Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico

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Faced with the rapid and extensive conversion of tropical rain forests to pasture lands and agricultural fields and with the need to preserve the remaining mammalian fauna, it is imperative to determine how the different species that form the mammalian community have responded to the anthropogenic alterations of their natural habitats. To provide data in this direction, we sampled bats in 45 forest islands, in 20 agricultural habitats representing five types of vegetation (cocoa, coffee, mixed, citrus and allspice), in four live-fence sites and in four pasture sites at Los Tuxtlas, Veracruz, Mexico. Sampling effort resulted in the capture of 2587 bats representing 35 species. In forest habitats we detected 32 species. We did not capture any bats at the four pasture sites, but the at the other agricultural habitats studied, we captured 38% of the bats and 77% of the species recorded. Thirty-four percent of the species recorded were present at the live-fence habitats. Isolating distance was an important variable influencing species richness in forests and in agricultural habitats. Only 10% of the species recorded occurred in all the habitats studied, but 77% of the species occurred in a habitat other than rain forest. Recaptures of bats indicated inter habitat movements in the fragmented landscape. We discuss the conservation value for the bat fauna of agricultural islands of vegetation as elements reducing isolating distances among forest fragments.

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Introduction

The transformation of tropical rain forests to pastures has resulted in the local and regional extinction of many species (Myers 1988). Fragmentation of tropical rain forest, a transitory stage in the process of total destruction, results in spatial, temporal and biotic isolation of plant and animal populations (Saunders et al. 1991). Physical and biotic isolation results also in a deterioration of ecological conditions that gradually or rapidly become inadequate for the persistence of species (Lovejoy et al. 1984, 1986, Saunders et al. 1991).

Members of the order Chiroptera are of particular importance in neotropical rain forests because they constitute c. 40–50% of the mammal species, greatly influencing the species richness and diversity of mammals in these ecosystems and through the acquisition of food, in the form of plant and animal matter, they participate in the recycling of nutrients and energy in the ecosystem (Fleming et al. 1972). In addition, a large number of species consume nectar and great quantities of fruits (Bonaccorso and Gush 1987) and act as pollen and seed dispersal agents for a broad spectrum of plant species and are thus important not only in the reproductive phenology and in the population structure of plants, but also in the natural process of rain forest regeneration (Heithaus et al. 1975, Heithaus 1982, Charles-Dominique 1986, Fleming 1988). Insectivorous bats may con-
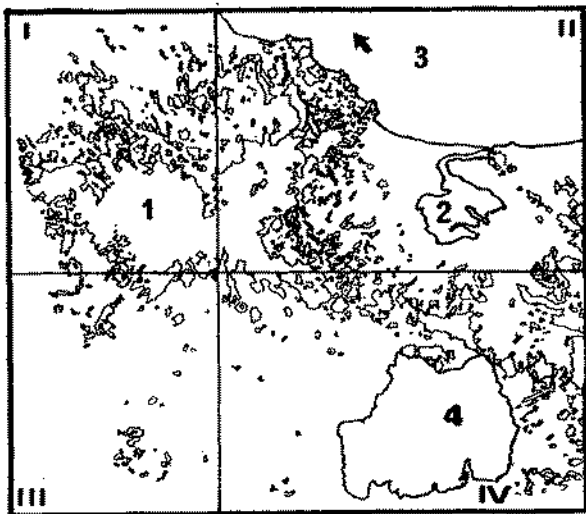
Fig. 1. Northeastern portion of the region of Los Tuxtlas in southern, Veracruz, Mexico. Lowland rain forest remaining shown as areas enclosed by thin continuous lines. The area was divided into four sections following latitude and longitude coordinates (95°10′W–18°30′N). Study sites (forests, agricultural habitats and live fences) located in sectors II and IV. Map drawn from a satellite image taken in April 1990. 1 = San Martin Volcano (1600 m), 2 = Lake Sontecomapan, 3 = Gulf of Mexico, 4 = Lake Catemaco. Distance between 2 and 4 c. 10 km.

sume up to 1.5 times their body weight in insects per night, regulating in important ways the populations of some invertebrates in the tropical ecosystem (McNab 1982).

In the region of Los Tuxtlas, in southern Veracruz, Mexico, lowland tropical rain forests reach their northernmost distribution in the American continent and are notable for their high biological diversity (Pennington and Sarukhan 1968, Estrada and Coates-Estrada in press). However, land management practices have converted 80–90% of these forests to cattle pastures. The remaining forests consist of fragments of various sizes and with different histories of isolation (Estrada and Coates-Estrada 1988, Dirzo and Garcia 1992).

Agricultural activities occur sporadically in a "sea" of pasture and consist of cultivation of non arboreal and seasonal crops such as corn, jalapeño chili pepper, beans and tobacco and of arboreal plants such as coffee, cocoa, allspice, citrus and mixed crops (coffee, cocoa, citrus, bananas). It is a common practice among farmers and ranchers of Los Tuxtlas, as elsewhere in the wet Neotropics, to use live posts of *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Leguminosae) to create barbed wire fences to parcel out the pasture land. Because the posts grow rapidly in height and produce moderately foliated crowns, single rows of these live fences resemble corridors of vegetation across the pasturelands.

