

Bat assemblages in a naturally fragmented ecosystem in the Yucatan Peninsula, Mexico: species richness, diversity and spatio-temporal dynamics

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Abstract: Investigations of bats in naturally fragmented ecosystems may help refine assumptions about bat responses to fragmentation of their habitats by human activity. Bat species assemblages were studied for a 3.5-y period in a naturally fragmented landscape in the north-west Yucatan Peninsula, Mexico. Bats were systematically sampled using mist nets in a total of 16 forest islands of four categories (four sites each): large (> 20 ha), small (< 5 ha), far and near (sites located > 10 km or < 1 km away from the nearest forest island, respectively). We captured a total of 1134 bats representing 17 species. Bat diversity and species richness were similar among categories of forest island. Fruit-eating bats (78–93% of captures) were significantly more abundant in large and in small than in forest islands in the far or near categories. Differences in density of *Manilkara zapota* trees in the forest islands might underlie the observed variations in the abundance of frugivorous bats. Distances traversed by bats (0.65–38 km) between forest islands (typically 100–300 m away), facilitates the mobility of bats across the landscape. However, the moderately rich bat species assemblage detected, suggests that other species may not be able to persist in such naturally fragmented ecosystems.

Key Words: Bats, forest fragmentation, habitat-island, Neotropics, coastal wetlands

INTRODUCTION

It has been suggested that bat tolerance to habitat loss and fragmentation may be related to an ability to traverse open areas to reach other forest fragments or other vegetation types and use resources within the matrix (Law *et al.* 1999, Schulze *et al.* 2000). However, in spite of their mobility and slow demographic turnover, the few studies available indicate that Neotropical bats seem to be sensitive to loss and fragmentation of their natural habitat, locally undergoing decreases in species diversity and size of populations (Brosset *et al.* 1996, Cosson *et al.* 1999, Estrada *et al.* 1993a, Gallard *et al.* 1989, Granjon *et al.* 1996, Schulze *et al.* 2000). Data available suggest that bat species and ecological guilds may respond differently to changes in the spatial and temporal arrangements of remnant forests and man-made vegetation in human-modified Neotropical

landscapes (Brosset *et al.* 1996, Estrada & Coates-Estrada 2001, Estrada *et al.* 1993a, Schulze *et al.* 2000). In these human-modified ecosystems, isolating distance, rather than area of the habitat island, may be an influential factor affecting the richness of bat species assemblages (Estrada & Coates-Estrada 2002, Estrada *et al.* 1993a). However, there is also some evidence indicating that bats may do well in naturally fragmented ecosystems (Aguirre 2002, Aguirre *et al.* 2003). Investigations of bats in naturally fragmented ecosystems can provide insight on how bats have adapted to the habitat-island nature of such habitats and may help refine assumptions about bat responses to fragmentation of their habitats by human activity.

In the coastal wetlands of north-west Yucatan Peninsula, tropical rain-forest vegetation is mainly represented by naturally formed forest islands in a matrix dominated by grasslands (typically with aquatic vegetation dominated by *Typha dominguensis* and the sawgrass *Cladium jamaicense*) which are seasonally flooded by rainfall (Rico-Gray 1982). In general, these forest islands, locally known as *petenes* (singular *peten*),

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constitute discrete units of forest vegetation in the landscape and most of them tend to be semicircular in shape and are located at variable distance from one another (Rico-Gray 1982). Vegetation in the forest islands is mainly semideciduous tropical rain forest, and in some cases, forest islands closer to the coast may harbour mangrove vegetation as well (Rico-Gray 1982). The forest islands originated as a result of two parallel factors. One, slight elevations of the terrain (predominant soil is of calcareous origin) above flooding levels during the rainy season, and two, the presence of sinkholes or *cenotes*. The cenotes in forest islands are openings where the calcareous rock has collapsed allowing the underground water to rise (Olmsted & Durán 1998).

The forest islands harbour a diverse assemblage of plant and animal species, with bats being an important component in the latter group (Montiel *et al.* in press). In spite of the ubiquity of the matrix of forest islands and grasslands along the western coast of the Yucatan Peninsula, little work has been done regarding its wildlife. The fragmented nature of that landscape and its resident biota hence provide an opportunity to investigate how bat populations and species are affected by the spatial arrangement of their naturally fragmented habitat.

In this paper we present data derived from a 3.5-year long (April 2001–August 2004) investigation of bat assemblages in the naturally fragmented petenes landscape in north-west Yucatan Peninsula, Mexico. We specifically document (1) the structure and composition of the bat assemblages inhabiting the forest islands known as *petenes*, (2) differences in bat species richness, diversity and abundance associated to differences in area and isolation distance of the habitat-island as well as seasons and years and (3) data on movements by bats among forest islands in the landscape.

