated tropical communities is unclear. Nonetheless, this zone is likely narrow and located somewhere around the area that divides tropic and temperate zones.

Most of our understanding of bat community structure in the New World comes from sites distributed throughout North and Central America (Findley 1993; Patterson et al. 2003; Stevens and Willig 2002). Few sites have been examined at the interface of tropical and temperate zones. Although fewer communities have been described in South America, the same bias holds true. Importantly, the number of descriptions of South American bat communities has increased over the last decade (Ascorra et al. 1996; Bernard 2001; Lim and Engstrom 2001; Simmons and Voss 1998), but most have focused on sites occurring in the Amazon basin. Nonetheless, as Mares (1992) suggested, non-Amazonian areas may contribute even greater amounts of diversity to the South American fauna than do Amazonian areas. Only a few studies located south of the Amazonian basin have addressed structure of bat communities (Aguirre 2002; Moura de Souza Aguiar 1994; Pedro and Taddei 1997). Information concerning structure and dynamics of non-Amazonian bat communities is needed to enhance understanding of ecology of bats in general.

The climatic, geologic, and biogeographic context of Paraguay provides an ideal setting in which to evaluate effects of spatial and temporal dynamics of species on community structure. Moreover, the enhanced spatial heterogeneity found

in Paraguay suggests that different communities can be found in close spatial proximity. The country is located at the junction of a number of different biomes including Cerrado, Pantanal, Atlantic rainforest, and Wet and Dry Chaco (Gorham 1973; Hayes 1995; Willig et al. 2000). Because Paraguay straddles the Tropic of Capricorn, the anticyclone of the Atlantic Ocean dominates the climate. Consequently, Paraguay experiences considerable annual climatic (temperature and precipitation) variability (Hayes 1995). As a result, a number of tropical bat species reach their biogeographic termini at latitudes within Paraguay (López-González 1998; Willig et al. 2000). Effects of such spatial and temporal dynamics are poorly understood, in part because of a paucity of comprehensive data collected at local scales in regions of elevated edaphic and climatic heterogeneity.

Herein, we quantify structure of 2 intensively surveyed Paraguayan bat communities. In addition, we evaluate differences in community structure in terms of species diversity and composition, as well as in terms of composition and diversity of functional groups. Finally, we compare these communities to a spectrum of other Amazonian and non-Amazonian communities in South America.

MATERIALS AND METHODS

Study sites.—Both bat communities we examined (Reserva Natural del Bosque Mbaracayú and Yaguareté Forests) occur in the Central Paraguay phytogeographic region (Fig. 1; Hayes 1995). Of the 7 geographical regions defined for Paraguay, this area exhibits the greatest spatial heterogeneity. From west to east, it extends from relatively flat terrain that comprises flat marshes, palm savannas, and patches of low humid forest along the Paraguay River to more topographically varied terrain that comprises tall humid forest along the border with Brazil. Humid forest once covered much of the Central Paraguay region, but the area has been forested extensively throughout the 20th century (Hayes 1995). The region is part of the drainage basins for the Paraguay and Paraná rivers. Dominant trees include *Astronium fraxinifolium*, *Patagonula americana*, *Peltophorum dubium*, *Piptadenia rigida*, *Sorocea bonplandii*, and *Actinostemon concolor* (Keel et al. 1993).

The climate of the Central Paraguay region is seasonal and subtropical with distinct wet (October to May) and dry (June to September) seasons that are characterized by marked temperature differences (Hill and Hurtado 1996; Hill et al. 1994). Average daily temperatures range from 27°C in January to 17°C in June and July. Annual average high and low daily temperatures range from 24°C to 33°C and 9°C to 21°C, respectively. Low temperatures of −3°C are not uncommon in winter, with several days of hard frost annually. Annual precipitation ranges between 1,500 and 1,700 mm from west to east (Hayes 1995) and is characterized by considerable interannual variation (Hill and Hurtado 1996). In some areas, precipitation is quite erratic. For example, based on 34 years of data from the Paraná Forest, Bertoni and Gorham (1973) were unable to discern which month would receive the most precipitation.

Yaguareté Forests.—Yaguareté Forests is located approximately 40 km east of Santa Rosa de Lima in the Department of San Pedro (23°48.50'S, 56°07.68'W) at an elevation of approximately 250 m (Willig et al. 2000). This private reserve was established to operate an economically viable but environmentally sound sustainable timber management and wildlife conservation program. Ostensibly, harvest of trees was light: only a portion of the property was logged selectively on

a 40-year rotation scheme (Yaguareté Forests 1996). Yaguareté Forests occupies approximately 16,000 ha and is bordered to the south and east by the Aguaray-Guazú River and on the west by the Verde River, both rivers are tributaries of the Jejuí-Guazú River. This site is embedded in a transition zone between the Amambay and Central Paraguay ecoregions defined by Keel et al. (1993), and the property is characterized by mesic tree species of low stature, although some tall-dry forest habitats dominated by peroba (*Aspidosperma polyneuron*) occur as well (Yaguareté Forests LDC 1996). Grassland-savanna habitats (Campos Cerrados) interdigitate with these forested habitats, enhancing spatial heterogeneity. Accordingly, 66% of the site is forested and 34% is mixed natural grassland and riparian habitats. The 5 most common plant species in rank abundance in the overstory were *Myrciaria bapoleti*, *Chrysophyllum gonocarpum*, *Coutarea hexandra*, *Sweetia elegans*, and *Dendropanax cuneatus*, whereas the 5 most common species in the understory were *Coussarea platyphylla*, *Sorocea bondplandii*, *Fagara naranjillo*, *C. hexandra*, and *S. elegans* (Jin and Oren 1997).

