

LANDSCAPE RESPONSES OF BATS TO HABITAT FRAGMENTATION IN ATLANTIC FOREST OF PARAGUAY

P. MARCOS GORRESEN* AND MICHAEL R. WILLIG

Department of Biological Sciences and the Museum, Texas Tech University, Lubbock, TX 79409-3131, USA
Present address of PMG: United States Geological Survey, Pacific Island Ecosystems Research Center, Kilauea Field Station, P.O. Box 44, Hawaii Volcanoes National Park, HI 96718, USA

Understanding effects of habitat loss and fragmentation on populations or communities is critical to effective conservation and restoration. This is particularly important for bats because they provide vital services to ecosystems via pollination and seed dispersal, especially in tropical and subtropical habitats. Based on more than 1,000 h of survey during a 15-month period, we quantified species abundances and community structure of phyllostomid bats at 14 sites in a 3,000-km² region of eastern Paraguay. Abundance was highest for *Artibeus lituratus* in deforested landscapes and for *Chrotopterus auritus* in forested habitats. In contrast, *Artibeus fimbriatus*, *Carollia perspicillata*, *Glossophaga soricina*, *Platyrrhinus lineatus*, *Pygoderma bilabiatum*, and *Sturnira lilium* attained highest abundance in moderately fragmented forest landscapes. Forest cover, patch size, and patch density frequently were associated with abundance of species. At the community level, species richness was highest in partly deforested landscapes, whereas evenness was greatest in forested habitat. In general, the highest diversity of bats occurred in landscapes comprising moderately fragmented forest habitat. This underscores the importance of remnant habitat patches to conservation strategies.

Key words: Chiroptera, community, conservation, diversity, evenness, landscape ecology, richness

Habitat fragmentation is one of the primary proximate causes of present-day extinction (Whitmore 1997). Indeed, informed conservation decisions require understanding population- and community-level responses of biota to deforestation and fragmentation. Consequently, interrelationships of habitat fragmentation, species persistence and community structure have become an increasingly important focus in ecology and conservation biology (Laurance and Bierregaard 1997; Schellhas and Greenberg 1996). Habitat patches exist in a complex landscape mosaic, and spatial pattern of patches may strongly influence dynamics of resident populations and communities (Wiens et al. 1993). As a result, research in the emerging discipline of landscape ecology promises to improve our understanding of spatial dynamics of biological diversity in general (Turner 1989), with relevance to conservation planning.

Forest fragmentation is occurring at unprecedented rates in tropical and subtropical environments (Whitmore 1997), especially in subtropical Atlantic forest (Viana and Tabanez 1996). This forest type currently covers less than 10% of its

former geographic expanse of approximately 1 million km² and exists almost entirely as small isolated remnants (International Union for the Conservation of Nature and Natural Resources 1988). In eastern Paraguay, forest was reduced to about 20% of its original extent as a result of an annual rate of deforestation of 5.4% between 1984 and 1991 (Universidad Nacional de Asunción 1994). Rapid conversion of forest to agricultural lands created a landscape comprising small isolated forest fragments. Consequently, development of effective conservation planning and remediation practices requires that land managers understand biological dynamics of habitat remnants and the degree to which species and communities are sensitive to habitat fragmentation (Bierregaard et al. 1992).

Bats are the 2nd most species-rich order of mammals (Wilson and Reeder 1993). At the local level, they are often the most species-rich and abundant mammals in tropical or subtropical sites (Patterson et al. 2003). Bats are important pollinators and seed dispersers (Fleming 1988; Patterson et al. 2003) and may be keystone taxa in tropical forests because of their effects in structuring plant communities, especially if they are sole or primary agents of pollination and dispersal (Fleming and Heithaus 1981). Bats, particularly many Phyllostomidae, promote secondary succession and revegetation of disturbed areas because they differentially disperse pioneer-plant species (Fleming 1988; Gorchov et al. 1993). The importance of bats in ecological systems underscores the need to understand effects

* Correspondent: marcos_gorresen@usgs.gov

of anthropogenically induced fragmentation of habitat on local and regional assemblages.

Several studies have examined relationships between bats and habitat fragmentation. However, evidence is equivocal regarding consequences of forest fragmentation on bats. Fenton et al. (1992) found that phyllostomid diversity was higher in undisturbed than in disturbed forest habitats, whereas species richness was indistinguishable between habitats. Medellín et al. (2000) determined phyllostomid richness, diversity, and number of rare species to be correlated positively with measures of forest disturbance. In contrast, Estrada et al. (1993) found that landscapes comprising forest fragments maintained a regional bat fauna close to their historic composition. Cosson et al. (1999) concluded that species composition differed between fragmented and unfragmented habitat, with capture rates, species richness, and diversity positively correlated with fragment size. In addition, de Jong (1995) found a positive correlation between species richness and forest area, but not between richness and distance of forest patches to contiguous forest (i.e., isolation).

