

COMPOSITION AND DISTRIBUTION OF A BAT ASSEMBLAGE DURING THE DRY SEASON IN A NATURALLY FRAGMENTED LANDSCAPE IN BOLIVIA

ANDREA P. LOAYZA* AND BETTE A. LOISELLE

Department of Biology, University of Missouri–St. Louis, One University Boulevard, St. Louis, MO 63121, USA

We investigated species composition of the bat assemblage in continuous forest and natural forest islands in a savanna ecosystem in northern Bolivia. We captured 396 bats of 24 species. Five species accounted for almost 70% of the captures: *Sturnira lilium*, *Artibeus obscurus*, *Carollia brevicauda*, *Carollia perspicillata*, and *Artibeus lituratus*. Species composition of the bat assemblage differed between continuous forest and forest islands; *Artibeus jamaicensis* and *S. lilium* were captured more often in islands, whereas *Platyrrhinus helleri* and *Mesophylla macconnelli* were more common in the continuous forest. The distribution of species over the forest islands and the continuous forest revealed a nested distribution pattern, with the continuous forest having the highest number of species, and the smallest island having the fewest species. However, bats were almost 5-fold more abundant in forest islands than in continuous forest. Examination of recapture data indicated movements of bats among forest islands and between islands and continuous forest. Our results suggest that bat populations, especially in the fruit-eating guild, can persist in a naturally fragmented landscape.

Key words: bats, Chiroptera, distribution, fragmentation, tropical savanna

Habitat fragmentation is widely recognized as one of the most serious threats to biodiversity (Whitmore 1997). It affects ecosystem functioning (Lord and Norton 1990) through changes in species richness and abundance (Cordeiro and Howe 2003; Cosson et al. 1999), forest structure (Echeverría et al. 2007), and through edge (Goosem 2002), isolation, and distance effects (Andrén 1994), among others. Ultimately, habitat fragmentation can result in the local extinction of many species (Laurance et al. 2002; Turner 1996).

In contrast to other groups such as primates and understory birds (Bierregaard and Stouffer 1997; Johns 1986; Lemos de Sa et al. 1990; van Roosmalen 1985), many species of bats, and particularly generalist ones, can persist in fragmented landscapes (Aguirre 2002; Aguirre et al. 2003; Fenton et al. 1992; Law et al. 1999; Schulze et al. 2000). This apparent tolerance to fragmentation is explained by the ability of bats to cross habitat boundaries and to fly over open areas to reach resources that are patchy in space and time (Montiel et al. 2006). Consequently, forest fragments may not represent isolated islands for such species.

Nonetheless, not all species of bats do well in fragments (Galindo-González and Sosa 2003). For example, carnivorous phyllostomines are generally restricted to forested habitats, and

their abundances are low in disturbed environments (Gorrensens and Willig 2004; Medellín et al. 2000). Moreover, even species that are abundant in fragments may be sensitive to fragmentation. In this sense, Henry et al. (2007) showed that even though *Artibeus obscurus* remained ubiquitous in the fragmented forest of Saint Eugene (French Guiana), the population in the fragments was under greater stress than the population in continuous forest, as revealed by a strong deviation in the population's sex ratio and higher hematocrit levels in fragments compared to the continuous forest. Additionally, changes in the structural characteristics of the forest in forest fragments also have been shown to affect occupancy of bats (Yates and Muzika 2006).

Although in the past 2 decades research has addressed bat composition in fragmented habitats (e.g., Aguirre 2002; Aguirre et al. 2003; Bernard and Fenton 2002, 2003; Brosset et al. 1996; Cosson et al. 1999; Estrada and Coates-Estrada 2001; Estrada et al. 1993a, 1993b; Gorrensens and Willig 2004; Montiel et al. 2006; Schulze et al. 2000; Wagner et al. 1995; Yates and Muzika 2006), very few of these studies have been carried out in natural forest fragments that, unlike anthropogenic fragments, have been isolated from the continuous forest for hundreds, and in some cases, thousands of years. Although the information acquired on anthropogenic fragments has provided insight regarding the “immediate” biological effects after habitat isolation, long-term processes and the fate of species after fragmentation cannot be studied in such fragments (Corlett and Turner 1997).

* Correspondent: andrea.loayza@umsl.edu

In northeastern Bolivia, the Moxos Plains consist of a complex mosaic of habitats that include continuous terra firma forest, forest islands, and open grasslands (Hanagarth 1993), which together constitute a naturally fragmented landscape. The forest islands form discrete units of forest vegetation in the landscape, frequently upon slightly elevated ground that stands above the annual flood line. They have a canopy height of up to 30 m, and although predominantly dominated by palms (*Attalea phalerata*), it is also common to find plant species typical of continuous forests (Comiskey et al. 2000; Moraes et al. 2000). The origin of the islands is debated. It has been suggested that processes such as termite and ant mound establishment, as well as tree grove establishment may in some instances account for island formation (e.g., Hanagarth and Sarmiento 1990). However, Langstroth (1996) recognized that the primary mode of island formation was the fragmentation and erosion of ancient natural levees and, in a few cases, the result of abandoned artificial mounds raised up to 2 m above the flooded savanna by Indians in the pre-Hispanic period. He also concluded that although forest islands in the Moxos Plains have been altered in some way by prehistoric or modern human activity, or both, this activity has led to only limited instances of forest fragmentation in the region (Langstroth 1996). Ultimately, the origin of the islands is estimated to be around 4,000 years ago, hence this landscape provides an opportunity to investigate how bats have adapted to long-term fragmentation, and can help understand the mechanisms of species impoverishment in fragmented landscapes.

Here, we compare the bat assemblage in a large area of continuous, mature tropical forest to that of naturally occurring forest fragments (hereafter, forest islands) during the dry season, in Beni Biological Station–Biosphere Reserve. Specifically, we addressed the following questions: how does the bat assemblage differ between continuous forest and forest islands–savanna habitat, and is the assemblage of bats in the forest islands nested within that of the continuous forest? We predicted distinct bat assemblages for the continuous forest and the forest island–savanna habitat, where the former would be characterized by specialists and canopy species, whereas the latter by generalist and understory species. Additionally, we hypothesized that the bat assemblage in forest islands would be nested within that of the continuous forest because nestedness is predominant in habitat fragments derived from a once continuous system with a common species pool that has subsequently become isolated (Atmar and Patterson 1993).

MATERIALS AND METHODS

Study area.—Fieldwork was conducted from June to August 2001 at Beni Biological Station–Biosphere Reserve in Beni, Bolivia (14°30′–14°50′S, 66°40′–65°50′W; approximate elevation 200 m). The area receives on average 1,900 mm of rain annually and has a mean annual temperature of 26°C (Miranda 2000). The reserve is located within the region of the Moxos Plains. Almost 60% of the reserve (80,000 ha) is represented by a large tract of continuous and largely undisturbed forest, whereas the rest consists of savanna (Ribera et al. 1990).

Within the savanna, forest islands are a prominent element of the Moxos Plains (Hanagarth 1993). Forest islands constitute isolated units of forest (0.5–20 ha), with canopy heights of up to 30 m (Moraes et al. 2000). The savanna encompassed by Beni Biological Station–Biosphere Reserve is divided into 2 sections. The section farthest from the forest is subject to cattle grazing, and managed with annual burns. Although the cattle density is low, degradation of the vegetation structure in the forest islands is evidenced by the fact that there is virtually no understory (Comiskey et al. 2000). In the section nearest to continuous forest no fire management is carried out and cattle have been excluded for more than 20 years. The islands selected for this study belonged to this latter group.