STUDY AREA

Fieldwork was conducted along the north-west coastline of the Yucatan Peninsula in the Biosphere Reserve 'Los Petenes' (BRLP from here on, 20°51'–19°49'N, 90°45'–90°20'W; area = 2829 km² (35.6% terrestrial surface, the rest marine surface); mean monthly temperature = 26 °C; mean annual precipitation = 819 mm). Rainfall is clearly seasonal, with a dry season from December to May (mean monthly precipitation ± SE = 13.2 ± 3.3 mm) and a rainy season from June to November (mean monthly precipitation = 149 ± 41.0 mm). Examination of aerial photographs (1998) and topographic maps (scale 1:75 000 and 1:50 000, respectively) as well as ground-truthing indicated the presence at least 329 clearly defined forest islands in the northern sector (*c.* 550 km²) of the BRLP. Area of these forest islands was 1–50 ha (mean =

13.4 ha). Minimum isolating distance among forest islands was 0.05–11 km (mean = 0.32 km).

METHODS

Study sites

Sampling of bats was conducted in a total of 16 forest islands in the BRLP. In eight of these forest islands, we systematically sampled bats during the first and second year of work (June 2001–May 2003). Four of these had similar isolation distance (< 1.0 km) and were selected to investigate the effects of area of the habitat-island on bat assemblages. Two of these forest islands were classified as large (area = 20 and 25 ha) and the other two as small (area = 2 ha in both cases). Another four forest islands of a similar size (12–15 ha) were selected to assess the influence of isolation distance of the habitat-island on bat assemblages. Two of these forest islands were classified as far (located > 10 km away from the nearest forest island) and two as near (located < 1.0 km away from the nearest forest island).

Another eight forest islands were added to the study during the second (two 'large' sites) and third year (the six remnant sites) of work. These forest islands were selected and assigned as two additional replicates for the large (area = 50 and 25 ha), small (area = 2 and 4 ha), far (located 10.2 and 11.5 km away from the nearest forest island) and near (located 0.2 km away from the nearest forest island in both cases) habitat-island categories. Before systematic sampling of bats began, each forest island was visited several times to assess the general state of conservation of the forest vegetation and to confirm their geographical coordinates.

Sampling of bats

Using sampling protocols described by Estrada *et al.* (1993a, b), Estrada & Coates-Estrada (2001, 2002) and Moreno & Halffter (2000), bats were sampled in each forest island during the dry and rainy seasons, in three and two instances per season in the first and the remnant two annual cycles, respectively. Bats were sampled using a line of 10 mist nets (each net = 12 m long × 3 m high) running sinuously through the centre of each forest island. In each site, we operated the nets for two consecutive nights from 19h00–24h00 on non-rainy and moonless nights, and checked the nets every 45 min for presence of bats. Each captured bat was weighed (to the nearest 0.5 g), measured (forearm length), sexed and identified to species level (following Coates-Estrada & Estrada 1986, Medellín *et al.* 1997, Sánchez-Hernández & Romero-Almaráz 1995). Each bat was marked with a

numbered plastic colour band (National Tag Co. TN, USA) placed on the forearm and released at the site of capture. We assigned each bat to one of seven general foraging guilds according to information reported by Bonaccorso (1979), Charles-Dominique (1991), Coates-Estrada & Estrada (1986), Fleming (1988), Gardner (1977), Lou & Yurrita (2005) and Sazima (1976). These foraging guilds were: frugivore, insectivore, sanguinivore, frugivore–insectivore or insectivore–frugivore (consumers of fruits and insects but one of them as primary item in the diet, respectively), carnivore–insectivore, and nectarivore–insectivore–frugivore. Since most Neotropical bat species might show a vertical stratification in their abundances (Kalko & Handley 2001) and our nets did not sample the forest canopy, we are aware that the reported data may represent a biased portrait more in abundance than in species richness of the bat assemblages present in the area.

Census of vegetation

During the first year of work, censuses of the forest vegetation were conducted in the first subset of eight forest islands that met the conditions of the experimental design. In each site we counted all trees ≥ 15 cm in dbh and identified each to species in three circular plots (radius = 15 m) covering 707 m² each. Average abundance values for all tree species in the plots and for some species known to be a principal source of fruits to Mesoamerican bats (*Manilkara zapota* (Sapotaceae) and *Ficus* spp. (Moraceae); Fleming 1981, Galíndo-González 1998, Vázquez-Yañes *et al.* 1975) were compared among types of forest island (large, small, far, near). Such comparison was done using a one-way ANOVA adjusting on the data a log-linear model with Poisson error in GLIM (see below).

Data analysis

The completeness of the bat inventory in forest islands, was assessed fitting models of species-accumulation functions (i.e. exponential, Clench and logarithmic models; Díaz-Francés & Gorostiza 2002, Díaz-Francés & Soberón 2005, Soberón & Llorente 1993) on the observed data. For this analysis, we generated the smoothed species-accumulation curve with the observed number of species in the pooled samples (netting nights) (S_{obs} –Mao Tau; Colwell *et al.* 2004) and did the statistical estimation with the Species Accumulation Functions software (<http://cimat.mx/info.php?m=1&ind=5>). This software uses the likelihood ratios between candidate models to select the best model for a given data set and calculates additionally, the total number of species

(TNS) for the best model that reaches an asymptote (Díaz-Francés & Soberón 2005).

