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Foraging Habits of *Alouatta palliata mexicana* in Three Forest Fragments

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Key Words
Howler monkey · *Alouatta palliata* · Foraging strategies · Activity patterns · Area size · Fragmentation

Abstract

The activity patterns and diet of howler monkeys *(Alouatta palliata mexicana)* were studied in 3 forest fragments in south-eastern Mexico: Playa Escondida (PLA), Agaltepec Island (AGA) and Arroyo Liza (LIZ). Intersite differences offered the opportunity to investigate the foraging adaptations of howler monkeys in response to population and habitat size. In the largest fragment (PLA), the howlers' diet was based on high-quality items (fruit and young leaves). In AGA, where the density of howlers was the highest, their diet was mostly folivorous with a marked exploitation of uncommon food items such as vines, lianas, shrubs and herbs. The dietary differences in AGA were accompanied by more time spent travelling and less time spent resting. Although LIZ was the smallest fragment and had a high howler density, the small group size and the use of energy-minimizing strategies (less time spent travelling and more time spent resting) probably allowed howlers to maintain a frugivorous diet.

Introduction

The ability of howler monkeys (*Alouatta* spp.) to adapt to different environments has been related to characteristics of their foraging strategy [Lovejoy et al., 1986; Schwarzkopf and Rylands, 1989; Chiarello, 1993; Estrada and Coates-Estrada, 1996; Crockett and Pope, 1988; Marsh, 1999; Gómez-Marín et al., 2001; Gilbert, 2003]. Howlers can increase the amount of leaves in their diet (up to 90% of the total feeding

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time) when fruit is scarce, either due to isolation of a forest fragment [Neves and Rylands, 1991; Juan et al., 2000; Rodríguez-Luna et al., 2003] or to seasonal variation [Glander, 1975; Milton, 1982; Estrada, 1984; Rylands and Keuroghlian, 1988]. Another important feature is their ability to adapt their diet to the plant species available in different habitats [Bicca-Marques and Calegaro-Marques, 1994; Crockett and Pope, 1988; Rodríguez-Luna et al., 2003; Silver and Marsh, 2003], even when they are not preferred plant species [Rodríguez-Luna et al., 2003]. Finally, howlers can improve their foraging efficiency by group fission [Rodríguez-Luna et al., 2003] and minimize energy expenditure by adjusting their activity patterns, either by reducing the total travelling time [Juan et al., 2000] or resting for longer periods and decreasing foraging time [Silver and Marsh, 2003]. Despite this wealth of evidence of the howler monkeys' adaptability to marginal habitats, research analysing the effects of habitat fragmentation on foraging behaviour is scarce and there is a need for comparative studies that consider varying degrees of habitat fragmentation [Bicca-Marques, 2003].

While habitat characteristics were not quantitatively measured in this study, differences in degree of degradation, area size and population density are good predictors of food availability [Saunders et al., 1991; Juan et al., 2000; Laurance et al., 2002; Arroyo-Rodríguez and Mandujano, 2003]. These studies demonstrated that food availability decreases in fragments with a high degree of degradation and small size by reducing plant species diversity and quantity available for howlers. Although the intensity of these effects may be affected by seasonality and age and sex group composition, it is still possible to explain the existence of diverse foraging strategies by examining differences in the habitat characteristics considered here.

In this paper, we investigate the foraging strategies of 3 mantled howler groups *(Alouatta palliata mexicana)* living in 3 markedly different socio-ecological conditions: Playa Escondida (PLA), a large fragment (approx. 40 ha), with a preserved forest and low population density (0.48 individuals/ha); Agaltepec (AGA), an island (8.3 ha) with a regenerating forest and an extremely high population density (9.5 individuals/ha), and Arroyo Liza (LIZ), a small fragment (1.3 ha), with degraded forest and a high population density (4.6 individuals/ha). We compare the activity patterns and diet of 3 groups living in each forest fragment, and discuss how the population density and area size at every site may be shaping their foraging strategies.