Site selection.—Five forest islands and 5 sites in the continuous forest were selected for the study. Islands ranged from approximately 0.5 to 3 ha and were within 3 km of the continuous forest. Site selection in the continuous forest was based on accessibility; however, sites had to be separated by at least 600 m from each other, and be within approximately 1 km of the forest's edge with the savanna (Fig. 1). Sampling within the continuous forest was designed to encompass approximately 1 ha to approximately match the area of sites in the forest islands. Sampling between continuous forest and forest islands was alternated between sites to control for possible seasonal effects.

Sampling bats.—We sampled bats from June to August 2001 using mist nets. Each site was sampled for 3 consecutive nights avoiding full or nearly full moon nights because bat activity can decrease during this moon phase (lunar phobia—Morrison 1978). During each sampling night, 7 (6 m, 36-mm mesh) mist nets were used to capture bats. In the forest islands, nets were placed so as to encompass the whole island, whereas in the continuous forest they were located in representative vegetation sites across approximately a 1-ha area. At each forest island, 2 additional nets were positioned in the savanna at 30 m from the island edge to capture bat species either leaving or entering the island, or traveling through the savanna. Nets were opened at 1830 h and were checked at 30-min intervals until closing at 0130 h. This 7-h period includes the peak foraging activity for phyllostomid bats (Heithaus and Fleming 1978). Sampling effort was standardized with net-hours as the unit of effort (one 6-m-long mist net set for 1 h equals 1 net-hour). Total sampling effort was 1,470 h (735 h each in continuous forest or forest islands) plus 210 net-hours in the savanna.

Bats were processed, marked, and released at the point of capture. Processing included species identification and determination of sex, reproductive stage (evidence of testicular descent, pregnancy, or lactation), relative age (juvenile, sub-adult, or adult), weight (to the nearest 0.1 g), forearm length (to the nearest 0.1 cm), body length, foraging associations (cf. Gardner 1977), time, and site of capture. We determined the relative age of bats by a combination of pelage features, body mass, and by degree of fusion of the metacarpal epiphyses (Edythe 1988). To document bat movement across sampling sites, we marked all bats by piercing between 2 and 8 small holes (<1 mm) in the wing membrane. This marking procedure is temporary (<1 year) and less injurious than attaching wing bands (L. F. Aguirre, Universidad Mayor de

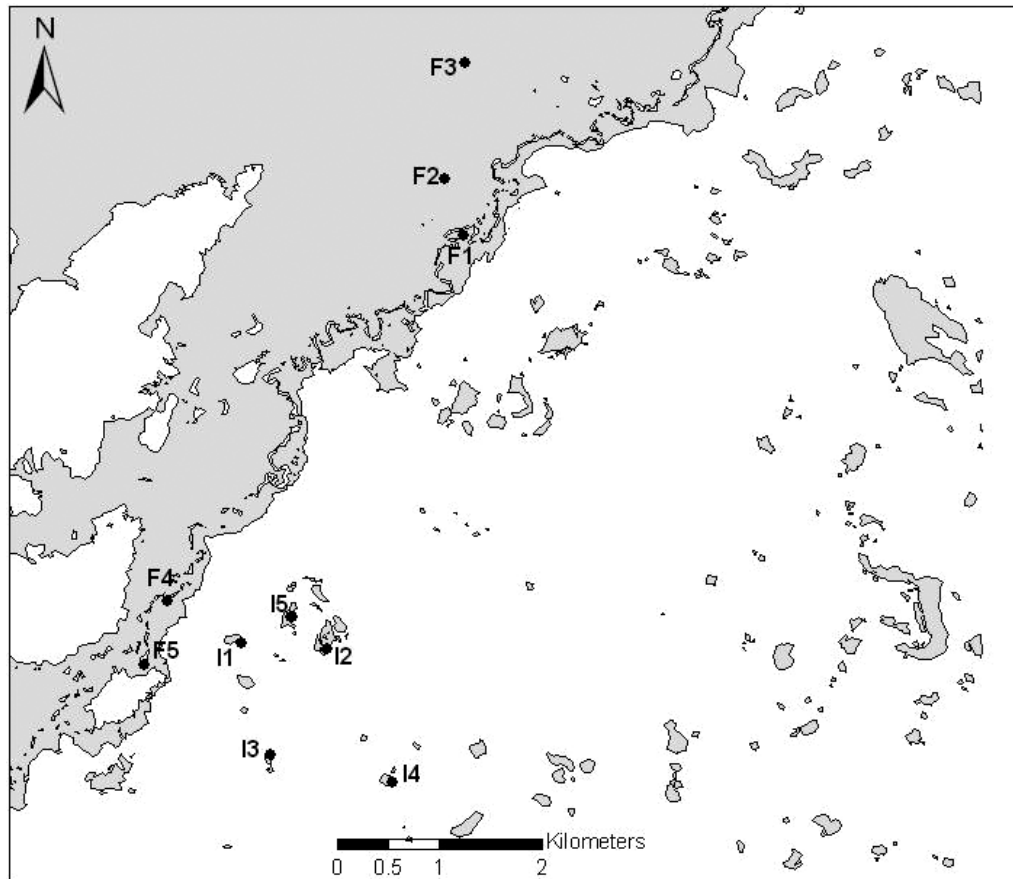


FIG. 1.—Sites sampled in the continuous forest (F) and forest islands (I) within the Beni Biological Station–Biosphere Reserve. Forested elements in the landscape are depicted in gray and the savanna matrix is shown in white.

San Simon, pers. comm.); however, rehandling of the bats is necessary for individual identification. Each capture site had a unique hole pattern. Consequently, when a bat was recaptured we could determine at which site the bat had been previously caught. Taxonomic nomenclature for bats followed Aguirre and Anderson (1997) and Anderson (1993). Field methods met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Data analysis.—We used several procedures to compare the species of bats that used forest islands with species that used continuous forest. First, we generated rarefaction curves for both habitats using EcoSim version 6.0 (Gotelli and Entsminger 2001) to determine if differences in the number of species found in each habitat were not simply a consequence of sample size (Gotelli and Colwell 2001). Second, we used a 2-tailed Fisher's exact test to determine if the frequencies of understory and canopy species of frugivorous bats are similar in both continuous forest and forest islands. Third, species composition of bat communities was compared between habitats using a Bray–Curtis ordination. In this case, the data matrix was relativized by species (columns) and sites (rows) so that the position of sites in relation to each other was graphed according to their similarities in relative species composition, rather than being influenced by number of captures or abundance of common species only. Fourth, we used a partial

Mantel test to determine whether there was spatial autocorrelation in the bat species composition. This test allows a comparison to be made between 2 variables, while controlling for a 3rd (Fortin and Gurevitch 1993). Specifically, we computed the correlation between 2 distance matrices, 1 matrix represented the euclidean distances among sites and the other the number of individuals captured of each species per site, while controlling for habitat type (continuous forest or forest island) using a 3rd matrix that indicated the habitat at each site. The null hypothesis for this test is that the relationship observed between the 2 distance matrices could have been obtained by any random arrangement in space of the observations through the study area.

Finally, we used the “nestedness temperature calculator” (Atmar and Patterson 1993; Patterson 1995) to determine whether patterns of bat occurrence in the continuous forest and forest islands created nested species distributions among the surveyed sites. This program maximally packs the presence–absence species matrix by ranking all sites according to their species richness (Cutler 1991). In a matrix that is perfectly nested, the set of species on an island is a perfect subset of the species on the island that precedes it in the matrix. In such a matrix, the hypothetical line that divides the occupied from the unoccupied area of the matrix is defined as the “extinction” or “occurrence” boundary (Atmar and Patterson 1993).

