



Resource Use in a Landscape Matrix by an Arboreal Primate: Evidence of Supplementation in Black howlers (*Alouatta pigra*)

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Abstract Across the tropics, landscapes of continuous rain forest are being replaced by forest fragments embedded in a matrix of pastures and farmlands. This conversion has endangered many species, including arboreal primates. Species vary, however, in how they are able to supplement their diets from the matrix, although this is rarely studied in primates. We studied two groups of black howlers (*Alouatta pigra*) for a total of 1156 h, one inhabiting a smaller fragment (0.4 ha) and the other a larger fragment (20 ha). Monkeys inhabiting the smaller fragment spent more time in the matrix than in the habitat fragment, spending 50 % of their time (335 of 667 h) in an abandoned mango (*Mangifera indica*) plantation, 8.8 % in scattered trees, and 0.2 % in pastures. In contrast, monkeys in the larger fragment spent 75 % of their time (368 of 489 h) in the forest fragment and only 25 % of their time in the matrix. Feeding in the matrix accounted for 53 % and 12 % of the foraging time for groups in the smaller and larger fragments respectively. We suggest that *Alouatta pigra* can use resources in

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the matrix to supplement their diet by means of crop raiding or taking other resources in many fragmented landscapes and that this may be true also for many fragment-dwelling primates. It is important to include a consideration of the matrix in conservation planning, considering both the total resources available to primates and the consequences of crop raiding for farmers.

Keywords Behavior · Dietary supplementation · Food · Fragmented landscapes · Matrix

Introduction

Deforestation, mainly the conversion of tropical forests into agricultural land, is showing signs of decreasing in a number of countries, but continues at an extremely high rate in others (FRAG 2010). Both deforestation and recovery from deforestation may lead to the fragmentation of animal habitats. Deforestation involves the elimination of areas important for the continuity of ecological processes of one or more species, whereas fragmentation creates discontinuity in the habitat and isolation in fragments surrounded by a matrix of anthropogenic vegetation, such as pasture, agricultural crops, and forest plantations (Declerck *et al.* 2010; Fischer and Lindenmayer 2007; Laurance *et al.* 2000; Manning *et al.* 2006; Markovchick-Nicholls *et al.* 2008; Naranjo 2003). Over the past decade, 130 million hectares of forest have disappeared worldwide, but 78 million hectares have been recovered, mainly by planting forest or by natural expansion of forests (FRAG 2010). This situation threatens the conservation of many species, including many arboreal primates, many of which are at risk of extinction as a result of fragmentation (Cowlshaw and Dunbar 2000).

Several researchers argue that fragmented habitats are able to sustain species capable of exploiting resources in anthropogenic habitats (Daily *et al.* 2003; Petit and Petit 2003; Sekercioglu *et al.* 2007). Primates can feed in a number of anthropogenic habitats, such as live fences, trees scattered across anthropogenic landscapes, cropland, plantations, and orchards (Asensio *et al.* 2009; Baranga *et al.* 2012; Bonilla-Sánchez *et al.* 2012; Estrada *et al.* 2006). However, the use of some of these habitats, e.g., cropland, is associated with considerable risk (Campbell-Smith *et al.* 2011). Such use has been termed landscape supplementation, i.e., the use of the same resource or one of different quality from nearby patches within the same landscape (*sensu* Dunning *et al.* 1992). However, primate research has focused on behavior in fragments and has generally not attempted to understand the complex mosaic of vegetation in which fragments are embedded, i.e., the matrix (Chapman and Peres 2001; Gascon *et al.* 1999; Ricketts 2001). There is little research on landscape supplementation for primates (*cf.* Asensio *et al.* 2009), and there is a need to investigate this in primates living in fragmented habitats and to examine the use of the surrounding matrix.

The matrix represents a landscape component that can function as a filter, facilitating the survival of some species but not others (Gascon *et al.* 2000). For several decades, it has been suggested that arboreal species such as howlers never descend to the ground, as they obtain their water and nutrients from arboreal leaves and fruits.