Faced with the rapid and extensive conversion of

tropical rain forests to pasturelands and agricultural fields and with the need to preserve the remaining mammalian fauna, it is imperative to determine how the different species of this animal community have responded to the anthropogenic alterations of their natural habitats. Our knowledge of which bat species have survived the fragmentation and isolation of tropical rain forests and how they are responding to the environmental change is practically nil for the neotropical region. Further, data on responses of entire guilds or assemblages to habitat fragmentation in the humid tropics are rare (but see Willis 1974, Lovejoy et al. 1984, 1986, Zimmerman and Bierregaard 1986, Klein 1989, Johns 1991). Such information is fundamental to determine, for particular localities, what remains of the original biological diversity, as represented by particular taxa, and for designing conservation strategies involving different sets of species under different types of land management systems. As an indispensable corollary to this, we also need the basic information on the little known patterns of composition and structure for different animal communities in various localities in the Neotropics.

This paper reports information on the bat species detected in isolated forest fragments, in man-made islands of vegetation representing five types of agricultural vegetation, in live fences and in pastures at Los Tuxtlas in southern Veracruz, Mexico.

Methods

We conducted field work in the northeastern portion of the region of Los Tuxtlas (95°00′W, 18°25′N; elevation sea level to 1600 m) in southern Veracruz, Mexico (Fig. 1). Original vegetation cover in the area was tall tropical rain forest (Miranda and Hernandez 1963), but today the landscape, dominated by pastures, contains many forest fragments and a few agricultural islands that were the subject of our biological surveys (Fig. 1). Mean annual temperature is 27°C and mean annual precipitation is 4964 mm (SD ± 862, N = 20 yr) (Estrada et al. 1985, Estrada and Coates-Estrada in press).

As part of a broader research program on responses of birds and mammals to forest fragmentation (Estrada et al. in press), bats were censused between August 1990 – August 1992 in 65 islands of vegetation of which 45 were rain forest and 20 were agricultural islands (altitude ranged from sea level to 1000 m). Forest islands varied in years of isolation (5–30 yr; isolation recorded as the time elapsed since the forest was separated from the major land mass of forest) and in isolating distance – distance to edge of the nearest forest fragment regardless of size (0.5–8.0 km). Area of forest fragments, estimated by digitizing aerial photos and by corroboration in the field, ranged from 1 to >2000 ha. Total area accumulated by forest sites was 8000 ha. For
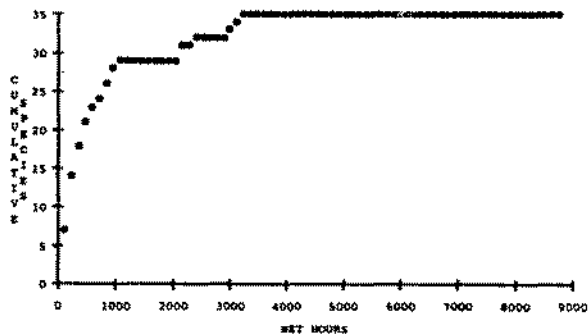
Fig. 2. Cumulative number of bat species captured in the study area.

each site we determined time since isolation by using aerial photographs taken in 1967 and 1979 and satellite images taken in 1986 and 1990 and by field surveys. The forest fragments studied represented different stages of conservation, regeneration and disturbance of the original vegetation.

We sampled four replicates in each of the following agricultural habitats: coffee, cocoa, allspice, citrus and mixed crops (coffee, cocoa, citrus, banana). Tall (> 15 m) rain forest trees left by the farmers provided shade in the case of coffee, cocoa and mixed plantation. The agricultural plots ranged in size from 2–10 ha for a total accumulated area of 100 ha and in age from 12–15 yr and were all fruit productive. Distance to the nearest forest fragment ranged from 200 m to 6000 m. We studied four areas of pasture, 25 ha each, totally devoid of the original forest vegetation and at least 10 km apart. We located the sampling area in the center of each of the 25 ha pasture plot.

To test the efficiency of our sampling procedures, we sampled bats at three forests and at three agricultural habitats for three consecutive nights from dusk to 04:00 h; captures declined significantly after the second night (no captures in 90% of the sites) and after 23:00 h (1% of captures). Maximum number of captures occurred in the first night (with a 50–70% decline in the second night) and between dusk and 23:00–24:00 h with an 80% decline after midnight. We placed sets of four unconnected nets (12 m long × 3 m high) at heights 10 and 20 m in five forest sites and in the pasture sites, but we discontinued use of these nets after 200 net hours because of few captures at the forest sites and because understory nets captured the same species; we did not capture any bats at the pasture sites. We decided upon the following sampling procedure in view of the above, but bearing in mind that because we only sampled one level of the habitats studied during part of the night and because species of bats are caught unequally by mist nets, the reported data may represent a biased portrait of the bat community present in the region.