TABLE 1.—Bat species captured in savanna (S), forest islands (I), and continuous forest (F) at Beni Biological Station, Bolivia, from June to August 2001.

Species ^a	Guild	No. captures			
		S	I	F	Total
<i>Sturnira lilium</i>	Understory frugivore	4	82	1	87
<i>Carollia brevicauda</i>	Understory frugivore	1	26	24	51
<i>Carollia perspicillata</i>	Understory frugivore	4	27	8	39
<i>Carollia castanea</i>	Understory frugivore	0	1	1	2
<i>Glossophaga soricina</i>	Nectarivore	4	14	8	26
<i>Artibeus obscurus</i>	Canopy frugivore	0	62	7	69
<i>Artibeus lituratus</i>	Canopy frugivore	1	23	8	32
<i>Artibeus jamaicensis</i>	Canopy frugivore	1	24	1	26
<i>Platyrrhinus helleri</i>	Canopy frugivore	0	0	6	6
<i>Platyrrhinus brachycephalus</i>	Canopy frugivore	0	1	0	1
<i>Chiroderma trinitatum</i>	Canopy frugivore	1	7	4	12
<i>Chiroderma villosum</i>	Canopy frugivore	1	0	0	1
<i>Uroderma bilobatum</i>	Canopy frugivore	4	16	1	21
<i>Mesophylla macconnelli</i>	Canopy frugivore	0	0	2	2
<i>Phyllostomus discolor</i>	Opportunistic frugivore, nectarivore	1	0	0	1
<i>Phyllostomus hastatus</i>	Carnivore	0	2	0	2
<i>Tonatia brasiliense</i>	Insectivore	0	1	0	1
<i>Tonatia silvicola</i>	Insectivore	0	3	2	5
<i>Myotis nigricans</i>	Insectivore	0	2	0	2
<i>Myotis simus</i>	Insectivore	0	0	1	1
<i>Lasiurus ega</i>	Insectivore	0	1	0	1
<i>Desmodus rotundus</i>	Sanguivore	0	3	0	3
<i>Trachops cirrhosus</i>	Carnivore	0	0	2	2
<i>Noctilio albiventris</i>	Insectivore	1	2	0	3
Total		23	297	76	396

^a Nomenclature according to Aguirre and Anderson (1997).

Species absences above the line and species presences below the line are classified as “unexpected.” Once the matrix has been maximally packed, the program then calculates a “matrix temperature,” which is interpreted as a relative measure of disorder in the extinction order of each site. This temperature ranges from 0° (completely replicable extinction order) to 100° (completely random extinction order—Atmar and Patterson 1993). An unexpected presence or absence of a species in a site (i.e., idiosyncratic species) will generate a higher matrix temperature (Atmar and Patterson 1993). Monte Carlo techniques are then used to assess the probability that a nested pattern could be obtained randomly from the species distribution. The program does have some limitations (Fischer and Lindenmayer 2002) and some absences within the matrix may be an artifact of undersampling (Cam et al. 2000) but this is only likely to be the case in the continuous forest sites. For this analysis the 5 forest islands were considered independently but all sites in the continuous forest were grouped and treated as one. The underlying assumption for this grouping is that the forest acts as a single unit and that all species can freely disperse within the forest.

RESULTS

Species composition.—We captured a total of 396 bats belonging to 24 species and 6 guilds (Table 1). Rarefaction analysis revealed that for a sample of 66 captures, the con-

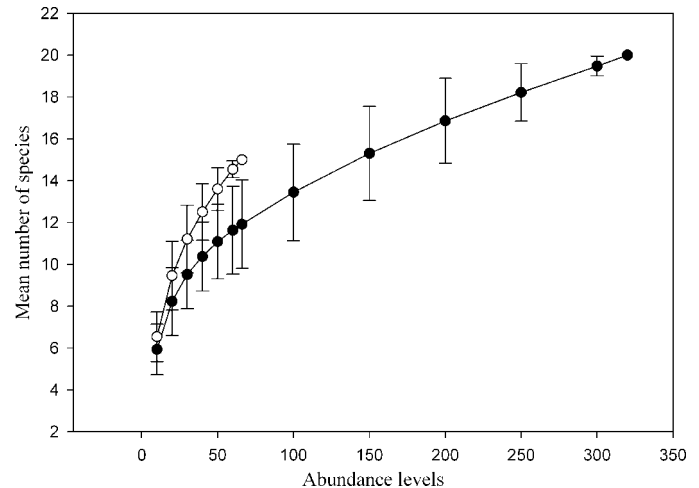


FIG. 2.—Species accumulation curves based on the number of captures in forest islands (solid circles) and continuous forest (blank circles). Error bars indicate variance of the mean.

tinuous forest had significantly higher bat species richness than the forest islands (15 species versus 12 ± 2.05 SD; $P < 0.05$). However, species accumulation curves did not reach an asymptote in either habitat indicating that species were still being added in both continuous forest and forest islands (Fig. 2). Fruit-eating bats (obligate or partially frugivorous) accounted for approximately 88% ($n = 350$) of the captures and represented 14 species from the family Phyllostomidae (Table 1; Fig. 3). Among these 14 species, 5 accounted for 70% of the total captures: *Sturnira lilium* (21.9%), *Artibeus obscurus* (17.4%), *Carollia brevicauda* (12.8%), *Carollia perspicillata* (9.8%), and *Artibeus lituratus* (8%). The frequencies of canopy and understory frugivorous species did not differ between forest islands and continuous forest ($n = 21$, $P = 0.34$; Fisher exact test), thus their relative proportion was maintained in both habitats.

Species composition of bats differed between continuous forest and forest islands as indicated by the Bray–Curtis ordination (Fig. 4); the first 3 axes accounted for 20.75%, 19.33%, and 17.18% of the variation, respectively. Continuous forest and forest islands separated largely along axes 2 and 3, where *Artibeus jamaicensis* and *S. lilium* were captured more often in forest islands, and *Platyrrhinus helleri* and *Mesophylla macconnelli* were captured more often within the continuous forest (Table 2; Fig. 4). However, bat composition did not show a spatial structure (partial Mantel $r = -0.19$, $P > 0.05$). Hence, bat compositions of sites that were close together (controlled by habitat) were not more similar than those of sites that were farther apart.

The distribution of species over the forest islands and the continuous forest revealed a nested distribution pattern (Fig. 5A). The distribution of the 21 species among the 5 forest islands and the continuous forest yielded 6 classes of species richness (range 3–15 species), with the pooled continuous-forest sites having the highest number of species (Fig. 5A). The “matrix temperature” observed was 15.17° and after 1,000 simulations the probability that the observed temperature fell