Thus, it was concluded that the landscape matrix was largely inhospitable and acted solely as a barrier (Glander 1975; Milton *et al.* 1979; Nagy and Milton 1979). However, concurrent with the rapid conversion of rain forests into pastures and cropland, some arboreal primates, including howlers (*Alouatta* spp.), colobus (*Colobus* spp.), and red-tailed monkeys (*Cercopithecus ascanius*) have been documented to exploit terrestrial resources (Anderson *et al.* 2007; Bicca-Marques and Calegario-Marques 1995; Naughton-Treves 1998; Naughton-Treves *et al.* 1998; Pozo-Montuy and Serio-Silva 2007; Pozo-Montuy *et al.* 2011). Thus, some primates can be ecologically and behaviorally flexible in response to environmental perturbations (Arroyo-Rodríguez and Dias 2009; Campbell-Smith *et al.* 2011; Dela 2011; Estrada *et al.* 2012). For example, the conversion of rain forests to agricultural croplands has permitted some primates to exploit the crops growing in the matrix (Cowlshaw and Dunbar 2000; Naughton-Treves *et al.* 1998). Thus, the matrix provides alternative foods (supplements) for folivorous species, such as colobus monkeys (Harris and Chapman 2007; Reynolds *et al.* 2003) and frugivorous/insectivorous monkeys, such as masked titi monkeys (*Callicebus nigrifrons*: Trevelin *et al.* 2007) or red-tailed monkeys (*Cercopithecus ascanius*: Baranga *et al.* 2012; Naughton-Treves *et al.* 1998). For example, exotic tree species such as mango (*Mangifera indica*), tamarind (*Tamarindus indica*), and citrus (*Citrus* spp.), as well as eggs from domestic birds, can provide food derived from the matrix for *Alouatta caraya* (Bicca-Marques and Calegario-Marques 1994; Bicca-Marques *et al.* 2009; Mattjie-Prates and Bicca-Marques 2008). Further, these primates can establish themselves and reproduce in cocoa plantations (*Theobroma cacao*: Baranga *et al.* 2012; Muñoz *et al.* 2005) and eucalyptus forests (*Eucalyptus* spp.: Bonilla-Sánchez *et al.* 2012). A recent review (Estrada *et al.* 2012) documented that 57 primate taxa from four regions — Mesoamerica, South America, Sub-Saharan Africa (including Madagascar), and Southeast Asia — used 38 types of agroecosystems as temporary or permanent habitats. Fifty-one percent of the primate taxa recorded in agroecosystems were classified as Least Concern in the IUCN Red List, but the rest were classified as Endangered (20 %), Vulnerable (18 %), Near Threatened (9 %), or Critically Endangered (2 %) (Estrada *et al.* 2012). In many of these studies, an unusual group structure and the cost–benefit trade-off faced in the matrix (Irwin *et al.* 2009; predation) indicate the need for further research on the use of the matrix (Anderson *et al.* 2007). Similarly, these studies reveal the behavioral flexibility that allows primates to coexist with humans, e.g., changes in temporal foraging patterns. Knowledge of this flexibility could be used to guide the development of specific human–wildlife conflict mitigation strategies to lessen future crop-raiding and conflicts (Campbell-Smith *et al.* 2011).

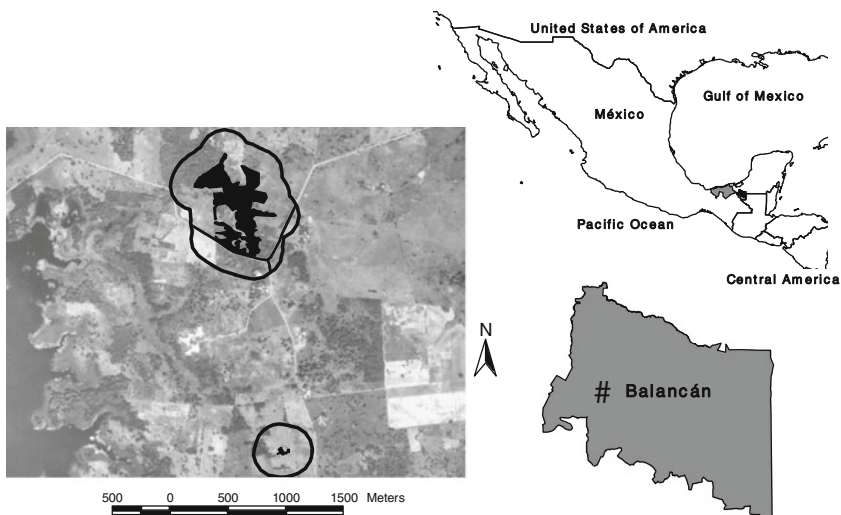
The use of the matrix by black howlers (*Alouatta pigra*) has been poorly studied, relative to other species in the genus, such as *A. palliata* and *A. caraya*, that have been documented feeding on exotic species (*Citrus* sp., *Eucalyptus* sp.) and on large trees found in living fences (Asensio *et al.* 2009; Bicca-Marques and Calegario-Marques 1995). Studies of *Alouatta pigra* have documented them feeding on the ground from vines and seedlings in Balancán in southeastern México (Pozo-Montuy and Serio-Silva 2006; Ramírez-Julian 2010). They have also been reported to occupy the edge between eucalyptus plantations and native vegetation. However, consumption of eucalyptus leaves and flowers represented <1 % of their feeding time (Bonilla-

Sánchez *et al.* 2012). monkeys used plantations of this species of commercial trees most frequently for resting and for accessing other food sources, such as vines (Bonilla-Sánchez *et al.* 2012). however, studies of *Alouatta pigra* in fragmented landscapes are few and the importance of landscape supplementation must be determined (Asensio *et al.* 2009; Dunning *et al.* 1992) to construct informed conservation plans for this species.

We studied two groups of *Alouatta pigra* at Laguna Colorada Ranch, Balancán, Tabasco, México to investigate how arboreal primates exploit resources when residing in a smaller fragment as opposed to larger ones, whether they supplement their diets using resources close to their habitat areas, what environments within the matrix they prefer, how much time they spend in the matrix and what sort of behaviors they engage in, what resources they feed on in the matrix, and whether some elements of matrix are part of the habitat.

