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The Influence of Large Tree Density on Howler Monkey (*Alouatta palliata mexicana*) Presence in Very Small Rain Forest Fragments

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ABSTRACT

The populations of the Mexican mantled howler monkey (*Alouatta palliata mexicana*) in the Los Tuxtlas region, Mexico, have declined drastically due to habitat loss and fragmentation. Nevertheless, several troops still inhabit very small and isolated rain forest fragments. We identified the main vegetation attributes that can favor the presence of howlers within 18 small (< 10-ha) fragments that did not differ significantly in size, shape, and isolation (nine occupied and nine unoccupied by howlers). We found that habitat quality (*i.e.*, food resources and vegetation structure) affected howler incidence in small fragments. Particularly, the occupied fragments showed greater density of big trees (dbh > 60 cm), greater total basal area, greater basal area of persistent tree species, and greater basal area of top food species than the unoccupied fragments; suggesting that even for small fragments the loss of big trees and particularly the decrease in size class of the top food species can negatively affect howler distribution in highly fragmented landscapes. These findings could be used to establish foreground conservation areas for this critically endangered subspecies in fragmented landscapes of Los Tuxtlas.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: fragmentation; habitat quality; Los Tuxtlas; Mexican mantled howler monkeys; Mexico.

ACCELERATED DEFORESTATION OF TROPICAL RAIN FORESTS AROUND THE WORLD has led to the destruction of suitable habitat for primates (Marsh 2003, Estrada *et al.* 2006). As deforestation increases, there is a reduction in fragment size and an increase in fragment isolation (Fahrig 2003). As fragments become smaller, more irregularly shaped, and more isolated, their floristic composition, plant species diversity, and vegetation structure are increasingly modified (Benítez-Malvido 1998; Laurance *et al.* 1998, 2000; Hill & Curran 2003; Arroyo-Rodríguez & Mandujano 2006a), potentially decreasing the quality and quantity of food resources for primates (Arroyo-Rodríguez & Mandujano 2006b). Furthermore, the magnitude of the negative fragmentation effects on the surviving fauna increases in small forest fragments due to anthropogenic activities, such as logging and hunting (Peres 1997, 2001; Chapman *et al.* 2000; Chiarello & de Melo 2001). Therefore, populations living in small fragments have higher probability of extinction (Hanski 1999).

Evidence from several primate species, including howler monkeys, suggests that < 10-ha fragments have little probability of being occupied (Cowlishaw & Dunbar 2000, Gilbert 2003, Mandujano & Estrada 2005, Mandujano *et al.* 2006). For instance, Cowlishaw and Dunbar (2000) reported that extinction rates of three primate species increased sharply when primates inhabited < 10-ha forest fragments in the Tana River, Kenya, whereas in Manaus, Brazil, Gilbert (2003) found higher number of primate species and groups in 10-ha and 100-ha fragments than in 1-ha fragments. Nevertheless, in some tropical regions the remaining forests are mainly represented by small habitat fragments scattered in human-dominated landscapes that can, however, support many native animal and plant species (Chiarello 2003, Daily *et al.* 2003, Mayfield & Daily 2005, Arroyo-Rodríguez & Mandujano 2006a). It is important to determine the key factors influencing the presence of particular species in these very small fragments as in some cases these fragments may represent the only remaining habitat for several species. Therefore, this information may help in designing management and conservation strategies.

Numerous studies have shown that fragment size and isolation are important spatial attributes in determining the presence (Chapman *et al.* 2003, Gilbert 2003, Wieczkowski 2004, Anzures-Dadda & Manson 2006) and abundance (Chiarello & de Melo 2001, Wieczkowski 2004, Martins 2005) of primates. However, evidence shows that, apart from fragment size and isolation, other habitat attributes, such as food resources play an important role in the occupation of fragments by several animal species including primates (Fleishman *et al.* 2002, Mbora & Meikle 2004, Anzures-Dadda & Manson 2006, Rode *et al.* 2006, Worman & Chapman 2006). Some studies have shown that the presence and abundance of primates are related to vegetation attributes, such as the diversity, abundance, and basal area of top food resources (Estrada &

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Coates-Estrada 1996, Balcomb *et al.* 2000, Cristóbal-Azkarate *et al.* 2005). In addition, for many primates, the number and size of trees correlate positively with primate abundance (Medley 1993, Mbora & Meikle 2004, Wieczkowski 2004, Anzures-Dadda & Manson 2006, Worman & Chapman 2006).