Study Area and Methods

Study Sites and Groups

Fieldwork was carried out at 3 different sites in the Los Tuxtlas Biosphere Reserve, southeastern Veracruz State, Mexico. The climate is warm and humid, with a mean annual temperature of 24–26°C and a mean annual precipitation of 3,000–4,000 mm. There are two seasons, a dry period from March to May and a wet season from June to February [Soto and Gama, 1997]. We studied the diet and activity patterns of 3 howler monkey groups living in each of the 3 forest fragments: PLA, AGA and LIZ.

PLA (18°27′–18°36′ N and 95°03′–95°03′ W) is a fragment of approximately 40 ha on the coast of the Gulf of Mexico, with an altitudinal gradient of 0–150 m above sea level. The vegetation is mainly evergreen rain forest with several patches of secondary forest [Miranda and Hernandez, 1963]. Canopy height is 20–25 m. The study group contained 7 individuals: 2 adult males, 2 adult females, 2 juveniles and 1 infant (following Clarke's age-sex classification [1990]). Serio-Silva and Rico-Gray [2002] estimated a density of 0.48 individuals/ha in the study area.

AGA (18°27′–18°28′ N and 95°02′–95°03′ W) is an 8.3-ha island located in the Catemaco Lake, at 360–390 m above sea level. The island has two general types of vegetation: 6.2 ha of semi-evergreen forest with several areas of secondary vegetation [López-Galindo and Acosta-Pérez, 1998] with a mean canopy height of 15–20 m and 2.3 ha of pasture which the howler monkeys do not occupy. In 1987, the Universidad Veracruzana translocated a group of 9 howler monkeys (1 male and 8 females) onto this island [Rodríguez-Luna et al., 1993]. At the time of the study this group had grown to 59 animals with a density of 9.5 individuals/ha: 19 adult males, 21 adult females, 11 juveniles and 8 infants.

Finally, LIZ (18°41′ N and 95°11′ W) is a forest fragment of 1.3 ha, also on the Gulf coast, with an altitude of 60–100 m above sea level. The original vegetation of this fragment was tall evergreen rain forest, but it has been highly degraded as attested by the low height of its canopy (10–15 m). The forest site is completely surrounded by pasture where the howler monkeys do not range. A more complete description of the site can be found in Gómez-Marín et al. [2002]. This fragment was inhabited by a group of 6 howler monkeys: 1 adult male, 4 adult females and 1 juvenile. The population density was 4.6 individuals/ha.

Behavioural Observations

N.A. collected data from August 1997 to June 1998 in PLA and AGA. Data in these 2 forest fragments were collected on alternating visits. Data were collected solely from LIZ from August 2000 to June 2001. Focal animal observation sessions were 5 h at every site [Altmann, 1974]. Focal individuals were chosen by random rotation. Individuals were easily identified by their natural marks (skin pigmentation on the hands and feet and sometimes scars). Focal observations occurred between 7.00–12.00 and 12.00–17.00 h, alternating mornings and afternoons, with a minimum of 7 days per month at each site. Focal observations shorter than the entire 5 h were not considered for data analysis. Each focal session was considered to represent the main activity of the group. Behavioural observations were categorized as the following: feeding (search and ingestion of food), travelling (movement to a new area, change of tree or movement within the tree without the clear purpose of feeding), resting (sleep or static without interaction) and other (remaining activities not categorized as feeding, travelling or resting). During feeding, the food item (mature fruit, young fruit, young leaf, mature leaf, flower or petiole) was recorded, and each consumed plant was identified to the species level.

Statistics

For comparative purposes every 5-hour focal session was taken as a unit of observation. Nine hundred hours of data were collected in the 3 study sites, with 300 h (60 observation units) at each site. After counting the number of food species and the time dedicated to each, dietary diversity for each group was estimated using the Shannon-Weaver index and its evenness using Biodap software [Magurran, 1988]. These indexes were run and then compared using t tests. To investigate differences in activity patterns and in time dedicated to the consumption of food from non-arboreal life forms (vines, lianas and epiphytes) we employed Friedman's ANOVA *(F)* and post hoc analysis. Kruskal-Wallis ANOVA and post hoc test were used to test differences in the frequencies of eaten food items (shoots, young leaves, mature leaves, petioles, flowers, young fruits and mature fruits) per session. Spearman's rank correlation was used to examine the relationship between locomotion time and number of food species consumed. The Kendall τ correlation index was run to relate the percentage of consumed plant parts between sites.