Methods

We worked in two fragments of different sizes at Laguna Colorada Ranch, Balancán, Tabasco, México (latitude: 17°44'05"N; longitude: 91°30'17"W): one of 0.4 ha, hereafter referred to as the smaller fragment, and one of 20 ha, the larger fragment (Fig. 1). The original vegetation in the region was described as rain forest, evergreen tropical forest, and spiny evergreen bloodwood (*Haematoxylum campechianum*) forest (López-Mendoza 1980). The government's development plans during the 1960s resulted in increased colonization in the region and land conversion for pasturing livestock and growing crops, all of which caused the loss and fragmentation of the original forest (Pozo-Montuy *et al.* 2008; Reyes-Castillo 1978). The conversion of forests to pasture



Created by: Pozo-Montuy G; Datum wgs84; Orthophotos 1:20 000 Scale; Zone15.

Fig. 1 Geographical location of the study areas in southeastern México. The semicircle in the upper part of the detailed image of the landscape depicts the larger fragment and the semicircle below is a smaller fragment.

has resulted in a loss of moisture and created an unusual climate, with long droughts lasting from February to September (8 month), when historically the dry season was only 3 month from march to may (Moguel and molina-Enríquez 2000). Climate change and land conversion have had another significant impact, as very dry years alternate with extensive flooding and increased silting in rivers, streams, and lakes, which occurs in the absence of forests that would normally retain the soil around bodies of water (Chapman and Chapman 2003; CNA 2010).

We considered a habitat fragment as a forest area of native trees with a continuous canopy having a mean height of ≥ 10 m, excluding live fences (Anzures-Dadda and manson 2007; Mandujano *et al.* 2006; Pozo-Montuy *et al.* 2011; Zunino *et al.* 2007). To describe the matrix, we obtained data from 1:20,000 orthophotos, provided and georeferenced by INEGI in 2008 (Fig. 2; Table I), and measured the coverage within a 200-m-wide buffer zone around the fragment (perimeter) as defined by ArcView 3.3. This 200-m distance was the maximum distance howlers had been observed to walk on the ground away from their habitat fragment to another site in the matrix using isolated trees as stepping stones (*sensu* Mandujano and Estrada 2005; Pozo-Montuy and Serio-Silva 2007; Pozo-Montuy *et al.* 2008). The matrix included scattered trees, live fences, annual crops, perennial crops, barbed wire fences, pastureland, plantations, young secondary vegetation, roads, and water bodies.

Alouatta pigra is mainly tree dwelling and is most frequently found in the upper canopy of the rain forest. Its diet consists of leaves and seasonally available fruit (Pavelka and Knopff 2004; Pozo-Montuy and Serio-Silva 2006). The group residing in the smaller fragment consisted of five individuals (one adult male, two adult females, and two male infants). Locating the focal groups within the area was facilitated by their calls and other characteristics (latrines and specific identifiers for each group, including scars). In addition, data from a concurrent radio telemetry project allowed us to determine the ranging distances for the howlers and thus reduce the search effort required in the matrix. halfway through the study (June 2009) the

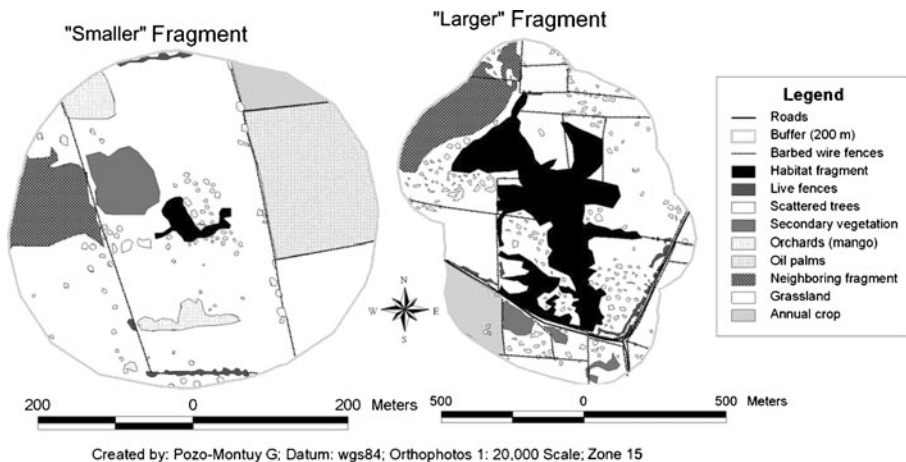


Fig. 2 Digital characterization of the landscape within the buffer area (200 m) around the two habitat fragments of black howler monkeys matrix in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009.

Table 1 A description of the landscape for a large and a small forest fragment in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009

Habitat	HabFrag (ha)	Past (ha)	LF (ha) ^a	Barb (m ^b)	Road (m ^b)	Pcrops (ha)	Acrops (ha)	ScT (ha) ^a	YSV (ha)	Water body (ha)	Total area (ha)
Smaller fragment	0.4	10.9	0.13	1089	0	3.9	0.7	1.35	0.6	0	17.98
Larger fragment	19.82	35.02	0.48	3749	1452.7	0	0	8.37	5.61	0.18	69.48

Areas include the 200-m buffer zone. habFrag = habitat fragment; Past = pasture land; LF = live fences; Barb = barbed wire fences; Road = unpaved road; Pcrops = perennial crops; Acrops = annual crops (plantations); ScT = scattered trees; YSV = young secondary vegetation

^a the area of scattered trees and living fences

^b Refers to lineal meters

group was attacked by feral dogs when they were on the ground, and the dogs killed a female and her offspring. Thus, for the remainder of the study the group consisted of three individuals. The group in the larger fragment consisted of five individuals (one adult male, two adult females, one juvenile female, and one juvenile male), and group size remained constant throughout the study. There were more than ten groups in the larger fragment, of which two were in regular competition with the focal group.