Mbaracayú.—The Reserva Natural del Bosque Mbaracayú is located approximately 30 km east of Ygatimí in the Department of Canindeyú (24°07.69'S, 55°30.34'W) at an elevation of 250 m (Willig et al. 2000). Mbaracayú has been the focus of a number of low-intensity mammal surveys (Brooks et al. 1992; López-González et al. 1998; Willig et al. 2000), as well as an examination of the effects of forest fragmentation on the distribution and abundance of phyllostomid taxa at the reserve and its surrounding region (Gorresen 2000; Gorresen and Willig, in press). This protected area was established through a federal mandate in 1992 to conserve in perpetuity one of the largest contiguous parcels of interior Atlantic rainforest that remains in South America. Mbaracayú comprises approximately 65,000 ha and is bisected by the Jejuí River. Although the reserve includes mesophytic broadleaf tall, medium, and short forests, tall forest is most common. The 5 most common plant species at this site were *S. bonplandii*, *Campomanasia xanthocarpa*, *C. gonocarpum*, *M. bapoleti*, and *Balfourodendron reidelianum* (Keel et al. 1993), all of which represent plant families that are included in diets of bats (Gardner 1977).

Sampling methods.—Bats were collected by mist netting from May through August 1996 and from January 1997 through April 1998. Between 5 and 10 locations at each of the 2 study sites were visited monthly. In general, 10 standard mist nets (3 × 12 m, 1.5-inch mesh) were erected on roads and trails and in open areas along edges of emergent vegetation each night. All nets were monitored from just prior to dusk for at least 4 h, and frequently (25% of nights) until dawn the next morning. Nets were checked hourly; bats were sacrificed and prepared as standard museum specimens or released after identification. One-half of the collection of specimens will be deposited at the Museum, Texas Tech University, and the other half will be deposited at the Museo Nacional de Historia Natural del Paraguay.

Quantitative analyses.—Based on netting records, we determined composition of species and functional groups at each site. We used sample-based species accumulation curves to estimate the completeness of mist-netting efforts at both sites. Sample-based curves are preferable to individual-based curves because they incorporate levels of spatial heterogeneity inherent to samples (Gotelli and Colwell 2001). Because differences between sites regarding number of individuals per sample will affect the shape of sample-based accumulation curves (Gotelli and Colwell 2001), we plotted the cumulative number of taxa against number of individuals constituting the sample (as opposed to plotting against number of samples). We also estimated the number of expected species at each site using Chao 1 (Chao 1984), Chao 2 (Chao 1987), and a jackknife species-richness estimator (Burnham and Overton 1978, 1979). Sample-based curves and species-richness

estimators were generated using the EstimateS software program (Colwell and Coddington 1994).

We evaluated differences between these 2 communities from perspectives of both species and functional groups. In general, we follow Koopman (1993) for taxonomic designations of Paraguayan bats but follow López-González (1998) in recognizing *Artibeus jamaicensis* (Handley 1987) instead of *Artibeus planirostris*, *Lasiurus blossevillii* instead of *Lasiurus borealis*, and *Eumops patagonicus* (Barquez et al. 1999) instead of *Eumops bonariensis beckeri* (while still recognizing *Eumops bonariensis bonariensis*). We divided species into 6 of 7 functional groups of bats present in the New World (e.g., aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, nectarivores, piscivores, and sanguinivores—Stevens and Willig 1999, 2001); piscivores were not detected in either community. Because the greatest difference between these communities involved number of species of high-flying insectivores, we conducted 2 suites of analyses, 1 suite including and 1 suite excluding this functional group. In analyses that evaluated differences between sites regarding community structure, we held experiment-wise error rate at 5% by conducting Bonferroni sequential adjustments (Rice 1989).