Due mainly to habitat loss and fragmentation, populations of the Mexican mantled howler monkey (*Alouatta palliata mexicana*) have declined drastically by 73–84 percent (Cuarón 1997), and this subspecies has been recently classified as critically endangered by the International Union for Conservation of Nature and Natural Resources (IUCN) (Cuarón *et al.* 2003). The populations of the Los Tuxtlas region, southeast Mexico, are the northernmost of the Neotropics (Estrada & Coates-Estrada 1996). This region has been severely fragmented during the last 60 yr (Dirzo & García 1992), and the remaining howler populations are isolated, inhabiting archipelagos of forest fragments that vary in size, degree of isolation, and habitat quality (Estrada & Coates-Estrada 1996, Cristóbal-Azkarate *et al.* 2005, Mandujano *et al.* 2006). To understand how the remaining howler populations can persist in small rain forest fragments, it is critical to identify which are the key habitat attributes favoring the distribution of howlers in this highly diverse but vanishing tropical system.

Studies at Los Tuxtlas have shown that the presence and abundance of howlers are positively related to fragment size and negatively related to fragment isolation (Estrada & Coates-Estrada 1996, Arroyo-Rodríguez *et al.* 2005, Cristóbal-Azkarate *et al.* 2005, Mandujano *et al.* 2006). However, little is known about the effect of habitat quality on fragment occupation (but see Estrada & Coates-Estrada 1996, Cristóbal-Azkarate *et al.* 2005).

Within the genus *Alouatta*, *A. palliata* has the largest home ranges (Bicca-Marques 2003) and howler troops at Los Tuxtlas have been shown to occupy an average home range of 28 ha (Cristóbal-Azkarate & Arroyo-Rodríguez 2007). Therefore, < 10-ha fragments could be considered unsuitable habitat, and it is highly relevant for the conservation of this endangered subspecies to study the factors favoring the occurrence of primates in these small fragments. In this study, we analyzed 18 very small (< 10-ha) fragments of Los Tuxtlas region to: (1) identify differences in vegetation structure and composition that could explain the distribution of howlers in these fragments; and (2) discuss some management implications for the conservation of this subspecies.

METHODS

STUDY AREA.—Los Tuxtlas region is in the southeast of the Veracruz state, Mexico (18°8′–18°45′ N, 94°37′–95°22′ W). The region, representing the northernmost tropical rain forest in the Neotropics, was decreed a Special Biosphere Reserve in 1998 (Diario Oficial de la Federación 1998) because of its great biodiversity (Dirzo & García 1992). The Biosphere Reserve covers an area of 155,122 ha, 19 percent of which corresponds to three core zones located mainly 600-m asl (Laborde 2004). The original dominant vegetation type below 700-m asl is tropical rain forest that has been heavily deforested and the remaining forest fragments are surrounded by a matrix of pastures and croplands (Castillo-Campos & Laborde 2004).

The fragments used in this study are located within three landscape units in the Los Tuxtlas region and are 0–400 m asl. The landscapes are naturally limited by the coast of the Gulf of Mexico and large rivers (Arroyo-Rodríguez *et al.* 2005). The landscapes were previously digitalized through ArcView 3.2 (Environmental System Research Institute, Inc., Redlands, CA, U.S.A.) software using aerial photographs (1:20,000), ortophotos, digital data, and field information (Arroyo-Rodríguez *et al.* 2005). Taking into account the pattern and rates of deforestation in the Los Tuxtlas region between 1972 and 1993 (Guevara *et al.* 2004), we assumed that all fragments studied were approximately of the same age and therefore this variable was not considered in the analysis.