Species richness of bat assemblage was compared among the four types of forest island (all sites $n = 16$), using the sample-based rarefaction curves with their 95% confidence intervals (Colwell *et al.* 2004, Mao *et al.* 2005) calculated for each case. The estimated values of such interpolation per type of forest island were obtained using the EstimateS software package (version 7.5; <http://viceroy.eeb.uconn.edu/estimates>). Statistical differences among types of forest island (large, small, far and near) were established when the confidence intervals of each rarefaction curve did not overlap with another from a different curve at a fixed sampling size (i.e. the minimum number of individuals from the four types of forest island). Effects of habitat-island, season and year on bat diversity, were evaluated using a repeated-measures ANOVA (ANOVAR, Zar 1996) with three factors: one factor (type of forest island) as the factor among sites and two factors (season and year) as the repeated measures within sites. For this analysis, we used a subset of eight sites that met the conditions of the experimental design with standardized sampling effort (200 net-hours per site per season) for the first and second annual cycle. In this case, the response variable was the Shannon's Diversity Index (H' using natural logarithms) calculated on the basis of the number of individuals of each species captured per site during each season (two instances per season). Under this mixed ANOVAR we adjusted on the data a generalized linear model with normal error (GLIM statistical package; Francis *et al.* 1993). Bat assemblage beta diversity was inferred using Sørensen's index of similarity (Baev & Penev 1995, Moreno 2001).

Using the same subset of eight forest islands and the same ANOVAR design, we also evaluated (1) the effects of habitat-island, season and year on bat foraging guilds (abundance of individuals for all species in a given guild) and (2) the effect of habitat-island and season on the number of bat recaptures from the same and different sites. In both cases, we adjusted on the data (number of individuals per site) a log-linear model with error Poisson in GLIM (Crawley 1993). Since Student's t-test cannot be used for multiple comparisons when several type errors are involved in the analysis (Crawley 1993), multiple comparisons among types of forest island were done removing, one at a time, each of the four levels of the factor habitat-island (i.e. large, small, far and near) from the model, and then tested the significance of the factor under the same ANOVAR design in GLIM. To test for differences in bat recaptures by sex, we ran a paired t-test (Zar 1996) on the percentages (arcsine transformed) of males and females recaptured per species. Bat movements among the forest islands investigated were assessed using ArcView GIS (version 3.1) in which the geographical locations of

Table 1. Species of bats and individuals captured in large (> 20 ha) small (< 5 ha) far (> 10 km) and near (< 1 km) forest islands during the 41-mo period (April 2000–August 2004). NS = Number of sites where the species was recorded. Also shown is the total sampling effort completed, including netting nights with no bat captures (*). Family code: 1 = Emballonuridae; 2 = Noctilionidae; 3 = Mormoopidae; 4 = Phyllostomidae; 5 = Natalidae; 6 = Molossidae. The acronym in parenthesis identifies each species. Foraging guild code (FG): 1 = frugivore–insectivore; 2 = frugivore; 3 = insectivore; 4 = insectivore–frugivore; 5 = nectarivore–insectivore–frugivore; 6 = carnivore–insectivore; 7 = sanguinivore.

Bat species	Type of forest island				Total	NS	FG
	Large	Small	Far	Near			
<i>Artibeus jamaicensis</i> Allen (AJ) ⁴	161	43	78	30	312	16	1
<i>Dermanura phaeotis</i> Miller (DP) ⁴	152	41	38	51	282	16	1
<i>Artibeus intermedius</i> Allen (AI) ⁴	123	32	65	32	252	16	1
<i>Glossophaga soricina</i> Webster & Jones (GS) ⁴	70	4	2	18	94	12	5
<i>Noctilio leporinus</i> Vahl (NL) ²	31	0	20	0	51	2	6
<i>Chiroderma villosum</i> Allen (CV) ⁴	28	3	1	3	35	9	2
<i>Sturnira lilium</i> Goldman (SL) ⁴	15	6	4	1	26	10	2
<i>Pteronotus parnelli</i> Smith (PP) ³	9	3	5	2	19	7	3
<i>Artibeus lituratus</i> Allen (AL) ⁴	7	6	1	3	17	8	1
<i>Micronycteris megalotis</i> Gray (MM) ⁴	8	0	9	0	17	4	4
<i>Molossus rufus</i> Geoffroy St.-Hilaire (MR) ⁶	9	0	0	0	9	4	3
<i>Natalus stramineus</i> Dalquest & Hall (NS) ⁵	3	1	0	1	5	4	3
<i>Centurio senex</i> Gray (CS) ⁴	4	0	0	0	4	2	2
<i>Mormoops megalophylla</i> Peters (MME) ³	3	0	1	0	4	3	3
<i>Saccopterix bilineata</i> Temminck (SB) ¹	3	0	1	0	4	2	3
<i>Nyctinomops laticaudatus</i> Miller (NLA) ⁶	1	1	0	0	2	6	4
<i>Diaemus youngi</i> Thomas (DY) ⁴	1	0	0	0	1	1	7
Total	628	140	225	141	1134		
Number of species	17	10	12	9	17		
Number of sites	4	4	4	4	16		
Number of netting nights	66 (5)	46 (11)	66 (15)	47 (9)	225 (40)		
Number of net-hours	4480	2781	3835	2904	14000		

original and recapture sites were used to estimate the straight-line distances traversed by bats.

