## CHAPTER SEVEN

# Forest Fragmentation and Its Effects on the Feeding Ecology of Black Howlers (*Alouatta pigra*) from the Calakmul Area in Mexico

*Andrómeda Rivera and Sophie Calmé*

## INTRODUCTION

The endemic Mesoamerican black howler monkey (*Alouatta pigra*) is found in the southern states of Campeche, Quintana Roo, parts of Tabasco and northern Chiapas, in Mexico, northern Guatemala, and Belize (Horwich and Johnson, 1986). Although Mexico harbors about 80% of the geographic distribution of *A. pigra*, it is the least studied of the three primate species that exist in Mexico. Until now, studies on this species in Mexico have consisted primarily of population surveys (Estrada *et al.*, 2002a,b, 2004), and a single study about diet and activity pattern (Barrueta, 2003). In the case of Guatemala,

---

**Andrómeda Rivera and Sophie Calmé** • El Colegio de la Frontera Sur, Division of Conservation of Biodiversity, AP 424, Chetumal, Quintana Roo, México.

*New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation*, edited by Alejandro Estrada, Paul A. Garber, Mary S. M. Pavelka, and LeAndra Luecke. Springer, New York, 2005.

population surveys (Coelho *et al.*, 1976 Baumgarten and Hernández, 2002; Estrada *et al.*, 2004), a study on seed dispersal (Ponce-Santizo, 2004) and another on fragmentation (Rosales-Meda, 2003) have been conducted. At present, almost all information on the species comes from Belize, in particular, regarding feeding behavior (Silver *et al.*, 1998, 2000; Pavelka and Knopff, 2004). The restricted distribution of *A. pigra* and the rapid fragmentation and conversion of its natural habitat to pasture lands and agricultural fields place populations of this primate species at risk (Estrada *et al.*, 2004).

This rapid loss of habitat associated with anthropogenic disturbance, such as logging and agriculture, is likely to have a significant impact on howler monkey feeding ecology and patterns of habitat utilization. In particular, the presence of distinct dry and rainy seasons is reported to influence leaf and fruit production by food trees. Typically, fruit production in tropical forests peaks in the late dry season or early rainy season (Janson and Chapman, 1999). This seasonality in food production affects primate behavior, impacting populations most strongly during times of resource limitation (Terborgh, 1986a).

*A. pigra* has been found to respond to variation in seasonal resource abundance by exploiting leaves from January to March and shifting to mostly fruits from April to July, which corresponds to the late dry season and the beginning of the rainy period (Pavelka and Knopff, 2004). Knowledge of the manner in which different primate species respond to seasonal changes in the availability and distribution of resources is critical for developing conservation and management policies. For example, if important feeding and refuge tree species are left standing in selective logging operations, population declines following logging are likely to be lower and/or the speed of recovery more rapid for those primate species requiring these resources (Chapman *et al.*, 2000).

Several studies have reported that the diet of howlers is comprised mainly of fruits, leaves, and flowers belonging to the Moraceae, Fabaceae, Sapotaceae, and Lauraceae families (Milton, 1980; Gaulin and Gaulin, 1982; Estrada, 1984; Julliot and Sabatier, 1993; Stoner, 1996; Estrada *et al.*, 1999). In fragmented habitats with introduced vegetation, they also consume exotic species like oranges, *Citrus sinensis* (Bicca-Marques and Calegaro-Marques, 1994) and mangos, *Mangifera indica* (Fuentes *et al.*, 2003). However, despite the fact that howlers are reported to consume a wide range of plant species, tradeoffs in the availability, distribution, and nutritional quality (i.e. ratio of protein to fiber and toxicity) of these resources suggest that commonly used resources are not necessarily the highest quality resources. In this regard, the words *use* and *selection* have been often applied interchangeably in the ecological literature (Litvaitis *et al.*, 1996). *Use* only indicates the consumption of food, whereas *selection* implies a choice among alternative foods that are available to the forager. Use is selective if components are exploited disproportional to their availability (Litvaitis *et al.*, 1996). Few primate studies have focused on food selection, i.e. using an index of selectivity (Sourd and Gautier-Hion, 1986; Julliot, 1996; McConkey *et al.*, 2002), and only one of them (Julliot, 1996) concerned a species of the genus *Alouatta*. Each of these studies demonstrated that monkeys are selective in their fruit choice using information on fruit color, fruit or seed size, amount of pulp, and water content in foraging decision.

Most forests in fragmented tropical landscapes offer both a reduced and disturbed space where monkeys are left with few opportunities to choose. If we succeed in understanding how black howler monkeys select the trees on which they feed, it should enable us to assess the quality of a fragmented and disturbed habitat for these monkeys. In this chapter, we compared the feeding ecology of five groups of black howler monkeys (*A. pigra*) existing in habitats that differ in land use patterns. Three troops of *A. pigra* were studied in the protected forest of the Calakmul Biosphere Reserve and two troops living in forest fragments managed as extractive reserves in community-owned land adjacent to the reserve. Specifically, we were interested in examining the effects of fragmentation on howlers' diet and determining the basis for selection of food trees using a selectivity index.

## MATERIALS AND METHODS

### Study Area

The Calakmul Biosphere Reserve (CBR) is located in the southeastern part of the state of Campeche in the municipality of Calakmul. It is bordered on the east by the state of Quintana Roo and on the south by Guatemala (17°45′–19°15′ N and 89°08′–90°08′ W; Figure 1). The Calakmul Biosphere Reserve protects the largest area of tropical forest in Mexico. It lies within the most important tropical forest region in North America and it forms part of the Mesoamerican Biological Corridor (Galindo-Leal, 1998).

The reserve covers 723,185 ha of largely homogeneous topography ranging in altitude from 260 to 385 m. It has two core areas, one of 147,915 ha in the southern portion where we worked, and another of 100,345 ha in the northern

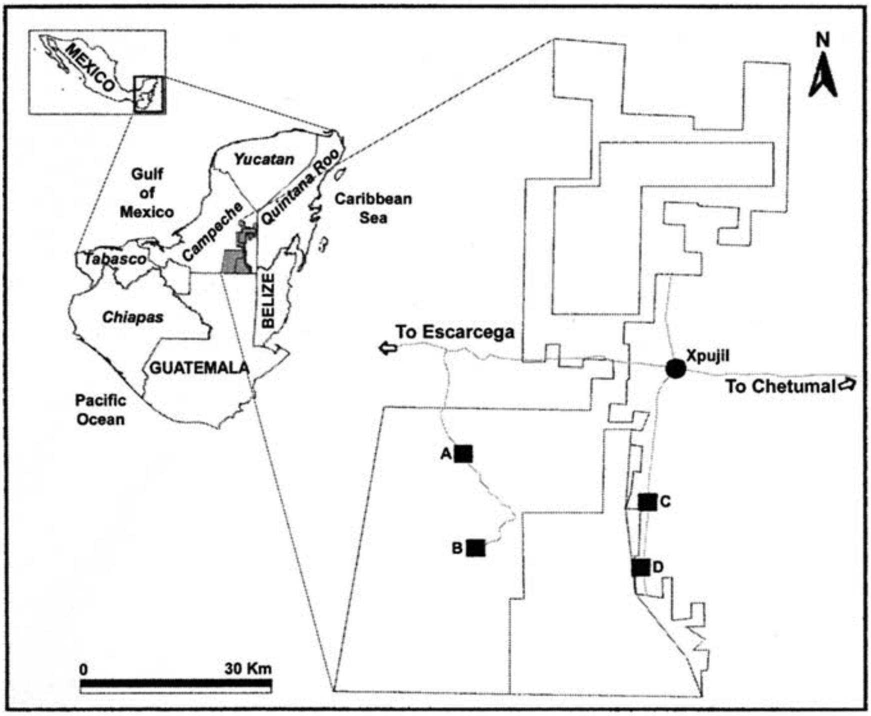

**Figure 1.** Location of study area (in grey) within the region that broadly encompasses black howler monkey's distribution range. Black squares on the main figure represent the location of the study sites within the study area of Calakmul, and letters refer to each site as illustrated in Figure 3; where A, El Sendero Ecológico; B, Mayan Ruins of Calakmul; C, Cristóbal Colón; and D, Once de Mayo.