The response of bat species to complex spatial features and fragmentation across a range of spatial scales remains unexplored. Given present threats to tropical and subtropical forests and limited resources available for conservation in many developing countries, it is critical that habitat fragments be evaluated for their potential contribution to the maintenance of biological diversity (Turner and Corlett 1996). This study appraises the degree to which landscape attributes of intact and fragmented forest habitat are associated with abundance and diversity of phyllostomid bats.

MATERIALS AND METHODS

Study area.—Research was conducted in a 3,000-km² region within and adjacent to the Reserva Natural del Bosque Mbaracayú (24°08'S, 55°30'W) in the Departamento de Canindeyú of eastern Paraguay. The habitats of Paraguay, as well as their associated bat faunas, are discussed in Willig et al. (2000). The Reserva Natural del Bosque Mbaracayú is located in the upper Río Jejuí basin of the Río Paraguay watershed. Elevation ranges between 140 and 450 m, and regional topography is characterized by gently undulating terrain and broad valley bottoms (Fundación Moisés Bertoni para la Conservación de la Naturaleza 1992; Hill and Hurtado 1996). Temperatures range from a mean daily average of 27°C in January to 17°C in June and July. The wet season is from October to April, and the dry season is from May to September. Total annual rainfall averages 1,650 mm in the study area. Vegetation of Reserva Natural del Bosque Mbaracayú primarily is subtropical semideciduous mesophytic broadleaf forest and includes high stature mature terra firme tropical forest, low stature dry forests, riparian flood forests, bamboo stands, cerrado grasslands, and palm dominated wetlands (Hill et al. 1996). High forest is the most common vegetation type within Reserva Natural del Bosque Mbaracayú and is characterized by a high density of liana vines and small- to medium-sized tree species (Keel et al. 1993).

Site selection.—Fourteen plots, spaced at approximately 10-km intervals, were established in Reserva Natural del Bosque Mbaracayú. Such spacing represented a compromise between establishing a study area sufficiently small that biogeographic factors did not complicate analyses and an area sufficiently large that measures of species abundance were more likely to have been obtained from statistically independent sampling units. Twelve of 14 sites were established within

fragmented forest habitats outside of Reserva Natural del Bosque Mbaracayú. Two sites were established within Reserva Natural del Bosque Mbaracayú to sample landscapes characterized by contiguous forest cover.

A 15-month survey period extended from 13 January 1997 to 24 May 1998, and duration of survey effort was assessed with species accumulation curves. At each site, five 2-night surveys were conducted every 2–3 months, for a total of 140 sampling nights (14 sites × 5 surveys/site × 2 nights/survey). Each site was sampled once with 180 m of mist net (AFO Mist Nets, Manomet, Massachusetts) deployed the entire night and 4 times with 228 m of net deployed for the first 6 h of the night, for a total of over 1,000 h of survey. The latter sampling schedule was adopted to facilitate survey logistics. Nets were set at ground level in 4 groups spaced between 100 and 200 m apart and were monitored continuously. Nomenclature follows Wilson and Reeder (1993).

Species abundance and community parameters.—Indices of abundance were based on number of captures per taxon and may have included recaptures (although rates of recapture are low for New World bats in tropical environments—Barclay and Bell 1988; Thomas and La Val 1988). Measures of community structure (species richness and evenness) were standardized with rarefaction methods to permit the comparison of indices among sites with different sample sizes (Gotelli and Graves 1996). Species richness was calculated as number of species within a rarefied sample. Evenness was estimated as likelihood that random selection of 2 individuals represents different species (Hurlbert 1971).

Ecological data often are autocorrelated spatially, thereby violating assumptions of standard statistical analyses and biasing type I error rates (Legendre 1993). Correlation analysis was used to assess degree to which proximate sites have more similar bat communities than do more distant sites. An ecological distance matrix was generated by calculating percentage dissimilarities among sites based on species abundance (i.e., Renkonen index—Krebs 1989). A geographic distance matrix was calculated based on straight-line distances between geographic coordinates for each site. Spearman rank correlation coefficients quantified association between pairs of elements from ecological and geographical distance matrices. A significant and high degree of association indicates that bat communities are sufficiently autocorrelated spatially to require corrective measures (e.g., regression with weighted errors—Legendre 1993).

Land cover classification.—Measurement of landscape characteristics was accomplished by processing Landsat Thematic Mapper imagery (path 255, row 77; recorded 5 January 1998) with ERDAS (ERDAS 1997) and ARC-INFO (Environmental Systems Research Institute 1997). Landscape characteristics were quantified with the spatial pattern analysis program LEAP II (Perera et al. 1997). Five categories of land cover (Fig. 1) were classified from satellite imagery of the study area: forest, early seral regrowth, grassland with little or no forest regrowth, bare soil, and water. The forest category included degraded (i.e., selectively or partially logged) and unmodified (i.e., not logged) primary forest because of difficulty of distinguishing these classes based on optical imagery (Rignot et al. 1997). Early seral regrowth included successional stages that follow clearing of forest for agricultural purposes and subsequent land abandonment. Grassland was defined as areas without early seral forest regrowth and included naturally occurring grasslands and managed pastures. Areas with bare soil included pasture with sparse vegetative cover due to overgrazing, recently tilled cropland, roads, and urban areas. Open water and wetlands in riverine or lacustrine systems were classified as water.

