General bat activity measured with an ultrasound detector in a fragmented tropical landscape in Los Tuxtlas, Mexico

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Abstract

General bat activity measured with an ultrasound detector in a fragmented tropical landscape in Los Tuxtlas, Mexico.— Bat tolerance to neotropical forest fragmentation may be related to ability by bats to use available habitats in the modified environmental matrix. This paper presents data on general bat activity (for three hours starting at dusk) measured with an ultrasound detector in a fragmented landscape in the region of Los Tuxtlas, Mexico. Bat activity was measured in continuous forest, forest fragments, forest–pasture edges, forest corridors, linear strips of vegetation, citrus groves, pastures and the vegetation present in local villages. The highest bat activity rates were recorded in the villages, in forest fragments and in linear strips of vegetation. The lowest activity rates were detected in pasture habitats. Data suggest that native and man–made arboreal vegetation may be important for sustaining bat activity in fragmented landscapes.

Key words: Chiroptera, Tropical forest fragmentation, Bat conservation, Bat ultrasounds, Los Tuxtlas, Mexico.

Resumen

Actividad general en los murciélagos registrada mediante un detector de ultrasonidos en una zona de selva fragmentada de Los Tuxtlas (México).— La tolerancia de los murciélagos a la fragmentación de las selvas neotropicales parece estar relacionada con su capacidad para utilizar los hábitats disponibles en la matriz ambiental modificada. En este trabajo se presentan datos sobre la actividad general de los murciélagos (durante las tres horas siguientes al atardecer) medida con un detector de ultrasonidos en una zona con fragmentos aislados de selva de la región de Los Tuxtlas (México). La actividad de los murciélagos se midió en una zona de selva continua, fragmentos aislados de selva, límites de la selva con zonas de pastos, corredores de vegetación, cercas vivas, plantaciones de cítricos, pastizales y la vegetación presente en los asentamientos humanos. Las mayores tasas de actividad se registraron en los asentamientos humanos, fragmentos de selva y cercas vivas. Las tasas más bajas de actividad se registraron en los pastizales. Los datos sugieren que las zonas con vegetación arbórea autóctona e introducida por el hombre pueden constituir un factor importante para sostener la actividad de los murciélagos en los fragmentos aislados de selva.

Palabras clave: Quirópteros, Fragmentación de la selva, Conservación de murciélagos, Ultrasonidos, Los Tuxtlas, México.

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Introduction

Members of the order Chiroptera are of particular importance in neotropical rain forests because they constitute about 40–50% of mammal species, greatly influencing the species richness and diversity of mammals in these ecosystems and have, as a result of their feeding habits, an important impact on the ecology of pollen and seed dispersal (Fleming et al., 1972; Heithaus et al., 1975; Fleming, 1982; Heithaus, 1982; Bonaccorso & Gush, 1987; Fleming, 1988; Charles–Dominique, 1991; Medellín & Gaona, 1999). Insectivorous bats may play an important role in regulating the populations of some invertebrates in the tropical ecosystem (MCNAB, 1982).

In spite of their mobility, 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., 1993; Brosset et al., 1996; Granjou et al., 1996; Schulze et al., 2000). Other studies suggest 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, documentation of bat activity in fragmented landscapes in the Neotropics is scanty. The few published studies available have been limited to trapping bats with mist nets and/or traps reporting presence or absence of species and describing aspects of bat assemblage structure and composition (Estrada et al., 1993; Brosset et al., 1996; Granjou et al., 1996; Cosson et al., 1999; Schulze et al., 2000; Estrada & Coates–Estrada, 2001a, 2001b, 2002). These studies have inferred activity of bats at various habitats from the number of bats captured at the sites investigated and have expanded our understanding of neotropical bat tolerance to habitat loss and fragmentation. However, to increase our understanding of bat responses to changes in the distribution of their natural habitat —additional evidence relating bat presence to bat activity at the habitats investigated is needed.

