

Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico

A. Estrada*, R. Coates-Estrada

Estación de Biología "Los Tuxtlas", Instituto de Biología-UNAM, Apdo 176, San Andrés Tuxtla, Veracruz, Mexico

Received 17 October 2000; received in revised form 11 April 2001; accepted 23 May 2001

Abstract

In order to document the responses of bats to destruction and fragmentation of their natural habitat and the value of different types of man-made vegetation for bat conservation in the Neotropics, bats were sampled with mist nets to compare species richness and species composition in a tract of continuous forest, forest fragments and a habitat-island consisting of a mosaic of forest and arboreal crops in Los Tuxtlas, southern Mexico. We captured 3835 bats representing 39 species: 76% were captured in continuous forest, 74% in the mosaic habitat and 87% in forest fragments. In the mosaic habitat we captured 43% of the total number of bats, 33% in the forest fragments and 24% in continuous forest. On average the habitats studied had 64% species in common. Evidence of continuous breeding activity was determined for a high number of species at the three habitats (> 70% lactating and 65% with embryos). A few bat species (*Carollia brevicauda*, *Pteronotus parnellii*, *Sturnira lilium*, *Artibeus jamaicensis*, *Dermanura phaeotis*, *Vampyroides caraccioli*, *Glossophaga soricina*, *Dermanuta toltecus*, *Cheoroniscus godmani*, *Platyrrhinus helleri*) dominated the sample, but their relative dominance varied among habitats. Recapture of bats provided evidence for inter-habitat movement. The co-occurrence of the three habitats helps conserve a diverse assemblage of bat species in the local landscape. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Chiroptera; Bat conservation; Forest fragmentation; Los Tuxtlas; Mexico; Neotropics

1. Introduction

Members of the order Chiroptera are of particular importance in Neotropical rainforests because they constitute about 40–50% of mammal species, greatly influencing the species richness and diversity of mammals in these ecosystems (Fleming, 1988). Through the acquisition of food, in the form of plant and animal matter, bats participate in the recycling of nutrients and energy in the ecosystem (Fleming, 1982, 1988). In addition, a significant number of species consume nectar and great quantities of fruits (Bonaccorso and Gush, 1987). These bats act as pollen and seed dispersal agents for a broad spectrum of plant species, participating in the reproductive phenology of plants and rainforest regeneration (Heithaus et al., 1975; Heithaus, 1982; Fleming, 1988; Charles-Dominique, 1991; Medellín and Gaona, 1999). It has also been suggested that insectivorous bats

may regulate the populations of some invertebrates in tropical ecosystems (McNab, 1982; Kunz and Pierson, 1994).

It has been suggested that bat tolerance to habitat loss and fragmentation may be related to their ability to traverse open areas to reach other forest fragments or other vegetation types and to use resources within the matrix (Law et al., 1999; Schulze et al., 2000). However, the few available studies indicate that, in spite of their mobility and slow demographic turn-over, Neotropical bats seem to be sensitive to loss and fragmentation of their natural habitat, locally undergoing decreases in species diversity and size of populations (Gallard et al., 1989; Estrada et al., 1993a; Brosset et al., 1996; Granjou et al., 1996; Schulze et al., 2000).

Very little data are available in the literature regarding the response by bats to destruction and fragmentation of their natural habitat and on the value of different spatial arrangements of remnant forests and man-made vegetation for bat persistence in modified Neotropical landscapes (Estrada et al., 1993a; Brosset et al., 1996; Schulze et al., 2000; Estrada and Coates-Estrada, 2001).

* Corresponding author. Tel.: +52-294-24668; fax: +52-294-24668.

E-mail address: aestrada@primatesmx.com (A. Estrada).

To redress this, here we describe aspects of community species composition and relative abundance for the bat fauna present in a continuous tract of pristine lowland rainforest, in a cluster of forest fragments and in an agricultural man-made mosaic of vegetation. These habitats form part of a landscape located in the north-eastern section of Los Tuxtlas region, Veracruz, Mexico. We attempt to infer what kind of landscape scenarios and mosaics might sustain maximum diversity and minimum species loss.

2. Methods

2.1. Study area

The tropical rainforest of Los Tuxtlas, in south-eastern Veracruz, Mexico, represents the northern limit of lowland rainforest on the American continent. Bat diversity in these forests is high with about 50 species reported (Coates-Estrada and Estrada, 1986). Human activity has converted approximately 75% of the original forest surface (2500 km²) to pastures, 20% exists as dispersed clusters of forest fragments in the lowlands, and 5% is still preserved as extensive forest mainly at elevations >800 m.a.s.l. (Estrada and Coates-Estrada, 1996). Weather monitoring stations indicate a mean annual temperature of 27 °C (range 20–28 °C), an average annual rainfall of 4900 mm but from March to May average monthly rainfall is $112 \pm \text{S.D. } 12$ mm and from June to February this average is $486 \pm \text{S.D. } 87$ mm.

2.2. Study habitats

The continuous tract of pristine lowland rainforest comprises the 700 ha forest of the “Los Tuxtlas” Biological Research Station of UNAM (95° 00' W, 18° 25' N) and this is connected to about 3500 ha of pristine rainforest that forms part of the Los Tuxtlas Biosphere Reserve (Fig. 1).