At each forest and at each agricultural site we set up 15 mist nets (12 m long × 3 m high) along 3-4 parallel lines at 25 m intervals, distance between lines was 25–30

m. Net lines were at least 10 m from the fragment's borders. We operated the nets for two consecutive nights beginning at dusk and ending at 23:00–24:00 h on nonrainy and moonless nights. We sampled bats at four live fence sites 2 km long each running across the pasture land. In these sites, we placed three net lines with nets adjacent to one another; lines were separated from each other by 50 m and ran parallel to the barbed wire fence.

We checked the nets, at all sites, every 45 min and marked captured bats with numbered plastic colored bands placed on the forearm. We recorded body weight, sex and age before releasing each animal and assigned each bat to one of four foraging guilds according to information reported by Villa (1967), Sazima (1976), Gardner (1977), Bonaccorso (1979), Coates-Estrada and Estrada (1986), Fleming (1988) and Charles-Dominique (1991). To have some control over seasonal variations in the presence and activity of bats, faunistic surveys in forest and in agricultural habitats included at least one sample in each quarter of the year. Taxonomic nomenclature for bats followed Hall (1981) and for plants Ibarra and Sinaca (1987).

We used the dissimilarity index (PD) and the polar ordination procedures of Bray-Curtis (Ludwig and Reynolds 1988) to measure the degree of resemblance when comparing forests and man-made habitats in terms of species richness and used rarefaction as an alternative to species richness indices to compare species richness between forests and agricultural habitats where sample sizes differed (James and Rathburn 1981).

Results

Our sampling effort (8760 net hours) resulted in the capture of 2587 bats of 35 species. Because the cumulative species curve tended to level off after 3500 net hours (60 nights of netting), we feel that our sample provides a reasonably good representation of the nettable species at ground level (Fig. 2). Ninetyone percent
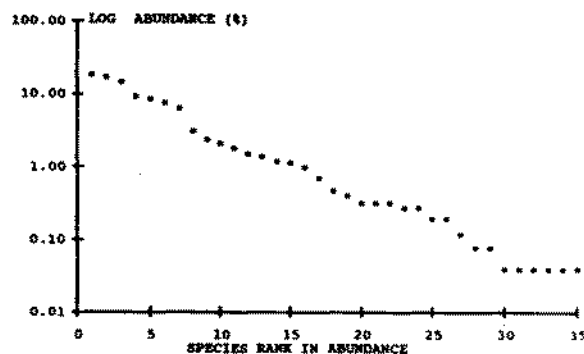

Fig. 3. Dominance diversity curve for the bat community detected. Note the asymmetry of the curve and the relatively high dominance of the first seven species.
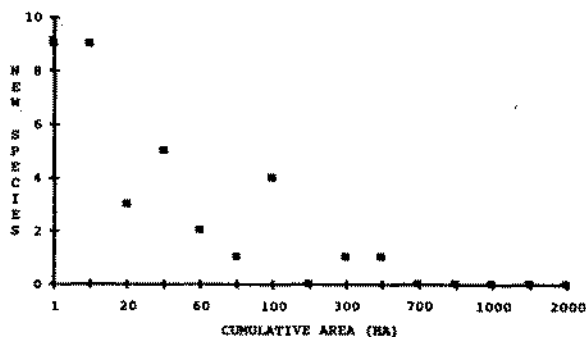
Fig. 4. Accumulation of new species of bats with increasing area. Ninety percent of the species accumulated with 100 ha of rain forest fragments.

of the species detected occurred in forest islands, 77% in agricultural habitats, and 34% in live fences; no bats were captured in the four pastures. Fiftyfour percent of captures occurred in forest fragments, 41% in agricultural habitats and 5% in live fences. Seven bat species (*Carollia brevicauda, Pteronotus parnelli, Sturnira lilium, Artibeus phaeotis, Vampyrodes major, A. jamaicensis, A. toltecus*) accounted for 81% of all bat records; the remaining species (80%) accounted for 19% of the captures (Fig. 3). Two species, *C. brevicauda* and *P. parnelli*, accounted for 18% and 17% the captures respectively; sixteen species had < 10 captures each; we captured very uncommon species such as *Vampyrum spectrum, Diclidurus virgo* and *Micronycteris megalotis* in the mixed plantations only (Appendix).

Bat species at forest fragments

At the forest fragments we captured 1407 bats representing 32 species. Five species (*C. brevicauda, P. parnelli, A. phaeotis, A. jamaicensis*, and *S. lilium*) accounted for 71% of the captures. The rest (86%), represented by < 100 individuals each, accounted for the remaining 29%. Among these, 16 species had < 10 captures (Appendix). On average, 60% of the species were present in all forest sites. The mean number of bat species caught per site was 8.4 (SD ± 2.9; range 4–14) and mean number of bat captures per site was 42.6 (SD ± 32.5; range 12–160).