Ultrasound detectors have been successfully used to study patterns of habitat use by bats in North America (Krusic et al., 1996; Thomas & Laval, 1988), in Britain (Vaughan et al., 1997), in New South Wales, Australia (Law et al., 1999) and in highly modified landscapes in Europe (Limpens & Kaptyen, 1991; Walsh & Harris,1996; Kalko & Schnitzler, 1993). The use of ultrasound detectors in the study of Paleotropical bats has been documented in several localities (Fenton & Thomas, 1980; Fenton, 1982). In the Neotropics, the use of ultrasound detectors has been restricted to a few inventories of bat vocal signatures (O´Farrel & Miller, 1997, 1999), to studies of assessment of intraspecific variation with respect to habitat and behavior and studies of location of food by frugivorous bats (Thies et al., 1998).

The central goal of this paper is to present data on bat activity measured with an ultrasound detector in a series of habitats that are part of a fragmented landscape located in the northeastern section of the region of Los Tuxtlas in southern Mexico: continuous forest, isolated forest fragments, forest–pasture edges, forest corridors, linear strips of vegetation, citrus groves, pastures and in the vegetation present in local villages. The data reported herein expands on earlier work based on trapping bats with mist nets at some of these habitats. These data and the results presented here are aimed at assessing which landscape scenarios may favor persistence of bat species assemblages in areas where the forest has been fragmented (Estrada et al., 1993; Estrada & Coates–Estrada, 2001a, 2001b, 2002).

Methods

Study area

The tropical rain forest of Los Tuxtlas, in southeastern Veracruz, Mexico, represents the northernmost limit of the lowland rainforests in the American continent. Bat diversity in these forests is high with about 50 species reported (Coates–Estrada & Estrada, 1986). Human activity in this region has converted large extensions of the original forest surface (2,500 km^2) to pastures, but constellations of forest fragments have remained in the lowlands (Estrada & Coates–Estrada, 1996). Some of the pasture land is used to cultivate arboreal cash crops such as citrus and allspice. These crops appear sporadically as islands of vegetation amidst the pastureland. Weather monitoring stations in the area indicate a mean annual temperature of 27^{o}C (range 20 to 28^{o}C). Average annual rainfall is 4,900 mm but from March to May average monthly rainfall is 111.7 SD $\pm$ 11.7 mm and from June to February this average equals 486.25 SD $\pm$ 87.0 mm.

Study habitats

The sites in which we sampled bat activity were located in a 126 km^2 landscape in the north–eastern section of the region of Los Tuxtlas where the altitudinal gradient ranges from sea level to about 500 m above sea level (fig. 1). The continuous tract of lowland rainforest comprised part of the land of the biological research station "Los Tuxtlas" of Universidad Nacional Autónoma de México (95^o 00' W, 18^o 25' N). The forest of this reserve (700 ha) is connected to about 4,000 ha of pristine rainforest that forms part of the Los Tuxtlas Biosphere Reserve. Three locations separated by 2.0 km within the continuous forest tract were used to sample bat activity. In the three locations in the interior of the continuous forest distance to the edge was 400–500 m. The forest–pasture edges consisted of three 1.0 km long sections of the edge that bordered the continuous forest tract in its northern boundary. These sections were separated from each other by about 1.5–2.0 km.