The original lowland rainforest immediately north of the continuous forest has been gradually converted to pasture lands between 1960–1970, but clusters of forest fragments remain in a 126 km² area. Sixteen of these forest fragments were selected randomly to sample the bat community (Fig. 1). Average area of these sites was 13 ha (range 1–80 ha) and total accumulated area of these fragments was 240 ha.

The mosaic of forest and fruit-productive man-made vegetation was located about 1.2 km north of the research station and about 0.5–1.2 km west from the cluster of forest fragments mentioned above. The mosaic habitat is an “island” of vegetation about 250 ha in size, surrounded by pastures. It consists of remnant rainforest and interdigitated 20–25 year-old stands of coffee and cacao shaded by rainforest trees and of citrus

and banana groves as well as patches of pineapple, avocado and papaya trees (Fig. 1).

2.3. Bat sampling

Between 1997 and 1999 bats were sampled in 16 locations within 250 ha of the continuous forest site, in one location within each of the 16 forest fragments and in 16 locations within the mosaic of agricultural vegetation. In the latter habitats four sampling locations were in forest and three locations were in each of the major agricultural habitats (coffee, cacao, citrus and banana) present. Distance among sampling locations in the continuous forest and mosaic habitat ranged from 500 to 1000 m.

Bats were sampled three times (February–March, May–June, September–October) over the 3 years at each sampling location in the continuous forest and in the mosaic habitat for a total of 288 nights. At each location we set up a line of 15 mist nets (12 m long × 3 m high) running sinuously through the site. We operated the nets for two consecutive nights at each location from 19:00 to 24:00 h on non-rainy and moonless nights. We checked the nets every 45 min. Each bat captured was identified to species, sexed, weighed (to the nearest 0.5g), measured (forearm length), classified as adult or non-adult, marked and released. Adult



Fig. 1. Study sites in the north-eastern region of Los Tuxtlas in southern Veracruz, Mexico. The continuous forest site (about 4000 ha), partly shown, is the shaded area at the bottom of figure. Forest fragments, to the right of the figure, shown in dark. Mosaic habitat is the lighter shaded area to the left of the figure. In this habitat, cacao and coffee groves shaded by forest trees are shown as gray rectangles. Open squares are citrus and banana groves. The broken line is a dirt road and continuous lines indicate streams. White areas are pastures.

females were examined to determine if they were lactating (lactating females usually had enlarged mammary glands and in some cases milk secretion was evident during palpation of glands) and their abdominal area was palpated to assess presence of larger embryos (Fleming et al., 1972). Each bat was marked with a coloured and numbered plastic colour band (National Tag Co. TN, USA) placed on the forearm and the bat released at the site of capture. Since we only sampled one level of the habitats studied during part of the night and because species of bats may be caught unequally by mist nets, we are aware that the reported data may represent a biased portrait of the bat community present in the area. Taxonomic nomenclature for bats followed Hall (1981) and Ramírez-Pulido et al. (1996). We assigned each bat to one of six general foraging guilds according to information reported by Bonaccorso (1979), Coates-Estrada and Estrada (1986), Charles-Dominique (1991), Fleming (1988), Gardner (1977), Sazima (1976) and Nowak (1994). These guilds were insectivore, frugivore-insectivore, frugivore, nectarivore-insectivore-frugivore, sanguinivore and carnivore-insectivore.

2.4. Data analysis

Since sampling effort (number of nets, netting nights, net hours and total net length) was the same across sampling locations and habitats, we compared bat and species counts across vegetation types using totals, averages and percentages. Rarefaction curves were used to compare species richness among habitats. This statistical method estimates the number of species that can be expected in a sample of n individuals (denoted by $E(S_n)$) drawn from a population of N total individuals distributed among S species (Ludwig and Reynolds, 1988). Published data on bat species richness documented at isolated plantations and at corridors of residual forest vegetation and at live fences (live posts of *Bursera simaruba*, Burseraceae, used by ranchers to hold barbed wire) were included here for comparative purposes (Estrada and Coates-Estrada, 2001). Shannon's diversity index (H') was used to compare habitats in species diversity. Sorensen's index of similarity was used to compare similarity in species assemblages among habitats (Ludwig and Reynolds, 1988). Non-parametric tests were used for statistical comparisons (Fitch, 1992).

3. Results

3.1. General aspects

A total of 3835 bats representing 39 species were captured. Seventy-six percent of the species were captured in the continuous forest habitat, 74% in the mosaic habitat and 87% in the forest fragments. The largest

proportion of bats were captured at the mosaic habitat (43%), while 33 and 24% were captured at the forest fragments and continuous forest habitats respectively (Table 1). The mean number of bats captured per location at the three habitats was 56.3 (± 11.4) for the continuous forest, 78.1 (± 23.6) for the forest fragments and 105.2 (± 12.9) for the mosaic habitat. These differences were significant only between the mosaic and the forest fragments ($z = -2.58$, $P = 0.004$) and between the mosaic and the continuous forest ($z = -3.25$, $P = 0.001$). The mean number of species captured per location at the three habitats were 10.2 (± 1.2) in the continuous forest, 10.0 (± 0.8) in the forest fragments, and 14.0 (± 1.0) in the mosaic habitat. The differences between the mosaic and continuous forest and between the mosaic and the forest fragments were significant ($z = -2.72$, $P = 0.003$ and $z = -3.05$, $P = 0.001$).