Area of forest fragments and bat species richness

We found no relationship between species richness and area of forest fragments ($r_s = -0.231$ ns), but when we ordered forest islands from small to large, an accumulated area of only about 100 ha, contributed by a constellation of forest fragments, was sufficient to accumulate 94% of the species recorded; addition of new species was very slow as additional area was added (Fig. 4).
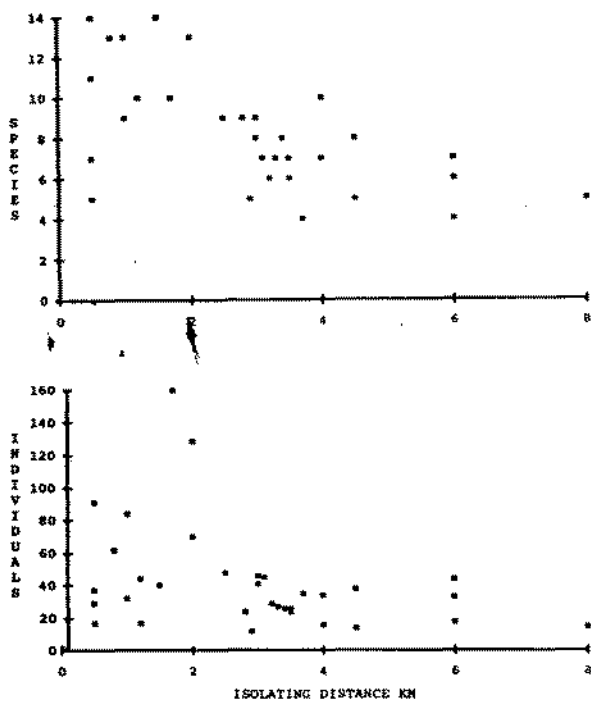

Fig. 5. Relationship between species richness and bat captures and isolating distance.

Bat species richness and isolating distance and age of forest fragments

A negative relationship existed between species richness and isolating distance of forest fragments ($r_s = -0.719$, p < 0.01) and a weaker negative association also existed between this variable and number of bats captured ($r_s = -0.387$, p = 0.05) (Fig. 5). No relationship was found with age of forest fragment ($r_s = -0.143$ ns).

Bat species richness in pastures

Our surveys in four pastures totaling 100 ha resulted in no detection of bats. A comparison with a similar area of forest (100 ha), represented by four forest islands,

Table 1. Species richness in equivalent areas of pastures and forests. Shown also is the species richness detected in 100 ha of agricultural habitats and in a 1 ha forest fragment.

Habitat	Number of species	Number of captures
Pastures 100 ha (4 sites)	0	0
Forests 100 ha (4 sites)	22	336
Agricultural habitats 100 ha; 20 sites)	27	1054
Agricultural habitats (4 replicates: 20 ha)	20	257
Forest 1 ha	9	24

Table 2. Recaptures of bats at forests and at man-made habitats.

Species	Original habitat*							Recapture habitat*							Total	Mean dist. m	Range m
	F	C	Cf	Mx	Ct	A	Lf	F	C	Cf	Mx	Ct	A	Lf			
C. brevicauda	28	2	17	2			2	36			13			2	51	1253	500–7000
S. lilium	2	2	2	2	3		3	4	1		2	2		5	14	2246	500–6500
A. phaeotis	3	1		5				5			4				9	1388	500–8000
V. major	1	2	1	3				1	1		5				7	757	500–1500
P. parnelli	3			1			1	1			2	1		1	5	710	500–1200
A. jamaicensis	2	1						3			2		1		3	600	500– 800
A. toltecus	1				1			1							2	525	500– 550
C. godmani	1		1					1			1		1		2	615	650– 580
C. perspicillata	1				1			1							2	525	500– 550
G. soricina	2							1			1				2	600	500– 700
V. helleri	1						1	1							2	700	500– 850
S. ludovici				1							1				1	580	
Total	45	8	20	15	3	2	7	54	2	0	30	3	2	8			

* F = forest, C = cocoa, Cof = coffee, Mx = mixed, Ct = citrus, A = allspice, Lf = live fence.

showed that forest habitats were significantly richer in bat species and individuals than pastures. Even a 1 ha forest patch resulted significantly richer in bats than the 100 times greater pasture habitat studied. The equivalent area (100 ha) of agricultural vegetation studied was significantly richer than pastures in bat species richness and individuals (Table 1).

Bats in agricultural habitats

While agricultural sites contributed to only 1% of the total area of vegetation sampled and to 27% of the sites studied, they accounted for 77% of all species recorded and for 38% of all bat captures. On average, agricultural habitats shared with one another 47% of the bat species detected in such habitats (range 10–15) (Appendix). Mean number of bat species caught per site was 10.0 (SD ± 4.8; range 3–14) and mean number of bats captured per site was 96.3 (SD ± 90.2; range 3–290).