STUDY SPECIES.—The Mexican mantled howler monkey (*Alouatta palliata mexicana*) has a natural distribution ranging from southeast Mexico to southern Guatemala (Rylands *et al.* 2006). The species is principally arboreal, and devotes about 50 percent of its feeding time consuming fruits (Milton 1980, Cristóbal-Azkarate & Arroyo-Rodríguez 2007). The species shows great fluctuations in population size (Fedigan *et al.* 1998; Zucker & Clarke 2003; Arroyo-Rodríguez *et al.*, in press), and social groups are characterized as multi-male–multi-female with both sexes dispersing (Jones 1980, Crockett & Eisenberg 1987, Arroyo-Rodríguez *et al.*, in press). Nevertheless, it is known that their movement capacity between forest fragments is limited, especially when the surrounding matrices are cattle pastures or croplands as in the present study site (Estrada & Coates-Estrada 1996, Mandujano *et al.* 2004, Anzures-Dadda & Manson 2006). The combination of these features makes *A. p. mexicana* a particularly sensitive species to the loss, transformation, and fragmentation of its habitat (see Henle *et al.* 2004).

FRAGMENT SELECTION.—The studied fragments were selected from a total of 45 randomly selected (range size ≤ 1–266 ha), 33 of which were < 10 ha (Arroyo-Rodríguez *et al.* 2005). Only 9 of the 33 small fragments were occupied by howlers. To isolate the effects of habitat quality from those of fragment size and isolation on the occurrence of primates in fragments, we selected nine small (< 10-ha) unoccupied fragments that did not differ significantly in size, shape, and isolation from occupied small fragments (Table 1). When two or more unoccupied small fragments had similar spatial characteristics we randomly selected one.

HABITAT ATTRIBUTES.—From January 2004 to May 2005, we collected data on 15 vegetation attributes for all fragments (Table 2). Vegetation was sampled following Gentry's (1982) protocol. We chose this method because it is logistically simple, it is economical (in both time and money), and it is appropriate for the analysis of species diversity in tropical forests (see Gentry 1982: 18–21, and the individual-based species accumulation curves for plant species in 15 forest fragments of our study area [Arroyo-Rodríguez & Mandujano 2006a]). To consider the heterogeneity in vegetation attributes within the fragments, ten 50 × 2 m transects were randomly located in each fragment. All tree, shrub, and liana species with diameter at breast height (dbh) ≥ 10 cm were recorded. Because the dominance of different ecological groups and dbh categories can

TABLE 1. *Differences in spatial attributes (mean ± SD) between occupied (N = 9) and unoccupied (N = 9) small rain forest fragments at Los Tuxtlas, Mexico.*[a]

Spatial attributes	Occupied fragments	Unoccupied fragments	χ^2
Fragment size (ha)	4.7 ± 2.5	4.0 ± 2.1	0.55 ns
Shape index[b]	2.1 ± 0.6	1.9 ± 0.6	0.49 ns
Distance to nearest fragment (*m*)	106 ± 205	165 ± 170	0.49 ns
Distance to nearest occupied fragment (*m*)	882 ± 1903	487 ± 605	0.40 ns
Distance to nearest village (*m*)	1433 ± 1052	1228 ± 1231	0.16 ns

[a]Differences were tested with analysis of deviance (df = 1, in all cases); ns = not significant ($P > 0.05$).
[b]$SI = P/2\sqrt{A\pi}$; where P and A are the fragment perimeter and area (*m*), respectively (Forman & Godron 1986). This index takes values equal to 1 when the fragment is round and increases to a maximum of 5 when the shape is highly irregular.