3.2. Species diversity, species richness and species overlap among habitats

Species diversity, measured by Shannon's function (H'), was 2.3 in the continuous forest, 2.3 in the forest fragments and 2.5 in the mosaic habitat. Rarefaction analysis showed that at $n = 500$, the continuous forest was the richest habitat in accumulated species, followed by the forest fragments and the mosaic habitat. The same analysis showed that the mosaic habitat was richer in species than isolated arboreal plantations and linear strips of vegetation in the same landscape (Fig. 2).

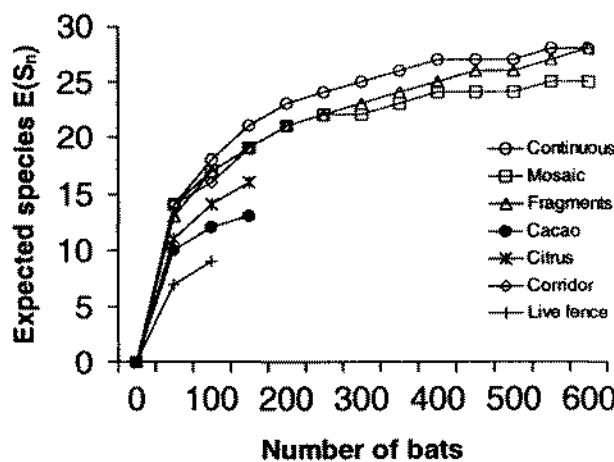


Fig. 2. Rarefaction curves for the three habitats investigated. $E(S_n)$ refers to the number of species that can be expected in a sample of n individuals drawn from a population of N total individuals distributed among S species. For comparative purposes we also show data from other studies (Estrada et al., 1993a; Estrada and Coates-Estrada, 2001) on bat species richness for an isolated cacao and citrus plantation, for a corridor of residual forest vegetation along the sides of a stream and for a linear strip of live posts of *Bursera simaruba* (Burseraceae), also sampled in the area. Comparison for the three habitats reported in this study were made at $n = 500$. Comparison for all habitats made at $n = 150$.

Kendall's rank coefficient calculated between the overall abundance rank of each species and their abundance rank in each habitat indicated that bat assemblages were similarly structured (continuous forest $r_t=0.79$, $P<0.001$; mosaic $r_t=0.93$, $P<0.001$; forest fragments $r_t=0.79$, $P<0.001$). However, a comparison between habitats showed that the continuous forest and forest fragments were more similar in species abundance ranking ($r_t=0.79$, $P<0.001$) than the continuous forest and mosaic habitat ($r_t=0.62$, $P<0.001$) and than the mosaic and forest fragments ($r_t=0.63$, $P<0.001$).

The number of common species between pairs of habitats ranged from 23 (continuous and mosaic) to 26 (mosaic and forest fragments). On average the habitats

studied had 25 species in common or 64% of all species detected ($N=39$). Sorensen's index of similarity was 0.79 for the continuous forest-mosaic habitats and had the same value for the continuous forest-forest fragments habitats. The index had a value of 0.85 for the mosaic-forest fragments habitats. The average value of the index among all habitats was 0.81.

3.3. Distribution of captured bats by sex and age among habitats

Forty-six percent of the captured bats were males and 54% females, 85% were adults and 15% non adults. The proportion of captured females was 51% for the

Table 1
Species captured at the three habitats investigated*

Species	Continuous forest	Mosaic habitat	Forest fragments	Total	Average mass g	Feeding guild
<i>Carollia brevicauda</i>	309	292	200	801	18.5	FRIN
<i>Pteronotus parnellii</i>	9	222	421	652	44.1	IN
<i>Sturnira lilium</i>	146	134	117	397	17.6	FR
<i>Artibeus jamaicensis</i>	85	166	72	323	46.1	FRIN
<i>Dermanura phaeotis</i>	93	153	52	298	13.9	FRIN
<i>Vampyroides caraccioli</i>	3	282	1	286	34.7	FR
<i>Glossophaga soricina</i>	38	67	64	169	10.9	NIFR
<i>Dermanura toltecus</i>	29	40	87	156	17.5	FRIN
<i>Choeronycteris godmani</i>	31	59	14	104	10.5	NIFR
<i>Platyrrhinus helleri</i>	19	63	20	102	17.4	FRIN
<i>Artibeus lituratus</i>	10	17	52	79	70.6	FRIN
<i>Desmodus rotundus</i>	17	37	17	71	38.2	S
<i>Carollia perspicillata</i>	23	19	17	59	19.5	FRIN
<i>Phyllostomus discolor</i>	7	30	14	51	36.4	NIFR
<i>Uroderma bilobatum</i>	8	20	10	38	21.9	FRIN
<i>Sturnira ludovici</i>	4	13	20	33	23.2	FR
<i>Vampyressa pusilla</i>	7	22	3	32	7.0	FRIN
<i>Moormops megalophylla</i>		4	24	28	15.8	IN
<i>Dermanura watsoni</i>	12	5	1	18	12.5	FRIN
<i>Chiroderma villosum</i>	6	1	9	16	34.3	FR
<i>Mimon bennettii</i>	15			15	26.2	FRIN
<i>Micronycteris brachyotis</i>	2	10	2	14	11.0	INFR
<i>Pteronotus davyi</i>		5	8	13	7.6	IN
<i>Saccopteryx bilineata</i>	3	6	3	12	7.3	IN
<i>Antrozous dubiaquercus</i>	6		5	11	16.9	IN
<i>Vampyrum spectrum</i>	2	8		10	110.7	CAIN
<i>Centurio senex</i>	5	2	1	8	20.0	FR
<i>Trachops cirrhosus</i>	7			7	41.4	CAIN
<i>Micronycteris megalotis</i>		3	2	5	9.5	INFR
<i>Natalus stramineus</i>			5	5	7.8	IN
<i>Thyroptera tricolor</i>	2		1	3	6.1	IN
<i>Diclidurus albus</i>	1		1	2	9.6	IN
<i>Hylonycteris underwoodi</i>		1	1	2	8.8	NIFR
<i>Leptonycteris nivalis</i>			2	2	32.0	NIFR
<i>Micronycteris sylvestris</i>			2	2	6.1	IN
<i>Myotis keaysi</i>		2		2	4.0	IN
<i>Noctilio leporinus</i>			2	2	18.0	CAIN
<i>Tonatia brasiliense</i>	2			2	6.1	IN
<i>Chrotopterus auritus</i>	1			1	125.0	CAIN
Total	902	1683	1250	3835		