Results

Activity Patterns

Howlers residing in the 3 study sites displayed significant differences in time spent resting ($F = 9.38$, $p < 0.001$) and travelling ($F = 168$, $p < 0.001$; fig. 1). Howlers in AGA spent less time resting than those in LIZ (post hoc test, $p < 0.001$) and in PLA

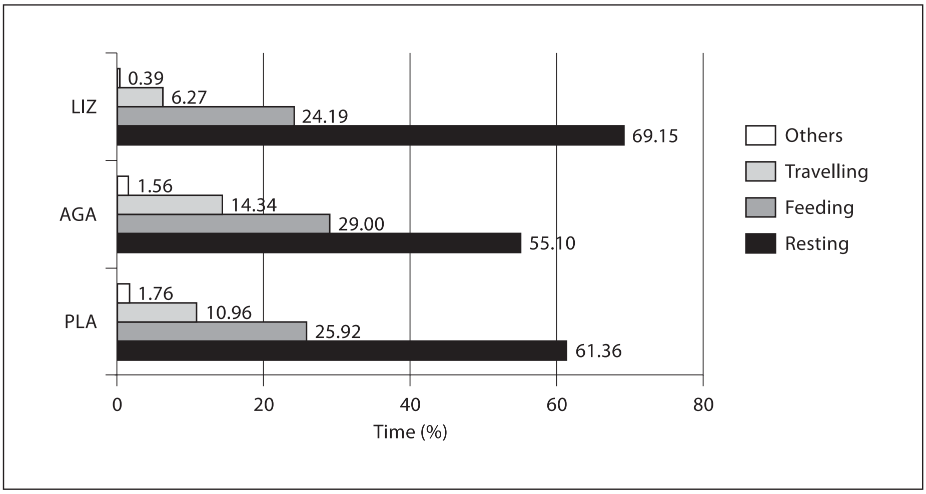

Fig. 1. Activity patterns: percentages of total observation time (300 h/study site).

(post hoc test, $p < 0.05$). The animals travelled less in LIZ than in AGA (post hoc test, $p < 0.0001$) and PLA (post hoc test, $p < 0.001$). Time dedicated to travel, however, was higher in AGA than in PLA (post hoc test, $p < 0.05$). No significant differences were found in time spent feeding between the 3 sites.

Diet

Howlers at the 3 sites consumed plant parts from a total of 100 species from 41 plant families (tables 1 and 2): 66 were tree species while the remaining 34 species were non-arboreal. In PLA the diet was composed of 49 plant species from 28 families: 36 trees, 4 vines, 7 lianas and 2 epiphytes. In AGA howlers consumed 56 species from 28 families: 32 trees, 3 shrubs, 2 herbs, 7 vines and 12 lianas. In LIZ 35 species belonged to 20 families: 26 trees, 2 vines, 6 lianas and 1 epiphyte were consumed. Eight species were shared between the 3 sites: 6 tree species *(Dendropanax arboreus, Bursera simaruba, Albizia purpuzii, Ficus lundelii, Ficus maxima* and *Ficus yoponensis)* and 2 liana species *(Cissus gosyphyfolia* and *Vitis tilifolia).* Moraceae, and especially the genus *Ficus*, was a particularly prominent part of the diet at the 3 sites; in PLA the consumption of *Ficus* represented 54.7% of the total feeding time, 51.9% in LIZ and 30.7% in AGA.

In AGA the Shannon index for diet diversity (table 2) was higher than in PLA ($t = 30.67$, $p < 0.001$) and in LIZ ($t = 18.96$, $p < 0.001$). Diet in PLA was more diverse than that in LIZ ($t = 10.82$, $p < 0.001$). We also found differences in the number of consumed species per observation session between sites (Kruskal-Wallis = 16.83, d.f. = 2, $p < 0.001$). Howlers in AGA ate more plant species per session (6.52) than in PLA (3.55; post hoc test, $p < 0.001$) and LIZ (4; post hoc test, $p < 0.001$). Locomotion time was correlated with species eaten per session in all study sites: PLA ($r_s = 0.67$, $n = 60$, $p < 0.001$), LIZ ($r_s = 0.6$, $n = 60$, $p < 0.001$) and AGA ($r_s = 0.6$, $n = 60$, $p < 0.001$).