portion. The buffer area covers the remaining 474,924 ha. Less than 4% of the buffer area is considered disturbed due to human activities. Surrounding the reserve are communal lands, called *ejidos.* Land use in these farming communities consists mainly of small agricultural plots of mixed crops, such as maize, squash, and beans. Some *ejidos*, especially on the southeastern edge of the CBR, also cultivate jalapeño pepper, and all have some cattle ranching (Klepeis and Roy Chowdhury, 2004). The remaining land cover is similar to CBR, i.e. tropical forest. The climate is warm subtropical, with a mean annual temperature of 22–26°C. Rainfall presents a north–south gradient. Annual precipitation ranges from 1200 to 1500 mm in the central portion of the Reserve, to 1500 to 2000 mm in the southern portion (García-Gil *et al.*, 2002). There are two well-marked seasons: the dry season is from December to May and the rainy

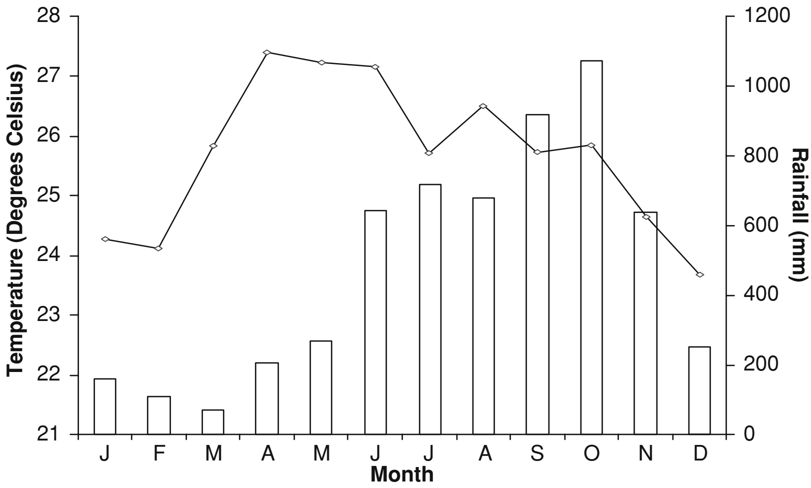

**Figure 2.** Temperature and rainfall collected by the National Water Commission in four sites at Calakmul for the period 1995–1999. Bars indicate mean rainfall, line indicates mean temperature.

season, which concentrates 81% of total rainfall, occurs from June to November (Figure 2).

Vegetation types in the reserve are: (1) tall semi-deciduous forests which reach heights of over 30 m, and cover a surface area of less than 10,000 ha; (2) medium semi-deciduous forests, which range in height from 15 to 25 m and cover the largest area of the reserve (480,000 ha); and (3) short semi-deciduous forests, with tree heights ranging from 4 to 15 m and covering an area of approximately 85,000 ha (Arriaga *et al.*, 2000).

## Study Sites and Focal Troops

Two study sites were located within CBR; that served as controls. The first site is known as El Sendero Ecológico (18°18′58″N, 89°51′23″W), and is situated at 26 km south of the Highway Escárcega-Chetumal (Figures 1 and 3a). The vegetation is medium semi-deciduous forest and tall semi-deciduous forest. When we began the study in February 2003, the troop contained seven individuals (3 females, 1 male, and 3 juveniles). During the second half of the study one infant was born in the troop. The study troop was the only one observed in this site.

The area surrounding the Mayan Ruins of Calakmul (18°06′43″N, 89°48′12″W) is the second study site within CBR (Figures 1 and 3B). It is located 23 km south of the first site, in the center of the southern part of CBR and covers an area of 30 $km^2$ (Estrada *et al.*, 2004). The vegetation is mainly medium semi-deciduous forest. Estrada *et al.* (2004) report the presence of eight howler monkey troops at this site; we studied two of them in different months, depending on whether we could find the main troop. The main troop had seven individuals at the beginning of the study (2 females, 2 males, 2 juveniles, and 1 infant) and eight individuals by the end (one additional newborn), and the second troop had four individuals (1 female, 1 male, and 2 juveniles).

Two other study sites were located outside CBR. The first is in the farming community *ejido* Cristóbal Colón and is a forest fragment 13.9 ha in size (18°11′25″N, 89°26′12″W; Figures 1 and 3C). The second site is located in the farming community *ejido* Once de Mayo, and consists of a forest fragment 11.6 ha in size (18°07′10″N, 89°27′03″W; Figures 1 and 3D). The distance between these fragments is 8 km. Medium semi-deciduous forest is the predominant vegetation in these sites and both are surrounded by crops (Figure 3). Both forest fragments have trails that people use for timber extraction, which is carried out for domestic purposes such as house construction or maintenance, usually during the dry season when access with a vehicle is possible. In Once de Mayo, the troop had seven individuals at the beginning of the study (2 males, 3 females, and 2 juveniles) and by April one infant was born. In Cristóbal Colón, the troop consisted of four individuals at the beginning of the study (1 male, 2 females, and 1 infant), and one infant was born during the study. Additionally, one adult male immigrated into the troop sometime around June and by December this male was gone. In each of these sites, only one troop was present.

## Feeding Behavior

The study was conducted in 2003, from February to May (dry season), and August to November (rainy season). Observations were done over two consecutive days each month, on each study troop, totaling 64 days (3152 records). We observed the monkeys a mean 4.2 ± 0.6 hours per day. To document feeding habits, we used the instantaneous scan-sampling method, recording at 15-minute intervals the activity (feeding, resting, traveling, playing, or vocalizing) displayed by each monkey of the focal troop at the moment they