We habituated the groups to our presence for 2 month (January–February 2009) before the initiation of systematic data collection. We collected focal animal behavioral data, changing subjects every 3 h from 06:00 to 18:00 h, for 5–10 d/mo, over 9 mo (March–November 2009). The order in which we observed individuals was random (we first selected the most visible individual and later changed the individual every 3 h). As observations progressed we attempted to balance the number of minutes recorded for each age–sex class per month. We observed only adults and juveniles. We quantified three main activities: feeding, locomotion, and resting. Other common activities were mainly social interactions (play, grooming, courtship, vocalizations, etc.), and we classified these as “other.”

We determined food availability for the smaller and larger fragments by counting all food trees in the 200-m buffer zone that were ≥ 5 cm diameter at breast height (DBH) and in the howler’s diet. This approach assumes that the greater the number of food trees (abundance), the greater the availability of leaves and fruit for monkeys; we did not consider changes in phenology. We determined which species were food trees based on data from this study and another study conducted near our study area (Pozo-Montuy and Serio-Silva 2006).

We used the *Animal movement* extension in Arc View 3.3 (Hooge and Eichenlaub 2000) to determine home ranges using the minimum convex polygon model with all sightings both in and out of the habitat fragments, recording hourly GPS coordinates using a Garmin eTrex Venture. We used the total number of food trees per species in each of the habitats to determine habitat use and preference. We applied the test of goodness of fit χ^2 statistics to test differences between the numbers of food trees counted at different habitats. We calculated the proportion of food trees in each habitat and tested for habitat differences with a goodness of fit test. We used this ratio to calculate Z Bonferroni confidence intervals of 95 %, using the selection or

rejection of habitat types by howlers. We calculated expected usage values for a given habitat (scattered trees, mango plantations, and habitat fragment) by multiplying the ratio of the availability of food trees and the proportion of observation time spent in each habitat type (Byers *et al.* 1984).

We determined the results of the Bonferroni test as follows: when the observed value and confidence intervals were higher than the expected value, we considered the coverage as preferred. If the expected value was within the confidence interval of the observed value, we considered habitats as not different. If the expected value was greater than the observed value and intervals, we considered the habitat as not preferred. We performed this analysis for the group in the smaller fragment, as it used the matrix the most. Finally, we considered elements of what our original definition would consider matrix, but were used a great deal by the howlers, as part of howler habitat. We used the time spent in the mango plantations by season to evaluate if howlers used mango plantations significantly more when the trees were fruiting in comparison with the nonfruiting season using a Kruskal–Wallis nonparametric test. Finally, we reanalyzed habitat preference considering our newly defined elements of howler habitat using the same methods as described earlier.

Results

We observed the group in the smaller fragment for 667 h, during which time the individuals spent 83 % of their time resting, 11 % feeding, and 4 % traveling; they shared the remaining time among social behavior, vocalization, and play. In the matrix (including scattered trees, pastures, and mango plantations), howlers spent 9.7 % of their time feeding, 83.2 % resting, 4.3 % in locomotion, and 2.9 % on other behaviors. These results suggest that the group distributed its time among activities in

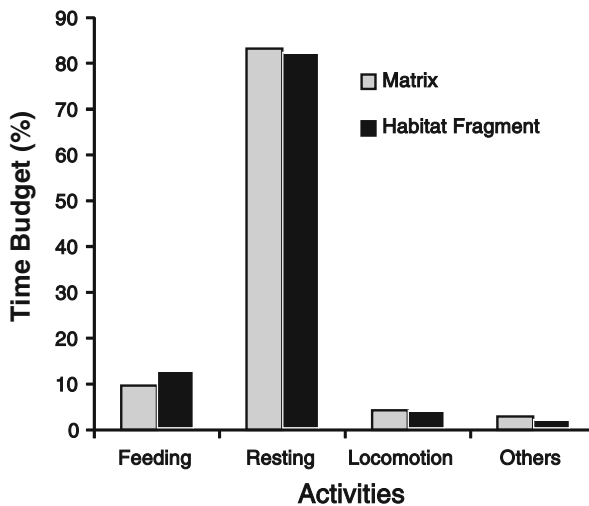


Fig. 3 Time budget of the black howler group inhabiting the smaller fragment compared between periods spent in the fragment and periods spent in the matrix in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009.

a similar manner in the matrix and habitat fragment ($H = 0.0833$, $df = 1$, $P = 0.886$) (Fig. 3). however, monkeys rested 50.2 % of the time when they were in the mango plantation, whereas in scattered trees they rested only 9.4 % of the time.