Table 1. Percentage of feeding time dedicated to each species by study troops

Family	Species	Growth form	Eaten part	PLA	AGA	LIZ
Amaranthaceae	*Iresine celosia*	herb	YL		0.08	
Anacardiaceae	*Astronium graveolens*	tree	YL, ML		4.93	
	Spondias mombin	tree	S, YL, MF		2.06	
	Spondias radlkoferi	tree	YL, ML, MF	0.49	0.35	5.83
	Tapirira mexicana	tree	MF	0.92		
Annonaceae	*Rollinia mucosa*	tree	YL, MF	2.86		0.04
Apocynaceae	*Fonsteronia viridenses*	liana	YL	1.43		
	Prestonia mexicana	vine	YL, ML		1.3	
	Stemadennia donnell-smithi	tree	YL, ML		0.11	
Araceae	*Monstera tuberculata*	vine	YL	0.44		
	Philodendron chiapensis	vine	YL	0.23		
	Philodendron radiatum	vine	YL, P	0.99		
	Philodendron scandens	vine	YL, P	0.53	0.63	
	Syngonium chiapensis	vine	YL, P		0.55	0.02
	Syngonium podophylum	vine	YL, P		2.41	0.05
Araliaceae	*Dendropanax arboreus*	tree	YL, MF		0.91	0.09
Aristolochiaceae	*Aristolochia ovalifolia*	liana	YL	0.05		
Asteraceae	*Eupatorium morifolium*	shrub	YL		0.11	
Bignonaceae	*Phitecoctenium crucigerum*	liana	ML		0.16	
Bombacaceae	*Pachira aquatica*	tree	FL		0.84	
Boraginaceae	*Cordia alliodora*	tree	YL, ML	1.26		2.06
	Cordia dodecandra	tree	MF	0.15		2.34
	Tournefortia hirsutissima	liana	MF			0.46
Burseraceae	*Bursera simaruba*	tree	S, YL	0.04	5.5	0.72
	Protium copal	tree	YL		0.73	
Caesalpiniaceae	*Cynometra retusa*	tree	YL	0.89		
	Machaerium falciforme	liana	YL		0.04	
Cecropiaceae	*Cecropia obtusifolia*	tree	YL, ML, P	4.84	0.94	
Chrysobalanaceae	*Hirtella triandra*	tree	MF, FL			1.83
Convulvulaceae	*Ipomoea batatas*	liana	YL		1.11	
	Ipomoea batatoides	liana	YL	0.04	0.04	
	Ipomoea philomega	liana	YL	0.84		
Cucurbitaceae	*Psyguria triphila*	vine	YL		2.97	
Ebenaceae	*Diospyros digyna*	tree	MF	7.79		
Euphorbiacae	*Croton schiedanus*	tree	YL			0.02
	Omphalea oleifera	tree	MF			0.46
	Sapium lateriflorum	tree	YL	0.13		
Fabaceae	*Andira galeotiana*	tree	S, YL, FL		4.61	
	Dussia mexicana	tree	S, YL, FL			0.39
	Gliricidia sepium	tree	YL		2.92	
	Lonchocarpus cruentus	tree	S, YL		1.93	
	Pterocarpus rohrii	tree	S, YL	4.92		
	Rynchosia minima	liana	YL, ML, FL		4.67	
Gutiferae	*Calophyllum brasiliense*	tree	YL	0.25		
	Rheedia edulis	tree	YF, MF	1.25		
Lauraceae	*Nectandra lundelli*	tree	YL		0.04	0.05
Malphygiaceae	*Malphygia coutierii*	shrub	YL, ML		0.29	
	Mascagnia vaccinifolia	liana	YL			0.76
Malvaceae	*Malvabiscus arboreus*	shrub	YL		0.57	
	Robinsonella mirandae	tree	YL	0.11		
Marcgraviaceae	*Sourobea loczi*	epiphyte	YL	0.46		0.37
Meliaceae	*Guarea glabra*	tree	YL	0.06		0.44

Table 1 (continued)