RESULTS

Species richness

Sampling effort resulted in an accumulation of 14 000 net-hours (225 nights of sampling; mean = 62.2 net-hours per night) and in the capture of 1134 bats in the 16 forest islands investigated (Table 1). We recorded a total of 17 bat species representing six families (Emballonuridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae and Phyllostomidae) (Table 1). The Phyllostomidae were the best represented with 10 species, while the others were represented by only one or two species. Eighty-two per cent of the species were recorded in the first 12 nights of sampling. The rest (*Mormoops megalophylla*, *Diaemus youngi* and *Nyctinomops laticaudatus*) were captured after 91 sampling nights. The asymptote reached in the cumulative species curve indicated that we recorded most of the species present in the study area (Figure 1a). The best-fitting model to our observed species-accumulation data was the exponential model (fitted parameters $a = 0.71$, $b = 0.03$; correlation

of errors $\rho = 0.99$; likelihood ratio = 1) followed by the Clench model (fitted parameters $a = 1.06$, $b = 0.05$; correlation of errors $\rho = 0.99$; likelihood ratio < 1). On the base of the exponential model, no more than 18 bat species can be expected in the petenes landscape (Figure 1a).

The abundance–diversity curve showed three types of bat species: abundant species (> 250 individuals; $n = 3$), moderately abundant species ($\geq 17 \leq 94$ individuals; $n = 7$), and rare species (≤ 9 individuals; $n = 7$) (Figure 1b). The number of sites in which a species was present was associated to the species' relative abundance rank ($r = 0.86$, $P < 0.001$); 29% of the species were present in ≥ 10 forest islands, 24% in 6–9 forest islands and 47% in < 5 sites (Table 1). The most abundant species in the total sample were *Artibeus jamaicensis*, *Dermanura phaeotis* and *A. intermedius*, which together accounted for 75% of all bats captured. The remaining 25% was represented by the other 14 species (Figure 1b and Table 1). Rarefaction curves and their confidence intervals showed that for a sample of 140 individuals (total captured in small forest islands), the bat species richness was similar among the four types of forest island investigated. However, the abundance of bats was clearly greater in large than in small forest islands and in far than in near forest islands (Figure 2).

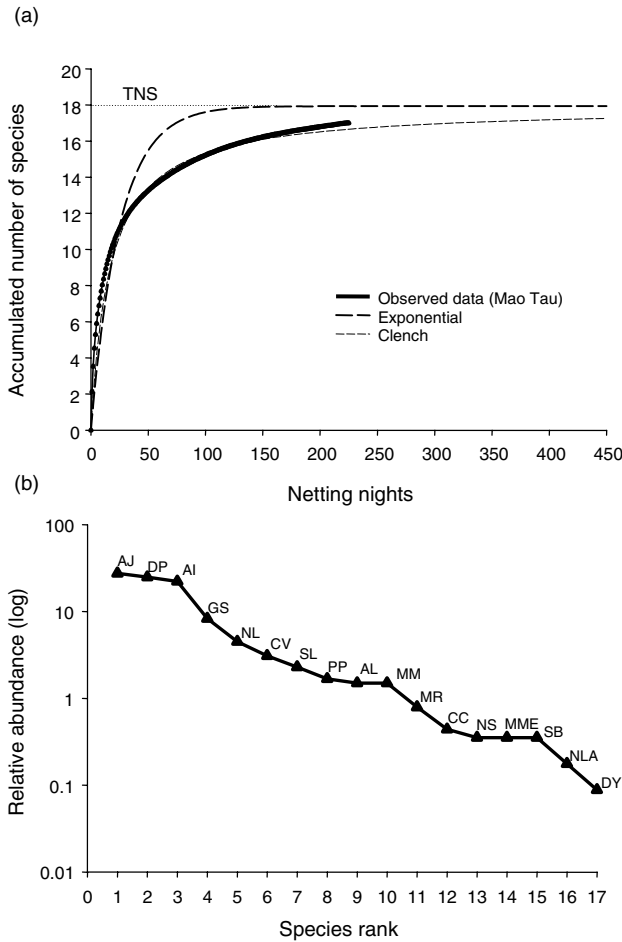


Figure 1. (a) Species-accumulation curves for the bat assemblages sampled in the petenes ecosystem. Shown is the smoothed species-accumulation curve with the observed number of species in the pooled samples (netting nights) from the 3.5-y sampling period ($n=225$ netting nights) (continuous line), the fitted curve to the exponential model (best fitted model), the fitted curve to the Clench model and the total number of species (TNS) expected for the exponential model. The last two curves were extrapolated to a duplicated sampling effort. (b) Abundance-diversity curve for bats sampled in the forest islands studied. Species codes match those in Table 1.