TABLE 2. *Differences in vegetation attributes (mean ± SD) between occupied (N = 9) and unoccupied (N = 9) rain forest fragments at Los Tuxtlas, Mexico.*[a]

Vegetation attributes	Occupied	Unoccupied	χ^2
Total species richness	35.8 (3.3)	34.7 (9.4)	0.1 ns
Richness of pioneer species	11.1 (2.7)	8.8 (4.7)	1.5 ns
Richness of persistent species	24.0 (3.0)	25.2 (6.4)	0.3 ns
Richness of top food species	9.7 (7.0)	7.3 (2.3)	1.2 ns
Density (plants/1000 m^2)	75.4 (17.4)	74.7 (25.6)	0.0 ns
Density of pioneer species (plants/1000 m^2)	27.2 (6.2)	27.3 (13.3)	0.0 ns
Density of persistent species (plants/1000 m^2)	47.3 (17.3)	46.6 (24.2)	0.0 ns
Density of top food species (plants/1000 m^2)	16.7 (7.0)	12.6 (4.3)	2.3 ns
dbh range 1(plants/1000 m^2)	40.4 (12.2)	44.2 (17.5)	0.3 ns
dbh range 2 (plants/1000 m^2)	31.6 (8.3)	28.0 (10.6)	0.6 ns
dbh range 3 (plants/1000 m^2)	5.2 (2.4)	2.9 (1.8)	4.4**
Total basal area (m^2)	6.7 (2.0)	4.5 (1.5)	7.6***
Basal area of pioneer species (m^2)	0.4 (0.8)	0.7 (1.2)	3.4*
Basal area of persistent species (m^2)	5.4 (1.7)	3.8 (1.5)	5.0**
Basal area of top food species (m^2)	2.7 (1.5)	1.5 (0.8)	5.6**

[a]Differences were tested with analysis of deviance (df = 1, in all cases).
*$P < 0.1$; **$P < 0.05$; ***$P < 0.01$; ns = not significant. Diameter at breast height (dbh) ranges: 1 = 10–30 cm, 2 = 31–60 cm, 3 = > 60 cm; species richness = total number of plant species found.

be indicative of different vegetation disturbances (Benítez-Malvido 1998; Laurance *et al.* 1998, 2000; Arroyo-Rodríguez & Mandujano 2006a), plant species were classified into three dbh categories (≥ 10–30 cm, ≥ 31–60 cm, and ≥ 60 cm; Arroyo-Rodríguez & Mandujano 2006b), and into two ecological groups: pioneer and persistent or nonpioneer (Ibarra-Manríquez *et al.* 2001). Although we recognize that there is no universally accepted categorization for tree regenerative guilds in the tropics (Swaine & Whitmore 1988), this categorization has been used in numerous studies carried out in Los Tuxtlas (Martínez-Ramos *et al.* 1989; Ibarra-Manríquez *et al.* 2001; Arroyo-Rodríguez & Mandujano 2006a, b). Pioneer species need intense light during the first stage of growth, establishing only under canopy gaps and forest edges. These species may persist in the forest under more diffuse light, such as older light gaps or the periphery of recent light gaps. Persistent species establish, and in some cases can mature and reproduce, under conditions of shade after the canopy has closed. We classified species following *Flora de Veracruz* and *Neotropical Flora*, as well as from numerous plant species lists (see further details in Arroyo-Rodríguez & Mandujano 2006a, b).

We pooled the transect data for each fragment and treated each fragment as a unit for all subsequent analyses. For each fragment, we quantified species richness, density, and basal area for all plant species. Based on a recent review on the diet of howler monkeys in Los Tuxtlas (Cristóbal-Azkarate & Arroyo-Rodríguez 2007), we selected the plant species that constituted > 80 percent of total feeding time and that were present in our studied fragments. We considered these species as the top food species (Table 3). Based on the sum of density (trees/9000 m^2), frequency (number of transects in which each species appeared/90 transects), and dominance (total basal area for each species in the 9000 m^2), the importance value index (IVI) was calculated for each plant species in fragments with and without howler monkeys (Moore & Chapman 1986). This index provides a more precise understanding of the importance of different plant species in the fragments.