Family	Species	Growth form	Eaten part	PLA	AGA	LIZ
Menispermaceae	*Cissampelos pareira*	vine	YL		2.08	
Mimosaceae	*Albizia purpusii*	tree	S, YL, YF, MF, FL	0.34	1.93	2.96
	Delonix regia	tree	YL	0.02		
	Inga acrocephala	tree	YL, ML, P, MF	1.56		7.73
	Inga paterno	tree	MF	0.13		
	Inga vera	tree	YL		0.65	
	Zacatecas tetragona	tree	YL, ML		0.25	
Moraceae	*Brosimum allicastrum*	tree	YL, YF, MF	5.66	0.52	
	Brosimum lactenses	tree	S, YL			2.8
	Castilla elastica	tree	MF			0.49
	Clorophora tinctoria	tree	S, YL		1.03	
	Ficus cotinifolia	tree	YL, P, MF		6.47	
	Ficus jimenezee	tree	MF	0.89		
	Ficus lundelii	tree	S, YL, YF, P, MF	5.09	0.5	29.82
	Ficus maxima	tree	S, YL, YF, MF	0.17	0.47	5.9
	Ficus obtusifolia	tree	S, YL, YF, P, MF	6.34	0.71	
	Ficus perforata	tree	S, YL, YF, MF	24.31		
	Ficus petenensis	tree	S, YL, YF, MF	3.87		4.91
	Ficus trigonata	tree	S, YL, YF, MF	22.74	8.01	
	Ficus tuerqueimii	tree	S, YL, P, MF		13.91	
	Ficus yoponensis	tree	S, YL, P, YF, MF	1.29	0.58	11.24
	Poulsenia armata	tree	S, MF	1.33		1.74
	Pseudolmedia oxyphylaria	tree	YL, YF, MF	0.65		0.51
	Trophis mexicana	tree	YL			0.19
	Trophis racemosa	tree	ML		0.17	
Myrtaceae	*Eugenia acapulcensis*	tree	YL, MF	1.84		9.46
Nyctaginaceae	*Neea psychotrioides*	tree	YL	0.27		
	Pisonia aculeata	liana	YL		0.08	0.23
Phitolacaceae	*Rivina humilis*	herb	YL		3.2	
Polygonaceae	*Coccoloba hondurensis*	tree	YL			2.55
	Coccoloba matudae	tree	S, YL	0.04		0.42
Rubiaceae	*Genipa americana*	tree	S	0.15		
Rutaceae	*Zantoxylum caribeum*	tree	YL		0.04	
	Zantoxylum kellermanii	tree	ML		0.16	
Sapindaceae	*Cupania dentata*	tree	MF		0.04	
	Paullinia clavijera	liana	YL		1.01	
	Paullinia schiedana	liana	YL		0.13	
	Serjania goniocarpa	liana	YL	0.04	0.15	
	Serjania mexicana	liana	YL		1.06	0.76
Sapotaceae	*Pouteria campechiana*	tree	S, YL	1.8		
	Pouteria durlandii	tree	S	0.11		
	Sideroxylon capiri	tree	YL, YF, MF		4.31	
Solanaceae	*Juanulloa mexicana*	epiphyte	YL	0.02		
Tiliaceae	*Heliocarpus donnell-smithii*	tree	YL		0.94	
Urticaceae	*Myriocarpa heterostacha*	tree	YL		0.8	
Vitaceae	*Cissus gosyphyfolia*	liana	YL, MF	0.15	0.71	0.16
	Cissus sicyoides	vine	YL		0.02	
	Vitis tilifolia	liana	S, YL	0.21	9.27	2.2

S = Shoots; Y = young leaves; ML = mature leaves; P = petioles; FL = flowers; YF = young fruits; MF = mature fruits.

Table 2. Different plant habits and diversity in diet

Study site	Trees	Shrubs	Vines	Lianas	Epi-phytes	Herbs	Total	Main species per observation session	Total feeding time min	H′	E
PLA	36	0	4	7	2	0	49	3.55	4,734	2.83	0.73
AGA	32	3	7	12	0	2	56	6.52	5,258	3.27	0.81
LIZ	26	0	2	6	1	0	35	4	4,322	2.56	0.72

H′ = Shannon Diversity Index; E = evenness.