* Also shown is the average body mass per species and the species' general feeding guild. FRIN fruit-eating insectivore, IN insectivore, FR frugivore, NIFR nectar-eating insectivore that also consumes fruit, S sanguinivore, CAIN carnivore-insectivore

continuous forest, 52% for the mosaic habitat and 58% for the forest fragments (Table 2). A comparison among habitats showed no significant differences between the continuous forest and the forest fragments in the number of females captured per location ($z=0.20$, $P=0.83$). However, significantly more females were captured in the mosaic habitat than in the continuous forest ($z=2.22$, $P=0.02$) and than in the forest fragments ($z=2.12$, $P=0.03$). The ratio of adults to non-adults was 1:0.19 in the continuous forest, 1:0.08 in the forest fragments and 1:0.23 in the mosaic habitat (Table 2). Evidence of lactation was present in 49% of adult females and 77% of the species captured in the continuous forest, in 59% of adult females and 70% of the species captured in the forest fragments and in 48% of adult females and 76% of the species captured in the mosaic habitat. Palpation for embryos gave positive results in 22% of adult females and 67% of species captured in the continuous forest, in 34% of adult females and 64% of species captured in the forest fragments and in 25% of adult females and 64% of species captured in the mosaic habitat.

3.4. Feeding guilds

In the continuous forest, fruit-eating insectivores and insectivores accounted for 86 and 3% of the bats captured, respectively. In the mosaic habitat these two guilds accounted for 73 and 15% of bats captured respectively. In contrast, in the forest fragments fruit-eating insectivores were represented by a lower proportion of individuals (53%), but insectivores were significantly more predominant (38%) than at the other two habitats. Less variation in proportion of individuals captured was evident in the case of the nectarivore-insectivore guild at the three habitats (Table 1). The only sanguivore species, *Desmodus rotundus*, was captured in the three habitats in similar proportions and the carnivore-insectivore species *Vampyrum spectrum* and *Chrotopterus auritus* were only captured in the continuous forest and mosaic habitat (Table 1).

3.5. Species ranking

The total sample was dominated by four species, *Carollia brevicauda*, *Pteronotus parnelli*, *Sturnira lilium* and *Artibeus jamaicensis* which accounted for slightly over 50% of the captures. Other common species were *Dermanura phaeotis*, *Vampyrodes caraccioli*, *Glossophaga soricina*, *Dermanura toltecus*, *Cheoroniscus godmani* and *Platyrrhinus helleri*, that together accounted for about 29% of captures (Table 1). However, the numerical ranking of these species varied from habitat to habitat. For example, *P. parnelli* was rarely captured in the continuous forest, but it was the first ranking species in the forest fragments and the third ranking in the

mosaic habitat. Another species, *V. caraccioli*, rarely captured in the continuous forest, was the second ranking species in the mosaic habitat, but it was also rarely captured in the forest fragments (Table 1).

Bat species overall abundance rank was correlated with the number of habitats in which a species was present ($r_s=0.80$, $P<0.0001$, $N=38$), but average body mass was not related to the number of habitats in which a species was present ($r_s=0.22$, $P=0.08$). Bat species average body mass, however, was found associated to bat species abundance rank in the forest fragments ($r_s=0.42$, $P=0.006$) and in the mosaic habitat ($r_s=0.33$, $P=0.04$), but not in the continuous forest ($r_s=0.04$, $P=0.41$).

3.6. Recaptures

During the study we recaptured 83 bats of 17 species. Within and inter-habitat recaptures contributed to 65 and 35% of individual recaptures, respectively. With respect to within-habitat recaptures, the mosaic habitat had the highest number of bat recaptures (42%) and the highest number of species represented in recaptures ($N=12$; Table 3). This habitat was followed by the continuous forest, with 14% of the recaptures and five species. The majority of between-habitat bat recaptures ($N=30$) were recorded between the mosaic and continuous forest (37%) and between the mosaic and forest

Table 2
Distribution of bat captures by age and sex class for the three habitats investigated^a

	Continuous forest	Mosaic habitat	Forest fragments	Total
Adults	757	1365	1154	3276
Non adults	145	318	96	559
Males	446	810	526	1782
Females	456	873	724	2053

^a Recaptures not included (see Table 3).