Landscape structure.—In examining relationships between bat populations and landscape characteristics, it is desirable to quantify

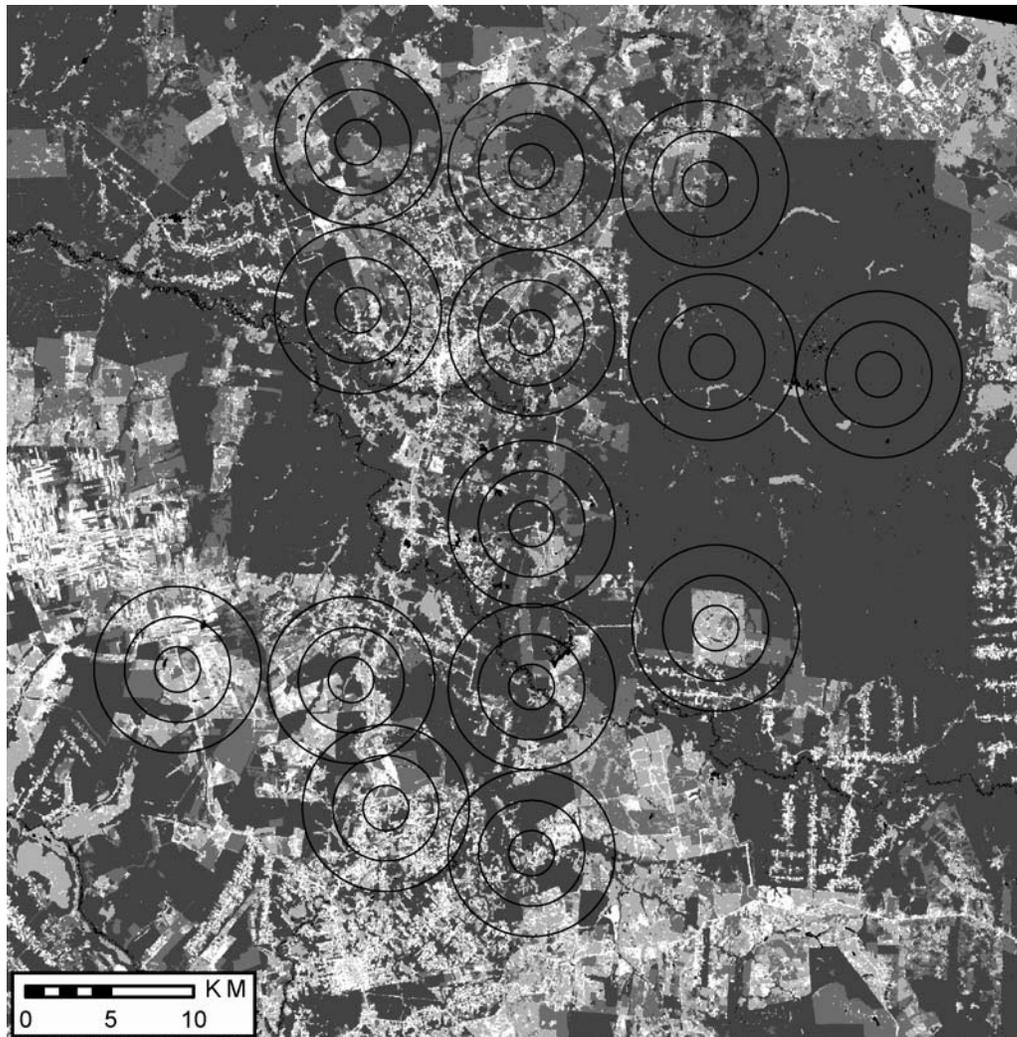


FIG. 1.—Landscape structure was measured in each of a nested sequence of concentric circles (1-, 3-, 5-km radius); species abundance and community composition were estimated at sites located at the center of each nested set of circles. Land cover types were classified from Landsat Thematic Mapper imagery and include water (black), forest (dark gray), regrowth (midtone gray), pasture or grassland (light gray), and bare soil (white). Forest habitat was the focal landscape element in all quantitative analyses. North is toward the top of the image. The upper left and lower right corners are located at 23°55'22"S, 55°54'40"W and 24°30'6"S, 55°16'43"W, respectively.

attributes that occur within home ranges of resident species. However, little is known about home range sizes of bat species in eastern Paraguay or elsewhere in the Neotropics. Therefore, concentric circles of 1-, 3-, and 5-km radii were centered on each site and used to delimit a nested series of sample plots (Fig. 1). Maximum plot size (5-km radius) was constrained by minimum distance between survey sites. The smallest plot size (1-km radius) was selected to encompass the expected home range of smaller bat species in the study area (e.g., perhaps as large as 0.5-km radius for *Glossophaga soricina*—Lemke 1984). Landscape characteristics were quantified and described for each of 3 nested landscapes at all 14 sites.