Table 3. Time spent eating non-arboreal foods (shrubs, herbs, vines, lianas and epiphytes)

Study site	Average time per session min	Total time min	Feeding time %
PLA	3.8	228	4.82
AGA	29.15	1,749	33.26
LIZ	3.65	219	5.07

Use of Non-Arboreal Species

We found differences in the time spent feeding on non-arboreal species between the study sites (*F* = 35.47, d.f. = 2, $p < 0.001$; table 3). Howlers in AGA ate more non-arboreal items than in PLA (post hoc test, $p < 0.001$) and LIZ (post hoc test, $p < 0.001$). In AGA 2 lianas were among the 10 most commonly eaten species (*Vitis tilifolia*, 9.28% of the feeding time, and *Rynchosia minima*, 4.68%), but this was not the case in PLA and LIZ (table 1). Furthermore, howlers in AGA used plant species that obliged them to go to the lower canopy or even to the ground: shrubs *(Eupatorium morifolium, Malphygia coutierii* and *Malvabiscus arboreus)* and herbs *(Iresine celosia* and *Rivina humilis)*. There were no differences in the feeding time on non-arboreal items between PLA and LIZ.

Food Items

Although mature fruits and young leaves were the main food plant parts at all study sites, there were some differences (fig. 2). In AGA the food items most eaten were young leaves (48.45%), followed by mature fruits (15.27%), petioles (9.76%), mature leaves (8.61%), shoots (6.51%), young fruits (6.08%) and flowers (5.32%). Feeding percentages on the different plant parts between LIZ and PLA were similar to each other ($\tau = 0.91$, $p < 0.005$) but different from the ones at AGA: mature fruit (40% in LIZ and 45.7% in PLA), young leaves (33.52 and 32.55%), young fruit (11.18 and 11.64%), shoots (8.87 and 5.07%), mature leaves (3.13 and 4.38%), flowers (2.13 and 0.17%) and petioles (1.17 and 0.48%).

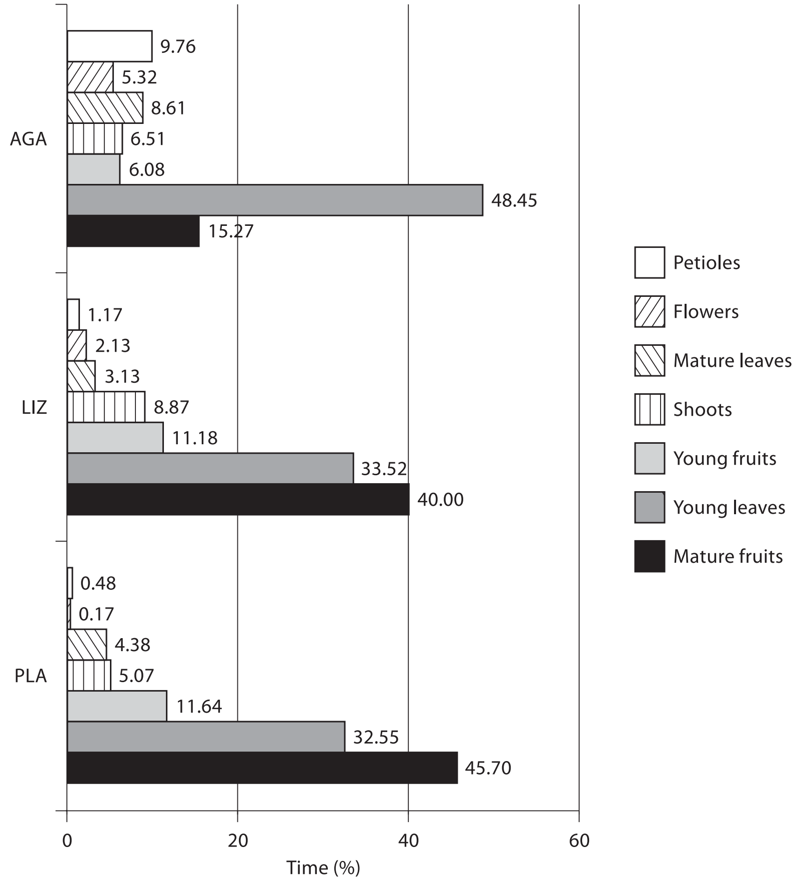

Fig. 2. Percentage of feeding time dedicated to each plant part. For total feeding time see table 2.