The group of monkeys in the smaller fragment spent 50.2 % of their time in mango plantations, 40.8 % in the habitat fragment, 8.8 % among scattered trees, and 0.2 % in pastures. Considering the mango plantations as part of howler habitat changes the results considerably: howlers spent 91 % of their time in their habitat (native vegetation and mango plantations) and 8 % in the matrix (pasture and scattered trees). They fed 92.8 % in their habitat and 7.2 % in scattered trees. They rested in 90.6 % in their habitat and 9.4 % in scattered trees in pastures. When feeding on mango (mean DBH $50.7 \pm SD 15.2$ cm) or *Spondias mombin* (mean DBH 40.7 ± 28.7 cm), the monkeys often remained in plantations or in isolated *S. mombin* for a day or two and then returned to the habitat fragment or to the other scattered trees. The time the monkeys spent near the 10 most consumed species accounted for 94.3 % of total time devoted to feeding, and of this, mango was the species most consumed by the monkeys, accounting for 34.3 % of total feeding time (Table II). They spent more time feeding in the mango plantation (86.4 %) than at the scattered trees (13.6 %). There were no significant statistical differences in the amount of time spent in the mango plantations between the fruiting and nonfruiting seasons ($H = 0.0053$, $df = 1$, $P = 0.942$), suggesting that howlers used the mango plantation independent of whether or not fruits were present.

Howlers from the smaller fragment carried out 49 movements on the ground, of which 32 were in pastureland, 10 were in the mango plantations, and 7 were to

Table II The 10 most consumed species by *Alouatta pigra* in the matrix and in the smaller fragment and their availability in the matrix in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009

Consumed species	Total feeding time (hours:minutes)	%	Feeding time in the matrix (hours:minutes)	%	Availability in the matrix (no. of individuals)	DBH (cm)
<i>Mangifera indica</i>	23:01	31.9	22:55	31.8	17	50.7
<i>Spondias mombin</i>	12:32	17.4	1:38	2.3	5	47.7
<i>Enterolobium cyclocarpum</i>	6:23	8.9	1:10	1.6	11	30.6
<i>Guazuma ulmifolia</i>	6:00	8.3	1:05	1.5	49	29.8
<i>Albizia guachapele</i>	4:27	6.2	3:15	4.5	1	27.8
<i>Lonchocarpus hondurensis</i>	3:29	4.8	0:07	0.2	6	13.0
<i>Sapindus saponaria</i>	3:10	4.4	3:10	4.4	1	14.2
<i>Ceiba pentandra</i>	2:03	2.8	2:03	2.8	4	67.7
<i>Cordia alliodora</i>	1:36	2.2	0:00	0.0	19	21.1
<i>Acacia angustissima</i>	1:26	2.0	1:26	2.0	3	31.3
Total time for top 10 consumed species	64:07	88.9	36:49	51.1		
Total time for all consumed species	72:06					

scattered trees. Of these 49 ground displacements, there were seven general routes, of which first route toward the mango plantation represented 24 (49 %) of the movements. The second most common route involved a movement from the mango plantation to scattered trees ($N = 12$), the third most frequent route was from the habitat fragment to scattered trees ($N = 9$), and the other four routes were each used only once. The group used the route between the habitat fragment and the plantation most when the mango trees were fruiting in may and June 2009. They used the route from the habitat fragment to the scattered trees most frequently between September and October, which coincided with the fruiting of *Spondias mombin*. The group that used the smaller fragment went beyond the 20-m buffer to a maximum distance of 312 m (straight-line distance from the edge of the habitat fragment to the farthest point) to use scattered trees beyond the mango plantation. The mean distance that the group moved through pastureland in one movement was 80 ± 10.5 m, with a maximum distance of 95 m and minimum of 5 m.

We observed the group living in the larger fragment for 489 h, of which feeding accounted for 18.5 %, resting for 72.3 %, and locomotion for 6.6 %; the remainder of the time was shared among social behavior, vocalization, and play. In the matrix, this group spent 17 % of its time feeding, 75.4 % resting, 4.8 % in locomotion, and 2.9 % in other behaviors. The distributions of time among activities in the habitat fragment and matrix were similar ($H = 0.00$, $df = 1$, $P = 1.000$) (Fig. 4). The group spent 75.2 % of its time in its fragment and 24.8 % in scattered trees near the edge of its habitat. Feeding in the landscape matrix represented 12.1 % of total feeding time. In the matrix the group fed on *Spondias mombin* for 87.4 % of their feeding time, followed by *Lonchocarpus hondurensis* (7.7 %; Table III). This group used only one foraging route outside its fragment that was in the direction of dispersed trees and moved only

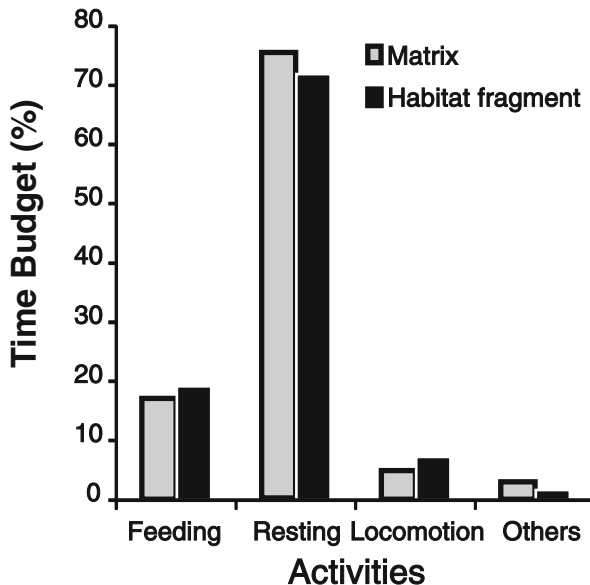


Fig. 4 Time budget of the black howler group inhabiting the larger fragment compared between periods spent in the fragment and periods spent in the matrix in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009.