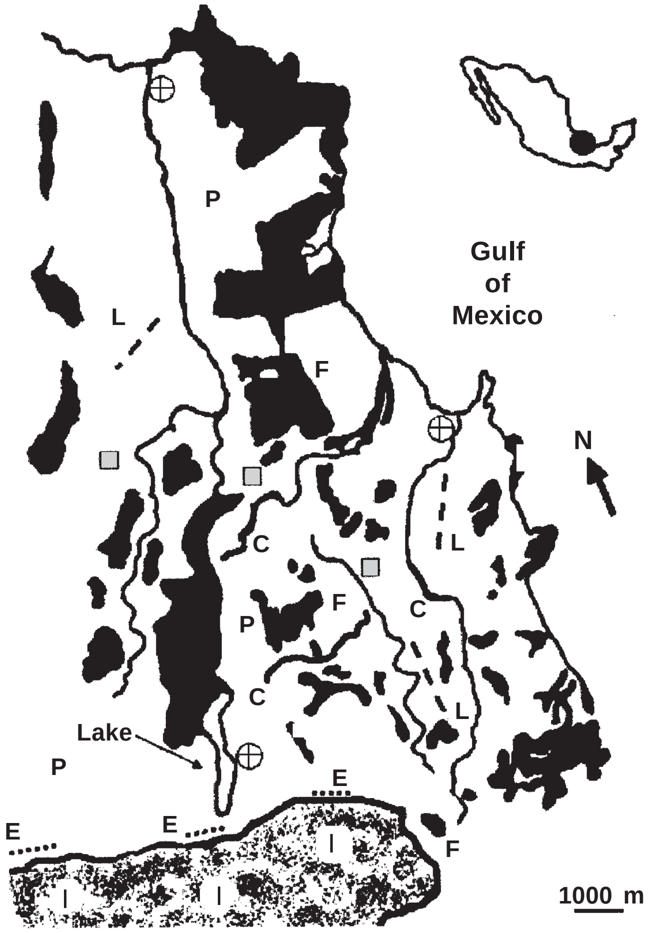

Fig. 1. Study sites in the region of Los Tuxtlas, Veracruz, Mexico. The fragmented landscape (forest fragments shown in black) north of the extensive forest tract that forms part of the biological field station Los Tuxtlas is shown: I. Forest interior sites; C. Corridors; E. Forest edges; F. Forest fragments; P. Pastures; L. Live fences; circles with a cross are villages and shaded squares are citrus groves.

Fig. 1. Áreas de estudio en la región de Los Tuxtlas, Veracruz, México. Se muestran los fragmentos de selva (indicados en negro) al norte de la selva extensa que forma parte de la Estación de Biología Los Tuxtlas: I. Emplazamientos del interior de la selva; C. Corredores; E. Límites de la selva; F. Fragmentos de selva; P. Pastizales; L. Setos vivos; los círculos con una cruz indican los asentamientos humanos y los cuadrados sombreados corresponden a las plantaciones de cítricos.

The original lowland rainforest immediately north of the continuous forest was gradually converted to pasture lands between 1960–1970, but clusters of forest fragments have remained in the 126 km^2 area. Three forest fragments, 10, 30 and 80 ha in size and located about 1, 3 and 6 km from the continuous forest were used to sample bats with the ultrasound detector. The linear strips of vegetation running across the pastures were of two types. One consisted of three corridors of remnant rainforest along the sides of three streams while another consisted of three live fences. The former habitats had an average length of 1.2 ± 0.10 km and an average width of 10.2 ± 3.5 m) and were located about 0.5–3 km from the forest edge sites. The residual forest vegetation at these sites was dominated by trees of the Lauraceae, Moraceae, Cecropiaceae, Boraginaceae and Fabaceae plant families. The sites had a few representatives of the forest palms *Astrocaryum mexicanum* and *Bactris trichophylla*, which are common in the understorey of undisturbed forest vegetation in this region (Bongers et al., 1988) reflecting the residual nature of the vegetation found at the site. The three live fence sites, formed by a single row of grown live posts of *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Leguminosae) planted at one

Table 1. Number of bat passes recorded at each habitat investigated. Each habitat was sampled for 1,620 minutes: S. Sampling points; Cf. Continuous forest; E. Forest pasture–edge; F. Forest fragments; C. Corridors; L. Live fences; Ci. Citrus; V. Villages; P. Pastures.

Tabla 1. Número de pases registrados en los hábitats investigados. En cada hábitat se realizó un muestreo durante 1.620 minutos: S. Puntos de muestreo; Cf. Selva continua; E. Límite de la selva con zonas de pasto; F. Fragmentos de selva; C. Corredores de vegetación; L. Setos vivos; Ci. Cítricos; V. Asentamientos humanos; P. Pastizales.

S	Cf	E	F	C	L	Ci	V	P
1	43	54	43	39	75	72	93	9
2	40	72	30	51	92	90	84	3
3	31	48	40	66	84	76	74	4
4	55	42	55	48	66	66	94	5
5	76	57	105	87	65	69	87	3
6	85	66	88	90	86	63	79	5
7	4	60	45	84	63	62	82	7
8	43	72	88	63	60	66	86	5
9	52	84	70	39	57	60	69	3
10	55	57	98	54	57	48	88	2
11	79	48	90	48	45	48	90	4
12	19	60	112	48	63	56	83	1
13	4	54	50	54	82	57	77	2
14	48	63	69	57	66	60	81	4
15	30	42	53	27	77	64	78	3
Total	664	879	1036	855	1038	957	1245	60
Mean	44.3	58.6	69.1	57	69.2	63.8	83.0	4.0
± SD	24.6	11.7	26.2	18.3	13.0	10.6	7.0	2.0

meter intervals a few years back by ranchers to hold the barbed wire, were separated from each other by about 2.5 km.