To evaluate significant differences between species rank-abundance distributions, we conducted a Kolmogorov-Smirnov 2-sample test (SPSS Inc. 1990). To evaluate differences between sites regarding composition of species and functional groups, we conducted 2-way chi-square contingency tests (Sokal and Rohlf 1995) in which we used a randomization approach to determine significance. More specifically, we randomly allocated individuals to species and sites under the constraint that row (species) and column (sites) totals summed to their original values. This randomization approach allowed us to relax more stringent requirements that 20% of expected values are ≥ 5 and none < 1 (Sokal and Rohlf 1995). Additionally, we evaluated differences between sites regarding taxonomic and functional diversity. We used number of species and number of functional groups as measures of richness. We also used the Shannon diversity index (Pielou 1975), Camargo evenness index (Camargo 1993), and Berger-Parker dominance index (Berger and Parker 1970) to characterize, respectively, diversity, evenness, and dominance of species and functional groups. Following Magurran (1988), the Berger-Parker index was scaled so that a large value represented low dominance and high diversity. We used a randomization procedure (Solow 1993) to infer significant pairwise differences in richness, evenness, diversity, and dominance between sites. In this procedure, the null hypothesis was that the 2 sites represent random samples from the same community (i.e., H_0 : difference in diversity = 0). To build a null distribution, individuals from both samples were pooled, and the same number of individuals as characterized each empirical sample were randomly drawn from the pool without replacement. Number of individual per species and number of species per functional group were tallied, a particular measure of diversity was then calculated for each of the simulated samples, and their difference was determined. This process was iterated 1,000 times to yield a distribution of 1,000 random differences. A P value then described magnitude of deviation of the empirical difference based on the distribution of random differences.

To evaluate biogeographic affinities of these communities, we compared Yaguareté and Mbaracayú with 14 other extensively sampled sites in South America that are available in the literature. More specifically, we used multidimensional scaling (SPSS Inc. 1990) to ordinate all 16 sites based on proximity matrices. To evaluate intersite patterns regarding species presences and absences, we calculated a binary Euclidean distance matrix based on species presences and absences. Also, we evaluated differences regarding structure of functional groups by calculating a standard Euclidean

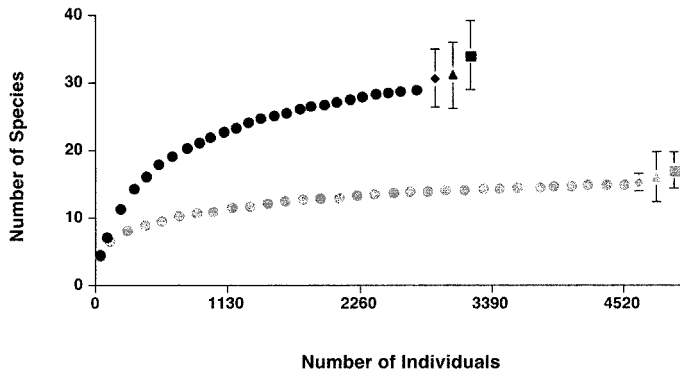


FIG. 2.—Species accumulation curves describing the average number of species for a given number of captured individuals in the Mbaracayú (gray) and Yaguareté communities (black). Both curves are asymptotic, suggesting that most species found in these communities were detected. Diamonds, triangles, and squares refer to estimated number of species that occur in these communities based on Chao 1, Chao 2, and jackknife estimators of species richness, respectively. Vertical lines represent 95% confidence intervals. The empirical species richness at each community was not significantly different than those based on estimation.

distance matrix based on number of species per functional group at each site. To determine significant differences between tropical forests as a group and tropical dry savanna and Atlantic rainforest sites as a group regarding positions in the space defined by the multidimensional scaling, we used multivariate analysis of variance (MANOVA; SPSS Inc. 1990).

RESULTS

More than 7,000 bats (62% at Mbaracayú and 38% at Yaguareté) representing 3 families, 17 genera, and 29 species were captured during 218 nights (55% at Mbaracayú and 45% at Yaguareté) of netting. Accumulation curves indicated that levels of species richness at each site were reasonably asymptotic (Fig. 2). Estimates of predicted species richness ranged from 15 to 17 at Mbaracayú and 32 to 34 at Yaguareté. The adequacy of sampling is supported by the observation that species richness of these sites detected from our netting efforts was indistinguishable from predicted estimates (i.e., observed species richness always occurred within confidence intervals about predicted estimates).

Phyllostomids were by far the most dominant species in each community (Fig. 3). *Artibeus lituratus*, *Sturnira lilium*, and *Pygoderma bilabiatum* were the 3 most abundant taxa at each site and together accounted for 85% and 91% of all captures at Yaguareté and Mbaracayú, respectively. Vespertilionids were uncommon and always accounted for <1% of captures. Molossids were typically uncommon but attained relative abundances of >1% at Yaguareté. The shape of species rank-abundance distributions differed significantly between Mbaracayú and Yaguareté (Table 1). When high-flying insectivores were excluded from the analysis, this difference was nonsignificant, suggesting that abundances of high-flying insectivorous species contribute to intersite differences regarding the shape of rank-abundance distributions.

Taxonomic diversity and species composition of these communities were significantly different as well (Table 1). Highly significant differences between sites existed regarding species composition and species richness. Nonetheless, no significant difference existed for diversity, dominance, or evenness of species. The exclusion of high-flying insectivores (i.e., excluding molossids) never altered decisions of significance regarding species composition or aspects of taxonomic diversity.