Table 3
Recaptures of bats indicating inter-habitat movements. The terms indicate the direction of the movement

Movement	Captures	Species
Continuous to continuous	12	5
Continuous to fragment	3	2
Continuous to mosaic	3	2
Fragment to fragment	7	3
Fragment to mosaic	3	2
Fragment to continuous	1	1
Mosaic to continuous	11	5
Mosaic to fragment	9	6
Mosaic to mosaic	34	12
Total	83	17

fragments (30%). In general, all combinations of between-habitat recaptures were recorded in our data and number of species involved ranged from 2 to 6 (Table 3). Among the species recorded in within-habitat recaptures ($N=15$), *C. brevicauda*, *P. parnellii*, *S. liliium* and *A. jamaicensis* accounted for 67% of recaptures. Ten bat species were recorded in the case of between-habitat recaptures of which *C. brevicauda*, *S. liliium* and *V. major* and *D. phaeotis* accounted for 66% of recaptures.

4. Discussion

4.1. General aspects

It may be assumed that because of their dispersal abilities Neotropical bats may be less vulnerable than other mammals to extensive deforestation and fragmentation of their habitats in the tropics (Estrada et al., 1994; Granjou et al., 1996; Offerman et al., 1996; Turner, 1996). The forest fragments and mosaic habitat were as rich in species as the continuous forest. Bats seem to display a strong preference for rainforest vegetation and may visit and/or reside in isolated forest fragments and may use those man-made habitats that most closely resemble the forest in vertical and horizontal complexity (Estrada et al., 1993a; Estrada and Coates-Estrada, 2001).

In the mosaic habitat the presence of forest tree species such as *Ficus* spp., *Brosimum alicastrum* (Moraceae), *Nectandra ambigens* (Lauraceae) and *Manilkara zapota*, *Pouteria campechiana* (Sapotaceae), among other species, preserved by farmers to provide shade for the cacao and coffee plants, are known to be important sources of food to bats (Vazquez-Yanes et al., 1975; Morrison, 1980; Fleming, 1988; Galetti and Morellato, 1994). Some of these trees may lend themselves for the establishment of roosting sites (AE personal observation) and many are laden with climbers, epiphytes, vines and lianas, contributing to high vertical and horizontal complexity of the vegetation. Such features may allow more bats and more bat species to co-occur in these habitats than at unshaded isolated plantations (Estrada et al., 1993a).

4.2. Species dominance and flexibility

While the majority of bat species were captured in low numbers, those species with the highest numerical representation in the total sample (e.g. *C. brevicauda*, *S. liliium*, *Artibeus* spp., *Dermanura* spp. and *G. soricina*) were also dominant in the mosaic habitat. These species are fast fliers and have been reported to forage in or above the canopy and in open spaces (Brosset et al., 1996). The fact that we caught many individuals of these species at net level suggests that these bats are capable

of using various strata of the vegetation. Such flexibility may allow them, in contrast to other bat species, to take advantage of the diversity of opportunities present in man-modified landscapes. Some other species may prevail under these conditions as a result of generalized habitat requirements or as a result of their preference for edges and/or habitats more open than those offered by the interior of continuous forest. For example, At Los Tuxtlas individuals of *P. parnellii* have been recaptured in forest fragments and in isolated man-made habitats located at distances of up to 2 km from the original site of capture (Estrada et al., 1993a; Estrada and Coates-Estrada, 2001), suggesting that these bats traverse long distances through open areas in the landscape.

The canopy frugivore species, *V. caraccioli*, with a few captures in the continuous forest and in the forest fragments, was the second most common species in the mosaic habitat. This species feeds on fruits of large canopy and sub-canopy trees and tends to prefer closed forest or creeks lined with closed forest (Bonaccorso, 1979; Morrison, 1980). The majority of captures of this species in the mosaic habitat were in the dense cacao and coffee groves and along the several creeks that cut across this site. Other fig specialists such as *A. jamaicensis*, common in our samples, have been documented to travel up to 10 km from day roosts to feeding sites (Fleming, 1982; Fenton et al., 1992) and it is possible that individuals of this species may include in their daily foraging range several forest fragments and patches of other vegetation types present in the landscape (Estrada et al., 1993a; Schulze et al., 2000).

The presence of high concentrations of plant species of the genera *Piper* and *Solanum* at the edges and interior of small forest fragments and at the edges and more open areas in the mosaic habitat, may benefit *Piper* specialists such as *Carollia* (Fleming, 1988) and *Solanum* specialists such as *Sturnira* (Marinho-Filho, 1991). These two frugivore species were numerically dominant in our samples and were captured in similar proportions in the three habitats investigated.

Nectarivorous species such as *G. soricina* may display similar generalized habitat requirements and amplitude of movements (Estrada et al., 1993a; Estrada and Coates-Estrada, 2001) and may also feed on insects, fruit pulp, and pollen (Bonaccorso, 1979; Fleming et al., 1972). These features may allow individuals of this species to take advantage of varied potential food resources in the various sub-habitats present within the mosaic habitat and in the cluster of isolated forest fragments present in the landscape (Brosset et al., 1996).

The capture of *V. spectrum*, a large bat that includes vertebrates in its diet (Norberg and Fenton, 1988), in the mosaic habitat contrasts with the reported absence of this bat outside of continuous forest in Tikal, Guatemala (Schulze et al., 2000). The rarity of these predators may suggest high sensitivity to fragmentation

of the forest, but captures of this bat species at the mosaic habitat suggests that this bat species may persist if some forest-type habitats are available in the landscape.