Selection of landscape characteristics was based on those metrics found in other studies to be associated with the occurrence or abundance of highly vagile and volant organisms such as birds (e.g., Rolstad 1991; Warburton 1997). Forest served as focal habitat type for all measures of landscape structure, and the other class types served as the matrix within which forest patches were dispersed. Landscape characteristics were estimated for each of 3 plot sizes and included forest cover, patch size, patch density, edge density, nearest neighbor

distances among patches, patch proximity, and patch shape (Perera et al. 1997). Forest cover was expressed as percentage of plot area designated as forest habitat. Patch density was the number of forest patches within a plot and was expressed as number of patches per 100 ha. Mean patch size was the average forest patch size within a plot. Edge density was the total perimeter of all forest patches within a plot. Mean shape index was calculated as a perimeter to area ratio for each patch and averaged for all patches within a plot. Mean nearest neighbor index describes average distance between each patch and its nearest neighbor. Index of mean proximity measures relative isolation by weighting distances among neighboring patches with the area of those neighbors. For example, 2 large patches are more proximate than 2 small patches with the same edge-to-edge distance between patches.

Relationships of species and community to landscape structure.—Species presence and abundance often are related to the amount of available habitat (e.g., McGarigal and McComb 1995; Villard et al. 1999). Because landscape configuration characteristics can be correlated moderately with habitat area, the response of species abundance to these characteristics may be confounded. Relationships

TABLE 1.—Indices of absolute and relative abundances for species of phyllostomid bats occupying Atlantic Rainforest habitats of eastern Paraguay.

Taxon	Abundance	
	Absolute	Relative (%)
Family Phyllostomidae		
Subfamily Phyllostominae		
<i>Chrotopterus auritus</i>	13	0.2
<i>Tonatia silvicola</i>	1	<0.1
Subfamily Glossophaginae		
<i>Glossophaga soricina</i>	22	0.3
Subfamily Carolliinae		
<i>Carollia perspicillata</i>	163	2.1
Subfamily Stenodermatinae		
<i>Artibeus fimbriatus</i>	193	2.5
<i>A. lituratus</i>	5350	69.3
<i>A. jamaicensis</i>	6	0.1
<i>Platyrrhinus lineatus</i>	51	0.7
<i>Pygoderma bilabiatum</i>	522	6.8
<i>Sturnira lilium</i>	1401	18.1
Subfamily Desmodontinae		
<i>Desmodus rotundus</i>	3	<0.1
Total	7725	100.0

between species abundance, community structure, and landscape characteristics were evaluated after controlling for habitat area. Regression was used to remove linear effects of associations between each landscape characteristic and forest cover. Residuals from regression values were used in subsequent analyses but, for the sake of simplicity, are referred to solely by the name of the characteristics whose residuals were analyzed. Relationships of species abundances and community indices to landscape structure were determined with multiple linear regression performed with the REG procedure in SAS (SAS Institute Inc. 1985). Forward stepwise selection was used to identify a parsimonious combination of landscape characteristics that maximizes R^2 . Rare phyllostomid species were not the subject of species-specific analyses because of the ubiquity of zeroes in capture data. Species were classified as rare if they were captured fewer than 10 times during the course of this study. However, all phyllostomid species, regardless of abundance, were included in the calculation of diversity measures at the community level.

RESULTS

Species composition, absolute abundance, and relative abundance.—Based on 7,781 bat captures, 20 species representing 3 families (Phyllostomidae, Molossidae, and Vespertilionidae) were encountered in the study area, of which 11 species were phyllostomids (Table 1). Total abundance ranged over 3 orders of magnitude, from 1 (*Tonatia silvicola*) to 5,350 captures (*Artibeus lituratus*). Three species (*A. lituratus*, *Sturnira lilium*, and *Pygoderma bilabiatum*) constituted 94% (69%, 18%, and 7%, respectively) of all phyllostomid captures ($n = 7725$). Molossid and vespertilionid bats were not examined for their response to forest fragmentation because of their low frequency of capture given the placement of mist nets (i.e., at ground level and away from open water bodies to avoid confounding effects of the presence of water bodies with that of landscape features related to forest habitat).

Spatial autocorrelation.—Spearman's test of correlation between ecological and geographic distances yielded $r = 0.38$ ($P = 0.08$) and a test power of 0.59 (Zar 1996). Although this degree of autocorrelation may slightly inflate type I error rates, low correlation and nonsignificant result indicated that spatial autocorrelation in phyllostomid assemblage structure was not sufficiently strong to warrant corrective measures.

Population and community effects of landscape composition and configuration.—Species showed variable patterns of association between abundance and particular landscape features (Table 2). Patch density and patch size were significant predictors of abundance for *Artibeus fimbriatus*, although at different landscape scales (3 and 5 km, respectively). The positive regression coefficient for the former indicated that abundance increased with higher patch density. Conversely, a negative coefficient indicated an association to smaller patch sizes at the larger scale. *A. lituratus* responded negatively to proximity and edge density of patches at small and large (1 and 5 km) scales, respectively. Abundance of *Chrotopterus auritus* was positively associated only with forest cover at 5-km landscape size. Abundance of *Carollia perspicillata* responded positively to forest cover and patch density and negatively to patch size at intermediate and large (3 and 5 km) scales. Abundance of *G. soricina* responded positively to patch size at the small scale and negatively to proximity at large scales. Abundance of *Platyrrhinus lineatus* was associated negatively with patch size at large scales and was associated positively with measures of patch and edge density at the small scale. Abundance of *P. bilabiatum* was associated positively with forest cover at intermediate and large landscape sizes, associated positively with proximity at large scales, and associated negatively with patch size at small scales. At large scales, abundance of *S. lilium* was associated positively with forest cover, patch density, and patch size, but associated negatively with edge density. Only forest cover and nearest neighbor distance elicited a response in abundance of *S. lilium* at intermediate scales.