The three citrus groves were located 2.5 km northeast of the continuous forest. These sites were rectangular in shape and each about 10 ha in size. The citrus trees arranged in rows were 3–4 m in height and fruit productive. The vegetation on the ground consisted of grass actively grazed by cattle. The vegetation patches forming part of three villages were located at 2, 5 and 8 km from the continuous forest. The vegetation in these sites consisted of planted tree species such as *B. simaruba, G. sepium,* coconut palms, citrus trees, almonds, avocados, and various other ornamental and shade providing trees and non tree plants such as papayas and bananas that people planted in their yards and to fence their house lots.

The pastures sites were three open areas about 100 ha in size located at 1, 2 and 6 km from the continuous forest. The pastures consisted of 10–15 cm high African star grass (*Cynodon plectostachyus*), grazed by free–ranging cattle.

Bat activity

Bat activity was monitored at each site using a Pettersson ultrasound detector model D230 (Pettersson Elektronic AB, Upsala, Sweden) in the broadband frequency division mode (10–120 kHz). The directional microphone had a reach of about 25 m. At each site a 750 m long sinuous transect was set up and sampling points were marked at 50 m intervals for a total of 15 points. In the forest fragments the transects ran sinuously through the middle of each site. In the corridors and live fences the sampling transects ran under the shadow of the tree vegetation and under the crown of the row of trees, respectively. In the citrus groves, three parallel transects were set up, separated from each other by 100 m, about 250 in length each. In the villages, the transect was established along one of 2–3 existing streets. No street lamps were present in the villages only indoor houselights were used by the inhabitants. In the pasture sites, the transects ran in a straight line N–S for 750 m.

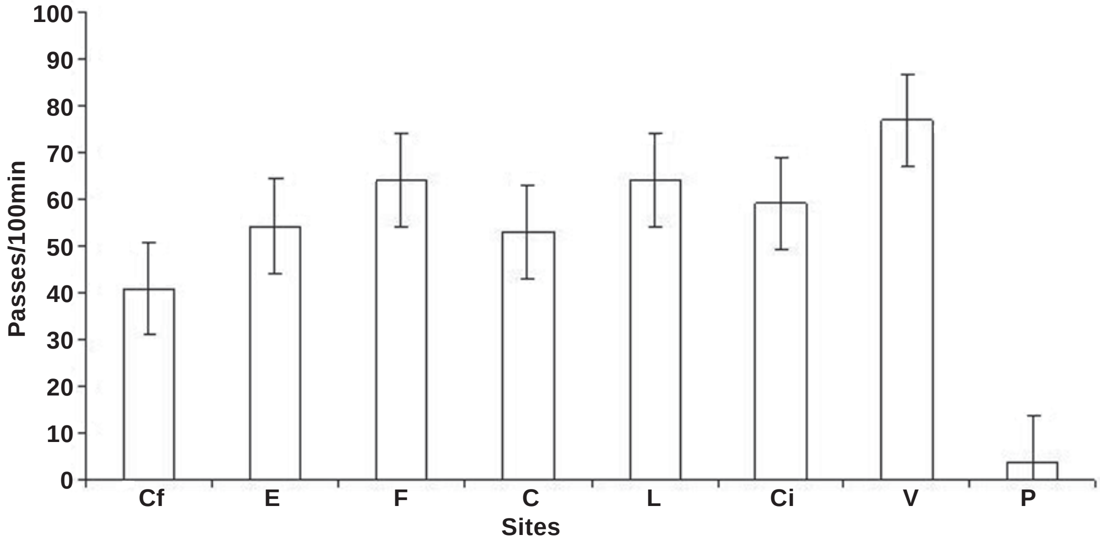

Fig. 2. Bat activity rates of bats (± SE), measured as passess/100 min with the ultrasound detector, at the habitats investigated. (For abbreviations see table 1.)