Five functional groups occur at Mbaracayú and 6 functional groups occur at Yaguareté (Fig. 4). Regardless of site, frugivores comprise the most species and the greatest number of individuals. Aerial insectivores also were relatively species rich but typically exhibited low abundances. The most conspicuous intersite difference involved the number of species of high-flying insectivores. Moreover, Yaguareté possessed all species of bats found at Mbaracayú and exhibited a greater number of species in 5 of 6 functional groups encountered at these 2 sites. Nonetheless, no significant differences exist between Mbaracayú and Yaguareté regarding composition of functional groups, or richness, evenness, diversity, or dominance of functional groups (Table 1).

A 2-dimensional ordination of South American sites based on presence and absence of bat species (Fig. 5) accounted for much variation among sites ($R^2 = 0.959$) and displayed intersite relationships with little distortion (stress = 0.098). Tropical forest sites exhibited greater variation on both multidimensional scaling axes and could be distinguished from tropical dry savanna sites and Atlantic rainforest sites based on their taxonomic composition (MANOVA, $F = 10.43$, $P < 0.001$). Mbaracayú was aligned most closely to Atlantic rainforest sites, whereas Yaguareté was aligned most closely to savanna sites.

The 2-dimensional ordination of sites based on number of species per functional group also accounted for much of the variation among sites in functional group composition ($R^2 = 0.992$) with little distortion (stress = 0.042). Intersite differences based on functional groupings were similar to those based on taxonomic composition. Tropical forest sites exhibited greater variation on both multidimensional scaling axes and could be distinguished from tropical dry savanna and Atlantic rainforest sites based on their functional group composition (MANOVA, $F = 14.96$, $P < 0.001$). Again, Mbaracayú was aligned most closely with Atlantic rainforest sites and Yaguareté was aligned most closely with tropical savanna sites.

DISCUSSION

Although bat communities at Mbaracayú and Yaguareté share a number of fundamental similarities, they are quite different with respect to shape of their rank-abundance distributions, species composition, and species richness. Moreover, these differences in community structure cannot be solely explained by difference in the number of high-flying insectivores. The interdigitating elements of forest and campos cerrado associated with the transition zone between Amambay and Central Paraguay ecoregions in general (Hayes 1995) and that found at Yaguareté in particular likely translate to greater habitat heterogeneity for bats that in turn allows for the coexistence of more species in this community.