Table III The 10 species most consumed by *Alouatta pigra* in the matrix and in the larger fragment and their availability in the nearest matrix in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009

Consumed species	Total feeding time (hours:minutes)	%	Feeding time in the matrix (hours:minutes)	%	Available in the matrix (no. of individuals)	DBH (cm)
<i>Spondias mombin</i>	41:47	46.1	9:36	10.6	7	19.7
<i>Lonchocarpus hondurensis</i>	12:10	13.4	0:46	0.8	5	24.8
<i>Maclura tinctoria</i>	6:32	7.2	-		1	16.2
<i>Albizia guachapele</i>	4:13	4.7	0:22	0.4	4	38.5
<i>Ficus</i> sp.	3:53	4.3	-		3	89.4
<i>Cordia alliodora</i>	3:55	4.3	-		2	21.3
<i>Guazuma ulmifolia</i>	3:51	4.2	0:09	0.2	22	26.7
Not tree species ^a	3:35	4.0	0:06	0.1	-	-
<i>Astronium graveolens</i>	3:25	3.8	-		1	24.0
<i>Acacia angustissima</i>	1:49	2.0	-		4	32.7
Total time for top 10 consumed species	85:10	94	10:59	12.1		
Total time for all consumed species	90:36					

^a Represents an exception, presenting higher consumption than some species of trees, in the form of vines and creepers; however, it was not possible to identify how many species were included in this category.

60 m from the fragment. On this route they descended to the ground and crossed an unpaved road and barbed wire fences to reach *Spondias mombin* bearing a very large quantity of fruit. The monkeys never revisited this area when *Spondias mombin* ceased fruiting.

The group living in the smaller fragment had a home range of 0.37 ha when we considered only movements within the fragment, but their home range increased 12 times to 4.59 ha when we also considered movements in the matrix (Fig. 5). In contrast, the group in the larger fragment had a home range of 5.82 ha, taking into account only movements within the fragment, but its home range increased by 10 % (6.40 ha) when we took the monkeys' few movements within the matrix into account.

We detected significant differences between the expected and observed use among habitat fragment, scattered trees, and mango plantation for the group using the smaller fragment ($\chi^2 = 7881.21$, $df = 2$, $P = 0.001$). This group preferred the mango plantation (preference value 0.4; Fig. 6a) compared to the habitat fragment, which had 243 food trees and scattered trees with 91 food trees (Fig. 6a). The mango plantations had only a few food trees (31), and monkeys used these more than expected.

When considering the mango plantation as part of the howlers' habitat, there was still a significant difference between expected and observed habitat use ($\chi^2 = 727.62$,