DATA ANALYSIS.—Differences in spatial and vegetation attributes between occupied and unoccupied fragments were tested with analysis of deviance (ANODE). ANODE is a statistical test analogous to analysis of variance (ANOVA). However, whereas in ANOVA the data must be normally distributed, that is, the distribution of residuals must be normal, in ANODE the structure of the error distribution is analyzed by a link-function, which is related to a specific distribution function (*e.g.*, Poisson, gamma, binomial). We analyzed count and continuous variables by generalized linear models (Crawley 2002). Thus, we selected a Poisson distribution with a log link-function to analyze plant species richness and density (count variables), whereas basal area (continuous variable) was analyzed with a normal error and identity link-function (Crawley 2002). For Poisson errors, we checked and corrected for overdispersion (Crawley 2002). All analyses were performed using the S-Plus Program for Windows, version 2000 (Anonymous 1999).

TABLE 3. *The importance value index (IVI) of the top food species for howler monkeys in 18 small forest fragments (9 occupied by howler monkeys and 9 unoccupied) at Los Tuxtlas, Mexico*

Family	Species[a]	IVI Occupied	IVI Unoccupied
Anacardiaceae	*Spondias* spp.	4.74	8.70
	Tapirira mexicana	2.16	4.94
Annonaceae	*Rollinia mucosa*	3.43	9.58
Burseraceae	*Bursera simaruba*	6.77	6.10*
Caesalpinaceae	*Cynometra retusa*	1.49	3.47
	Dialium guianense	1.43	3.66
Cecropiaceae	*Cecropia obtusifolia*	9.52	2.86*
Combretaceae	*Terminalia amazonia*	6.42	3.56*
Ebenaceae	*Diospyros digyna*	0.56	0*
Fabaceae	*Dussia mexicana*	2.11	1.16*
	Lonchocarpus cruentus	2.79	1.52*
	Platymiscium pinnatum	1.09	0.57*
	Pterocarpus rohrii	5.63	1.26*
Lauraceae	*Nectandra ambigens*	0	2.14
Mimosaceae	*Albizia purpusii*	1.82	0*
	Inga acrocephala	0.67	0.43*
Moraceae	*Brosimum* spp.	21.86	1.55*
	Ficus spp.	4.64	10.02
	Poulsenia armata	2.99	6.37
	Pseudolmedia oxyphyllaria	6.39	1.66*
	Total	86.51	69.56

*Indicates the cases in which IVI was greater in occupied than in unoccupied forest fragments.

[a]*Spondias* spp. = *S. mombin*, *S. radlkoferi*; *Brosimum* spp. = *B. alicastrum*, *B. lactencens*; *Ficus* spp. = *F. eugeniaefolia*, *F. lundellii*, *F. oerstediana*, *F. petenensis*, *F. tecolutensis*, *F. yoponensis*.

RESULTS

We recorded a total of 1351 plants, from 194 species, within 51 families in a sampled area of 18,000 m^2, distributed in the 18 selected fragments. We identified 99.3 percent of plants to species. The families with the highest number of individuals were Euphorbiaceae (11.8% of all plants recorded), Moraceae (7.3%), Lauraceae (4.4%), Anacardiaceae (4.1%), and Annonaceae (4.1%). We found that certain pioneer species were notably abundant, representing 13 percent of all plants recorded (Table 4): *Croton schiedeanus* (Euphorbiaceae), *Siparuna andina* (Monimiaceae), *Myriocarpa longipes* (Urticaceae), *Hampea nutricia* (Malvaceae), *Cecropia obtusifolia* (Cecropiaceae).

Both occupied and unoccupied fragments presented top food species for howlers (Table 4). However, the IVI of top food species was greater in the occupied (IVI = 85.5) than in the unoccupied (IVI = 69.6) fragments (Table 3). It was interesting that both *Brosimum alicastrum* (Moraceae) and *C. obtusifolia* (Cecropiaceae) were found among the four most important plant species of the occupied fragments (Tables 3 and 4).