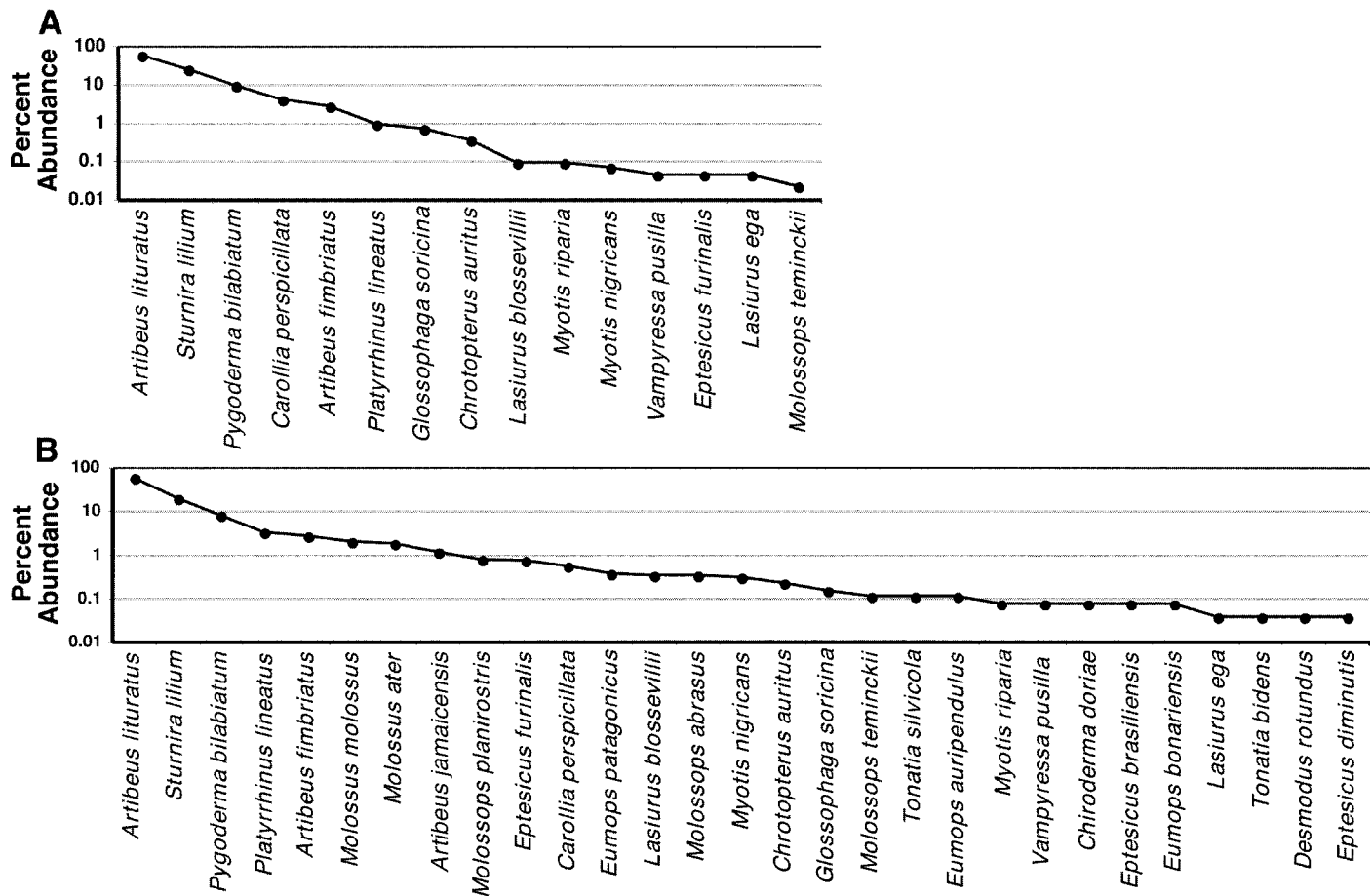


FIG. 3.—Species composition and rank-abundance distributions of the (A) Mbaracayú and (B) Yaguareté communities.

Although these 2 communities are significantly different from each other in a number of ways, their distinction with respect to other South American communities derives from their high number of cosmopolitan species. Indeed, a number of populations persist in these communities that are at the edge of their species or even subfamilial and familial geographic ranges. For example, of the 54 species that have been reported from Paraguay (López-González 1998; Willig et al. 2000) all noctilionids, emballonurids, natalids, 85% of phyllostomids, 31% of vespertilionids, and 59% of molossids reach their biogeographic termini in either Paraguay or adjacent Brazil or northern Argentina (Barquez et al. 1999; Koopman 1982; Redford and Eisenberg 1992). Moreover, these tropical bats face temperate seasons in which winters are characterized by a drastic reduction in resources and freezing temperatures (Fariña-Sánchez 1973). These factors interact to create communities of bats with a noteworthy combination of characteristics: moderate species richness, taxonomic simplicity, and species with generalist habits. Twenty-one of the 29 species found in these 2 communities (72%) have range sizes that are in the upper quartile for all New World bats (M. R. Willig and S. J. Andelman, in litt.). Moreover, *Desmodus rotundus*, *S. lilium*, *Glossophaga soricina*, *A. lituratus*, *Carollia perspicillata*, *A. jamaicensis*, and *Tonatia silvicola*, common bats in eastern

Paraguay, possess the 7 largest range sizes of any phyllostomid species. Twelve species, almost half of those found in these 2 communities, are in the top hemispheric abundance quartile of 150 bats examined from the New World, and 13 species in these communities are considered among the most common bats based on size of their geographic distribution combined with their average abundance at the local level (Arita 1993). Although the bat fauna of this region and in these communities in particular possess few remarkable species, the degree to which these communities are inhabited by generalist taxa is exceptional.

Given their moderate species richness, these communities are relatively complex from an ecological perspective in possessing 6 of 7 functional groups comprised by New World bats. Nonetheless, Mbaracayú and Yaguareté possess 3 and 2 functional groups, respectively, that are represented by only a single species. It has been suggested that decreases in species richness associated with increasing elevation is nonrandom with respect to ecological characteristics of bat species (Kalko 1997). More specifically, species richness decreases within ecological groups (i.e., feeding guilds), and this ultimately leads to a decrease in the number of groups with those comprising phyllostomids (i.e., nectarivores, frugivores, sanguinivores) disappearing first and those composed of species from other

TABLE 1.—Significance tests evaluating differences between Mbaracayú and Yaguareté regarding community attributes.^a

Criterion	Yaguareté	Mbaracayú	Test statistic	P
Rank abundance distributions			1.84	0.002*
Excluding molossids			1.08	0.940
Species composition			514.13	<0.001*
Excluding molossids			266.68	<0.001*
Species richness	29	15	14	<0.001*
Excluding molossids	21	14	7	0.009*
Species evenness	0.13	0.17	0.04	0.403
Excluding molossids	0.13	0.19	0.05	0.404
Species diversity	1.50	1.24	0.26	0.034
Excluding molossids	1.27	1.24	0.04	0.834
Species dominance	1.74	1.75	0.01	0.997
Excluding molossids	1.65	1.75	0.10	0.973
Guild composition			3.98	0.617
Excluding molossids			1.23	0.943
Guild richness	6	5	1	0.765
Excluding molossids	5	4	1	0.756
Guild evenness	0.63	0.57	0.05	0.632
Excluding molossids	0.58	0.61	0.03	0.822
Guild diversity	1.53	1.26	0.26	0.394
Excluding molossids	1.30	1.09	0.21	0.517
Guild dominance	3.22	2.14	1.08	0.409
Excluding molossids	2.33	2.00	0.33	0.733

^a Three types of analyses were used: Kolmogorov-Smirnov tests (test statistic z) on rank abundance distributions, chi-square tests (χ^2) on species and guild composition, and randomization tests to evaluate differences (d) between communities regarding aspects of diversity. An asterisk indicates significant difference between the 2 communities after a Bonferroni sequential adjustment (Rice 1989).

families (i.e., insectivores) disappearing last. A similar diminution transpires along latitudinal gradients (Stevens 2004; Willig and Selcer 1989). Accordingly, the latitudinal position of Mbaracayú and Yaguareté likely accounts for low species richness and relative abundances of nectarivore, gleaning animalivore, and sanguinivore bats. Nonetheless, this latitudinal position does not explain the relatively high species richness and dominance of frugivores.