The only sanguinivore species, *D. rotundus*, was present in the three habitats studied. This species has been reported to be more common in second growth vegetation than in continuous forest in Panama (Bonaccorso, 1979). It is possible that the mosaic habitat may resemble, as a result of its highly variable vegetation structure and composition, second growth vegetation, and *D. rotundus* may use these habitats to roost and/or as stepping stones when searching for food in the pasture dominated landscape.

While some bat species may take advantage of available opportunities in the man-modified landscape, possibly a result of generalized habitat and/or feeding requirements and high mobility, other species may be less mobile or may have specialized habitat requirements making them unable to move to and use other habitats in the landscape. For example, 31% of the species were captured only in the continuous forest and/or in forest fragments. Most of these species were rare (≤ 15 captures) and also have specialized foraging requirements, feeding mostly on nectar (e.g. *L. nivalis*), small insects (e.g. *D. albus*) and small vertebrates (e.g. *T. cirrhosus*, *C. auritus*) and may display restricted mobility (Bonaccorso, 1979; Nowak, 1994, Kalko et al., 1999), features that may put them at risk (Brosset et al., 1996).

4.3. The mosaic habitat-island and forest fragments

The high number of bats and bat species captured at the mosaic habitat suggests that these environments are attractive to bats and may be suitable for bat sustenance and persistence. The high structural vertical diversity of the remaining forest and that of the forest that shades coffee and cacao groves coupled to the presence of different types of cultivated vegetation in this kind of habitat, may provide bats with varied food resources (insects, fruits, nectar, pollen) and potential roosting sites in foliage (e.g. *T. tricolor*, *U. bilobatum*) and tree cavities (e.g. *A. jamaicensis*, *N. leporinus*).

Individually, the forest fragments studied may be unsuitable for holding large populations of bats (average size of forest fragments was 13 ha), but collectively they may support, as a result of their close spatial proximity, a large bat population and a large array of bat species in the local landscape (Estrada et al., 1993a,b). Bats may reside in isolated forest fragments and the vicinity of other fragments 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 habitats. In this case even small or poor quality fragments may be a valuable resource for bats (Estrada and Coates-Estrada, 1993a; Law et al., 1999). However, the small size and spatial separation of rem-

nant forests may pressure bats to range more widely than usual, exerting strong demands on their time and energy budgets (MacClintock et al., 1977; Urban et al., 1988; Offerman et al., 1995; Hagan et al., 1996; Schulze et al., 2000). The fact that forest fragment to forest fragment recaptures accounted for 64% of recaptures in these habitats, suggests that individual bats are traveling variable distances across the open landscape and may be involved in higher expenditure of time and energy and in higher exposure to predators (e.g. bat falcons, owls) as they search for resources.

4.4. Breeding activity and tolerance to fragmentation

Data on bat flexibility to drastic reductions and fragmentation of their natural habitat may not be conclusive, unless evidence is available indicating continuous breeding activity in the remaining population occupying or using residual pockets of native and co-existing man-made vegetation. Our study showed that on average, about 50 and 27% of the adult females captured were lactating and/or gave positive results for embryo presence respectively, indicating continuous breeding activity. The large number of species involved in these cases (> 70 and 65%, respectively) suggests tolerance by many bat species to significant reductions in area and fragmentation of their natural habitats. Such tolerance may be the result of an ability to move through open spaces and through different types of vegetation to take advantage of opportunities present in man-modified landscapes (Laurance, 1991; Law et al., 1999).

It is evident from our study that a large number of bat species seem to have responded with some flexibility to the disappearance of rainforest habitat by using forest fragments and patches of man-made vegetation. However, the majority of the species seem to occur in low numbers, a trait that may put them at risk (Offerman et al., 1995; Brosset et al., 1996). Further, the observed lower proportion of non-adults in the forest fragments may suggest higher mortality of individuals in this age class in these habitats, probably resulting from poor dispersal or mobility. In contrast, the average ratio of adults to non-adults at the mosaic habitat more closely matched the one detected in the continuous forest.

The high number of within-habitat recaptures in the continuous forest and mosaic habitat may suggest a large resident population of bats in these habitats. The species richness detected in the mosaic habitat closely matched that of the continuous forest and 77% of the species captured in this latter habitat were also captured in the mosaic. Such richness was higher than the one detected by us in isolated plantations shaded by forest vegetation (Estrada et al., 1993a), in corridors of residual forest vegetation and in linear strips of vegetation (Estrada and Coates-Estrada, 2001).

4.5. General implications

Bearing in mind the limitations of our study (the use of ground-level nets, the few sites sampled and the few points in time sampled), our study suggests that conservation planning of isolated forest fragments in pasture-dominated landscapes is incomplete unless consideration is accrued also to assessing the conservation value of other types of man-introduced vegetation present in Neotropical landscapes. Some of these may be valuable in reducing isolating distances among forest fragments and between these and continuous forest. They may also provide habitat not only for generalist bat species, but also for those displaying more specialized ecological requirements (e.g. *L. nivalis*, *S. ludovici*, *V. spectrum*, *V. caraccioli*; Bocaccorso, 1979; Fleming et al., 1982; Brosset et al., 1996). Consistent with this idea, our study showed high number of bats and rich species pool in the mosaic habitat. It also showed that both small (e.g., the 4.0 g *Myotis keaysi*) and large (e.g. the 110 g *V. spectrum*) species, males and females, adults and non-adults and bats from five feeding guilds were present in this habitat. Our study also provided evidence of continuous reproductive activity and between-habitat movements by bats of several species present in the mosaic habitat, stressing the value of this kind of habitat for bat conservation.