Considering the 15 vegetation attributes analyzed, only four attributes significantly differed between occupied and unoccupied fragments (Table 2). Occupied fragments presented greater total basal area (Wald $\chi^2 = 7.6$, df = 1, $P = 0.006$), greater basal area of top food species (Wald $\chi^2 = 5.6$, df = 1, $P = 0.02$), greater basal area of persistent species (Wald $\chi^2 = 5.0$, df = 1, $P = 0.03$), and greater density of large trees (dbh > 60 cm) (Wald $\chi^2 = 4.4$, df = 1, $P = 0.04$) than unoccupied ones (Table 2).

DISCUSSION

As the occupied and unoccupied fragments showed no significant differences in size, shape, and degree of isolation (Table 1), we expected few differences in vegetation attributes between the two types of fragments (Benítez-Malvido 1998; Laurance *et al.* 1998, 2000; Hill & Curran 2003; Arroyo-Rodríguez & Mandujano 2006a). However, we found that some important vegetation attributes differed significantly between occupied and unoccupied fragments, which could explain the presence of howlers in some of the small fragments. Occupied fragments showed greater density of large trees (dbh > 60 cm) and greater basal area than unoccupied fragments. In particular, basal area in occupied fragments was greater for persistent species characteristic of old-growth forests and for the top food tree species. These findings suggest that, even for small fragments, the presence of large trees and trees of the top food species influence howler distribution in the strongly fragmented landscapes of Los Tuxtlas.

Other studies have also shown that the presence and abundance of several primate species are strongly associated with basal area and with the presence of the most important food resources (Balcomb *et al.* 2000, Juan *et al.* 2000, Stevenson 2001). The lack of large trees may reduce the food availability for numerous animal species (see Coates-Estrada & Estrada 1986, Shanahan *et al.* 2001), because larger trees (measured through basal area) produce a greater amount of food resources than smaller ones (Chapman *et al.* 1992). Studies from the Old-World showed that the number of large trees in a given forest area is positively related to the number of primates (Medley 1993, Mbora & Meikle 2004, Wieczkowski 2004, Worman & Chapman 2006). As availability of food resources decreases, so does the carrying capacity of the fragment (see Medley 1993, Wieczkowski 2004).

Evidence suggests that howlers feed from a wide variety of plant species but generally, they spend most of their time feeding on a small, selected number of species (Milton 1980, Bicca-Marques 2003, Cristóbal-Azkarate & Arroyo-Rodríguez 2007). The IVI values of the top food species in our study were greater in occupied fragments. In the Yucatán Peninsula, howlers (*Alouatta pigra*) are more abundant in forests dominated by *B. alicastrum*, an important food species, than in other vegetation types (J. Cristóbal-Azkarate, pers. comm). Worman and Chapman (2006) demonstrated that forest areas used by blue monkeys (*Cercopithecus mitis*) and gray-cheeked mangabeys (*Lophocebus albigena*) in Kibale

TABLE 4. *The ten plant species with the highest importance value indices (IVI) within occupied and unoccupied small forest fragments by howler monkeys at Los Tuxtlas, Mexico.*[a]