A characteristic that distinguishes these communities from others found in South America is the high degree to which they are dominated by phyllostomid frugivores, particularly *A. lituratus*, *S. lilium*, and *P. bilabiatum*. These communities are among the 3 most dominated communities of 15 from South America evaluated by Stevens and Willig (2002). A general notion in biogeography and macroecology, the abundant-center hypothesis (Sagarin and Gaines 2002), is that abundances of species are highest at the center of their geographic range and uniformly decrease toward their periphery (Brown et al. 1996; Enquist et al. 1995). This may result because local abundance of a species reflects how well a particular site satisfies its ecological needs along multiple niche axes (Brown 1984; Hall et al. 1992). Thus, the position of sites along an environmental gradient is coupled to the abundances of populations inhabiting those sites. Because environmental conditions are spatially autocorrelated, abundances are too, and the greater the distance from the optimum site for a species, the lower abundances should become. Ultimately, the environment becomes too inhospitable for persistence of a population at a point called the geographic terminus. That species exhibit their lowest

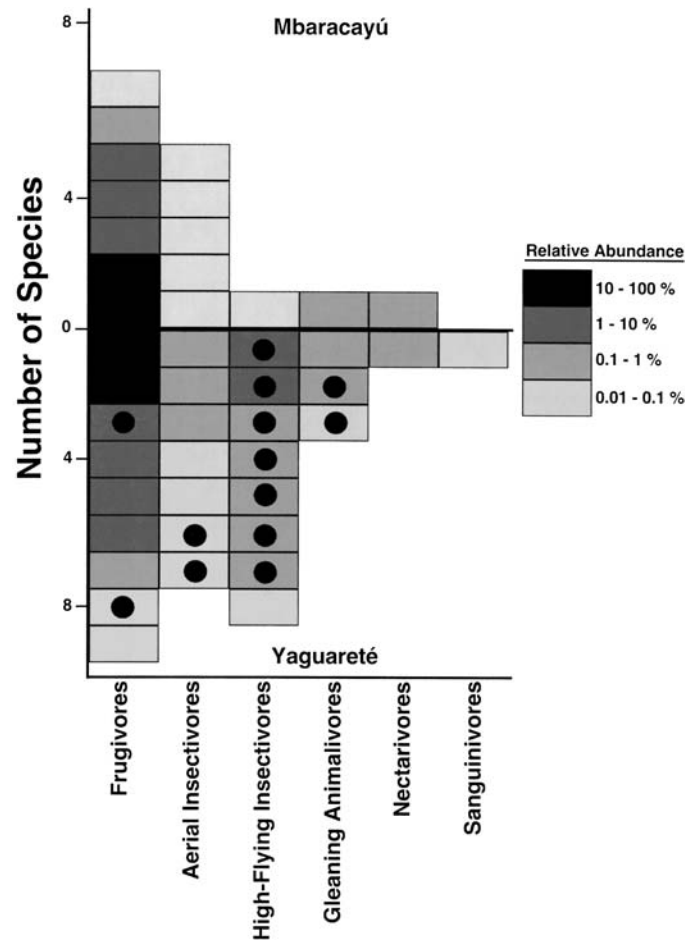


FIG. 4.—Composition of functional groups found in the Mbaracayú (upper) and Yaguareté (lower) communities. Rectangles represent species and black dots represent those species that are unique to the Yaguareté community. The shade of the rectangle represents relative abundance of that species.

abundances at the edge of their geographic range is clearly not the case for the 3 most abundant taxa in these communities. All 3 are within close proximity of the edge of their geographic distribution. Nonetheless, these species exhibit exceptionally high absolute and relative abundances in these communities. The reasoning behind the abundant-center distribution (Sagarin and Gaines 2002) may be reasonable in a simple world, but environmental parameters may not be the only characteristics that vary along spatial gradients. For example, to the degree that the position along climatic or edaphic gradients reflects harshness of the environment, biotic gradients may run opposite of climatic and edaphic gradients for some species. Those species that can persist in relatively harsh environments may be able to enjoy higher abundances in those environments because of fewer interspecific interactions. Success of these 3 frugivorous species in these communities may be further enhanced by their specialization on 3 fairly distinct types of fruit. Although substantial geographic and temporal variation characterizes the diets of these bats, in this part of South America *A. lituratus* is a fig and *Cecropia* specialist (Galetti and Morellato 1994; Zortea and Chiarello 1994), *S. lilium* is