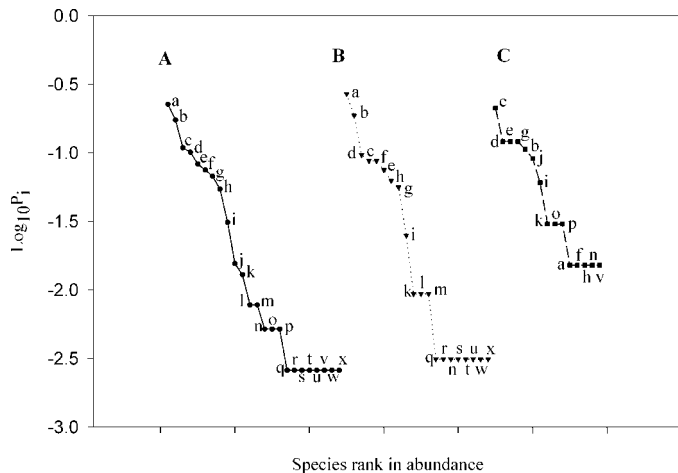


FIG. 3.—Dominance diversity curves for the bat assemblage detected. A) Grouping forest islands, continuous forest, and savanna. B) Forest islands. C) Continuous forest. In all cases, note the relatively high dominance of a few species. Lowercase letters indicate species identity as follows: a) *Sturnira lilium*, b) *Artibeus obscurus*, c) *Carollia brevicauda*, d) *Carollia perspicillata*, e) *Artibeus lituratus*, f) *Artibeus jamaicensis*, g) *Glossophaga soricina*, h) *Uroderma bilobatum*, i) *Chiroderma trinitatum*, j) *Platyrrhinus helleri*, k) *Tonatia silvicola*, l) *Desmodus rotundus*, m) *Noctilio albiventris*, n) *Carollia castanea*, o) *Mesophylla macconnelli*, p) *Trachops cirrhosus*, q) *Myotis nigricans*, r) *Phyllostomus hastatus*, s) *Lasiurus ega*, t) *Tonatia brasiliense*, u) *Platyrrhinus brachycephalus*, v) *Myotis simus*, w) *Phyllostomus discolor*, and x) *Chiroderma villosum*.

within the range of simulated scores was 2.49^{-4} (Fig. 5B). This supports a replicable pattern of extinction. Eight of the 21 species were idiosyncratically distributed (i.e., had a higher temperature than the system temperature of the matrix) among the islands and the forest (Fig. 5C). These species were *Glossophaga soricina*, *Desmodus rotundus*, *Platyrrhinus brachycephalus*, *Noctilio albiventris*, *Myotis nigricans*, *Phyllostomus hastatus*, *Lasiurus ega*, and *Tonatia brasiliense*.

Recaptures from other sites.—We recaptured 25 bats of 8 species; 13 of these individuals were recaptured at sites different from that of the marking site. Distance from the original marking site ranged from approximately 0.5 to 2 km. The most commonly recaptured species were *C. brevicauda*, which accounted for 36% of the recaptures, followed by *S. lilium*, which accounted for 28%. Recaptures indicated movements of bats among forest islands and between forest islands and continuous forest. For example, among the 4 individuals of *C. brevicauda* recaptured, 3 were recaptured at forest islands between 450 and 2,000 m from their original capture islands, and 1 individual was recaptured in the continuous forest approximately 800 m from the original capture island (Table 3).

DISCUSSION

In a world where conversion of forest to farmland and pastures is occurring at an accelerating rate (Turner and Corlett 1996), studies documenting the patterns of species abundance and composition in the remaining forest fragments are a critical

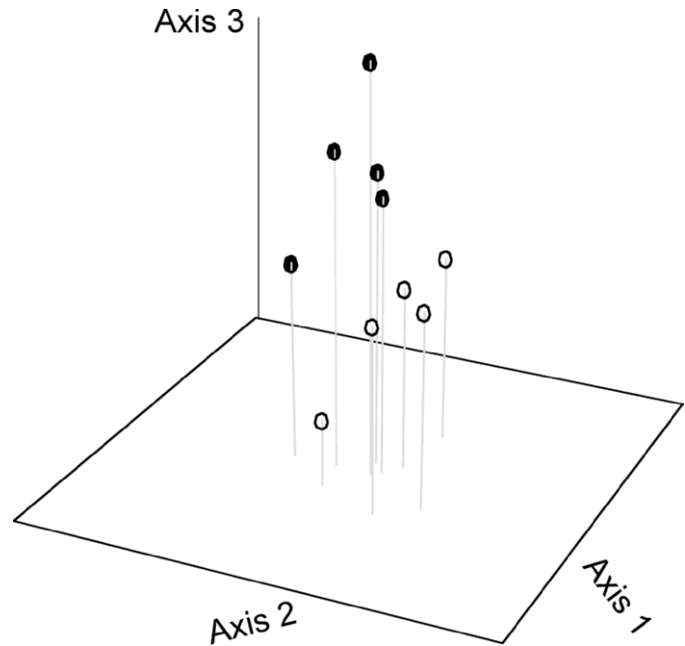


FIG. 4.—Ordination of sites in the continuous forest (blank circles, $n = 5$) and forest islands (solid circles, $n = 5$) in bat species space. Sites in both habitats are plotted according to their factor scores along the first 3 ordination axes (see Table 2).

1st step to understanding the dynamics of a fragmented landscape. Thus far, most studies have focused on anthropogenic fragments (e.g., Gorrensens and Willig 2004; Laurance and Bierregaard 1997), whereas less attention has been paid to natural fragments (but see Montiel et al. 2006). Unlike anthropogenic fragments, natural forest fragments have experienced long-term isolation and can thus provide new insight into the effect of long-term fragmentation on ecosystem processes.

In this study, the most prominent difference observed between the continuous forest and forest islands was that bats were almost 5-fold more abundant in the latter than the former. At equal sample sizes, however, the continuous forest was

TABLE 2.—Results of Bray–Curtis ordination based on bat species using forest islands and continuous forest at Beni Biological Station–Biosphere Reserve (see text).

Variable	Axis 1	Axis 2	Axis 3
<i>Artibeus jamaicensis</i>			0.82
<i>Artibeus lituratus</i>	0.887		
<i>Artibeus obscurus</i>		0.684	
<i>Chiroderma trinitatum</i>	0.806		
<i>Desmodus rotundus</i>			0.673
<i>Glossophaga soricina</i>		0.727	
<i>Lasiurus ega</i>		0.650	
<i>Mesophylla macconnelli</i>	-0.620	-0.651	
<i>Myotis simus</i>	0.737		
<i>Phyllostomus hastatus</i>			0.650
<i>Sturnira lilium</i>			0.646
<i>Tonatia brasiliense</i>		0.650	
<i>Platyrrhinus helleri</i>	-0.607		-0.686
% of information	20.75	19.33	17.18
Total	20.75	40.07	57.25