Fig. 2. Tasa de actividad de los murciélagos (± EE), indicada como el número de pases cada 100 minutos en los hábitats investigados. (Para las abreviaturas ver tabla 1.)

Each site was visited three times between May and August of 2000. Echolocation calls were monitored at each site for three hours starting at dusk. At each of the 15 points in each site, we counted the number of bat passes, defined as a sequence of ≥ 2 echolocation calls including feeding buzzes (Thomas, 1988; Law et al., 1999) for a total of 12 minutes. The ultrasound detector was held at elbow height at a 45 degree angle with respect to the ground and aerial space at each cardinal point was scanned for three minutes. Samples were conducted on moonless nights and on non rainy days at all sites.

Measures of habitat clutter

To obtain an indirect measure of vegetation clutter at the habitats investigated, a light meter at knee height was used to measure the amount of light illuminating the ground at each of the 15 points in each site where sampling of bat activity was carried out with the ultrasound detector. Readings were taken between 12:00–14:00 hrs on sunny and clear days. Data were expressed as mean number of lumens per square meter.

Data analysis

Bat activity recorded with the ultrasound detector was standardized as number of passes per 100 min (Thomas, 1988). The non–parametric Kruskal–Wallis (data could not be transformed to fit a normal distribution) or the Mann–Whitney tests were used to determine whether bat activity differed among habitats and between pairs of habitats (MINITAB for Windows, version12).

Results

A total of 216 hours was accumulated monitoring the activity of bats at all habitats (1620 min per habitat) and a total of 6,734 passes was recorded. Bat activity was not homogeous among habitats (Kruskal–Wallis H = 62.97; df = 7; P = 0.001) (table 1). The lowest bat activity rates were recorded at the pasture habitats (3.7 passes/100 min) (fig. 2). The highest bat activity rates (76.9 passes/100 min) were recorded in villages followed by the forest fragments, live fences, citrus groves, forest pasture edges, corridors and the continuous forest sites (fig. 2).

A pair–wise comparison in activity rates between the continuous forests and the non–pasture habitats showed that non–significant differences in bat activity rates existed only with respect to the forest pasture-edge and the corridors (U–test P > 0.05). In all other cases, bat activity rates were significantly higher at the other habitats than in the continuous forest (U–test P = 0.002) All habitats differed significantly in activity rates from the pasture sites (U–test P < 0.001 in all cases) (table 1).

Measures of habitat clutter

Light meter readings (lumens/m^2) were lower at the forest sites than at the other habitats investi-

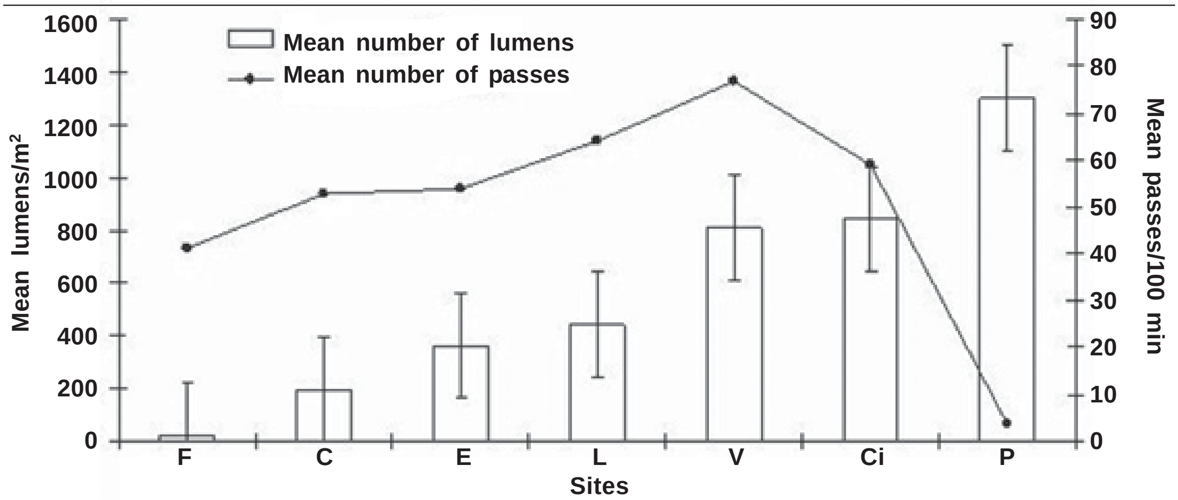

Fig. 3. Reading (lumens/m^2) recorded with a lightmeter at the sites investigated. (For abbreviations see table 1.)