The amount of variation in abundance described by regression models also differed greatly among species regardless of landscape scale. For example, the largest adjusted coefficient of multiple determination (model R^2) was 73% for *S. lilium*. In contrast, the largest model R^2 for *A. lituratus* was only 24% (Table 2). Separately, particular landscape characteristics accounted for a wide range of variance in abundance. For example, the largest variance accounted for by a single landscape feature in a regression model was 52% for patch proximity (*A. lituratus*). This feature also significantly accounted for abundance of *G. soricina* ($\Delta R^2 = 38\%$) and *P. bilabiatum* ($\Delta R^2 = 22\%$).

Landscape characteristics differed in the ubiquity of their effects on phyllostomid species. For instance, patch size consistently accounted for the greatest amount of variance in abundance ($\Delta R^2 = 31\%$, 39%, 42%, and 48% for *P. lineatus*, *A. fimbriatus*, *G. soricina*, and *P. bilabiatum*, respectively). Relative amount of forest cover accounted for a low to moderate amount of variation in the abundance of 4 species ($\Delta R^2 = 21\%$, 29%, 43%, and 49% for *C. perspicillata*, *C. auritus*, *P.*

TABLE 2.—Multiple regression analyses of bat species abundance and community indices as a function of landscape characteristics at each of 3 scales (1 km, 3 km, and 5 km radii).^a

	1 km landscape			3 km landscape			5 km landscape		
	ΔR^2	<i>P</i>	sign	ΔR^2	<i>P</i>	sign	ΔR^2	<i>P</i>	sign
<i>Artibeus fimbriatus</i>									
Patch density				34	0.030	+			
Patch size							39	0.018	-
Model <i>R</i> ²				30	0.030		33	0.018	
<i>A. lituratus</i>									
Edge density				25	0.072	-	30	0.043	-
Patch proximity	52	0.013	-						
Model <i>R</i> ²	46	0.013		18	0.072		24	0.043	
<i>Chrotopterus auritus</i>									
Forest cover				26	0.061	+	29	0.045	+
Patch proximity	29	0.090	+						
Model <i>R</i> ²	21	0.090		20	0.061		24	0.045	
<i>Carollia perspicillata</i>									
Forest cover				21	0.044	+	16	0.095	+
Patch density				36	0.015	+			
Patch size							34	0.028	-
Patch shape	36	0.052	+						
Patch proximity							10	0.135	-
Model <i>R</i> ²	29	0.052		48	0.011		49	0.021	
<i>Glossophaga soricina</i>									
Patch density				23	0.084	+			
Patch size	42	0.032	+				14	0.105	-
Patch proximity							38	0.015	-
Model <i>R</i> ²	35	0.032		16	0.084		43	0.019	
<i>Platyrrhinus lineatus</i>									
Patch density				28	0.053	+			
Patch size							31	0.040	-
Model <i>R</i> ²				22	0.053		30	0.040	
<i>Pygoderma bilabiatum</i>									
Forest cover				38	0.019	+	43	0.003	+
Patch size	48	0.017	-						
Patch proximity							22	0.024	+
Model <i>R</i> ²	43	0.017		32	0.019		59	0.003	
<i>Sturnira lilium</i>									
Forest cover				49	0.002	+	44	0.001	+
Patch density							11	0.011	+
Patch size	24	0.124	-				14	0.038	+
Edge density							7	0.039	-
Nearest neighbor				14	0.068	+	7	0.106	+
Model <i>R</i> ²	16	0.124		56	0.004		73	0.006	
Richness									
Patch density							11	0.079	+
Forest cover	28	0.094	+						
Patch density							15	0.032	-
Patch size				42	0.012	-	44	0.005	-
Patch proximity							12	0.065	-
Model <i>R</i> ²	20	0.094		37	0.012		62	0.005	
Evenness									
Forest cover				60	0.001	+	56	0.001	+
Patch density							11	0.079	+
Patch shape	40	0.038	+						

TABLE 2.—Continued.