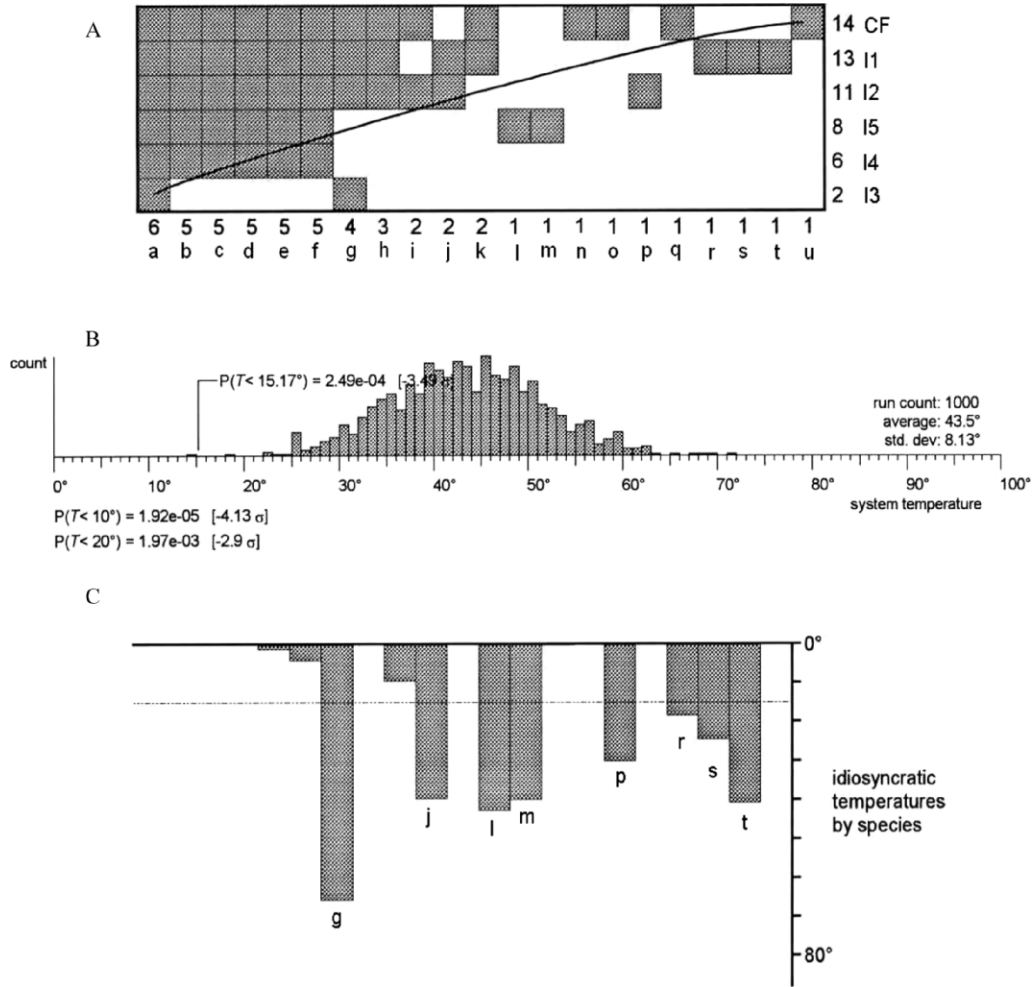


FIG. 5.—A) Maximally packed matrix (fill 42.8%) of bats captured at 5 forest islands and the continuous forest from July to August 2001 at Beni Biological Station–Biosphere Reserve (species captured only in the savanna were excluded). Rows numbers on the right indicates richness; letters or letter/number combinations indicate site as follows: CF = continuous forest, I1 = Island 1, I2 = Island 2, and so on. Column numbers indicate the number of sites where a species was found. Column letters indicate species identity as follows: a) *Artibeus obscurus* and *C. perspicillata*, b) *Sturnira lilium*, c) *Carollia brevicauda*, d) *Artibeus jamaicensis*, e) *Artibeus lituratus*, f) *Uroderma bilobatum*, g) *Glossophaga soricina*, h) *Chiroderma trinitatum*, i) *Carollia castanea*, j) *Desmodus rotundus*, k) *Tonatia silvicola*, l) *Platyrrhinus brachycephalus*, m) *Noctilio albiventris*, n) *Platyrrhinus helleri*, o) *Mesophylla macconnelli*, p) *Myotis nigricans*, q) *Trachops cirrhosus*, r) *Phyllostomus hastatus*, s) *Lasiurus ega*, t) *Tonatia brasiliense*, and u) *Myotis simus*. Note that the 1st column in the graph is represented by the 2 species that occurred at all sites. B) Distribution of simulated temperatures after 1,000 runs. C) Idiosyncratic species are identified by an unexpected presence or absence of a species in a site.

richer than the forest islands and showed a steeper curve (Fig. 2), suggesting that this habitat is accumulating species at a much higher rate than the forest islands.

The lower capture rates of bats, particularly frugivorous bats that were recorded in the continuous forest, are probably associated with fruit availability, because it has been shown that frugivores respond to spatial and temporal changes in fruit availability (Fleming 1988; Loisele and Blake 1991). During our study, the number of fruiting species in the forest was 3-fold lower than in the forest islands; moreover, the mean amount (g) of fruit biomass available per night was 9-fold higher in forest islands than in continuous forest (7,102.4 g in islands compared to 765.8 g in the forest). However, low captures rates also may result from the lower probability of a bat being caught in a net in the continuous forest. In com-

parison to the continuous forest, bats in forest islands are concentrated within a relatively small area (e.g., within 0.5–3.0 ha), hence they are more likely to be caught by nets placed across the island than in nets placed in extensive tracts. Additionally, although canopy height of forest islands can reach up to 30 m, it is more common to see islands with a canopy of 15–20 m. Therefore, it is likely that at least some species of bats in forest islands fly at lower heights than bats in continuous forest, where the canopy is much higher, ultimately also resulting in higher capture rates in forest islands.

Low capture rates in the continuous forest at Beni Biological Station–Biosphere Reserve, in contrast to the forest islands, is generally the opposite pattern to that found in other areas. In other areas of the Neotropics, lower capture rates in forest fragments have been explained by lower resource availability

TABLE 3.—Recaptures of bats in forest islands and continuous forest at Beni Biological Station, Bolivia, from June to August 2001.

Species	Original capture site ^a							Recapture site ^a							Total	Total recaptured at other sites	Mean distance (m)	Range (m)	
	I1	I2	I3	I4	I5	F3	F5	I1	I2	I4	I5	F3	F4	F5					
<i>Carollia brevicauda</i>	4	2		1		1	1	5				1	1	1	1	9	4	950	450–2,000
<i>Carollia perspicillata</i>	1			2				2		1					3	1	2,000		
<i>Sturnira lilium</i>	5	1	1					5		1	1				7	3	831	371–1,656	
<i>Artibeus obscurus</i>	1				1				1		1				2	1	467		
<i>Artibeus jamaicensis</i>					1					1					1	1	1,860		
<i>Artibeus lituratus</i>	1										1				1	1	371		
<i>Uroderma bilobatum</i>		1								1					1	1	1,485		
<i>Glossophaga soricina</i>		1								1					1	1	467		
Total	12	5	1	3	2	1	1	12	2	4	4	1	1	1	25	13			

^a I = forest island; F = continuous forest.

in these habitats (e.g., Cosson et al. 1999). Once a habitat is fragmented, pioneer understory species colonize the fragments and in some cases replace mature forest tree species (Laurance et al. 1998; Viana et al. 1997). This inevitably leads to a reduction of fruit availability of forest canopy species, which may limit the occurrence of bats that use these resources (e.g., Stenoderminae). Contrary to other fragmented sites in the Neotropics (e.g., Schulze and Whitacre 1999), the forest islands at Beni Biological Station–Biosphere Reserve have retained much of the mature forest species component. Moreover, Comiskey et al. (1998, 2000) found that of thirteen 1-ha biodiversity monitoring plots located throughout the reserve, the plots located in forest island sites had the highest tree diversity per hectare (trees ≥ 10 cm diameter at breast height) with woodland species of both lowland forest and savanna.