Our results suggest that the preservation of landscapes containing clusters of forest fragments and islands of man-made arboreal vegetation or islands of managed forests may result in benefits to remnant bat populations such as increased area of vegetation, increased diversity of resources and habitats available and reduction of isolating distances among habitat islands. The presence of these habitats in the vicinity of continuous forest may support ecological sustainability (sensu Recher et al., 1987) by providing increased opportunities for bat persistence, reduced isolation, and facilitation of contact among conspecifics.

Scenarios such as the above would help sustain common, rare, generalist and specialist bat species, increasing the number of species preserved. Economic dividends resulting from the marketing of cash crops obtained from mosaic type habitats may help strengthen the subsistence economy of local inhabitants (Estrada and Coates-Estrada, 1996). Other added benefits derived from the presence of mosaic type habitats and the conservation of forest fragments may be soil, nutrient and water retention, as well as sources of wood, firewood and medicinal, ornamental and edible plants (Myers, 1988). Such benefits may outweigh the benefits obtained from turning fragmented landscapes into pastures (Saunders and de Rebeira, 1991; Pimentel et al., 1992; Lindenmayer and Nix, 1993; Turner and Corlett, 1996; Beier and Noss, 1998). Further important consequences resulting from preserving the remaining

bat populations would be the potential restoration of the forest via the seed and pollen dispersal services of fruit and nectar eating bats that move across such landscapes (Estrada et al., 1993b; Guevara and Laborde, 1993; Medellín and Ganoa, 1999).

Acknowledgements

Support provided by Universidad Nacional Autónoma de México. We are grateful to the late John Scott and Peg Scott for their encouragement and additional support. We also thank the three anonymous referees for helpful comments.

References

- Beier, R.I., Noss, R.F., 1988. Do habitat corridors provide connectivity? *Conservation Biology* 6, 1241–1252.
- Bocaccorso, F.J., Gush, T.J., 1987. An experimental study of feeding behavior and foraging strategies of phyllostomid fruit bats. *Journal of Animal Ecology* 56, 907–920.
- Bocaccorso, F.J., 1979. Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum, Biological Sciences* 24, 340–359.
- Brosset, A., Charles-Dominique, P., Cockie, A., Cosson, J.C., Masson, D., 1996. Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology* 74, 1974–1982.
- Charles-Dominique, P., 1991. Feeding strategy and activity budget of the frugivorous bat *Carollia perspicillata* (Chiroptera: Phyllostomidae) in French Guiana. *Journal of Tropical Ecology* 7, 243–256.
- Coates-Estrada, R., Estrada, A., 1986. *Manual de Identificación de Campo de los Mamíferos de la Estación de Biología "Los Tuxtlas"*. Instituto de Biología. Dirección General de Publicaciones, UNAM, México.
- Estrada, A., Coates-Estrada, R., 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas. *International Journal of Primatology* 5, 759–783.
- Estrada, A., Coates-Estrada, R., 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography* 24, 94–102.
- Estrada, A., Coates-Estrada, R., Meritt Jr., D., 1993a. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography* 16, 309–318.
- Estrada, A., Coates-Estrada, R., Meritt Jr., D., 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography* 17, 229–241.
- Estrada, A., Coates-Estrada, R., Meritt Jr., D., Montiel, S., Curiel, D., 1993b. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. In: Fleming, T.H., Estrada, A. (Eds.), *Frugivores and Seed dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Press, The Hague, pp. 245–257.
- Fenton, M.B., Acharva, L., Audent, D., Hickey, M.B.C., Merriman, C., Obrust, K., Syme, D.M., Adkins, B., 1992. Phyllostomid bats (Chiroptera, Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica* 24, 440–446.
- Fitch, R., 1992. *WinSTAT, The Statistics Program for Windows*. Kalmia, Cambridge, MA.
- Fleming, T.H., 1982. Foraging strategies of plant-visiting bats. In: Kuntz, T.H. (Ed.), *Ecology of Bats*. Plenum Press, New York, pp. 287–325.
- Fleming, T.H., 1988. *The Short-tailed Fruit Bat*. The University of Chicago Press, Chicago.