Fig. 3. Luminosidad (lúmenes/m^2) registrada por medio de un exposímetro en los emplazamientos investigados. (Para las abreviaturas ver tabla 1.)

gated. Average light meter readings were 196 lumens/m^2 and 442 lumens/m^2 in the corridors and live fences, respectively (fig. 3). Higher readings were recorded at the villages and the citrus groves, 812 lumens/m^2 and 840 lumens/m^2, respectively. Maximum readings were obtained at the pasture sites (1200 lumens/m^2). Bat activity roughly paralleled the observed increases in luminosity from forest to the villages, dropping sharply in the pastures (fig. 3).

Discussion

While a catalogue of vocal signatures for the bat species present in Los Tuxtlas does not yet exist, mist netting of bats in the continuous forest, forest fragments, live fences and citrus grove sites used in this study indicated the presence of a rich species pool represented by 39 species of bats (about 80% of species historically recorded; Estrada et al., 1994). The proportion of bat species captured with mist nets in the habitats sampled with the ultrasound detector were 77% in the continuous forest, 85% in forest fragments, 46% in citrus groves, 31% in live fences and zero percent in pastures. This indicates a high diversity of bat species in the arboreal habitats investigated and the likelihood that bat activity measured with the ultrasound detector reflects the activity of many of the bat species identified with the use of mist nets in these habitats. For example, *C. brevicauda, S. lilium, Artibeus* spp., *Dermanura* spp. and *G. soricina* dominant bat species in continuous forest and forest fragments are fast fliers and have been reported to forage in or above the canopy and in open spaces (Brosset et al., 1996) and frequent the edges and interior of small forest fragments (Fleming, 1988), live fences and citrus groves (Estrada et al., 1993). Even bat species with more specialized feeding habitats and habitat requirements (e.g., *Leptonycteris curasoae, S. ludovici, V. spectrum*; Fleming, 1982) are present in these habitats (Estrada et al., 1994; Estrada & Coates–Estrada, 2001a, 2001b, 2002).

Our study showed that bat activity rates were higher in the non–pasture habitats examined than in the continuous forest. While habitat clutter in the continuous forest habitats may have influenced detection of echolocation calls produced by bats, our results nevertheless suggest that bats living in fragmented landscapes in Los Tuxtlas, regularly use linear strips of vegetation, forest fragments and human–made vegetation patches (including the vegetation of home gardens in human settlements) (Estrada et al., 1993; Estrada & Coates–Estrada, 2001a, 2001b). As feeding rates of bats have been reported to be positively correlated with aerial insect densities (Racey & Swift, 1985), areas where bats may achieve high rates of activity may be good quality habitats for movement and/or foraging, and deserve protection (Vaughn et al., 1997). The high activity rates of bats recorded at the forest fragments suggest that even small or poor quality remnants constitute a significant conservation resource for bats (Shafer, 1995; Law et al., 1999). The intense bat activity recorded in the live fence sites and in the corridors of residual forest vegetation suggests the presence of resources used by bats in these habitats. It has been noted that wind speed affects the distribution of nocturnal insects (Peng et al., 1992a, 1992b) and linear strips of vegetation such as hedgerows and wind breaks affect insect distribution, probably because of their effect on local wind speed (Lewis, 1969).