	1 km landscape			3 km landscape			5 km landscape		
	ΔR^2	<i>P</i>	sign	ΔR^2	<i>P</i>	sign	ΔR^2	<i>P</i>	sign
Nearest neighbor				22	0.004	+			
Model <i>R</i> ²	33	0.038		78	0.001		62	0.002	

^a ΔR^2 represents the individual percentage contribution of landscape characteristics to the regression model. The sign of regression coefficients associated with a particular landscape characteristic are indicated with plus or minus. Coefficients of multiple determination (model *R*²) are adjusted for number of selected variables in the model. Significant regression models or parameters (*P* ≤ 0.05) are indicated in bold.

bilabiatum, and *S. lilium*, respectively). Patch density was significant with a ΔR^2 of 11%, 34%, and 36% for *S. lilium*, *A. fimbriatus*, and *C. perspicillata*, respectively. Edge density was significant for only 2 species (ΔR^2 of 7% for *S. lilium* and 30% for *A. lituratus*). Patch shape and nearest neighbor distance were moderately to marginally significant indicators of abundance (ΔR^2 = 36% for *C. perspicillata* and 14% for *S. lilium*).

A variety of landscape characteristics was associated with structure of the phyllostomid assemblage (Table 2). Species richness was associated significantly and negatively with patch size and density at intermediate and large scales. Evenness was associated positively with forest cover at intermediate and large scales, and with patch shape and nearest neighbor distance at small and intermediate scales, respectively. In addition, forest cover consistently accounted for the greatest amount of variation in community attributes (ΔR^2 = 28% for species richness and 60% for evenness). Other landscape characteristics that effect a relatively high amount of variation were patch shape for species evenness (ΔR^2 = 53%) and patch size for species richness (ΔR^2 = 44%).

DISCUSSION

Species abundances and structure of phyllostomid assemblages varied greatly with landscape configuration, and the identity and strength of associations were species and index specific. In accordance with other studies of habitat fragmentation (e.g., McGarigal and McComb 1995; Villard et al. 1999), landscape composition (i.e., amount of forest habitat, patch size, and patch density) was a significant predictor of abundance of most species and of assemblage structure. Moreover, bat species and their assemblages are associated significantly with measures of landscape configuration (e.g., edge density, shape complexity, and patch proximity). Spatially explicit measures that characterize landscape provide a more comprehensive picture of biotic response to habitat fragmentation.

Species-specific responses.—Elevated abundances of phyllostomid species were associated with particular landscape types. These landscape types represent gradations of deforestation and include the following: forested areas with little or no fragmentation, forested areas with large closely situated patches, partly forested areas with small patches within a matrix of dispersed large patches, partly forested areas comprising many small patches, and deforested areas with few and small patches of forest.

Chrotopterus auritus attained highest abundance in highly forested areas, corroborating the observation that carnivorous phyllostomines are more abundant in undisturbed than in disturbed forest (Fenton et al. 1992; Medellín et al. 2000; but see Wilson et al. 1996). This species may be restricted to forested habitats for reasons related to prey availability and foraging behavior. However, the varied responses of potential prey items to deforestation render difficult an understanding of associations between prey availability and abundance of *C. auritus*. For example, species richness for most insect groups is generally higher and overall abundance is lower in undisturbed forest habitats compared to cultivated areas (Power 1996). Likewise, species richness, abundance, and biomass of small terrestrial mammals are higher in Amazonian forest fragments, although arboreal assemblages may remain unchanged (Malcolm 1997). Despite the equivocal effects of deforestation on prey density, predation success may be greater in undisturbed mature forest than in degraded forest and deforested areas because the former habitat retains a greater degree of vertical structure that is more conducive to the arboreal foraging behavior of *C. auritus* (Kalko and Schnitzler 1998). Primary forests also may provide roosting refugia in foliage and tree hollows that are likely limiting in more deforested landscapes.

Although *S. lilium* is common in open and secondary growth areas, this understory frugivore (Fleming 1988) occurred at higher abundances in landscapes with numerous, large, proximate patches of forest with little forest edge. Forested areas may confer a greater or more suitable range of resources to *S. lilium* than do deforested and young secondary forests. Primary forests have a higher diversity of fruiting species than do young secondary forests (Opler et al. 1980; but see Levey 1988), which contributes to a more even production of fruit throughout the year. In addition, fruit production of primary forest understory species generally is less seasonal than that of canopy or secondary species (Levey 1988; Opler et al. 1980). Nevertheless, moderate levels of deforestation increase spatial diversity of structural types in forests and enhance abundances of early successional plants. Many early successional plants use a steady-state strategy to produce a small amount of fruit over extended (seasonal) periods (Frankie et al. 1974). Consequently, moderate deforestation may increase overall food availability and contribute to higher reproductive rates and abundances for frugivorous bat species that exploit disturbance-adapted plant species (e.g., *Sturnira ludovici*—Dinerstein 1986).

The nectarivorous *G. soricina* had higher abundances in areas characterized by large and proximate patches of forest. Lemke (1984) observed that the greatest recorded distance between sites visited by the same foraging individual was 1,450 m. In addition, he noted that individuals adopt an energetically costly territorial behavior in environments of low plant diversity and food reliability. Consequently, landscapes that have undergone loss of floristically species-rich forests of the region (Keel et al. 1993) may represent habitats of lesser quality for *G. soricina*. Limited foraging movements and a preference for floristically diverse habitats may account for higher abundances in landscapes with closely situated and large forest patches.