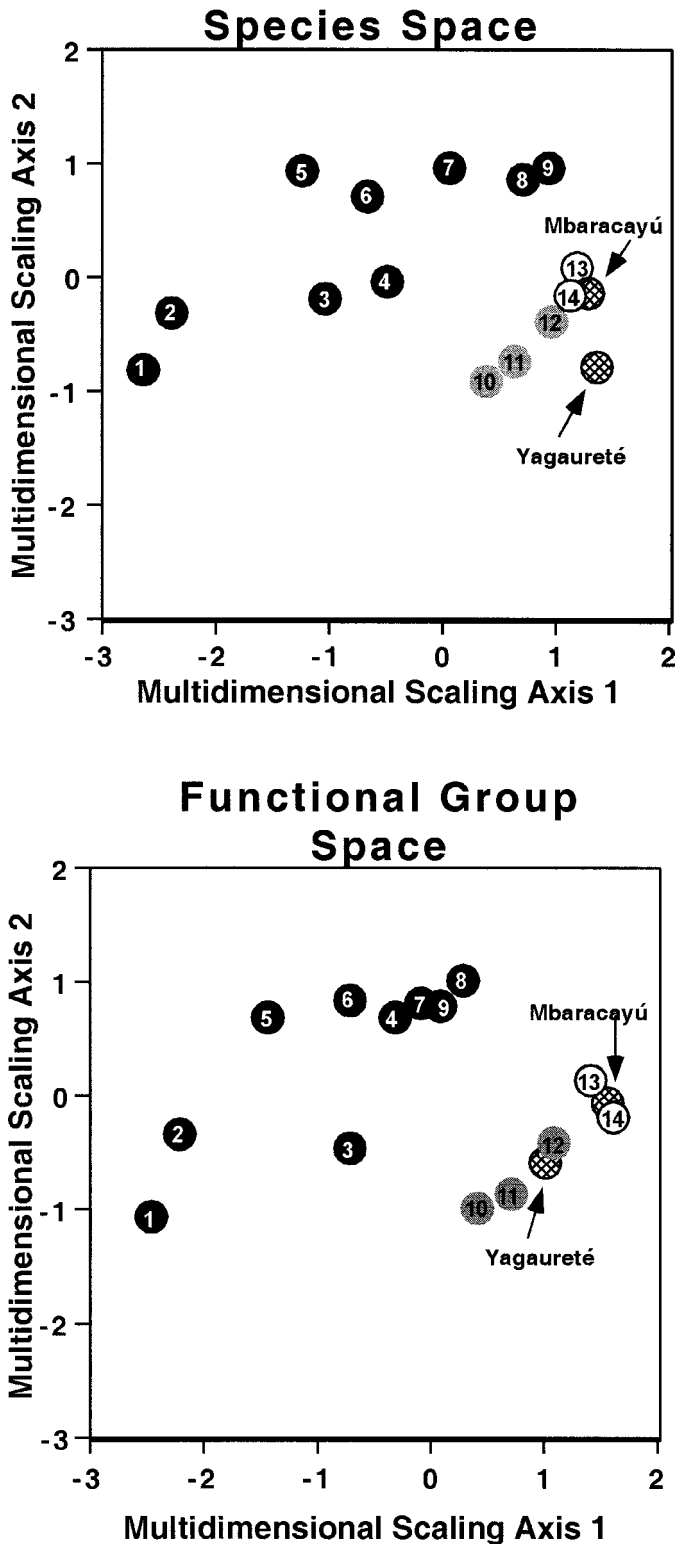


FIG. 5.—Proximity of the Mbaracayú and Yaguareté communities (hatched circles) to 14 other extensively sampled sites in South America, based on first 2 axes of multidimensional scaling. Numbers in circles refer to sites: (1) Paracaou, French Guiana (Simmons and Voss 1998); (2) Iwokrama Forest, Guyana (Lim and Engstrom 2001); (3) Manaus, Brazil (dos Reis 1984); (4) Duida-Marahuaka National Park, Venezuela (Pérez Eman 1995); (5) Jenaro Herrera, Perú (Gorchov and Ascorra in litt.; Gorchov et al. 1995); (6) Pakitza, Perú

a *Solanum* specialist (Marinho-Filho 1991), and *P. bilabiatum* is a specialist on large ripe fleshy fruit (Myers 1981). Accordingly, high abundances of these frugivores may be a consequence of ecological release (Losos and de Queiroz 1997; Terborgh and Faaborg 1973) in these relatively species-poor communities due to an absence of numerous competitors and the effects of direct and diffuse competitive interactions.

Paraguay lies at the interface of a number of major South American biomes. However, it exhibits little topographic relief and few barriers to promote the development of an endemic bat fauna (López-González 1998). Species that compose this fauna likely were preadapted by conditions occurring in other faunas and have extended their distribution into the country by migration (Myers 1982). If true, this bat fauna has resulted from exclusion of species from neighboring faunas rather than from in situ speciation (Meyers and Wetzel 1983). Nonetheless, major vegetational differences exist on east and west sides of the Paraguay River that facilitate maintenance of distinct assemblages of bats (López-González 1998; Myers and Wetzel 1983; Willig et al. 2000) in the absence of an impenetrable biogeography barrier.