Bats are usually loyal to foraging sites and may find new roosts if the sites where roosts were located disappear (Brinham & Fenton, 1986), suggesting that the conservation of foraging and flyway habitats such as corridors of residual forest vegetation and live fences is important. The presence of linear strips of residual forest or of man–made vegetation may also reduce isolation distances between forest fragments and between these habitats and other types of vegetation patches, a feature that may facilitate movement of bats in the landscape and may also function as foraging trap–lines for bats (Fleming, 1982; Estrada et al., 1993; Estrada & Coates–Estrada, 2001a). Similarly, the high bat activity rates recorded at the forest–pasture edges may stress the importance of linear landscape elements to bats for commuting and navigating across the landscape (Krusic et al., 1996). Some fruit–eating neotropical bats use echolocation to locate their food, as studies have shown for species of *Carollia* (Thies et al., 1998) and *Phyllostomus* (Kalko & Condon, 1998). It is thus possible that some of our records in the linear strips of vegetation and at the forest–asture edge may be of fruit–eating bats tracking food resources such as fruits of *Piper* and *Solanum,* plants that become established in these environments (Fleming, 1988).

Readings of light illumination at the sites investigated suggest less cover is available at live fences, citrus groves and villages when compared to the other non–pasture habitats studied. Increases in bat activity roughly paralleled the presence of less vegetation clutter in these habitats, suggesting that, in spite of greater exposure of bats to potential predators (e.g., bat falcons, *Falco rufigularis* and owls, *Tyto alba*) in these habitats, bats were active in these sites. While bats may face potential predation and higher time and energy expenditure due to exposure and distances flown when visiting different habitat patches in the landscape, by reaching various vegetation patches available in the matrix, outside the forest fragment in which they reside, they may encounter a greater variety of habitats in which to find resources and meet survival requirements, avoiding over exploitation of resources and increased competition (Offerman et al., 1995).

General implicatons

The use of ultrasonic detectors to record bat activity may detect soft–calling species (whispering bats, e.g., Phyllostomidae) less frequently than loud calling species (e.g. *Pteronotus parnelli*). In addition, these devices do not provide data that can be translated directly into estimates of population density (Thomas, 1988). However, ultrasound detectors provide a relatively unbiased index of levels of use among habitats (Thomas & Laval, 1988) and, in contrast to ground level nets, the devices may detect canopy and high flying taxa (O´Farrel & Miller, 1999).

The low record of bat activity in the pasture habitats corresponds well with the lack of captures of bats using mist nets in these habitats (Estrada et al., 1994). Although we observed bats in pastures at dawn or dusk but flying high (> 20 m) toward scattered groups of forest fragments), it is possible that some species may forage on insects in high grass. 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, while the other could be potential predation. During the study, bat falcons (*Falco rufigularis*) and owls (*Tyto alba*) were observed preying on bats at dusk as they flew out of forest fragments into the pasture, suggesting that exposure to predators may be greater in these habitats (see Fenton & Thomas, 1980).

Surely, the ability to fly and to traverse open areas using patches of native and introduced vegetation as well as linear strips of vegetation, seems to allow bat species more flexibility in their responses to habitat fragmentation as compared to non–flying mammals (Estrada et al.,1993; Estrada et al., 1994; Cosson et al., 1999; Schulze et al., 2000). The high diversity of the bat assemblages still present in the investigated landscape, attested by our ealier studies using mist nets, and the data presented here suggest that bats not only pass through native and man–made habitats in the landscape, but that they are active in these habitats searching and harvesting food, thus enhancing their capacity to persist in landscapes modified by man and in which arboreal agricultural vegetation is an important component (Laurance, 1991; Estrada & Coates–Estrada, 1994; Walsh & Harris, 1996; Turner, 1996; Law et al., 1999). Clearly, in this scenario, conservation of isolated forest fragments is incomplete and consideration must also be given to the value, as stepping–stones and as foraging sites, of other types of vegetation in the matrix, including the vegetation found in the home gardens of local villages, for bats (Lindenmayer & Nix, 1993; Neiman et al., 1993; Turner, 1996; Estrada & Coates–Estrada, 2002). The fact that not only insectivorous bats and those that feed on vertebrates use echolocation to locate their food, but also that frugivorous bats employ these tactics (Thies et al., 1998; Kalko & Condon, 1998) suggests that bat activity in the human–modified landscape investigated involves a great number of bat species that differ in dietary and habitat requirements. These species may be important in the natural control of insect populations as well as in the natural process of forest regeneration via the pollen and seed dispersal services bat species provide for forest plants in human–modified landscapes.

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