Diversity of bat assemblages

The ANOVAR showed that bat diversity (average Shannon’s index H') was similar ($P > 0.05$) among types of forest island (large = 1.48, small = 0.92, far = 1.11 and near = 0.87; $F_{3,3} = 4.57$), seasons (rainy season = 1.22 and dry season = 0.97; $F_{1,4} = 4.1$) and years (1.27 and 0.92 the first and the second year of sampling, respectively; $F_{1,4} = 2.6$). However, the only significant interaction was between type of forest island and season ($F_{3,4} = 7.58$, $P < 0.05$). Only bat diversity of small forest islands was higher in the rainy than in the dry season (average Shannon’s index $H' = 1.54$ and 0.31; respectively). The values of the Sørensen’s index of

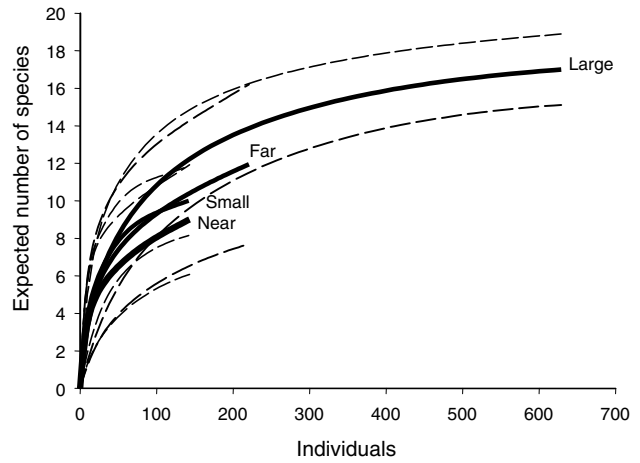


Figure 2. Rarefaction curves with 95% confidence intervals for the four types of forest island investigated. Comparisons among types of forest island were made at $n = 140$.

similarity showed low bat beta diversity among forest islands (large vs. small = 0.80, large vs. far = 0.70, large vs. near = 0.77; small vs. far = 0.66; small vs. near = 0.87, far vs. near = 0.62). On average, 70% of the species were common among most of the different types of forest island studied.

Foraging guilds

Classification of bats into foraging guilds showed 41% of species in the insectivore guild, 41% in the frugivore or frugivore-insectivore, 6% in the nectarivore-insectivore-frugivore, and 12% fitted in the carnivore-insectivore or sanguinivore guilds (Table 1). Fruit-eating bats (consuming fruits as primary items in their diets) were the most common, accounting for 78–93% of individual captures in each type of forest island. Focusing on this guild, the log-linear ANOVAR in GLIM showed that abundance of fruit-eating bats was different among forest islands ($\chi^2 = 76.6$, $df = 3$, $P < 0.001$), between seasons ($\chi^2 = 80.4$, $P < 0.001$) and between years ($\chi^2 = 26.8$, $P < 0.001$). The same analysis showed that fruit-eating bat abundance was different between seasons in relation to type of forest island ($\chi^2 = 35.5$, $df = 3$, $P < 0.001$). Thus, mean ($\pm SE$) number of fruit-eating bats captured (individuals per 200 net-hours) was greater in large ($n = 19 \pm 4.8$ individuals) and in small ($n = 12 \pm 4.1$), than in forest islands in the far or near categories ($n = 7 \pm 1.6$ and 5 ± 1.2 individuals, respectively). Similarly, bats in this guild were more abundant in the rainy ($n = 16 \pm 3$) than in the dry season ($n = 6 \pm 1$), and were also more abundant in the first of the two annual cycles examined ($n = 14 \pm 2.6$ and 8 ± 2.4 individuals, respectively). Only in large and small forest