In the agricultural habitats four species (V. major, S. lilium, C. brevicauda, and A. phaeotis) numerically dominated (> 100 individuals each) the sample, accounting for 59% of the captures (Appendix). The number of bat species detected at each type of agricultural vegetation ranged from 14 (coffee) to 23 (mixed plantation). We detected more species at the mixed plantations than at the other habitats where the number of species detected was similar (range 14–18). We found no differences between shaded and unshaded habitats in species richness (t = 0.25, p = 0.81) or in number of bats captured (t = 0.14, p = 0.67). Total bat biomass at these sites was 42% of the total biomass detected at all habitats (58.4 kg) and it ranged from 1825 g (coffee) to 7080 g (mixed plantation) (Appendix).

Bats in live fences

In the live fences we captured 34% of the species detected in the total sample and 12% of the bats captured

in the man-made habitats. Two species, P. parnelli and S. lilium, accounted for 78% of the captures. Mean number of species caught per site was 6.6 (SD ± 4.0; range 3–11) and mean number of bats captured per site was 71.6 (SD ± 24.8; range 44–92) (Appendix).

Vegetation types used by bat species

The distribution of species censused was not homogeneous across the vegetation types studied (tropical rain forest, cocoa, coffee, mixed plantation, citrus, allspice and live fences) (Appendix). Only 10 species (29%) occurred in forest habitats and in the five types of agricultural vegetation studied. These species, except V. major, occurred also at the live fence habitat. Fortyeight percent of the species occurred in 2–5 types of vegetation that encompassed forest and agricultural habitats and 23% of the species were present in forest habitats only (Appendix). The number of vegetation types in which a species occurred was not correlated with the species' mean body mass ($r_s = 0.04$ ns), but an association was found with the rank order of individuals censused per species ($r_s = 0.92$, p < 0.05).

Recaptures from other sites

We recaptured 100 bats of 12 species banded at habitat islands different from the banding site. Distance from the original banding site ranged from 0.5 to 8.0 km. Recaptures indicated movements of bats from forest to forest, forest to agricultural habitat, agricultural habitat to forest and from forest to agricultural habitat to forest. Species such as C. brevicauda accounted for 51% of the recaptures, S. lilium for 14% and A. phaeotis and V. major for 9% and 7% respectively. These species also had the longest scored travel distances (Table 2).
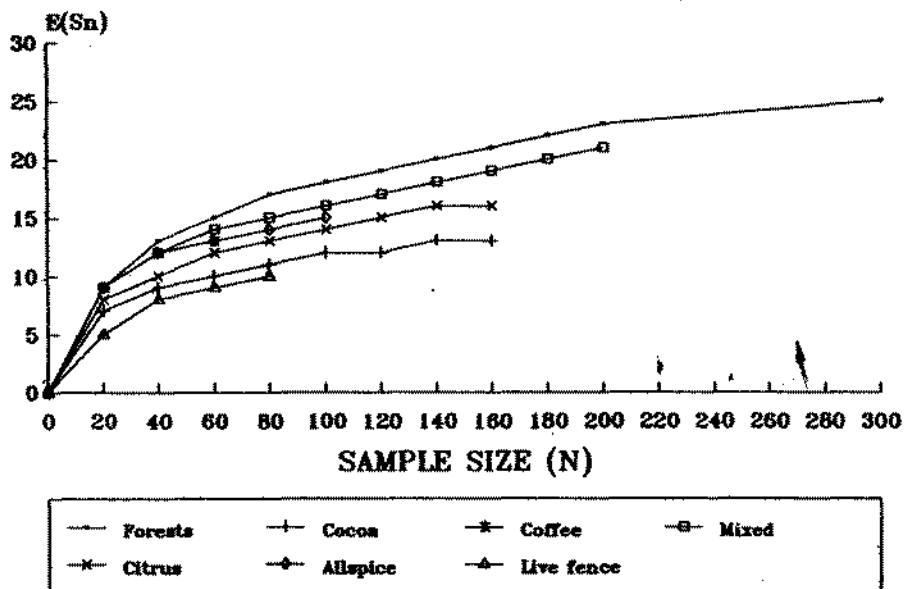
Fig. 6. Rarefaction curves for bats in all habitats examined. $E(S_n)$ is the expected number of species in a random sample of size n where S is the sum of the probabilities that each species will be included in the sample. Comparisons can be made of the expected number of species at different sample sizes. Comparison was made here at n = 60 and at n = 80 where all or most habitats studied are included.