- Fleming, T.H., Hooper, E.T., Wilson, D.E., 1972. Three Central American bat communities: structure, reproductive cycles and movement patterns. *Ecology* 5, 555–569.
- Gallard, J.M., Ponter, D., Allain, D., Lebreton, J.D., Trouvillez, J., Clovert, J., 1989. An analysis of demographic tactics in birds and mammals. *Oikos* 56, 59–76.
- Galett, M., Morellato, L.P.C., 1994. Diet of the large fruit-eating bat *Artibeus lituratus* in a forest fragment in Brazil. *Mammalia* 58, 661–665.
- Gardner, A.L., 1977. Feeding habits. In: Baker, J., Jones, J.K., Carter, D.C. (Eds.), *Biology of Bats of the New World Family Phyllostomidae*. Part II. Special Publications 13. The Museum. Texas Technical University Press, Lubock, Texas, pp. 223–250.
- Granjou, L., Crosson, J.F., Judas, J.N., Ringet, S., 1996. Influence of tropical rain forest fragmentation on mammal communities in French Guiana: short term effects. *Acta Oecologica* 17, 673–684.
- Guevara, S., Laborde, L., 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. In: Fleming, T.H., Estrada, A. (Eds.), *Frugivory And Seed Dispersal: Ecological And Evolutionary Aspects*. Kluwer Academic Publishers, The Hague, pp. 319–338.
- Hagan, J.M., Vander Haegen, M., McKinley, P.S., 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* 10, 188–202.
- Hall, E.R., 1981. *The Mammals of North America*. Vol. I and II. John Wiley, New York.
- Heithaus, R.E., 1982. Coevolution between bats and plants. In: Kunz, T.H. (Ed.), *Ecology of Bats*. Plenum Publishing Company, New York, pp. 327–367.
- Heithaus, R.E., Fleming, T.H., Opler, P.A., 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 4, 841–854.
- Kalko, E.K.V., Fiernel, D., Handley Jr., C.P., Schnitzler, N.V., 1999. Roosting and foraging behavior of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica* 34, 344–353.
- Kunz, T.H., Pierson, E.D., 1994. Bats of the world: an introduction. In: Nowak, R.M. (Ed.), *Walker's Bats of the World*. The Johns Hopkins University Press, Baltimore, pp. 1–46.
- Laurance, W.F., 1991. Ecological correlates of extinction proneness in Australian rain forest mammals. *Conservation Biology* 5, 79–89.
- Law, B.S., Anderson, J., Chidel, M., 1999. Bat communities in a fragmented landscape on the south-west slopes of New South Wales, Australia. *Biological Conservation* 88, 333–345.
- Ludwig, J.A., Reynolds, J.F., 1988. *Statistical Ecology*. John Wiley, New York.
- Lindemayer, D.B., Nix, H.A., 1993. Ecological principles for the design of wildlife corridors. *Conservation Biology* 3, 627–630.
- MacClintock, L., Whitcomb, R.F., Whitcomb, B.L., 1977. Island biogeography and habitat islands of eastern forest. II. Evidence for the value of corridors and minimization of isolation in the preservation of biotic diversity. *American Birds* 31, 6–12.
- Marinho-Filho, J.S., 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. *Journal of Tropical Ecology* 7, 59–67.
- McNab, B.K., 1982. Evolutionary alternatives in the physiological ecology of bats. In: Kunz, T.H. (Ed.), *Ecology of Bats*. Plenum Publishing Corporation, New York, pp. 151–196.
- Medellin, R., Gaona, O., 1999. Seed dispersal by bats and birds in forest and disturbed habitats in Chiapas, Mexico. *Biotropica* 31, 478–485.
- Myers, N., 1988. Tropical forests: much more than stocks of woods. *Journal of Tropical Ecology* 4, 209–221.
- Morrison, D.W., 1980. Foraging and day-roosting dynamics of canopy fruit bats in Panama. *Journal of Mammalogy* 61, 20–29.
- Norberg, U.M., Fenton, M.B., 1988. Carnivorous bats? *Biological Journal of the Linnean Society* 33, 383–394.
- Nowak, R.M., 1994. *Walker's Bats of the World*. The Johns Hopkins University Press, Baltimore.
- Offerman, H.L., Dale, V.N., Pearson, S.M., Bierregaard Jr., O., O'Neill, R.V., 1995. Effects of forest fragmentation on Neotropical fauna: current research and data availability. *Environmental Review* 3, 190–211.
- Pimentel, D., Stachow, D.A., Takacs, H.W., Brubaker, A.R., Dumas, J.J., Meaney, J.A.S., O'Neil, D., Onsi, E., Corzilius, D.B., 1992. Conserving biological diversity in agricultural/forestry systems. *BioScience* 5, 354–362.
- Ramirez-Pulido, J., Castro-Campillo, A., Arroyo-Cabrales, J., Cervantes, F.A., 1996. A taxonomic list of the terrestrial mammals of Mexico. *Occasional Papers. The Museum Texas Tech University* 158, 1–62.
- Recher, H.F., Shield, J., Kavanagh, R., Webb, G., 1987. Retaining remnant mature forest for nature conservation at Eden, New South Wales: review of theory and practice. In: Saunders, D.A., Arnold, G.W., Burbidge, A.A., Hopkins, A.J.M. (Eds.), *Nature Conservation: The Role of Remnants of Native Vegetation*. Surrey Beatty, Sydney, Australia, pp. 177–194.
- Saunders, D.A., De Rebeira, C.P., 1991. Values of Corridors to Avian Populations in a Fragmented Landscape. In: Saunders, D.A., Hobbs, R.J. (Eds.), *Nature conservation 2: The role of Corridors*. Surrey, Beatty, Chipping Norton, Australia, pp. 221–240.
- Sazima, I., 1976. Observations on the feeding habits of phyllostomid bats (*Carollia*, *Anoura* and *Vampyrops*) in southeastern Brazil. *Journal of Mammalogy* 57, 381–382.
- Schulze, M.D., Seavy, N.E., Whitacre, D.F., 2000. A comparison of phyllostomid bat assemblages in undisturbed Neotropical forest and in forest fragments of a 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., Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. *Tree* 11, 330–333.
- Urban, D.L., Shugart Jr., H.H., De Angelis, D.L., O'Neil, R.V., 1988. Forest bird demography in a landscape mosaic. Publication No. 2853. Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Vazquez-Yanes, C.A., Orozco, A., Francois, G., Trejo, L., 1975. Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico. *Biotropica* 7, 73–76.