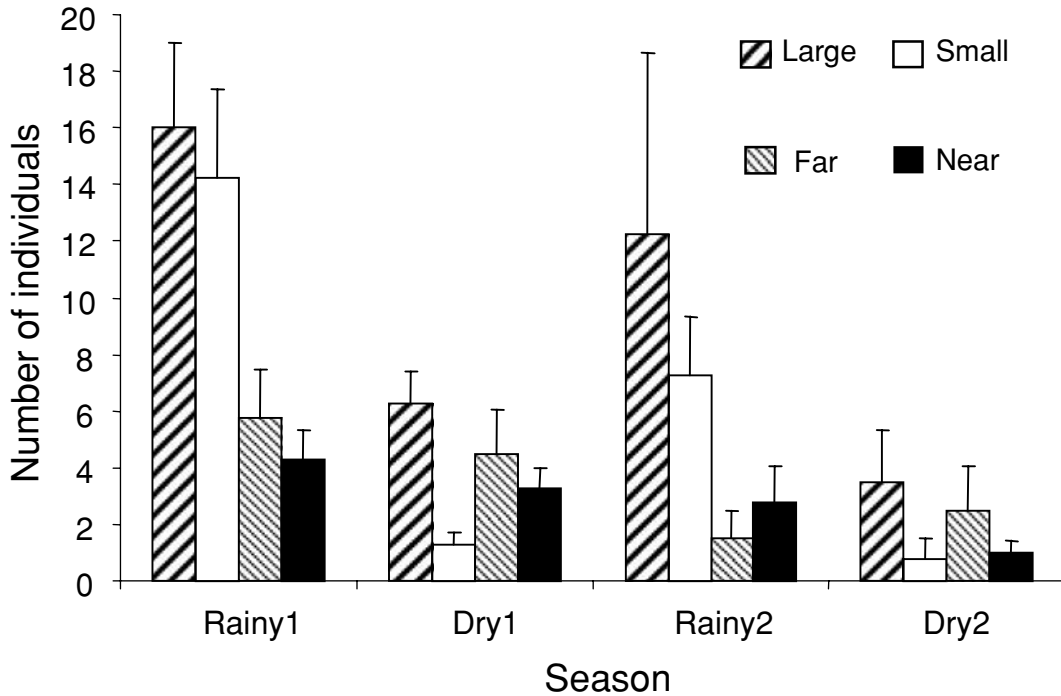


Figure 3. Mean abundances for fruit-eating bats in a subset of eight forest islands with standardized sampling effort (n = 200 net-hours × site × season) for each rainy and dry season in two consecutive annual cycles (August 2001–July 2003).

islands fruit-eating bats were notably more abundant in both annual cycles and in the rainy (n = 28 and 21) than in the dry season (n = 10 and 2 individuals) (Figure 3).

Vegetation census showed that the density of the tree species *M. zapota* was different among forest island categories (log-linear one-way ANOVA, $\chi^2 = 15.1$, $df = 3$, $P < 0.05$; Table 2). Mean (\pm SE) and density of this tree species was significantly lower in forest islands in the far category than in those in the large, small and near categories (Table 2). The latter three were not significantly different from one another (log-linear one-way ANOVA, $\chi^2 = 1.94$, $df = 2$, $P > 0.05$). In the case of *Ficus* spp. no significant differences were evident among the forest island categories (Table 2).

Recaptures

We recaptured 126 bats of eight species during the study (Table 3). Fruit-eating bats such as *D. phaeotis*, *A. jamaicensis* and *A. intermedius* accounted for 94% of the recaptures. The rest was accounted for by another five species, but recaptures for these were three individuals or fewer. Relative abundance was positively associated with bat species recaptures ($r = 0.76$, $P < 0.05$). No statistical differences were evident in the proportions of males and females recaptures from the eight species ($t = 0.33$, $df = 7$, $P > 0.05$).

Seventy-two per cent of recaptured bats were within-site recaptures and the remaining 28% were of bats that had been banded at a different site. The latter group (78%

Table 2. Mean (\pm SE) density of tree species in the vegetation plots in the forest islands investigated. Also shown are the Chi-square values ($\alpha = 0.05$) obtained from the log-linear one-way ANOVA for each comparison. All trees > 15 cm in dbh were measured in three circular plots (15 m radius) in each of eight forest islands within the categories of small, large, near and far. *Manilkara zapota* and *Ficus* spp. were examined separately as the fruits of these species are known to be an important source of food to fruit-eating bats.

Trees	Type of forest island				χ^2	P
	Large	Small	Far	Near		
All species	552 ± 75	852 ± 104	874 ± 190	940 ± 123	5.9	n.s
<i>Manilkara zapota</i>	106 ± 32	217 ± 45	40 ± 18	165 ± 28	18.3	< 0.05
<i>Ficus</i> spp.	52 ± 15	14 ± 12	12 ± 8	17 ± 9	6.1	n.s

Table 3. Number of adult male and female bats recaptured in the forest islands during the study period. Also shown are the estimated mean distances traversed between forest islands by recaptured bats.