Legend:
— Forests   —+— Cocoa   —*— Coffee   —□— Mixed
—×— Citrus   —◆— Allspice   —△— Live fence

Forests and agricultural habitats

Forests and agricultural habitats had 74% of the species in common. Rarefaction curves showed that at n = 60 and at n = 80, forests and mixed plantations had the highest species richness followed by the coffee, allspice and citrus habitats; the cocoa and live fence habitats had the lowest species richness (Fig. 6). Polar ordination showed that the citrus, mixed and cocoa plantations were the habitats most similar to forest fragments in species composition and distribution. The least similar were the coffee, allspice and live fence habitats. The citrus, mixed and cocoa plantations were more similar to each other than to the rest of the man-made habitats (Fig. 7).

Foraging guilds

Fruit-eating bats accounted for 67% of the captures in forest habitats and from 73–92% of the captures in
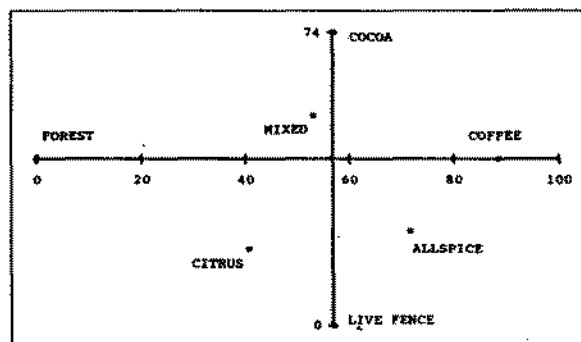

Fig. 7. Polar ordination of PD index (bat species composition and distribution) for the habitats studied.

agricultural habitats. In live fences they accounted for 61% of the samples. Fruit-eating bats also accounted for 78% of the total bat biomass recorded. Insectivorous bats (e.g., *P. parnelli*) accounted for 19% of the bat biomass. Nectarivores (e.g., *G. soricina, C. godmani*), specially common at the coffee plantations, accounted for 2% of the biomass and sanguivores (*D. rotundus*) for 1% (Table 3).

Discussion

Our study showed the existence of a rich bat species pool still occurring in the forest fragments surveyed (80% of the species historically reported; Estrada and Coates-Estrada in press). We found that both small and large forest fragments dispersed in the study area were rich in bat species and that isolating distance plays an important role influencing the fragments species' richness. This and the fact that, on average, 60% of the species detected were present in all forest sites and 47% were present in all agricultural habitats, suggest that the spatial dispersion of a diversity of macrohabitats (forest and agricultural) is paralleled by the spatial dispersion of bat species. If this is true, the conservation of small and large forest fragments may have an important additive effect in the number of species persisting in time and space at Los Tuxtlas.

While we report that bats moved between forest patches and between forests and agricultural islands in the landscape, the use of all the habitats examined seemingly applies only to a limited number (29%) of the species detected; the rest are less resilient. Bat species such as *C. brevicauda, A. phaeotis, A. jamaicensis, A. toltecus, P. parnelli, S. lilium, G. soricina, V. helleri,*

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Table 3. Proportional representation of foraging guilds in the vegetation types studied.

Guild	Forest	Cocoa	Coffee	Mixed	Citrus	All-spice	Live fence
Fruit-eating/insectivore	67.2	91.8	72.9	80.9	89.7	74.5	61.1
Insectivore	25.3	4.3	5.8	15.2	14.5	19.0	31.7
Nectarivore/insectivore	6.0	2.5	17.6	3.7	0.7	6.3	4.7
Sanguivore	1.2	0.7	3.5	0	1.0	0	2.3

and *V. major* were the species present in both forests and in all agricultural habitats studied, which is consistent with the generalist habitat and feeding preferences of these taxa (Fleming et al. 1972, Heithaus et al. 1975, Bonaccorso 1979, Fleming 1986, 1988). At the other extreme were species such as *Centurio senex*, *Diclidurus virgo*, and *Macrotus waterhousi* that occurred in forest habitats only.

The absence of bats in pastures (we observed bats in pastures at dawn or dusk but flying high (>20 m) toward scattered groups of forest fragments) suggests that these are unsuitable habitats for them. Two factors may mitigate against use of pastures by bats. One is the scarcity of food resources (fruit/insects) and lack of roost sites in these habitats. The other could be potential predation. We observed bat falcons (*Falco rufigularis*) and owls (*Tyto alba*) preying on bats at dusk as these flew out of forest fragments into the pasture, suggesting that exposure to predators may be greater at these habitats (see Fenton and Fleming 1976).

While there is a cost (e.g. potential predation and higher time and energy expenditure due to the distances covered), bat species capable of reaching forest habitats outside of the patch in which they reside may encounter a greater variety of habitats in which to find resources and meet survival requirements, simply because a single large forest fragment will not contain all of the habitats likely to occur in an area (Saunders et al. 1991). Such diversity of opportunities will increase significantly if a species can also make use of the man-made islands of vegetation. In this context, it is important to point out that 77% of the species detected were present in at least a habitat other than rain forest, suggesting the existence of variable habitat plasticity among bat species.