Thus, given that the forest islands at Beni Biological Station–Biosphere Reserve are maintaining higher tree diversity than continuous forest, they are unlike other fragments in that they retain some extent of the continuous forest structure and composition and thus provide a wider array of resources for frugivores. If this is so, then forest islands at the study site should attract not only species of bats that feed mostly upon pioneer understory species (i.e., *Carollia* and *Sturnira*), but also bats that feed in the canopy of mature forest tree species. Given that there are no differences in the relative proportions of understory and canopy frugivores between the forest islands and the continuous forest, the results from this study suggest that forest islands provide resources for both groups of fruit-eating bats. In this sense, we found that at the time of the study 4 species of *Ficus* were fruiting in the islands, as compared to only 1 in the continuous forest. Additionally, with the exception of *M. macconnelli* and *P. helleri*, all canopy frugivores recorded in the area were present in the forest islands. Both *M. macconnelli* and *P. helleri* have been previously detected either in forest fragments or in disturbed habitats in other areas (Cosson et al. 1999; Estrada et al. 1993a, 1993b; Galindo-González et al. 2000; Schulze et al. 2000). Thus, it is likely that they are able to use the forest islands. However, it has been suggested that even though *P. helleri* can use fragments, it needs either riparian vegetation or habitat corridors to reach these fragments, because it seldom crosses open areas (Galindo-González 2004). Isolation also would explain why

this species was not detected in the forest islands. Both *P. helleri* and *M. macconnelli* are rare (Ferrell and Wilson 1991; Kunz and Pena 1992), but were only detected in the continuous forest even though sample size there was 5-fold lower than in forest islands. This finding is contrary to what would be expected by chance and may indicate that *M. macconnelli* and *P. helleri* do indeed prefer continuous forest.

The bat fauna in the continuous forest and forest islands at Beni Biological Station–Biosphere Reserve during this study exhibited a nonrandom pattern of distribution. Instead, distribution of bats followed a nested pattern: most species occurred in the continuous forest with the forest islands supporting fewer species. Nested subset distributions are usually found to be a result of area effects where successively smaller fragments contain a subset of species found in larger fragments (e.g., Blake 1991). Interestingly, the smallest forest island (I3) was the one in which the fewest number of species was detected. However, this result needs to be interpreted with caution because numerous factors may have helped shape the species distribution. For example, although I3 had the fewest species, this island also was sampled during unusually cold nights that followed a storm system. Thus, results may reflect low activity patterns (i.e., only 9 bats were captured during the 3 sampling nights) rather than a bat-depauperate island. Results also are difficult to interpret because the proximity among islands and, most importantly, the high mobility of bats can cause changes in distribution patterns (Bernard and Fenton 2003; Montiel et al. 2006). Thus, the nested distribution may change with greater sampling effort or sampling in a different season.

Most of the idiosyncratic species identified in the nested subsets are species that were detected only once during the study (e.g., *P. brachycephalus*, *M. nigricans*, *Phyllostomus discolor*, *L. ega*, and *T. brasiliense*) and, thus, we cannot really conclude anything regarding their distributions because of small sample size. Three species had idiosyncratic distributions even though the number of captures was higher: *G. soricina* ($n = 26$), *D. rotundus* ($n = 3$), and *N. albiventris* ($n = 3$). The “temperature” of *G. soricina* results from its unexpected presence in I3, the most depauperate island. *G. soricina* is a bat commonly found throughout the Neotropics (Alvarez et al. 1991; Medellín et al. 2000) and it has been reported to have large home ranges (Heithaus et al. 1975). Finding this species

at I3 may be related to the presence of a large bat roost in that island. Although we cannot confirm whether *G. soricina* used that roost, we observed several other species of bats using it. The distribution of *D. rotundus* is likely related to its ecology. This species was absent from the continuous forest, but was present in the 2 most-speciose forest islands (Figs. 5A and 5C). This is likely because *D. rotundus* is a sanguivore that feeds mainly on blood of livestock (Greenhall et al. 1983), and some sections of the savanna at Beni Biological Station–Biosphere Reserve are used for cattle grazing. Furthermore, the savanna in ranches adjacent to the station is used for cattle grazing at much higher densities than that at Beni Biological Station–Biosphere Reserve. Finally, the distribution of *N. albiventris* was likely influenced by the presence of a roost of this species at I4 (Fig. 5A). *N. albiventris* is an insectivore that forages over rivers, streams, and marshes (Hood and Pitocchelli 1983), and it is unlikely to be caught within a forest island. At I4, individuals of *N. albiventris* were caught in nets near the roost. Consequently, the capture of this species is probably a direct result of the presence of the roost.

To what extent do bats live in the forest islands as opposed to just visiting the islands while foraging over a wide area? Evidence from recapture data as well as movement patterns of *S. lilium* (Loayza and Loisel 2008) reveals that bats move freely across this landscape and, thus, forage over large areas. However, islands are not just visited by bats but also provide roosting sites. During our study, we observed active roosts of at least 5 species of bats (*C. brevicauda*, *C. perspicillata*, *S. lilium*, *A. obscurus*, and *N. albiventris*) in almost all islands. We monitored a roost of *S. lilium* and found several individuals with evidence of lactation or embryos suggesting that some bat species also may reproduce within the islands.

Our results suggest that bats can persist and reproduce in this naturally fragmented landscape, most likely because they are capable of crossing the savanna matrix and therefore able to use different habitats (Bernard and Fenton 2003; Montiel et al. 2006). Malcom (1997) suggested that, compared to diurnal mammals, nocturnal mammals such as bats are more likely to cross a nonforested matrix because they perceive less difference in risk between the forested and the nonforested habitat when flying in the dark. In this study, evidence of movements across the savanna is given by the recapture of individuals at sites other than their original capture sites and by the fact that many species ($n = 11$; Table 1) were captured in the nets in the savanna. Movement across habitats is highly influenced by the matrix, which can act as a filter agent enabling some species and not others to cross (e.g., Cosson et al. 1999). In this sense, Laurance et al. (1998) suggested that matrices could be ranked in terms of their capacity to allow movement among the elements in a landscape. They determined that water, row crops, and pastures were the most unfavorable matrices for gene flow. Nonetheless, despite a pasture being an unfavorable matrix, our study shows that there is movement of bats across the savanna, which indicates that this matrix may not be impermeable, at least to some species of bats. Although crossing the savanna matrix can impose a cost, such as higher predation risk (Janzen et al. 1976), bat species reaching forest habitats

outside the forest may be rewarded by encountering patches that are resource rich (Comiskey et al. 1998).

In summary, the results from our study show that bat populations, especially in the fruit-eating guild, can persist in a naturally fragmented landscape. Although individual forest islands may not be able to sustain large populations of bats, these habitats provide abundant fruit resources in comparison to the forest. Although it is uncertain if this pattern is maintained throughout the year, at least during the dry season, forest islands at our site provided more fruit resources than the continuous forest. Because forest islands at Beni Biological Station–Biosphere Reserve retain similar vegetation structure and tree composition as the continuous forest, they also provide the roosting requirements for several species of bats. Furthermore, the rarefaction curves for neither habitat reached an asymptote, indicating that more species will be added to both habitats with more sampling effort. Additional sampling methods, such as canopy nets, harp traps, and passive monitoring system are undoubtedly necessary to completely sample the bat assemblage in this landscape. Finally, we concur with Gorrensens and Willig (2004) in that forest fragments should be considered in management plans because they can contribute to the maintenance of biodiversity.

RESUMEN

Investigamos la composición de especies del ensamble de murciélagos en bosque continuo e islas naturales de bosque en un ecosistema de sabanas en el norte de Bolivia. Capturamos 396 murciélagos de 24 especies. Cinco especies representaron el 70% de las capturas: *Sturnira lilium*, *Artibeus obscurus*, *Carollia brevicauda*, *C. perspicillata* y *Artibeus lituratus*. La composición de especies del ensamble de murciélagos difirió entre el bosque continuo y las islas de bosque. *Artibeus jamaicensis* y *S. lilium* fueron capturados con mayor frecuencia en las islas de bosque, y *Platyrrhinus helleri* y *Mesophylla macconnelli* en el bosque continuo. Los murciélagos presentaron un patrón de distribución anidado. El bosque continuo tuvo el mayor número de especies, y la isla más pequeña el menor número de especies. Sin embargo, los murciélagos fueron cinco veces más abundantes en las islas de bosque que en el bosque continuo. Los datos de recaptura muestran movimientos de murciélagos tanto entre islas, como entre islas de bosque y bosque continuo. Nuestros resultados sugieren que las poblaciones de murciélagos, y particularmente de murciélagos frugívoros, pueden persistir en un paisaje naturalmente fragmentado.