Species	Family	EG	Abundance	Basal area (m^2)	IVI	Top food
Occupied fragments ($N = 9$)						
Brosimum alicastrum	Moraceae	Pers	16	8.87	19.62	Yes
Dendropanax arboreus	Araliaceae	Pers	25	3.14	11.43	
Myriocarpa longipes	Urticaceae	Pion	35	0.89	10.61	
Cecropia obtusifolia	Cecropiaceae	Pion	26	1.15	9.52	Yes
Orthion oblanceolatum	Violaceae	Pers	18	0.98	7.34	
Cordia alliodora	Boraginaceae	Pers	8	2.75	7.55	
Pseudolmedia oxyphyllaria	Moraceae	Pers	20	1.42	6.39	Yes
Hampea nutricia	Malvaceae	Pion	25	0.96	8.34	
Terminalia amazonia	Combretaceae	Pers	3	2.19	6.42	Yes
Siparuna andina	Monimiaceae	Pion	26	0.64	5.43	
Unoccupied fragments ($N = 9$)						
Vochysia guatemalensis	Vochysiaceae	Pers	48	3.94	20.97	
Croton schiedeanus	Euphorbiaceae	Pion	47	1.55	16.32	
Dendropanax arboreus	Araliaceae	Pers	21	1.59	10.63	
Rollinia mucosa	Annonaceae	Pers	15	1.91	9.58	Yes
Spondias radlkoferi	Anacardiaceae	Pers	14	1.57	8.20	Yes
Alchornea latifolia	Euphorbiaceae	Pers	17	1.30	8.01	
Poulsenia armata	Moraceae	Pers	10	1.37	6.37	Yes
Cymbopetalum baillonii	Annonaceae	Pers	17	0.61	6.30	
Siparuna andina	Monimiaceae	Pion	17	0.31	6.14	
Bursera simaruba	Burseraceae	Pers	9	1.25	6.10	Yes

[a]Species that are top food resources for howlers are indicated. Ecological groups (EG): Pion = pioneer species, Pers = persistent species.

National Park, Uganda, had higher basal area and densities of food resources than unused areas of the forest. Similarly, we found that important food species, such as *B. alicastrum*, *C. obtusifolia*, *Pseudolmedia oxyphyllaria*, *Lonchocarpus cruentus*, *Pterocarpus rohrii*, and *Dussia mexicana* were larger and much more abundant within occupied fragments, suggesting that the loss of these species can influence the distribution of howlers in very small fragments of Los Tuxtlas.

As has been reported for other tropical fragmented areas (Benítez-Malvido 1998; Hill & Curran 2003; Arroyo-Rodríguez & Mandujano 2006a, b), the fragments in our study presented a high density and richness of pioneer species. Nevertheless, howlers showed preference for fragments with greater basal area of persistent species. Studies at Los Tuxtlas (reviewed by Cristóbal-Azkarate & Arroyo-Rodríguez 2007) showed that while many plant species consumed by howlers are pioneer species, they principally consume persistent forest species. Although the ability of primates to forage on secondary vegetation has often been cited as a key explanation for their capacity to survive in small fragments (Lovejoy *et al.* 1986, Chiarello 2003, Gilbert 2003, Cristóbal-Azkarate *et al.* 2005), our findings highlight the importance of persistent tree species on primate survival in small fragments.

Edge effects are stronger in small fragments than in larger ones (Laurance & Yensen 1991, Malcolm 1994), resulting in increased mortality of big trees (Laurance *et al.* 1998, 2000) that could decrease the quality and quantity of food resources for howlers in the long term (Arroyo-Rodríguez & Mandujano 2006b). Furthermore, hunting pressure could be more intense in the smallest fragments, where primates are easily found and targeted (Peres 1997, 2001; Chiarello & de Melo 2001). In our study, all fragments selected were of a similar size and distance from human settlements, therefore hunting pressure is unlikely to be the principal factor explaining howler distribution within these fragments.

The strong relationships between occupancy, the density of large trees (dbh > 60 cm), the total basal area, the basal area of persistent species, and the basal area of top food plant species are useful management tools to be considered in conservation efforts. We support the idea that even forest fragments of a few hectares are unquestionably valuable for primate conservation in tropical regions, such as Los Tuxtlas, where small fragments are the only remaining habitat for numerous plant and animal species, some of which are unique to this region (Castillo-Campos & Laborde 2004, Arroyo-Rodríguez & Mandujano 2006a). In Los Tuxtlas, the largest forest fragments are located above 700-m asl (Mendoza *et al.* 2005) falling outside the distribution range of howler monkeys (Estrada & Coates-Estrada 1996). Therefore, it is necessary to restore the small- and medium-sized fragments on the lowlands of the Biosphere Reserve. Such action could diminish numerous edge effects that contribute to the death of big trees (Malcolm 1994; Laurance *et al.* 1998, 2000).

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