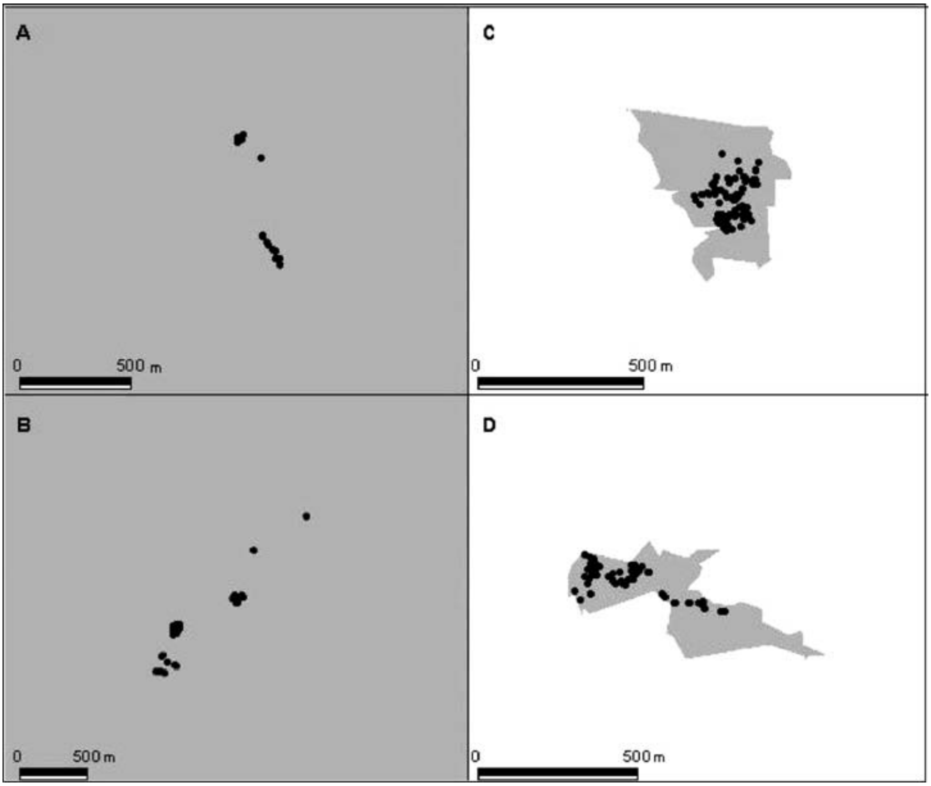

**Figure 3.** Land cover of the study sites and surroundings (grey represents forest and white represents agriculture). A, El Sendero Ecológico; B, Mayan Ruins of Calakmul; C, Cristóbal Colón; and D, Once de Mayo. Black dots represent locations where howlers were recorded eating and moving from one feeding tree to another.

were observed. If the activity was feeding, we recorded the species and plant part eaten. We chose to use the scan-sampling method because it is well-suited for non-social behavior observations (Altmann, 1974), and it enabled us to collect a large sample of behavioral data. Mitlöhner *et al.* (2001), working with heifers, argued that data collected across 15-min intervals were sufficient to ensure some degree of statistical independence, especially for feeding events, while capturing the whole spectrum of behavior.

## Vegetation Sampling

To evaluate how trees used by monkeys for feeding differed from neighboring trees they do not use, we established plots (hereafter named focal plots) of 10 m radius around the focal trees. Plots never overlapped using a 10 m radius, which avoided including the same trees, and thus problems of spatial dependency. We classified trees into three categories: (1) focal trees, where the majority of the monkeys of a given focal troop were feeding; (2) used trees, i.e. trees on which a minority of monkeys of a focal troop were feeding; and (3) non-used trees, i.e. trees not used for feeding. Within each plot, we determined the diameter at breast height (dbh), height, species, and phenology (ripe or unripe fruits, young or mature leaves, leafless, flowers, and buds) of all trees >10 cm dbh. Additionally, we conducted a vegetation census using similar 10-m-radius plots established at random 100–300 m around the areas used by focal troops, in forest stands* where no howler monkey had been observed. We only determined the species of all trees >10 cm dbh, and used this census to assess whether tree species selection is at the stand level by comparing the composition and abundance of tree species between these plots and focal plots.

## Statistical Analyses

For the purpose of the present study, we analyzed data corresponding to only adult howlers to avoid any possible age-related bias. To estimate and compare howler monkey's diet composition in each type of forest (continuous, Figures 1A and 1B versus fragments, Figures 1C and 1D), we evaluated the relative percentage of consumption of each species by dividing the number of feeding records of a given species by the total number of feeding records. We did not relate these data to the number of available trees, as we considered that one single tree could provide unlimited resources to a given troop, provided that the tree part they consumed was present (e.g. fruits). For further comparisons between forest fragments and the reserve, we selected only the species that represented >10% of the total number of feeding records, and performed independent likelihood ratio chi-square tests (*G*-tests).

To compare the consumption of the different food items between the reserve and the fragments, we also performed independent *G*-tests. For these analyses,

---

* Forest stand: A community of trees possessing sufficient uniformity in composition, age, arrangement or condition to be distinguishable from the forest or other growth on adjoining areas, thus forming a temporary silvicultural or management entity. Silvaterm Database, International Union of Forest Research Organizations http://iufro.boku.ac.at/iufro/silvavoc/svdatabase.htm

we selected those species that (1) had various food items consumed, and (2) were used as food sources in both types of forest.

To assess food preference, we compared the proportion of a given tree species in the diet with the proportion of that tree species available in focal plots. We measured diet selection by the howlers using the electivity index ($\varepsilon$) presented by Chesson (1983). The major advantage of this measure of preference is that it is not influenced by food density (i.e. trees in our case), because it is standardized. The Chesson index is based on Manly's alpha selection index ($\alpha$), which allows to rank plants in order according to frequency in the diet:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} (r_j/n_j)}$$

where $r_i$ and $r_j$ are the proportions of the tree species $i$ and $j$, respectively, in the diet; $n_i$ and $n_j$ are the proportions of the tree species $i$ and $j$, respectively, available in focal plots; and $m$ is the total number of tree species.

Manly's alpha is applicable in situations where the diet plant population can be assumed not to be significantly depleted by feeding activity (Manly, 1974; Chesson, 1983). To obtain results that are comparable between cases in which the number of available tree species varies, we converted Manly's alpha to the selectivity index presented by Chesson (1983):

$$\varepsilon_i = \frac{m\alpha_i - 1}{(m-2)\alpha_i + 1}$$

Chesson's $\varepsilon$ potentially ranges between −1 and +1. Plant species having negative values are avoided[†] and species with positive values are preferred (Chesson, 1983). If the index value is zero, this represents non-selective feeding on that plant species. We computed the selectivity value for each of the 10 species used for feeding in the CBR and the 16 species used for feeding in the fragments.

To determine if there were structural differences between feeding trees and non-used trees, we compared the dbh and height of the three categories of trees (focal, used, and non-used), using a Tukey–Kramer test for multiple comparisons.

Finally, we compared the frequency distributions of the tree species found in the focal and random plots (where the monkeys did not feed) using the

---

[†] Avoid: We use this term *sensu* Chesson (1983), who defines that those species less present in the diet than their availability would allow, are avoided.

Kolmogorov–Smirnov two-sample test, after correcting for the unequal number of plots. Then, we selected the most-consumed tree species (>10% of total consumption), and we compared their abundances in focal and random plots using *G*-tests.

## RESULTS

### Comparison of Diet Composition

In total, 20 tree species were used as sources of food by the howlers, in both the CBR and the forest fragments. Sixteen of these species were consumed in the forest fragments and 10 in CBR (Table 1). Eight out of 10 species consumed in CBR were also a source of food in the fragments.