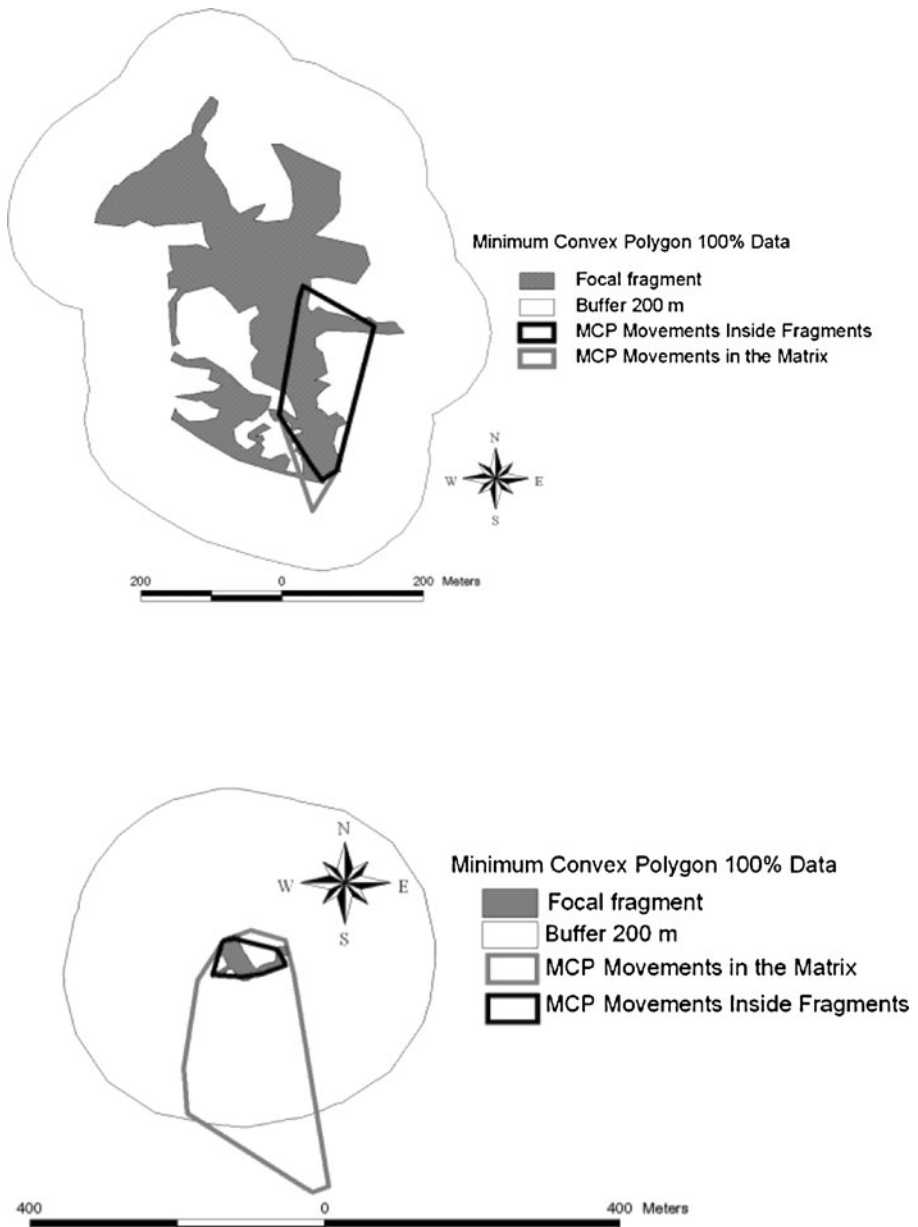


Fig. 5 Home ranges of groups of howlers inhabiting the large (above) and small (down) fragment in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009.

$df = 1$, $P = 0.001$), with monkeys preferring habitats that consisted of fragments of native vegetation with mango plantations over matrix habitats consisting of pastures and scattered trees (preference 0.2) (Fig. 6b).

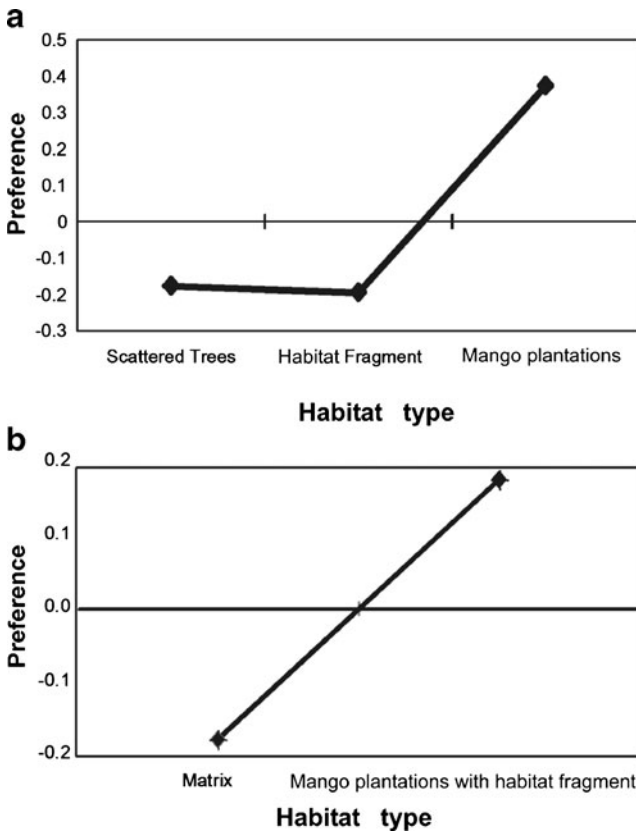


Fig. 6 Feeding preferences by ground cover for the howler group in the “smaller” fragment in Laguna Colorada Ranch, Balancán, Tabasco, México in 2009. Values <0 indicate that coverage is not preferred; values >0 indicate coverage is preferred. The upper plot shows values if mango plantations are considered a part of the matrix and the lower plot if mango plantations are classified as part of the habitat.

Discussion

Our study revealed considerable use of the matrix by an arboreal primate, specifically two black howler groups living in two habitat fragments of different sizes. The use of the matrix appeared to be strongly influenced by the abundance of food in the matrix and monkeys used the matrix when it contained food. By supplementing their diets outside their resident fragments, howlers were able to increase their fruit consumption and therefore likely the quality of their diet. Thus, they supplemented their diet with resources derived from the matrix, via landscape supplementation (Asensio *et al.* 2009; Dunning *et al.* 1992). This may allow populations to be maintained at higher densities or to be viable even when the remaining fragments are small. Our study supports previous statements that a nonhostile or good quality matrix can provide resources permitting animals to survive in fragmented landscapes (Fahrig 2005); however, this likely relates to the structure of the matrix, the displacement capacity of the species, and the landscape connectivity (Pozo-Montuy *et al.* 2011; Taylor *et al.* 1993). Species that manage to leave their fragments when faced with highly disturbed

conditions increase their resistance to adverse habitat changes in their fragments and are more likely to persist relative to species unable to venture into the matrix (Chapman *et al.* 2007; Laurance 1991).