Species	Males	Females	Total of recaptures	Inter site recaptures (males/females)	Mean (range) distance (km)
<i>Dermanura phaeotis</i>	51	24	75	29 (21/8)	1.79 (0.65–4.66)
<i>Artibeus jamaicensis</i>	20	4	24	2 (2/0)	2.89 (1.13–4.66)
<i>Artibeus intermedius</i>	15	4	19	3 (2/1)	15.11(0.65–38.28)
<i>Chiroderma villosum</i>	2	1	3	–	–
<i>Noctilio leporinus</i>	2	0	2	–	–
<i>Centurio senex</i>	1	0	1	1 (1/0)	4.66
<i>Sturnira lilium</i>	0	1	1	–	–
<i>Micronycteris megalotis</i>	0	1	1	–	–
Total	91	35	126	35 (26/9)	–

and 22% male and female bats, respectively) indicated minimum and maximum distances traversed through the natural grassland of 0.65 (*D. phaeotis*) to 38.28 km (*A. intermedius*). About 74% of these movements were between forest islands located at distances exceeding 3.0 km. Recapture data indicated that mean distance traversed by bats between forest islands was higher for individuals of *A. intermedius* (15.11 km) than for individuals of *Centurio senex*, *A. jamaicensis* and *D. phaeotis* (< 5 km in all three cases) (Table 3).

The log-linear ANOVAR in GLIM showed that number of recaptures was significantly different ($P < 0.05$) only among types of forest island ($\chi^2 = 58.1$, $df = 3$) and types of recapture (within and among forest islands) ($\chi^2 = 10.2$). No significant influence of season was detected on the probability of bat recaptures ($\chi^2 = 1.4$, $P > 0.05$). Interactions of second and third order among factors in the model were not significant. A larger average number of recaptures was found in the large ($n = 5.3$ recaptures) than in the small ($n = 1.2$), far ($n = 1.7$) and near ($n = 0.12$) forest islands. On average we recaptured more individuals from the same site ($n = 2.9$ recaptures) than from different sites ($n = 1.3$ recaptures). No influence of season was detected in the recaptures ($\chi^2 = 1.4$, $P > 0.05$).

DISCUSSION

Our study showed the existence of a moderately rich bat community ($n = 17$ species) inhabiting the naturally fragmented petenes landscape. After 225 sampling nights, the best predictor of species accumulation (exponential model) indicates that only one bat species is missing in our inventory (even duplicating the sampling effort done in this study). Thus, the bat community in the petenes landscape includes, at least, 56% of species occurring in the north sector of the Yucatan Peninsula ($n = 32$ species for the Yucatan state; Arita 1997). However, the fact that only a moderately rich bat species assemblage was detected in the forest island matrix,

suggest that other species may not be able to persist in the naturally fragmented landscape.

The abundance–diversity curve showed that the bat assemblages in the forest islands were strongly dominated by a few species (*A. intermedius*, *A. jamaicensis* and *D. phaeotis*). Similar profiles for abundance–diversity curves for bat species assemblages in human fragmented landscapes have been reported in other localities in south-east Mexico (Estrada *et al.* 1993a, b; Moreno & Halffter 2000) and in other parts of the Neotropics (Bernard & Fenton 2002, Brosset *et al.* 1996, Granjon *et al.* 1996). Data also indicated that forest island size had not had a significant effect upon the richness of bat assemblages. Similarly, in human-fragmented landscapes no effects of area on species richness were detected for bat assemblages. Instead, in such landscapes isolating distance was the variable more strongly associated to richness of bat species assemblages (Estrada *et al.* 1993a, b).

Several studies have documented high species richness in large (> 10 ha) man-made forest fragments and in heterogeneous human-modified landscapes (forest patches and various types of agroecosystems) in other Neotropical localities. In these systems bat assemblages are strongly dominated by species such as *Artibeus* spp., *Dermanura* spp., *Glossophaga soricina*, *Sturnira lilium* and *Pteronotus parnelli* (Aguirre *et al.* 2003, Bernard & Fenton 2003, Estrada & Coates-Estrada 2001, 2002; Estrada *et al.* 1993a, b). These bat species are fast fliers and have been reported to forage in or above the canopy and in open spaces (Brosset *et al.* 1996). Our data showed that these bat species also dominated bat species assemblages in the petenes landscape. It is likely that the generalized habitat requirements coupled to the preference by these bat species for edges and/or habitats more open than those offered by the interior of the forest, may explain their predominance and possible ecological success in the petenes landscape of the Yucatan Peninsula.

In the petenes forest islands the relationship between functional (the specific mobility of the organism; Tischendorf & Fahrig 2000) and structural (the spatial arrangements and orientation of landscape

components; Murphy & Lovett-Doust 2004, Ricketts 2001) connectivity, rather than distance effects alone (Moilanen & Neimeien 2002), probably explains the richness and persistence of the bat assemblages that exist there. Our results suggest a low bat species turnover among forest islands, each of which shared at least 70% of the species recorded. The close vicinity of other forest islands may result in continuous visitation by bats to these sites to secure resources or to use them in a stepping stone fashion to reach other forest islands. Thus, even small or poor-quality forest islands may be valuable resources (foraging and roosting sites) for bats, as has also been reported for small forest fragments in human fragmented landscapes (Bernard & Fenton 2003, Estrada & Coates-Estrada 2002, Estrada *et al.* 1993a, b; Law *et al.* 1999).