**Table 1.** Tree species used for feeding by *Alouatta pigra* at CBR (two sites) and the forest fragments (two sites)

| | Occurrences (%) | | | |
|---|---|---|---|---|
| Species | Fragments | CBR | *G* | *p* |
| *Aspidosperma megalocarpon* (Apocynaceae) | 0.8 | 0.0 | 1.09 | 0.295 |
| *Brosimum alicastrum* (Moraceae) | 24.9 | 31.6 | 0.80 | 0.372 |
| *Bursera simaruba* (Burseraceae) | 0.0 | 1.8 | 2.52 | 0.112 |
| *Caesalpinia mollis* (Leguminosae) | 3.1 | 0.9 | 1.32 | 0.250 |
| *Celtis trinervia* (Ulmaceae) | –[*] | 1.8 | – | – |
| *Coccoloba acapulcensis* (Polygonaceae) | 1.8 | 1.3 | 0.08 | 0.781 |
| *Croton arboreus* (Euphorbiaceae) | 0.3 | – | – | – |
| *Eheretia tinifolia* (Boraginaceae) | 8.7 | 0.0 | 12.00 | <0.001 |
| *Ficus* sp (Moraceae) | – | 50.5 | – | – |
| *Krugiodendron ferreum* (Rhamnaceae) | 0.0 | 0.9 | 1.26 | 0.262 |
| *Lonchocarpus xuul* (Leguminosae) | 0.5 | 0.0 | 0.73 | 0.392 |
| *Manilkara zapota* (Sapotaceae) | 22.0 | 8.4 | 6.31 | 0.012 |
| *Neea choriophylla* (Nyctaginaceae) | 0.8 | 0.0 | 1.09 | 0.295 |
| *Platymiscium yucatanum* (Leguminosae) | 7.9 | 2.2 | 3.30 | 0.069 |
| *Protium copal* (Burseraceae) | 0.3 | 0.0 | 0.42 | 0.519 |
| *Sideroxylon salicifolium* (Sapotaceae) | 2.4 | 0.0 | 3.29 | 0.070 |
| *Tabebuia chrysanta* (Bignonaceae) | 3.1 | – | – | – |
| *Talisia olivaeformis* (Sapindaceae) | 17.1 | 0.5 | 20.10 | <0.001 |
| *Vitex gaumeri* (Verbenaceae) | 1.8 | – | – | – |
| Unknown | 4.2 | 0.0 | 5.85 | 0.016 |
| Number of consumed species | 16 | 10 | 1.40 | 0.237 |

[*] A dash in place of a value for occurrence indicated that the species was not present in the focal plots; if the species was not used for feeding but present, the corresponding value was 0. The likelihood ratio chi-square (*G*) is the result of the comparison of the frequency of consumption between fragments and the reserve. The associated probability is noted as *p*.

In CBR, feeding records totaled 440; *Ficus* sp. and *Brosimum alicastrum* contributed approximately 82% of the feeding records. In the fragments, feeding records totaled 381, with *B. alicastrum*, *Manilkara zapota*, and *Talisia olivaeformis* contributing 64% of all feeding records (Table 1).

We found no significant difference in the overall consumption (fruits and leaves) of *B. alicastrum* between fragments and the reserve. This species was the most consumed in fragments and the second most consumed in CBR, contributing to 24.9% and 31.6% of the total consumption, respectively (Table 1). We found significant differences in the consumption of *M. zapota* and *T. olivaeformis* between fragments and CBR. Both the species contributed significantly more to the diet in the forest fragments. Finally, the most important species as source of food (50% of total consumption) in the CBR, *Ficus* sp., was absent in the forest fragments.

## Comparison of Tree Parts Consumed

Among the 20 species used for feeding by black howlers, only *B. alicastrum* and *M. zapota* were consumed in both types of forest and for each species a range of different food types were consumed. We found that there were no significant differences in the consumption of young leaves, matures leaves, and fruits of *B. alicastrum* between CBR and the forest fragments (Table 2). However, young leaves represented half the consumption of this species in the fragments, whereas consumption of young leaves (36.7%), mature leaves (28%),

**Table 2.** Consumption of leaves and fruits of *B. alicastrum* and *M. zapota* in the CBR (two sites) and the forest fragments (two sites). The likelihood ratio chi-square ($G$) is the result of the comparison of the frequency of consumption between fragments and the reserve. The associated probability is noted as $p$

| | Consumption (%) | | | |
|---|---|---|---|---|
| Tree part | Fragments | CBR | $G$ | $p$ |
| *Brosimum alicastrum* | | | | |
| Young leaves | 49.47 | 36.69 | 1.90 | 0.170 |
| Mature leaves | 29.47 | 28.06 | 0.03 | 0.850 |
| Fruit | 21.05 | 35.25 | 3.62 | 0.060 |
| *Manilkara zapota* | | | | |
| Young leaves | 14.29 | 40.54 | 13.10 | <0.001 |
| Mature leaves | <0.01 | 21.62 | 29.97 | <0.001 |
| Fruit | 85.71 | 37.84 | 19.05 | <0.001 |

and fruits (35.2%) of *B. alicastrum* were almost equally represented in the diet at CBR. For *M. zapota*, howlers ate significantly more young and mature leaves in CBR than in the forest fragments. Conversely, they ate significantly more *Manilkara* fruits in the fragments than in CBR (Table 2).

For both *B. alicastrum* and *M. zapota*, we found that howlers always ate ripe fruits whenever they were available. In the case of *M. zapota*, we registered 14 and 72 feeding records on ripe fruits in the CBR and the forest fragments, respectively; and only in two cases, howlers also ate young leaves. There was no difference in the consumption of unripe fruits of *Manilkara* between CBR and the fragments ($G = 1.03$, $p = 0.3$). However, in both the forest fragments and the CBR, howlers ate significantly more ripe than unripe *Manilkara* fruits (both $G \geq 4.8$, $p \leq 0.02$). We also found that they consumed mature leaves of this species only when fruits were unavailable or immature.

Unlike the case of *M. zapota*, black howlers ate significantly more unripe fruits of *B. alicastrum* in the CBR than in the fragmented sites ($G = 11.3$, $p < 0.001$). However, as for *Manilkara*, howlers ate significantly more ripe than unripe fruits of *B. alicastrum* in both types of forest (both $G \geq 27.7$, $p < 0.001$). In fact, in the forest fragments, when ripe fruits were available, black howlers never ate unripe fruits of *B. alicastrum*. We also found that in fragments they consumed mature and young leaves of this species only when ripe fruits were unavailable. In the CBR, however, black howlers also ate mature or young leaves as well as ripe fruits of *B. alicastrum*.

## Dietary Selectivity in Fragments and CBR

We computed the Chesson's electivity index for the 20 tree species that were consumed both in the fragments and the CBR, and only if species were present in the focal plots. We omitted the species not used by monkeys for feeding, as we had no local evidence of their edibility.

Howlers in the forest fragments fed selectively on 12 of the 16 species they consumed, while *T. olivaeformis* and *Caesalpinia mollis* were not used selectively. *Lonchocarpus xuul*, *Protium copal*, *Bursera simaruba*, and *Krugiodendron ferreum* were avoided (Figure 4), although the former two, which represented only 0.8% of the feeding records, were consumed.

Of the 10 tree species used as a source of food in the CBR, 9 species were selected (i.e. had positive electivity indices). Eight species were negatively selected, one of which was consumed however (*T. olivaeformis*; Figure 4).