While no bat species is endemic to Paraguay (López-González 1998), species from 3 distinct faunas intergrade there. The 1st group of species are of tropical affinity and can be found throughout the country. Phyllostomids dominate east of the Paraguay River, whereas molossids and vespertilionids dominate to the west (López-González 1998; Willig et al. 2000). Second, species that share affinities with the Atlantic rainforest (i.e., *Artibeus fimbriatus*, *Chiroderma doriae*, *P. bilabiatum*) remain in forest remnants that occur in the eastern part of the country. Third, species of primarily Patagonian affinity (i.e., *Histiotus macrotus*, *Histiotus velatus*, *Myotis ruber*, *E. bonariensis*, *E. patagonicus*) occur throughout eastern and western Paraguay.

Bat faunas that intergrade in Paraguay characterize 2 biogeographic crossroads (Spector 2002) that present themselves at regional scales (eastern as opposed to western Paraguay) and continental scales (e.g., different faunal regions of South America). Within Paraguay, flooded lands (sensu López-González 1998, in litt.) represent the transition zone between the eastern and western regions of the country, where phyllostomid-dominated communities come into contact with communities dominated by molossid and vespertilionid taxa. At the level of the entire country, biotic elements of tropical, Atlantic rainforest, and Patagonian regions converge and result in the distinctive Paraguayan bat fauna. Although biogeographic

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(Ascorra et al. 1996); (7) Marcarena, Colombia (Sánchez-Palomino et al. 1993); (8) Zabelitas, Colombia (Thomas 1972); (9) Cordillera Central, Colombia (Muñoz Arango 1990); (10) Espíritu, Bolivia (Aguirre 2002); (11) Caatingas, Brazil (Willig 1982); (12) Edaphic Cerrado, Brazil (Willig 1982); (13) Minas Gerais, Brazil (Moura de Souza Aguiar 1994); (14) Panga, Brazil (Pedro and Taddei 1997). Sites in black are communities in tropical forest, sites in gray are communities in savanna-grassland, and sites in white are from the Atlantic rainforest.

intersections represent areas of high turnover of species and habitats, and hence areas of high beta diversity (Spector 2002), these 2 bat communities still retain all 3 of the biotic elements found in Paraguay.

Populations found within biogeographic zones of intergradation have a number of unique characteristics. Contrary to the abundant-center hypothesis, Lomolino and Channell (1995) suggest that peripheral populations have higher abundances and are more preadapted to a larger range of ecological conditions than are more central populations. Moreover, environmental heterogeneity and different selection pressures experienced across ecotones can enhance rapid evolutionary change among populations despite gene flow (Schnieder et al. 1999; Spector 2002). These characteristics possibly drive evolution within zones of intergradation and ultimately enrich biotas (Spector 2002). Furthermore, these conditions predispose peripheral populations and not more central ones to be among those that survive when ranges contract (Lomolino and Channell 1995), as well as predispose them to be able to adapt more favorably and rapidly to future environmental change (Araujo 2002). Conservation of species within areas of biogeographic intergradation may be even more effective because such practices protect areas with elevated species richness and elevated amounts of adaptive variation, relative to areas in the center of any particular region (Spector 2002). Although conservation efforts should focus on maximizing the protection of as many species as possible (Andelman and Willig 2002), the conservation of adaptive variation of species may be as important as the conservation of the particular species in question (Araujo 2002). Thus, protection should not only maximize the number of protected species but should maximize variation in the attributes of species as well. The current system of protected areas established in Paraguay may be adequate to safeguard the most common bat species, but additional sites may be necessary to enhance the protection of all species (Andelman and Willig 2002). The protection of particular attributes associated with ecological and evolutionary processes in which bats are involved may require even more effort. This may be particularly true given the intersite differences among communities described here, as well as the spatial heterogeneity described at other sites throughout the entire country (López-González 1998; Willig et al. 2000).

RESUMEN

En base a más de un año y medio de intenso trabajo de campo, el presente estudio documenta la estructura de las comunidades de murciélagos en dos sitios al este de Paraguay (Reserva Natural del Bosque Mbaracayú y Yaguareté Forests). A partir de más de 7.000 capturas se documentan 29 especies de murciélagos pertenecientes a 17 géneros y tres familias. En general, estas comunidades comparten muchas similitudes con el Bosque Atlántico y las savanas de Sudamérica; sin embargo existen diferencias significativas entre ambas comunidades con respecto a la distribución de la abundancia y a la composición de especies. Además, Yaguareté Forest presenta un número significativamente mayor de especies que Mbaracayú, aun luego de extraer los efectos de dicha diferencia provocada por

los insectívoros de alto vuelo. También existen diferencias no significativas entre estas comunidades en cuanto a otros aspectos de diversidad taxonómica—equitatividad, diversidad y dominancia de especies—y algunos aspectos de diversidad funcional. El alto grado de heterogeneidad del hábitat en Yaguareté Forest probablemente produce las diferencias en la estructura de dichas comunidades.

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