Our results are consistent with another study that established that some of the matrix attributes have a very strong effect on monkey presence (Pozo-Montuy *et al.* 2011). For example, the number of trees providing a valuable supplement to the diet of *Alouatta pigra* in the landscape matrix was positively related to howler presence. Other studies also document a strong association between the presence and abundance of primate species and the presence of their most important food resources (Juan *et al.* 2000; Stevenson 2001). Another study found a growing population of black howlers (*Alouatta pigra*) in eucalyptus plantations (Bonilla-Sánchez *et al.* 2012). Our work, as well as many other investigations of primates in fragmented landscapes, has limitations, such as the small number of groups and conditions evaluated. However, obtaining field data is difficult and the future challenge is to study a larger number of groups and conditions.

Another methodological problem in our and similar studies is the categorization of habitat types, specifically the mango plantation. Like other elements of the landscape, e.g., plantations of *Eucalyptus* spp., one may classify these forested areas as monkey habitat rather than part of the matrix, despite the fact that they are introduced species managed by people. Habitat may be broadly defined as the range of environments suitable for a given species (Hall *et al.* 1997). Thus, it is a species-specific concept that generally refers to broad vegetation types, such as tropical rain forest, tropical dry forest, and cloud forest. Because native vegetation is important for many species, many researchers equate habitat with native vegetation (Fischer and Lindenmayer 2007; Umapathy and Kumar 2003). Nevertheless, primate species may have different habitat requirements and most of them can use resources from many habitats (Bicca-Marques 2003; Michalski and Peres 2005), as well as from a number of agroecosystems (Estrada *et al.* 2006, 2012). Therefore, some elements that traditionally have been considered as part of the matrix could be considered part of an animal's habitat. Based on our finding we now consider the most appropriate definition of a habitat fragment for howlers to be a forest area of native trees with a continuous canopy with an average height of ≥ 10 m, and where there are resources in the matrix within 300 m, including live fences, scattered trees, and orchards. However, we recognize the difficulty in classifying the mango orchard and encourage researchers encountering similar difficulties to present their results to enable readers to evaluate different definitions of habitat fragments.

The inclusion of matrix elements as part of the habitat of howlers increases the home range and reduces the time spent in the matrix 12-fold in the case of the smaller fragment group. Similar patterns have been documented for *Alouatta palliata* in Nicaragua, where the largest home range contained a higher proportion of secondary and recovering vegetation (Williams-Guillén 2003; Williams-Guillén *et al.* 2006). In this sense, it seems that a group must expand its home range to meet its needs in a low-quality environment, allowing individuals to survive in small forest fragments.

Social behavior and food competition have been shown to influence the reproductive capabilities of primates (Jones *et al.* 2008; Kitchen 2004; Snaith and Chapman 2008; Van Belle *et al.* 2008) and may influence the use of the matrix. For example, differences between the numbers of groups in the two fragments may have influenced

the level of feeding competition and thus the value of using the matrix (Rosales-Meda 2008). The quantity and value of the food items in the matrix may be elevated over those in the fragment, as trees in the pastureland are not competing for light and thus may be able to produce more fruit with higher value (Houle *et al.* 2010; Rothman *et al.* 2012). However, the use of the matrix is not without costs. Dogs (*Canis familiaris*) often use the matrix and may kill howlers when monkeys travel on the ground in a stepping stone manner between scattered trees (Candelero-Rueda and Pozo-Montuy 2011). We observed this when a group of feral dogs attacked a female and her young in the group from the small fragment, resulting in the death of the monkeys. Although it is unfortunate that two members of our focal group were killed by dogs, this is valuable data as it replaces statements of possible risk with actual cost. Likewise, crop raiding will promote human–primate conflicts and cause the removal of primates or changes in their survival strategies (Baranga *et al.* 2012; Campbell-Smith *et al.* 2011; Sillero-Zubiri and Switzer 2001).

The consequences of consuming exotic species have not been evaluated extensively. The excessive consumption of domesticated fruits by some primates may create digestive problems to the extent of causing acidosis or even death (Danish *et al.* 2006). For example, a group of mantled howlers (*Alouatta palliata mexicana*) that lived in the La Venta museum Park in Tabasco, México, died from eating mangos that were introduced into the park. An autopsy revealed constipation resulting from large amounts of mango seeds in the monkeys' digestive tracts (Pozo-Montuy *pers. obs.*). The howlers ate the mangos although many other native species were available. Similarly, several species of primates have been documented to eat the leaves and bark of introduced eucalyptus trees, and these plant parts contain phytoestrogens, which are speculated to have a detrimental influence on reproductive function (Wasserman *et al.* 2012). This indicates that as well as considering supplements derived from the landscape, theoretical reflection concerning the nonoptimal movement of animals in anthropogenic landscapes must consider the costs involved in these movements, such as predation risk or dangers associated with the consumption of introduced plant foods.

The processes of habitat loss and fragmentation are considered the most important threats to biodiversity (Declerck *et al.* 2010; Laurance *et al.* 2000; Markovchick-Nicholls *et al.* 2008). Thus, it is clear that we must understand the conservation value of fragments, because they may represent opportunities to make important conservation gains, particularly for species whose ranges are not in protected areas. Our results clearly demonstrate the importance of considering the matrix within which the fragment is embedded in conservation plans, including the nature and type of matrix food and ease of traveling in the matrix, including predation risk.

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