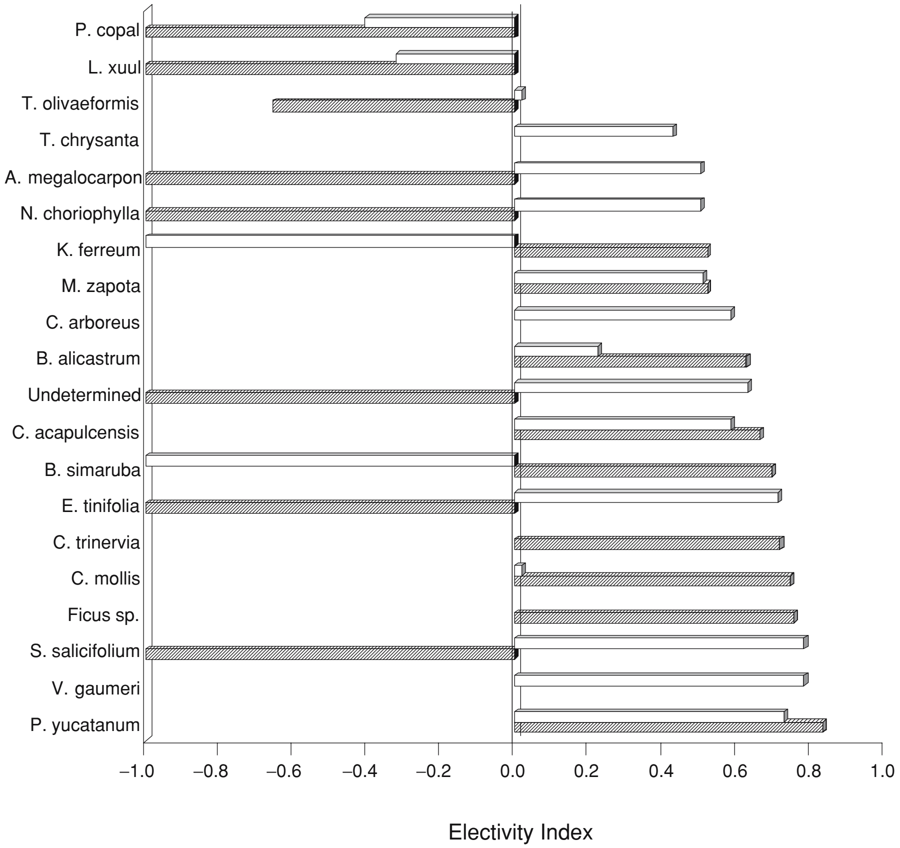

**Figure 4.** Electivity values (Chesson's ε) for the species used as food sources by black howler monkeys in the Calakmul Biosphere Reserve (hatched bars) and forest fragments (white bars). The more howlers select a species, the higher the value (maximum value is 1). Complete avoidance is denoted by −1, while 0 represents random selection.

## Characteristics of Consumed and Non-consumed Trees

In the CBR and the forest fragments, heights of focal and used trees were similar between and among sites. However, in these forests, non-used trees were significantly shorter (by 4–6 m) than both focal and used trees (Tukey–Kramer multiple comparisons, $p < 0.05$ in all the cases; Table 3).

Among the fragments, dbh of focal and used trees also were similar, and greater (by ≥13 cm) than non-used trees (T–K multiple comparison, $p < 0.05$). At CBR, focal trees were greater in diameter than used trees (46 cm), whereas used trees were larger (25 cm) than non-used trees (T–K multiple comparison, $p < 0.05$). Both focal and used trees at CBR were also larger than their

**Table 3.** Characteristics of used and non-used trees within the Calakmul Biosphere Reserve and in the forest fragments outside the reserve

| | | Height (m) | | | | | Diameter at breast height (cm) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Tree category | *N* | Mean | SD | T–K | Median | Range | Mean | SD | T–K | Median | Range |
| *Fragments* | | | | | | | | | | | |
| Focal tree | 21 | 17.8 | 3.9 | a | 18 | [14–26.5] | 35.2 | 15.4 | a | 32 | [22.5–65.5] |
| Used tree | 51 | 16.5 | 2.9 | a | 16 | [11–27.8] | 33.0 | 14.8 | a | 31 | [12–69] |
| Non-used tree | 488 | 12.6 | 3.6 | b | 12 | [6–29] | 20.1 | 9.7 | d | 17 | [10–80.2] |
| *CBR* | | | | | | | | | | | |
| Focal tree | 24 | 18.0 | 4.5 | a | 18 | [10–30] | 95.2 | 91.6 | b | 54 | [17–357] |
| Used tree | 56 | 16.4 | 3.5 | a | 17 | [10–25] | 48.7 | 40.1 | ac | 35 | [11–196] |
| Non-used tree | 261 | 12.0 | 4.1 | b | 11 | [4–25] | 23.3 | 15.8 | ad | 19 | [10–143] |

**Table 4.** Comparisons of the distribution of frequency of tree species between focal and random plots using the two-sample Kolmogorov–Smirnov test (statistics D). All plots had a 10 m radius

| Site | D | P |
|---|---|---|
| *Fragments* | | |
| Once de mayo | 0.2449 | 0.006 |
| Cristóbal Colón | 0.1633 | 0.147 |
| *CBR* | | |
| Sendero | 0.3367 | <0.001 |
| Mayan Ruins of Calakmul | 0.1429 | 0.270 |
| All sites | 0.2347 | 0.009 |

counterparts in the fragments by 60 and 15.7 cm, respectively (significant only for focal trees). On the other hand, non-used trees had similar diameters in the reserve and in the fragments (Table 3).

### Tree Species Composition and Abundance in Focal and Random Plots

We counted a mean number of 20.5 trees larger than 10 cm at breast height in the focal plots, and similarly, 18.5 trees in the additional random plots. Considering both focal and random plots, there were a total of 74 tree species in CBR, and 57 in the fragments. Overall, the frequency distribution of tree species in focal and random plots was significantly different (Table 4). However, random plots were different from focal plots only in the ejido Once de Mayo, outside the reserve, and in El Sendero Ecológico, within the reserve.

*B. alicastrum* was more abundant in the focal plots than in the random plots, but this difference only approached statistical significance ($G = 3.32$, $p = 0.068$). *Ficus* sp. and *M. zapota* were significantly more abundant in the focal plots (both $G > 6.8$, $p \leq 0.009$). For *Ficus*, the analysis was done only for the sites in the reserve, as no *Ficus* tree was detected in the forest fragments. The fourth species most used for feeding in the fragments, *T. olivaeformis*, was equally abundant in focal and random plots in these sites ($G = 0.06$, $p = 0.79$).

## DISCUSSION

### Feeding Habits in CBR and the Forest Fragments

The diet of black howler monkeys in the protected and extensive forest of CBR and forest fragments outside CBR differed in the number of tree species they used as sources of food, and in dietary composition. For instance, in the extensive forest, 50% of feeding time was devoted to a single species, *Ficus* sp., while the most frequent species in the diet of howlers in the fragments, *B. alicastrum*, represented only one quarter of the total consumption. Thus, howlers were found to have a more narrow-based diet in the reserve, whereas their diet was more broad-based in the fragments. Several factors could account for this, including the fact that *Ficus* sp. was very rare in the fragments (and absent from all plots), and that when available, *Ficus* fruits and leaves are reported to be major food resources for howlers at other sites in Mesoamerica (Silver *et al.*, 1998; Estrada *et al.*, 1999; Serio-Silva *et al.*, 2002; Pavelka and Knopff, 2004).

Our results on diet composition and diversity differ from those of Silver *et al.* (1998) in the Community Baboon Sanctuary (CBS) in Belize. At this site, black howlers are reported to feed on 53 tree species (of a total of 60 tree species identified), with no single species accounting for more than 12.5% of feeding time, although all *Ficus* species together accounted for 31% of feeding time. The top five tree species consumed at CBS contributed 42.8% of feeding time, far from the 80.6% and 96.3% of the top five species consumed in fragments and CBR, respectively, in this study. Black howlers in CBS thus appear to exploit a highly broad-based diet. The habitat at CBS is more disturbed than even the forest fragments in our study, as suggested by the presence of pioneer trees like *Cecropia* spp., and exotics like *C. sinensis.* On the other hand, black howlers of El Tormento, a large managed forest fragment (1400 ha) in Southwestern Campeche, are reported to exploit 19 tree species (Barrueta, 2003), similar to what we report here for fragments.