Recapture data indicated that individuals of several bat species were traversing distances to reach other forest islands up to 38 km away (measured in a straight line). The majority of the distances among forest islands in the study area fell between 100 and 300 m, a feature that makes them very accessible to long-distance flying bats as well as to those with more restricted mobility. Bats may use forest islands as stopover sites in their movements across the landscape, as flyways, as foraging sites, and in the case of the large forest islands as potential sites for colonization and residency, thus avoiding saturation in the forest islands from which they originated (Estrada & Coates-Estrada 2001, Estrada *et al.* 1993a, b, 1994, 1997, 2000; Gascon *et al.* 1999, Lovett-Doust *et al.* 2003, Murphy & Lovett-Doust 2004, Taylor *et al.* 1993, Turner & Corlett 1996). Another study in a naturally fragmented landscape in Brazil reports that radio-tagged bats usually travelled distances of 2.2 km between sites and used areas from 65 to 530 ha (Bernard & Fenton 2003). In this scenario, bats were highly mobile and savannas did not appear to inhibit the movements of some species, suggesting the existence of a persistent biological flow among isolated forest fragments (Bernard & Fenton 2003). A similar proposition has been argued for bat responses to anthropogenically induced fragmentation of their habitat in other localities in Mesoamerica, where bats survive in the heterogeneous fragmented landscape by making use not only of isolated remnant forest patches, but also of patches of different types of agroforestry ecosystem (Estrada & Coates-Estrada 2002, Estrada *et al.* 1993a, b).

Season or year did not, in general, influence the diversity of bat species assemblages among the different types of forest islands investigated, probably the result of the high mobility of bats and of the relatively short distance among forest islands. These features may allow bats to overcome any spatial variation in the availability of preferred food resources. Yet, our data showed a greater density of *M. zapota* trees in small, large and in near than in far forest islands, a tree species that fruits during the

rainy season (June–November), possibly explaining the high abundance of fruit-eating bats captured in these three types of forest islands during the rainy season. The asynchronous nature of another important source of fruits to bats (*Ficus* spp.) found in the forest islands does not seem to explain the association between abundance of fruit-eating bats and seasons. The lower number of captures of fruit-eating bats during the second annual cycle of sampling may have been due to the impact of hurricane Isidore that went through the study area in September of 2002. We observed that the strong hurricane winds dislodged many fruits of *M. zapota* and of other tree species and also caused the fall of many trees.

While tolerance of bat species to forest fragmentation and loss may be related to the ability of individuals to traverse open areas to reach other forest fragments (Law *et al.* 1999, Schulze *et al.* 2000), large rates of emigration may result in higher mortality rates when populations may move into a dangerous matrix (Murphy & Lovett-Doust 2004). In the petenes landscape bats may be more exposed to predation as they leave the protective cover of the forest islands interior. Although we currently lack precise data, predation pressures upon bat populations in our study area may come from several nocturnal vertebrates such as *Didelphis virginianus*, *Philander opossum*, *Potos flavus*, *Falco rufigularis*, *Bubo virginianus* and *Ciccaba virgata*, usually observed by us in several of the study sites.

Our data showed that while the number of forest islands in which a species was present was associated to the species relative abundance, 55% of the species were present in less than five sites. This suggests the existence of a subset of species that may be more habitat-restricted and may display less mobility in the landscape. These may be forest-interior species such as gleaning insectivorous bats (e.g. *Natalus stramineus*, *M. megalophylla*), some fruit-eating bats (e.g. *C. senex*) (Bonaccorso 1979, Brosset *et al.* 1996, Fenton *et al.* 1992, Fleming 1982, Medellín & Gaona 1999), and possibly bats with more specialized feeding habits such as *Noctilio leporinus* (Schnitzler *et al.* 1994). Studies in human-fragmented landscapes in other Neotropical localities report that bat species most affected are those that depend on pristine forest habitat having also more restricted mobility (Aguirre *et al.* 2003, Bernard & Fenton 2003, Estrada *et al.* 1993a, b, 2002; Schulze *et al.* 2000).

Data from long-term monitoring of bat populations in heterogeneous landscapes consisting of forest fragments and agricultural areas in Los Tuxtlas, Mexico, indicate the existence of close to 85% of the species historically reported as well as continued breeding activity by > 70% of the species detected (n = 39) (see Estrada & Coates-Estrada 2001, 2002, Estrada *et al.* 1993a, b). In these circumstances, the high mobility of bats coupled to a strong resilience to environmental changes by many

species, especially in the fruit-eating guild, seems to explain, on an ecological time scale, their persistence in human-modified landscapes. In the petenes landscape where fragmentation has been a natural condition in geologic time, bat species assemblages seem to have responded in a similar fashion. However, in contrast to the human-fragmented landscape where landscape heterogeneity seems to be important in facilitating the persistence of bat species assemblages, in the naturally fragmented ecosystem of the petenes it is the homogeneous nature of the landscape that may have favoured the colonization and continued persistence of a moderately diverse assemblage of bat species.

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