The frugivorous *P. bilabiatum* was associated positively with forested landscapes subdivided into isolated patches at large scales and small patches at small, local scales. These apparently contradictory results are only interpretable within a landscape context. They indicate that abundance is higher in areas of small forest patches within a larger matrix of well-forested, but dispersed patches. This was the only species clearly demonstrating an association with characteristics of both forested and deforested habitats segregated across landscape scales. Little is known about the foraging behavior and diet of *P. bilabiatum* (Webster and Owen 1984); however, its association with heterogeneous landscapes may reflect a capacity for consumption of fruits from both forest and secondary vegetation.

Carollia perspicillata, *P. lineatus*, and *A. fimbriatus* each exhibited higher abundances in fragmented forested habitat with numerous patches of small size. *C. perspicillata* is a generalist frugivore that primarily consumes fruit of species common to the understory of primary forest and 2nd-growth vegetation (Fleming 1988). This trait may permit this bat to use a wide variety of successional habitats. Although this abundant colonial species has generalized roost requirements, it may compete with other species for predator-free roost space (Fleming 1988). Therefore, the limited availability of adequate roost habitat in young secondary vegetation may restrict *C. perspicillata* to areas with at least a few patches of forest. Forest patches may also provide it with a greater diversity of food items during periods of scarcity in disturbed plant communities.

Platyrrhinus lineatus is a generalist frugivore that consumes fruit from both the primary forest canopy (e.g., *Ficus* spp.) and 2nd growth (e.g., *Vismia*—Willig and Hollander 1987; Willig et al. 1993). In the study area, *P. lineatus* exhibited highest abundance in landscapes with many small forest patches and abundant secondary vegetation. As with *C. perspicillata*, these areas may provide diverse food items and patches of heavily foliated roost habitat for groups of *P. lineatus*.

Artibeus fimbriatus and *A. lituratus* are large-bodied frugivores, and in many forest biomes the latter, and likely the former, feed extensively on the fruit of fig species in the canopy (Handley et al. 1991). Figs are abundant but irregularly available during the year in moist tropical forests (Milton et al. 1982). As such, *A. fimbriatus* and *A. lituratus* may be more likely to occupy landscapes comprising a variety of successional habitats that provide food items that seasonally complement production of figs in primary forest. Although common in forested habitat, *A. lituratus* was the only species that showed highest abundance in extensively deforested areas. The ability of *Artibeus* species to commute extensive distances (Morrison 1978) may facilitate use of highly fragmented forest that provides both fig resources in distant forest remnants and alternate food items in 2nd growth. In addition, the foliage roosting habits of *A. lituratus* (Morrison and Handley 1991), and possibly that of *A. fimbriatus*, may allow the species to occupy landscapes comprising mostly early 2nd growth, with only minor components of primary and old secondary forests patches.

Community responses.—Indices of bat community structure were related to landscape characteristics in a number of ways.

Community-level analyses generally support the findings of Cosson et al. (1999), Fenton et al. (1992), and Medellín et al. (2000): diversity is higher in relatively undisturbed forest than in deforested habitats. More specifically, bat community evenness was highest in forested landscapes comprising many dispersed patches. Nonetheless, contrary to other observations by these same authors, phyllostomid species richness was higher in fragmented forest comprising few, small forest patches than in less fragmented areas. This difference in the association of community indices with landscape characteristics occurs because each index integrates responses of constituent species in different ways. Because species richness measures only species presence and is insensitive to relative abundance, the index includes both species found in preferred habitat and those able to persist in marginal or sink habitats. For example, 4 of 8 phyllostomids had highest abundance in moderately to highly fragmented forest habitats. The remaining species were present in fragmented forest habitats, although at lower abundances. In addition, the 3 phyllostomids (*A. planirostris*, *D. rotundus*, *T. silvicola*) for which sample sizes were insufficient to develop regression models were present in areas with low to moderate amounts of forest cover.

Caveats and considerations.—Caution is required in interpretation of causal factors and response. For instance, bat use of habitat physiognomy (i.e., physical structure) may bias analyses of associations to landscape characteristics. Bat species commute and forage at different heights within forest (Fleming 1988) and can preferentially use roads and trails (Palmerim and Etheridge 1985). Therefore, abundance may reflect differences in susceptibility to capture among habitat types, above and beyond effects of habitat quality and landscape structure, per se. In addition, association of elevated species abundances with particular landscape characteristics may not necessarily indicate a correspondence to high habitat quality (Van Horne 1983). Factors such as territoriality and other social interactions may cause juveniles or subdominant individuals to have higher densities in suboptimal habitat.

Spatial habitat patterns were derived from satellite imagery and do not incorporate more fine-grained habitat features below the scale of imagery resolution (30 m²). In addition, forest class served as the focal patch type from which landscape attributes were derived. Other class types such as early seral secondary forest were not used to describe landscape characteristics because of limitations imposed by sample size on statistical analyses. These habitats may provide phyllostomid bats with suitable resources and confound determination of important species-habitat associations.