Moreover, as in CBR and forest fragments in Calakmul, *M. zapota* and *B. alicastrum* also were important species in the diet of howlers at El Tormento. These two species were absent from CBS forest (Silver *et al.*, 1998). Our study suggests that, when possible, howlers may limit their diet to a small number of particular plant species present in sufficient abundance and available over a large time span (and probably highly palatable). In the case of *Ficus*, for example, a single tree may produce a sufficiently large fruit and leaf crop to feed a group for several months. Serio-Silva *et al.* (2002) previously suggested that mantled howlers (*A. palliata*) may concentrate their feeding activities on a single or small number of *Ficus* trees. Such a pattern may reduce time and energy spent traveling, permitting more time and energy for the digestion of a high fiber diet. This is consistent with an energy-minimizing foraging strategy (Milton, 1980).

We hypothesize that in the fragments, howlers compensated for the lack of *Ficus* by eating more *Manilkara* fruits plus "alternative" species, all of them consumed significantly more in the fragments (Table 1). Three of these four species, *Eheretia tinifolia*, *T. olivaeformis*, and the unknown species, were also selected in the fragments, whereas they were strongly avoided in CBR (Figure 4). The four species accounted for 52.1% of howlers feeding time in the fragments. This was not significantly different from the value of 50.5% that *Ficus* represented in the diet of howlers in the reserve ($G = 0.57$, $p = 0.45$), suggesting that howlers might respond to the absence of figs by selecting alternative species and increasing the consumption of other species already present in the diet. The exploitation of *Ficus*, *Brosimum*, and *Manilkara* appear to represent staple resources for many howler populations (Estrada *et al.*, 1999; García del Valle, 2001; Barrueta, 2003). Factors affecting the use of "alternative" species remain unclear and require analyzing the nutritional quality and phytochemical components of these resources.

Howlers ate significantly more ripe fruits than unripe fruits and leaves of *M. zapota* and *B. alicastrum* in both the forest types. Thus, ripe fruits appeared to be a preferred food type when available. In forest fragments, however, leaf consumption of *B. alicastrum* was correlated with a decrease in fruit availability. A similar relationship was found when consuming mature leaves of *M. zapota* in both the fragments and the reserve. Our results are in agreement with that of Silver *et al.* (1998), who mentioned that mature leaves may be secondary or supplemental choices to howlers. These results are consistent with Yeager's (1989) suggestion that increased dietary diversity is associated with food scarcity.

We expected leaf and unripe fruit consumption of *B. alicastrum* and *M. zapota* to be higher in the fragments, because we assumed that trees with ripe fruits should be less numerous in a reduced and disturbed space and both tree species are subject to extraction in the forest fragments. However, we found no differences in the relative consumption of young and mature leaves of *B. alicastrum* between fragments and CBR. In addition, unripe fruits were consumed more in CBR. For *M. zapota*, the relative consumption of young and mature leaves was higher in CBR, and unripe fruit consumption was similar between the two types of forest. In contrast with our results, Fairgrieve and Muhumuza (2003) found that overall consumption of unripe fruits by *Cercopithecus mitis* was higher in a disturbed (logged) forest in Uganda. More detailed analysis of the relationship between habitat disturbance and its effects on forest composition and primate behavior are needed to clearly understand changes in dietary food items.

## Food Selection in CBR and the Forest Fragments

If howlers did not behave selectively in their dietary choice, we should expect diet diversity to be broadly similar to that of tree species diversity in the studied sites. Thus, howlers' diet is expected to be more diverse in CBR than in the fragments, as 74 species were identified in the vegetation plots in CBR compared to 57 in the fragments. However, of the 20 species that were used for feeding in both types of forests, 16 species were consumed in the forest fragments and 10 were consumed in the CBR. This is best explained by the predominance of figs (*Ficus* sp.) in howlers' diet in CBR, which was highly selected and represented half of all consumption events. In fact, many fruit-eating primates are reported to preferentially consume figs even when other food is abundant (O'Brien *et al.*, 1998). Figs also have been suggested as keystone resources in tropical forests (Terborgh, 1986b), and in playing a special role in howler conservation (Coates-Estrada and Estrada, 1986; Milton, 1991; Serio-Silva *et al.*, 2002).

In general, most species present in the diet were highly selected. Our data also show that 9 of the 10 species consumed in CBR, and 12 of the 16 species consumed in the fragments were preferentially selected by the howlers. However, it was striking that some species reported to be commonly eaten by howlers at other sites (e.g. Estrada, 1984; Serio-Silva, 1992; Julliot, 1996; Silver *et al.*, 1998; Barrueta, 2003) were not seen being consumed by black howlers during the present study. This was the case of *L. castilloi*, *P. campechiana*, *Spondias mombin*, *Hampea tribolata*, and *Chrysophyllum mexicanum*. Species of the genera *Drypetes*, *Piscidia*, *Pouteria*, *Guettarda*, *Diospyros*, and *Trichilia*, which are known to be consumed by other species of *Alouatta* (Milton, 1980; Julliot, 1996), though present in the fragments and in the reserve also were not consumed. There are several explanations to account for this, first the fact that we did not observe howlers feed on these species does not necessarily mean that they were not consumed. Second, perhaps our observations did not correspond to the period of maximum fruiting of these species (e.g. *P. piscipula* and *Trichilia minutiflora*), and third, in the case of CBR, the extended and asynchronous pattern of fig fruiting and leafing may have enabled the howlers to exploit this species throughout much of the year as it occurred at high enough densities (O'Brien *et al.*, 1998).

Within suitable habitats, the quality of different plants is probably the main factor leading to diet selection (Markkola *et al.*, 2003). The quality of food varies according to energy, protein and water content, soluble carbohydrates, digestibility and toxicity, and several studies on howler diet indicate that selection appears to be based on phytochemical factors rather than the relative availability of potential food (Milton, 1980; Silver *et al.*, 2000). Chemical analyses on the plant species and food items consumed by black howlers in Calakmul would provide greater insight into the criteria used in food selection.

## Selection of Feeding Sites at Tree and Stand Levels

The selectivity analysis clearly indicates that howlers are not feeding on tree species based on their availability, but have marked preferences for some species and aversions to others. In general, we found that tree species used by howlers as sources of food were taller and larger than non-used species in both the forest fragments and the reserve. Used trees were usually dominant trees in the canopy, and were either older trees or individuals of species reaching larger dimensions. Non-used trees were usually components of the under-canopy. In fact, all the abundant species clearly avoided by howlers (i.e. abundant in focal plots but not consumed, such as *Drypetes lateriflora*, *Pouteria reticulata*, and *T. minutiflora*) were very small and barely reached the mean values for height and dbh of non-used trees. Other authors who have studied *A. pigra* (Barrueta, 2003) or *A. palliata* (Estrada and Coates-Estrada, 1986; García del Valle, 2001) have found similar mean heights and diameters of the feeding trees in their study sites; however, they did not provide a basis for comparison as they did not measure non-used trees.