ACKNOWLEDGMENTS

We thank the staff at Beni Biological Station–Biosphere Reserve for their assistance during this study. We are thankful for the help from Colección Boliviana de Fauna of the Instituto de Ecología in La Paz, Bolivia, to obtain permits. We are particularly grateful to our field assistants R. Tarquino and I. Moya, as well as our field guides “Jechu” and Nataniel Burgos. The manuscript benefited from comments from R. Rios, G. Camilo, and 2 anonymous reviewers. This work received financial support from the Wildlife Conservation Society through their Research Fellowship Program, the Scholarship Program of Bat

Conservation International, Ideawild, and the Goldie Millstone Scholarship of the Whitney Harris World Ecology Center at University of Missouri–St. Louis. This research was executed as partial fulfillment of the requirements of the M.S. degree by APL at the University of Missouri–St. Louis.

LITERATURE CITED

- AGUIRRE, L. F. 2002. Structure of a neotropical savanna bat community. *Journal of Mammalogy* 83:775–784.
- AGUIRRE, L. F., AND S. ANDERSON. 1997. Clave de campo para la identificación de los murciélagos en Bolivia. Instituto de Ecología, La Paz, Bolivia, Serie Zoología 5:1–38.
- AGUIRRE, L. F., L. LENS, AND ERIK MATTHYSEN. 2003. Patterns of roost use by bats in a neotropical savanna: implications for conservation. *Biological Conservation* 111:435–443.
- ALVAREZ, J., M. R. WILLIG, J. K. JONES, JR., AND W. D. WEBSTER. 1991. *Glossophaga soricina*. *Mammalian Species* 379:1–7.
- ANDERSON, S. 1993. Los mamíferos bolivianos: notas de distribución y claves de identificación. Instituto de Ecología, La Paz, Bolivia.
- ANDRÉN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366.
- ATMAR, W., AND B. D. PATTERSON. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382.
- BERNARD, E., AND M. B. FENTON. 2002. Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in central Amazonia, Brazil. *Canadian Journal of Zoology* 80:1124–1140.
- BERNARD, E., AND M. B. FENTON. 2003. Bat mobility and roosts in a fragmented landscape in central Amazonia, Brazil. *Biotropica* 35:262–277.
- BIERREGAARD, R. O., JR., AND P. C. STOFFER. 1997. Understory birds and dynamic habitat mosaics in Amazonian rainforests. Pp. 138–155 in *Tropical forest remnants: ecology, management, and conservation in fragmented communities* (W. F. Laurance and R. O. Bierregaard, Jr., eds.). University of Chicago Press, Chicago, Illinois.
- BLAKE, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. *Conservation Biology* 5:95–103.
- BROSSET, A., P. CHARLES-DOMINIQUE, A. COCKE, J. F. COSSON, AND D. MASSON. 1996. Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology* 74:1974–1982.
- CAM, E., J. D. NICHOLS, J. E. HINES, AND J. R. SAUER. 2000. Inferences about nested subsets structure when not all species are detected. *Oikos* 91:428–434.
- COMISKEY, J. A., F. DALLMEIER, AND G. AYMARD. 2000. Floristic composition and diversity of forested habitats in the Estación Biológica del Beni, Amazonia, Bolivia. Pp. 89–112 in *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia* (O. Herrera-MacBryde, F. Dallmeier, B. MacBryde, J. A. Comiskey, and C. Miranda, eds.). Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB), Rockville, Maryland.
- COMISKEY, J. A., F. DALLMEIER, AND R. B. FOSTER. 1998. Forest structure and diversity in managed and unmanaged rainforest of Beni, Bolivia. Pp. 663–680 in *Forest biodiversity in North, Central and South America, and the Caribbean: research and monitoring* (F. Dallmeier and J. A. Comiskey, eds.). Man and the Biosphere Series Vol. 21. Parthenon Publishing, Pearle River, New York.
- CORDEIRO, N. J., AND H. F. HOWE. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences* 100:14052–14056.
- CORLETT, R. T., AND I. M. TURNER. 1997. Long-term survival in tropical forest remnants in Singapore and Hong Kong. Pp. 333–350 in *Tropical forest remnants: ecology, management, and conservation in fragmented communities* (W. F. Laurance and R. O. Bierregaard, Jr., eds.). University of Chicago Press, Chicago, Illinois.
- COSSON, J. F., J. M. PONS, AND D. MASSON. 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology* 15:515–534.
- CUTLER, A. 1991. Nested faunas and extinction in fragmented habitats. *Conservation Biology* 5:496–505.
- ECHEVERRÍA, C., A. C. NEWTON, A. LARA, J. M. REY BENAYAS, AND D. A. COOMES. 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Global Ecology and Biogeography* 16:426–439.
- EDYTHE, L. P. A. 1988. Age determination in bats. Pp. 47–58 in *Ecological and behavioral methods for the study of bats* (T. E. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- ESTRADA, A., AND R. COATES-ESTRADA. 2001. Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 17:627–646.
- ESTRADA, A., R. COATES-ESTRADA, AND D. MERITT, JR. 1993a. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, México. *Ecography* 16:309–318.
- ESTRADA, A., R. COATES-ESTRADA, D. MERITT, JR., S. MONTIEL, AND D. CURIEL. 1993b. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. *Vegetatio* 107/108:245–257.
- FENTON, M. B., ET AL. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica* 24:440–446.
- FERRELL, C. S., AND D. E. WILSON. 1991. *Platyrrhinus helleri*. *Mammalian Species* 373:1–5.
- FISCHER, J., AND D. B. LINDENMAYER. 2002. Treating the nestedness temperature calculator as a “black box” can lead to false conclusions. *Oikos* 99:193–199.
- FLEMING, T. H. 1988. The short-tailed fruit bat: a study in plant–animal interactions. University of Chicago Press, Chicago, Illinois.
- FORTIN, M., AND J. GUREVITCH. 1993. Mantel tests: spatial structure in field experiments. Pp. 342–359 in *Design and analysis of ecological experiments* (S. M. Scheiner and J. Gurevitch, eds.). Chapman & Hall, New York.
- GALINDO-GONZÁLEZ, J. 2004. Clasificación de los murciélagos de la región de Los Tuxtlas, Veracruz, respecto a su respuesta a la fragmentación del hábitat. *Acta Zoológica Mexicana (Nueva Serie)* 20:239–243.
- GALINDO-GONZÁLEZ, J., S. GUEVARA, AND V. J. SOSA. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology* 14:1693–1703.
- GALINDO-GONZÁLEZ, J., AND V. J. SOSA. 2003. Frugivorous bats in isolated trees and riparian vegetation associated with human-made pastures in a fragmented tropical landscape. *Southwestern Naturalist* 48:579–589.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GARDNER, A. L. 1977. Feeding habits. Pp. 293–350 in *Biology of bats of the New World family Phyllostomidae. Part I* (R. J. Baker, J. K.