The presence of bats in the man-made habitat, however, does not equal suitablity of the habitat for bats, unless we can demonstrate that bats can survive and breed in these habitats. Although our observations and recaptures indicate that bats live in the forest fragments, the same data indicate that they are capable of leaving the forest to visit nearby agricultural islands. Such use may reduce time and energy and predation when moving among forest fragments and may sustain connectivity among the fragmented bat populations.

Removal of the native vegetation and the isolation of remnants, which become the only area of suitable habitat remaining for biota displaced by clearing, may lead to concentration of mobile elements of the biota in the remnants (Lovejoy et al. 1986). Our data showed that isolating distance was an important variable influencing species richness and individual captures at forest fragments. The use of forest patches and of agricultural islands by bats as stepping stones may reduce isolation and ease crowding effects resulting from forest fragmentation. These effects may be rapid and may result in saturation of the remnant by some species altering intra and interspecific interactions and resource availability (Walker 1981). In these circumstances, over exploitation of resources may result in increased competition and predation that can produce changes in fecundity and the potential collapse of the population (Karr 1990). The capacity of bat species to move out of the forest patch in which they reside and use other forest patches and other types of vegetation in the landscape may provide them with an edge with respect to other bat and vertebrate species incapable of such ability, particularly in a landscape where pastures have replaced the tropical rain forest as the dominant type of vegetation.

Our study indicated that the majority of species occurred in low numbers. Those species with the highest numerical representation in our samples were also those detected at all non-forest habitats. It is possible that these species are capable of sustaining their populations as a result of their capacity to access a greater diversity of opportunities in the landscape. For example, the presence of high concentrations of plant species of the genus *Piper* and *Solanum* at the edges of the forest fragments studied and along live fences suggests the occurrence of abundant food supplies (large numbers of fruits produced per plant and year long availability) for *Piper* specialists such as *Carollia* (Fleming 1988) and *Solanum* specialists such as *Sturnira* (Marinho-Filho 1991), the first and third ranking species in our sample. Another bat common in all habitats and numerically dominant in our sample was *P. parnelli*, an insectivorous species with generalized habitat requirements (Fleming et al. 1972).

The large number of bats captured at the mixed and at the cocoa plantations was probably due to the presence of forest trees 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 cultivated plant and which are known to be important sources of food to bats (Morri-

son 1980, Orozco-Segovia and Vazquez-Yanes 1982) and some lend themselves for the establishment of roosting sites (Estrada pers. obs.). While at the mixed plantations the mean number of bat species captured was 15.6 ($\pm$ SD 2.0), at the other plantations the mean ranged from 3.7–6.4 (Appendix). The higher diversity of cultivated plants in the understory (cocoa, coffee, bananas, citrus, avocado) coupled to the remaining forest trees providing shade at the mixed plantations suggests a greater vertical and horizontal complexity of the vegetation in these habitats compared to the other man-made habitats examined. This may allow more bat species to co-occur in these habitats than at the other plantations. The high number of bats at the citrus plantations is more difficult to explain, but preliminary investigations by colleagues studying insects indicate higher numbers of insects present in the arboreal structures at the citrus groves compared to allspice plantations (A. Aldrete unpubl. data).

Distance from forest fragments seems to be an important factor associated with the richness of species in man-made habitats. Polar ordination showed that the coffee and allspice plantations and the live fence sites were the most dissimilar, as measured by the PD index, to forest habitats. These were also the most isolated man-made habitats we studied with mean isolating distance (distance to the edge of the nearest forest patch) equalling 2556 m (range 500–6000 m). In contrast, in the cocoa, mixed and citrus plantations mean isolating distance was 439 m (range 200–1000 m). A high correlation found between the PD index and isolating distance ($r_s = 0.98$, $p < 0.01$) confirmed, in this case, the relative importance of isolating distance as a significant variable influencing species richness and number of bats present in agricultural habitats.

The conservation value for bats of agricultural islands as a mechanism to reduce isolating distances among forest fragments remaining in Los Tuxtlas could be enhanced by the interconnection provided by live fences. The trees forming the live fences not only provide a rich set of microhabitats in which insects become established, but they also fruit during the year adding to the opportunities available to bats in a landscape where the present forest is a limited resource. These landscape conditions may have the net result of reducing time and energy expenditure and exposure and in addition provide some degree of connectivity to the species' fragmented population, in contrast to a landscape devoid of these intermediate stop-over points (see Johns 1991 for an example with birds in Amazon rain forests). Moreover, availability of suitable breeding habitats (e.g. potential roosting sites) needs consideration. However, lack of field data limits us to ask to what extent forest destruction and fragmentation and continued removal by man of trees in forest fragments has affected roost site availability for bats to sustain sufficient numbers to avoid extinction (see Karr 1990, Newark 1991 and Blake 1991 for examples with birds) and which are the species most affected?