In terms of forest management, the characteristics of used trees have clear implications for the conservation of howlers. In effect, selective logging implies the removal of individuals of commercial tree species above a minimum diameter. Most species on which howlers fed are used commercially (e.g. *B. alicastrum*, *C. mollis*, *E. tinifolia*, *M. zapota*, and *P. yucatanum*). Logging decreases the densities of these trees and increases the openness of the canopy from less than 5% to more than 30% in this type of forest (Dickinson, 1998). Thus, in managed forests, howlers have to face both the lack of continuity in the canopy that makes movements more difficult and the loss of many vital trees for feeding. In the forest fragments we studied, the diameter of focal trees was smaller than in the reserve, even after excluding *Ficus* trees from the analyses (mean $\text{dbh}_{\text{fragment}} = 35.2 \pm 15.4$ cm versus mean $\text{dbh}_{\text{reserve}} = 45.0 \pm 18.2$ cm). This suggests that the small-scale logging for domestic purposes that local inhabitants practice has an important impact on the trees howlers use for feeding. Chapman *et al.* (2000) reported that a reduction of food availability due to logging leads to increased infant and juvenile mortality in species such as *Macaca sinica* and *Papio cynocephalus.* Therefore, it is necessary to understand how the effects of vegetation changes commonly associated with logging influence primate feeding ecology (Fairgrieve and Muhumuza, 2003); this will help in the implementation of management plans based on conservation of howler food trees.

We also were interested in determining if the forest stands in which howlers were feeding differed from surrounding stands where howlers had not been observed, in order to evaluate the spatial scale at which they select feeding trees. However, focal plots differed from random plots in only two of the four study sites, one within the reserve and the other in a forest fragment, making conclusions unclear. Nevertheless, the four species that accounted for more than 75% of the feeding records overall provide interesting insight. Actively selected species such as *Ficus*, *M. zapota*, and to a lesser extent *B. alicastrum*, were more abundant in the focal plots than in random plots. In contrast, *T. olivaeformis* was equally abundant in focal and random plots, but was not a selected species in fragments and was avoided in the reserve. This suggests that selection at the stand level might be linked to the presence/abundance of the preferred tree species.

In conclusion, black howler monkeys showed strong selection for the consumption of plant food of particular tree species. Forest fragmentation may have served to relax the degree of dietary selectivity in howlers. Howlers depended on a small number of tree species, the lowest ever reported for *A. pigra*, and this was relatively independent of their availability. In fact, the second most abundant tree species in this study, *P. reticulata*, was never used as a source of food by howlers. However, this species is of low stature and small diameter. Black howlers selected the trees on which they fed based at least partially on their stature, dbh, and maturity. Moreover, areas they selected to spend most of their time contained higher abundances of their preferred feeding tree species. As tree species selected by howlers also are commonly exploited, these findings provide a good basis for establishing criteria useful in forest management plans compatible with the conservation of *A. pigra.*

## SUMMARY

Information on food selection and feeding habits is critical for species conservation, particularly in the context of forest landscapes heavily transformed by human activities. In this study, we examined the degree to which *A. pigra* feeding habits differed between two sites in the conserved forest of the Calakmul Biosphere Reserve (CBR) and two forest fragments outside the reserve, and how monkeys select the trees on which they feed. Our results suggest that howlers tended to exploit a smaller set of fruit and leaf species in the conserved sites, whereas their diet was more diverse in the fragments. This can be explained probably by the role, at CBR, of *Ficus* sp. in howlers' diet, as it was highly selected and represented half of all feeding events. Chesson's electivity index showed that howlers in fragments selected 12 of the 16 species used for feeding; while in CBR, they selected 9 of the 10 species used for feeding. At both types of forests, feeding trees were taller and were greater in diameter than non-feeding trees. Trees exploited by howlers for feeding have commercial dimensions and most of these species are commercially logged. As a result, in fragments and logged forests, howlers have to face the lack of continuity in the canopy and the loss of many vital trees for feeding. We expect howler monkeys to survive in fragmented sites if tree species important in their diet are conserved.

## ACKNOWLEDGMENTS

This study would not have been possible without the help in the field of Oscar Fernando Ramírez, Roberto "Chibebo" Rojo, Johannes Hechenbichler, Rubén Aguilar, Luciano Pérez, Margarito Tuz, and Andrés Sánchez. The identification work of nearly 1000 trees was realized by Demetrio "Coyote" Álvarez. We are indebted to the people of the *ejidos* Once de Mayo and Cristóbal Colón for granting us access to their land. We are also grateful to the Direction of Calakmul Biosphere Reserve for allowing us to study howler monkeys and SEMARNAT for the plant collection license No./SGPA/DGVS/02475. Earlier drafts of this manuscript benefited from helpful comments from Gabriel Ramos Fernández, Jorge León Cortés, Alejandro Estrada, Mary Pavelka, Paul Garber, and an anonymous reviewer. Figures 1 and 3 were produced by Holger Weissenberger. Financial and logistic support for the project was provided by

ECOSUR. AR benefited from a scholarship granted by CONACYT (contract number 169607).

## REFERENCES

Altmann, J. 1974, Observational study of behavior: Sampling methods. *Behaviour* 49:227–267.

Arriaga, L., Espinoza, J. M., Aguilar, C., Martínez, E., Gómez, L., and Loa, E. (Coordinators). 2000, Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México.

Barrueta, T. 2003, Reconocimiento demográfico y dieta de Alouatta pigra en un fragmento de selva en El Tormento, Campeche, México. MSc Thesis, El Colegio de la Frontera Sur, México, p. 49.

Baumgarten, A. and Hernández, J. F. 2002, Características poblacionales y uso de hábitat del mono aullador negro (*Alouatta pigra*) en la zona de influencia del Parque Nacional Laguna Lachua, Alta Verapaz. Revista Científica del Instituto de Investigaciones Químicas y Biológicas, Universidad de San Carlos de Guatemala 15:1–9.

Bicca-Marques, J. C. and Calegaro-Marques, C. 1994, Exotic plant species can serve as staple food sources for wild howler populations. *Folia Primatol.* 63:209–211.

Chapman, C. A., Balcomb, S. R., Guillespie, T. R., Skorupa, J. P., and Struhsaker, T. T. 2000, Long-term effects of logging on african primate communities: A 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* 14:207–217.

Chesson, J. 1983, The estimation and analysis of preference and its relation to foraging models. *Ecology* 64:1297–1304.

Coelho, A. M., Bramblett, C. A., Quick, L. B., and Bramblett S. S. 1976. Resource availability and population density in primates: A socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates* 17:63–80.

Coates-Estrada, R. and Estrada, A. 1986, Fruiting and frugivores at strangler fig in the tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 2:349–357.

Dickinson, M. B. 1998, Tree regeneration in natural and logging canopy gaps in a semideciduous forest. PhD Thesis, Florida State University, p. 177.

Estrada, A. 1984, Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. *Int. J. Primatol.* 5:105–131.

Estrada, A. and Coates-Estrada, R. 1986, Use of leaf resources by howling monkeys (*Alouatta palliata*) and leaf-cutting ants (*Atta cephalotes*) in the tropical rain forest of Los Tuxtlas, Mexico. *Am. J. Primatol.* 10:51–66.

Estrada, A., Juan-Solano, S., Ortiz, T., and Coates-Estrada, R. 1999, Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living in a forest fragment at Los Tuxtlas, Mexico. *Am. J. Primatol.* 48:167–183.

Estrada, A., Luecke, L., Van Belle, S., Barrueta, E., and Rosales, M. 2004, Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan Sites of Calakmul and Yaxchilan, Mexico and Tikal, Guatemala. *Primates* 45:33–39.