- Jones, Jr., and D. Carter, eds.). Special Publications, The Museum, Texas Technical University.
- GOOSEM, M. 2002. Effects of tropical rainforest roads on small mammals: fragmentation, edge effects and traffic disturbance. *Wildlife Research* 29:277–289.
- GORRENSEN, P. A., AND M. R. WILLIG. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. *Journal of Mammalogy* 85:688–697.
- GOTELLI, N. J., AND R. K. COLWELL. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- GOTELLI, N. J., AND G. L. ENTSMINGER. 2001. EcoSim: null models software for ecology. Version 6.0. Acquired Intelligence Inc. & Kesity-Bear. <http://homepages.together.net/~gentsmin/ecosim.htm>. Accessed 22 May 2002.
- GREENHALL, H. M., G. JOERMANN, AND U. SCHMIDT. 1983. *Desmodus rotundus*. *Mammalian Species* 202:1–6.
- HANAGARTH, W. 1993. Acerca de la geología de las sabanas del Beni en el Noreste de Bolivia. Instituto de Ecología, La Paz, Bolivia.
- HANAGARTH, W., AND J. SARMIENTO. 1990. Reporte preliminar sobre la geología de la sabana de Espíritu y sus alrededores (Llanos de Moxos, departamento del Beni, Bolivia). *Ecología en Bolivia* 16:47–75.
- HEITHAUS, E. R., AND T. H. FLEMING. 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomatidae). *Ecological Monographs* 48:127–143.
- HEITHAUS, E. R., T. H. FLEMING, AND P. A. OPLER. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56:841–854.
- HENRY, M., J. F. COSSON, AND J. M. PONS. 2007. Abundance may be a misleading indicator of fragmentation-sensitivity: the case of fig-eating bats. *Biological Conservation* 139:462–467.
- HOOD, C. S., AND J. PITOCHELLI. 1983. *Noctilio albiventris*. *Mammalian Species* 197:1–5.
- JANZEN, D. H., G. A. MILLER, J. HACKFORTH-JONES, C. M. POND, K. HOOPER, AND D. P. JANOS. 1976. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology* 57:1068–1075.
- JOHNS, A. D. 1986. Effects of selective logging in the behavioral ecology of West Malaysian primates. *Ecology* 67:684–694.
- KUNZ, T. H., AND I. M. PENA. 1992. *Mesophylla macconnelli*. *Mammalian Species* 405:1–5.
- LANGSTROTH, R. P. 1996. Forest islands in an Amazonian savanna of northeastern Bolivia. Ph.D. dissertation, University of Wisconsin–Madison.
- LAURANCE, W. F., AND R. O. BIERREGAARD, JR. 1997. Tropical forest remnants: ecology management and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois.
- LAURANCE, W. F., L. V. FERREIRA, J. M. RANKIN-DE-MERONA, S. G. LAURANCE, R. W. HUTCHINGS, AND T. E. LOVEJOY. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12:460–464.
- LAURANCE, W. F., ET AL. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605–618.
- LAW, B. S., J. ANDERSON, AND M. CHIDEL. 1999. Bat communities in a fragmented landscape on the south-west slopes of New South Wales, Australia. *Biological Conservation* 88:333–345.
- LEMONS DE SA, R. M., T. R. POPE, K. E. GLANDER, T. T. STRUHSAKER, AND G. A. B. DA FONSECA. 1990. A pilot study of genetic and morphological variation in the muriqui (*Brachyteles arachnoides*). *Primate Conservation* 11:26–30.
- LOAYZA, A. P., AND B. A. LOISELLE. 2008. Preliminary information on the home range and movement patterns of *Sturnira lilium* (Phyllostomidae) in a naturally fragmented landscape in Bolivia. *Biotropica* 40:630–635.
- LOISELLE, B. A., AND J. G. BLAKE. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. *Auk* 108:114–130.
- LORD, J., AND D. NORTON. 1990. Scale and the spatial concept of fragmentation. *Conservation Biology* 4:197–202.
- MALCOM, J. R. 1997. Biomass and diversity of small mammals in Amazonian forest fragments. Pp. 207–221 in *Tropical forest remnants: ecology, management, and conservation in fragmented communities* (W. F. Laurance and R. O. Bierregaard, Jr., eds.). University of Chicago Press, Chicago, Illinois.
- MEDELLÍN, R. A., M. EQUIHUA, AND M. A. AMIN. 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conservation Biology* 14:1666–1675.
- MIRANDA, C. L. 2000. La Reserva de la Biosfera Estación Biológica del Beni, Bolivia. Pp. 21–25 in *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia* (O. Herrera-MacBryde, F. Dallmeier, B. MacBryde, J. A. Comiskey, and C. Miranda, eds.). Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB), Rockville, Maryland.
- MONTIEL, S., A. ESTRADA, AND P. LEÓN. 2006. Bat assemblages in a naturally fragmented ecosystem in the Yucatan Peninsula, Mexico: species richness, diversity and spatio-temporal dynamics. *Journal of Tropical Ecology* 22:267–276.
- MORAES, M. R., M. O. RIBERA, AND E. VILLANUEVA. 2000. La vegetación de la Reserva ed la Biosfera Estación Biológica del Beni y su importancia para la conservación. Pp. 59–73 in *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia* (O. Herrera-MacBryde, F. Dallmeier, B. MacBryde, J. A. Comiskey, and C. Miranda, eds.). Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB), Rockville, Maryland.
- MORRISON, D. W. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behaviour* 26:852–855.
- PATTERSON, B. D. 1995. The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices. AICS Research and The Field Museum, Chicago. <http://aics-research.com/nestedness/tempcalc.html>. Accessed 15 May 2002.
- RIBERA, M. O., M. MORAES, AND E. VILLANUEVA. 1990. Formaciones de vegetación en la Reserva de la Biosfera Estación Biológica Beni, bajo un marco ecológico. Informe Final para el Proyecto Bioecología del Ecosistema Beni, OEA, La Paz, Bolivia.
- SCHULZE, M., AND P. WHITACRE. 1999. A classification and ordination of the tree community of Tikal National Park, Petén, Guatemala. *Bulletin of the Florida Museum of Natural History*. 41:169–297.
- SCHULZE, M. D., N. E. SEAVY, AND F. F. WHITACRE. 2000. A comparison of the phyllostomid bat assemblages in undisturbed forest and in forest fragments of slash-and-burn farming mosaic in Petén, Guatemala. *Biotropica* 32:174–184.
- TURNER, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33:200–209.
- TURNER, I. M., AND R. T. CORLETT. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology & Evolution* 11:330–333.
- VAN ROOSMALEN, M. G. M. 1985. Habitat preferences, diet, feeding behaviour and social organization of the black spider monkey

- (*Ateles paniscus paniscus*) in Surinam. *Acta Amazónica* 15, supplement:1–238.
- VIANA, V. M., A. A. J. TABANEZ, AND J. L. F. BATISTA. 1997. Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. Pp. 351–365 in *Tropical forest remnants: ecology, management, and conservation in fragmented communities* (W. F. Laurance and R. O. Bierregaard, Jr., eds.). University of Chicago Press, Chicago, Illinois.
- WAGNER, A. P., M. P. GERALDES, G. G. LOPEZ, AND C. J. RODRIGUES A. 1995. Fragmentação de habitat e a estrutura de uma taxocenose de morcegos em São Paulo (Brasil). *Quiropeira Neotropical* 1: 4–6.
- WHITMORE, T. C. 1997. Tropical forest disturbance, disappearance, and species loss. Pp. 3–12 in *Tropical forest remnants: ecology, management, and conservation in fragmented communities* (W. F. Laurance and R. O. Bierregaard, Jr., eds.). University of Chicago Press, Chicago, Illinois.
- YATES, M. D., AND R. M. MUZIKA. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management* 70:1238–1248.

Submitted 9 July 2008. Accepted 18 September 2008.

Associate Editor was David S. Jacobs.