Hierarchy theory proposes that large-scale processes can affect or constrain smaller scale phenomena (Allen and Starr 1982). For example, local abundance may be determined, in part, by large-scale source population dynamics elsewhere in the range of a species (Ricklefs 1987). If large-scale events such as deforestation and loss of Atlantic and gallery forest habitats in other regions operate to limit immigration into the study area, presence of ample high-quality habitat at the local scale may not be sufficient to offset population declines through rescue effects or mass effects (Brown and Kodric-

Brown 1977). More specifically, large-scale loss of forest habitat outside the study area over past decades (e.g., 90% loss of Atlantic forest in the nearby state of São Paulo by the late 1960s—Viana and Tabanez 1996) may act as a filter and reduce the regional species pool to a subset of species either able to use anthropogenically modified habitats or able to traverse extensive tracts of poor quality or inhospitable habitat.

Conservation implications.—The difficulties inherent in sampling bat abundance, the effects of social interactions on the assessment of habitat quality, and the influence of factors above and below the scales of analyses complicate interpretations of bat responses to landscape structure. Nonetheless, this study demonstrated specific and spatially explicit ecological relationships for phyllostomid species and the regional assemblage. The relative strength and direction of the associations between population and community-level attributes and landscape characteristics may be incorporated into models to predict patch occupancy (e.g., Wahlberg et al. 1996), as well as to identify habitat patches important to species persistence (e.g., Keitt et al. 1997). Such models may determine thresholds of regional habitat occupancy contingent on minimum patch size and maximum isolation distances.

Presence of forest remnants is important to the persistence of phyllostomid species. In general, phyllostomids maintain relatively high diversity in landscapes comprising moderately fragmented forest habitat. Forest fragments may satisfy autoecological requirements related to roosting habitat and permit continued occupancy if the surrounding deforested matrix provides adequate food resources (e.g., pioneer plants such as *Piper*, *Solanum*, and *Cecropia*—Fleming 1988; Galetti and Morellato 1994; Marinho-Filho 1991). As such, forest remnants may be highly relevant to the conservation of phyllostomid bat species and to conservation strategies in general.

The suitability of forest fragments as phyllostomid habitat, in turn, may assist in the restoration of forest habitat. Frugivorous bats disperse the seeds of pioneer and some primary forest plant species (Fleming 1988; Galetti and Morellato 1994; Gorchov et al. 1993). As such, frugivorous bats promote revegetation of disturbed areas, secondary succession, and reestablishment of plant species of primary forests (Willig and McGinley 1999). Frugivorous bats also may play critical roles in sustaining genetic connectivity among populations of plant species (Estrada et al. 1993). Use of roosts between feeding sites results in dispersal and deposition of seed while bats are in transit (Thomas et al. 1988). Therefore, succession in clearings between forest patches is enhanced by bat mobility and feeding behavior, particularly for areas occurring in proximity with larger tracts of undisturbed forest (Lamb et al. 1997; Wunderle 1997).

The principal conservation recommendation derived from this study is that forest fragments in areas outside of ecological reserves should be considered integral to regional management plans. Generally, large reserves are essential components of forest conservation strategies (e.g., Peres and Terborgh 1995), but it is increasingly appreciated that smaller forest fragments can contribute to the maintenance of biological diversity as well (Laurance and Bierregaard 1997; Schelhas and Greenberg

1996; Turner and Corlett 1996). Conservation strategies should be expanded to incorporate the presence of forest remnants in areas surrounding reserves. This may involve development and strengthening of regulatory directives that stipulate retention of a measure of forest cover in private landholdings (e.g., 50% retention of forest cover in Amazonia required by Brazilian law—Nepstad et al. 1996). It may also entail implementation of forest restoration programs amenable to the socioeconomic and cultural perspectives of local landowners.

RESUMEN

Comprender los efectos de la pérdida de hábitat y fragmentación en las poblaciones o comunidades es crítico para una efectiva conservación y restauración. Esto es particularmente importante para los murciélagos debido a que ellos proveen servicios vitales a los ecosistemas por medio de la polinización y dispersión de semillas, especialmente en hábitats tropicales y subtropicales. Basados en más de 1000 horas de muestreo durante un período de 15 meses, cuantificamos la abundancia de especies y la estructura de la comunidad de murciélagos filostomidos en una región de 3000 km² al este de Paraguay. Para *Artibeus lituratus* la abundancia más alta se dio en ambientes deforestados y para *Chrotopterus auritus* en hábitats de bosque. En contraste, *Artibeus fimbriatus*, *Carollia perspicillata*, *Glossophaga soricina*, *Platyrrhinus lineatus*, *Pygoderma bilabiatum* y *Sturnira lilium* tuvieron abundancias más elevadas en bosques moderadamente fragmentados. La cubierta del bosque, el tamaño del parche y la densidad del parche frecuentemente fueron asociados con la abundancia de especies. Al nivel de comunidad, la riqueza de especies fue más elevada en ambientes parcialmente deforestados, mientras la uniformidad fue más grande en hábitats de bosque. En general la más alta diversidad para murciélagos ocurrió en ambientes que comprendían hábitats moderadamente fragmentados. Esto subraya la importancia de los parches de hábitat remanentes para las estrategias de conservación.

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