Estrada, A., Luecke, L., Van Belle, S., French, K., Muñoz, D., García, Y., Castellanos, L., and Mendoza, A. 2002a, The black howler monkey (*Alouatta pigra*) and spider monkey (*Ateles geoffroyi*) in the Mayan Site of Yaxchilán, Chiapas, Mexico: A preliminary survey. *Neotrop. Primates* 10:89–95.

Estrada, A., Mendoza, A., Castellanos, L., Pacheco, R., Van Belle, S., García, Y., and Muñoz, D. 2002b, Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. *Am. J. Primatol.* 58:45–55.

Fairgrieve, C. and Muhumuza, G. 2003, Feeding ecology and dietary differences between blue monkey (*Cercopithecus mitis stuhlmanni* Matschie) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *Afr. J. Ecol.* 41:141–149.

Fuentes, E., Estrada, A., Franco, B., Magaña, M., Decena, Y., Muñoz, D., and García, Y. 2003, Reporte preliminar sobre el uso de recursos alimenticios por una tropa de monos aulladores, *Alouatta palliata*, en El Parque La Venta, Tabasco, México. *Neotrop. Primates* 11:24–29.

Galindo-Leal, C. 1998, El mal congénito de Calakmul. *Biodiversitas* 17:9–15.

García del Valle, Y. 2001, Estudio preliminar de los patrones de alimentación de monos aulladores (*Alouatta palliata*) en semilibertad en el parque Yumka', Tabasco, México. BSc Thesis, Universidad Juárez Autónoma de Tabasco, México, p. 70.

García-Gil, G., Palacio-Prieto, J. L., and Ortíz-Pérez, M. A. 2002, Reconocimiento geomorfológico e hidrográfico de la Reserva de la Biosfera Calakmul, México. Investigaciones Geográficas. Boletín del Instituto de Geografía. Universidad Nacional Autónoma de México 48:7–23.

Gaulin, J. C. and Gaulin, C. K. 1982, Behavioral ecology of *Alouatta seniculus* in cloud forest. *Int. J. Primatol.* 3:1–32.

Horwich, R. H. and Johnson, E. D. 1986, Geographical distribution of the black howler (*Alouatta pigra*) in Central America. *Primates* 27:53–62.

Janson, C. H. and Chapman, C. A. 1999, Resources and primates community structure, in: J. G. Fleagle, C. H. Janson, and K. E. Reed, eds., *Primates Communities*, Cambridge University Press, Cambridge, pp. 237–267.

Julliot, C. 1996, Fruit choice by red howler monkey (*Alouatta seniculus*) in a tropical rain forest. *Am. J. Primatol.* 40:261–282.

Julliot, C. and Sabatier, D. 1993, Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. *Int. J. Primatol.* 14:527–550.

Klepeis, P. and Roy Chowdhury, R. 2004, Institutions, organizations, and policy affecting land change: Complexity within and beyond the *ejido*, in: B. L. Turner II, J. Geoghegan, and D. R. Foster, eds., *Integrated Land-Change Science and Tropical*

*Deforestation in the Southern Yucatán*, Oxford University Press, Oxford, pp. 145–169.

Litvaitis, J. A., Titus, K., and Anderson, E. M. 1996, Measuring vertebrate use of terrestrial habitats and food, in: T. A. Bookhout, ed., *Research and Management Techniques for Wildlife and Habitats*, The Wildlife Society, Bethesda, MD, pp. 254–274.

Manly, B. F. J. 1974, A model for certain types of selection experiments. *Biometrics* 30:281–294.

Markkola, J., Niñéemela, M., and Rytkönen, S. 2003, Diet selection of lesser white-fronted geese *Anser erythropus* at a spring staging area. *Ecography* 26:705–714.

McConkey, K. F., Aldy, F., Ario, A., and Chivers, D. J. 2002, Selection of fruit by gibbons (Hylobates muelleri × agilis) in the rain forest of Central Borneo. *Int. J. Primatol.* 23:123–145.

Milton, K. 1980, *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics.* Columbia University Press, New York, p. 165.

Milton, K. 1991, Leaf change and fruit production in six neotropical Moraceae species. *J. Ecol.* 79:1–26.

Mitlöhner, F. M., Morrow-Tesch, J. L, Wilson, S. C., Dailey, J. W. and McGlone, J. J. 2001, Behavioral sampling techniques for feedlot cattle. *J. Anim. Sci.* 79:1189-1193.

O'Brien, T. G., Kinnaird, M. F., Dierenfeld, E. S., Conklin-Brittain, N. L., Wrangham, R. W., and Silver, S. C. 1998, What's so special about figs? *Nature* 392:668.

Pavelka, M. S. M. and Knopff, K. H. 2004, Diet and activity in black howler monkeys (*Alouatta pigra*) in southern Belize: Does degree of frugivory influence activity level? *Primates* 45:105–111.

Ponce-Santizo, G. 2004, Dispersión de semillas por mono araña (*Ateles geoffroyi*), saraguate negro (*Alouatta pigra*) y escarabajos coprófagos en el Parque Nacional Tikal, Guatemala. BSc Thesis, Departamento de Biología, Universidad del Valle de Guatemala, Guatemala, p. 89.

Rosales-Meda, M. M. 2003, Abundancia, distribución y composición de tropas del mono aullador negro (*Alouatta pigra*) en diferentes remanentes de bosque en la ecoregión Lachuá, Guatemala. BSc Thesis, Facultad de Ciencias Químicas y Farmacia, Universidad de San Carlos de Guatemala, Guatemala, p. 105.

Serio-Silva, J. C. 1992, Patrón diario de actividades y hábitos alimenticios de *Alouatta palliata* en semilibertad. BSc Thesis, Facultad de Biología, Universidad Veracruzana, Córdoba, México, p. 66.

Serio-Silva, J. C., Rico-Gray, V., Hernández-Salazar, L. T., and Espinosa-Gómez, R. 2002, The role of *Ficus* (Moraceae) in the diet and nutrition of a troop of Mexican howler monkeys, *Alouatta palliata mexicana*, released on an island in southern Veracruz, Mexico. *J. Trop. Ecol.* 18:913–928.

Silver, S. C., Ostro, L. E. T., Yeager, C. P., and Dierenfeld, E. S. 2000, Phytochemical and mineral components of foods consumed by black howler monkeys (*Alouatta pigra*) at two sites in Belize. *Zoo Biol.* 19:95–109.

Silver S. C., Ostro L. E. T., Yeager C. P., and Horwich, R. 1998, Feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. *Am. J. Primatol.* 45:263–279.

Sourd, C. and Gautier-Hion, A. 1986, Fruit selection by a forest guenon. *J. Anim. Ecol.* 55:235–244.

Stoner, K. E. 1996, Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *Int. J. Primatol.* 17:1–30.

Terborgh, J. 1986a, Community aspects of frugivory in tropical forests, in: A. Estrada and T. H. Fleming, eds., *Frugivores and Seed Dispersal*, Dr. W. Junk Publishers, The Hague, The Netherlands, pp. 371–384.

Terborgh, J. 1986b, Keystone plant resources in the tropical rain forest, in: M. Soule, ed., *Conservation Biology*, Sinauer Associates, Sunderland, pp. 330–344.

Yeager, C. P. 1989, Feeding ecology of the proboscis monkey (*Nasalis lavvatus*). *Int. J. Primatol.* 10:497–530.