The predominance of fruit-eating bats at all habitats studied coupled to their movements between forest fragments and between forest and man-made habitats suggests that movement of seeds across the landscape may be sustaining some degree of genetic connectivity among plant populations and may be contributing to the formation of scattered clusters of seed and seedling banks outside of forest fragments, with an unexplored hitherto impact on the self regenerating capacity of the rain forest (Estrada et al. in press).

Neotropical fruit-eating bats are also important consumers of insects (Fleming 1988) and our observations and interviews with the farmers indicated that very few of the bats detected in the agricultural habitats studied feed on the economically important fruits and the damage they cause to the crops is insignificant. Instead they seem to feed on insects living in the tree canopy. Thus, it is likely that bats may contribute at the plantations in important ways in the regulation of insect populations that are the major damaging agents of the plant's foliar and fruit parts.

Economic surveys conducted by us showed that although the plantations studied required significantly many more man hours of work in the field than pastures, they may, singly or as a group, be a more economically productive mode of managing the tropical landscape than pastures. For example, the estimated economic yield of mixed plantations per ha per year was 2.1 times greater than that obtained from cattle ranching and the average yield of the five plantations under consideration here was 1.4 times greater than that derived from pastures (Estrada unpubl. data).

Thus, at Los Tuxtlas, we have bat species that can successfully occupy a variety of man-made habitats. At the other extreme are species that display intolerance and exist in a truly fragmented landscape. The majority of the species, however, seem to fall between these extremes. In this instance, a variegated model rather than a fragmentation model may be more adequate as a conservation approach at the landscape level (McIntyre and Barret 1992). Turning pasture area into agricultural parcels of the sort studied by us rather than turning more forest into pasture coupled to the obligatory conservation of the remaining forest fragments may result in 1) the persistence in time and space of forest bats, 2) the retention of some of the regenerating capacity of the ecosystem via the pollen and seed dispersal services provided by fruit and nectar eating bats and 3) important economic benefits to the local human populations.

Dept of Forest Management at The University of Maine for the 1990 satellite images.

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Appendix 1.

Bats captured at forests and at agricultural habitats. Nomenclature follows Hall (1981).

Species	Forest	Coc	Cof	Mix	Citr	Alls	Lfen	Total	Weight* g
Emballonuridae									
Saccopteryx bilineata	4			1		3		8	7
Diclidurus virgo	1							1	19
Mormopidae									
Pteronotus parnelli	306	11	5	38	33	8	40	441	19
Pteronotus davyi	8	1		2	4	3		18	8
Mormoops megalophylla	24			2	3	10		39	15
Phyllostomidae									
Micronycteris brachyotis	3		1	1				5	8
Micronycteris megalotis				1				1	11
Mimon bennettii	7							7	32
Phyllostomus discolor	10			1	1			12	38
Vampyrum spectrum				3				3	170
Glossophaga soricina	55	6	7	2	2	5	3	80	11
Leptonycteris sanborni	1							1	32
Hylonycteris underwoodi	2							2	9
Choeroniscus godmani	29	1	8	9		3	3	53	10
Carollia brevicauda	335	46	22	38	5	13	8	467	18
Carollia perspicillata	20		1			10		31	20
Sturnira lilium	115	17	9	28	105	34	59	367	19
Sturnira ludovici	21		1	5	9			36	25
Uroderma bilobatum	15	2		5	1	1	1	25	20
Vampyrops helleri	30	9	3	14	1	2	1	60	20
Vampyrodes major	22	121	3	64	5	2		217	34
Vampyressa pusilla	4	1		1	1			7	10
Chiroderma villosum	6				4			10	30
Artibeus phaeotis	126	42	7	34	25	4	2	240	13
Artibeus toltecus	74	9	4	11	41	19	4	162	17
Artibeus watsoni	6			2				8	14
Artibeus jamaicensis	121	7	11	26	18	9	1	193	47
Artibeus lituratus	28	2			15		1	46	62
Artibeus hartii	1							1	13
Centurio senex	1			1				2	20
Desmodus rotundus	18	2	3		3		3	29	35
Natalidae									
Natalus stramineus	5							5	7
Thyropteridae									
Thyroptera tricolor	1							1	4
Vespertilionidae									
Antrozous dubiaquercus	8							8	20
Myotis keaysi				1				1	5
Individuals	1407	277	85	290	276	126	126	2587	
Mean per site	42.6	92	28.3	96.6	92	42	71.6		
S.D.	32.5	44	22.7	22.5	15	39.5	24.8		
No. of species	32	15	14	23	18	15	12	35	
Mean per site	8.4	8	7.3	15.6	10.3	9	6.6		
S.D.	2.9	4.5	3.7	2	6.4	4	4		
Biomass g	29979	7049	1825	7080	6121	2334	4068	58456	
Mean	21	21	21	21	21	21	21		
Range	7–100	7–65	8–65	4–170	8–76	7–57	9–62		

* Average weight; Coc: cocoa, Cof: coffee, Mix: mixed, Citr: citrus, Alls: allspice, Lfen: live fence.