Discussion

In general, activity patterns and diet in the 3 howler monkey groups studied are similar to reports of *Alouatta* elsewhere; long periods of resting followed by short bouts of travelling and feeding are the norm in the genus in both continuous (reviewed in Neville et al. [1988]) and fragmented habitats (reviewed in Bicca-Marques [2003]).

Howler monkeys ate a total of 100 species belonging to 41 families: 66 trees and 34 plants of other growth habits. *Ficus* in particular was the most frequently eaten plant taxon at the 3 study sites. Figs are an important component of the diet of *Al-*

ouatta palliata [Milton, 1980; Estrada, 1984; Bicca-Marques, 2003]. Given their high fruit production and asynchronous phenological cycles [Ibarra and Wendt, 1992; Shanahan et al., 2001], fig trees are a preferred item in environments with secondary vegetation [Julliot and Sabatier, 1993]. These general aspects were common to the 3 study sites; however, there were some differences between them.

Playa Escondida

Of the 3 study sites, PLA most resembled a continuous forest. The population density at PLA (0.48 individuals/ha) did not differ from the average reported by Chapman and Balcomb [1998] for several howler monkey populations. This group inhabited a large area with a high canopy that was relatively intact. Under conditions of low monkey density and undisturbed habitat we expect howlers to have a more frugivorous diet because fruit patches are generally less common and less rich in disturbed compared to undisturbed forests [Saunders et al., 1991; Juan et al., 2000; Laurance et al., 2002; Arroyo-Rodríguez and Mandujano, 2003]. Estrada [1984] observed that the diet of a howler monkey group in continuous forest at Los Tuxtlas included 41% of feeding time on mature fruit and 39% on young leaves. Howler monkeys in PLA foraged preferentially on mature fruits (45.7%) and young leaves (32.55%), both of which are high-quality food items [Milton, 1980]. In summary, these howlers spent 61.36% of their time resting, 10.96% moving and 25.92% feeding in a habitat with presumably high food availability (low population density, small group size and large area).

Agaltepec Island

In times of resource scarcity, primates can respond by feeding more frequently on lower-quality and/or unusual food items [Hladik, 1977; Glander, 1979], travelling greater distances to find food [Dunbar, 1988] or minimizing group size by forming smaller parties [Symington, 1990]. In AGA, the howlers had a highly folivorous diet with significant proportions of food plants that appear to be uncommon resources for other groups. On this island, the howler monkeys travelled for longer, rested for a shorter length of time and fragmented into subgroups.

It is reasonable to consider that the extremely high population density on this island (9.5 individuals/ha) reduced food availability for the howler monkeys. Furthermore, when so many animals coexist in a closed area, patch depletion occurs quickly and all group members are not able to feed on high-quality food items (fruits and young leaves) for long periods. Fruit patches are temporally and spatially more limited than leaves, and the relation between food intake and foraging effort restricts frugivory in a large group [Milton, 1980]. Howlers can increase the amount of leaves in their diet when fruit availability is reduced due to isolation in a forest fragment [Neves and Rylands, 1991; Juan et al., 2000]. Accordingly, we found that howler monkeys in AGA foraged mainly on young leaves (almost 50% of total time feeding) and to a much lesser extent on mature fruits (approx. 15% of time spent feeding). The observation that over the last 15 years howler monkeys in AGA have changed from an essentially frugivorous diet to one which is more folivorous [Rodríguez-Luna et al., 2003] reinforces the idea that this mainly folivorous diet is in response to high population density. This change has coincided with an increase in population size from 9 individuals in 1987 to 59 in 2001. Therefore, diet in AGA appears to be that of an opportunistic frugivore, in the sense that animals are as frugivorous as possible, but are as folivorous as necessary, since an exclusive dependence on fruits would prevent animals from satisfying their minimum nutritional requirements [Nagy and Milton, 1979; Milton, 1980].

At another level of dietary adaptation, when preferential food resources were not available, howler monkeys have been observed to forage upon plants that are not a common part of their diet [Bicca-Marques and Calegaro-Marques, 1994; Crockett, 1998; Rodríguez-Luna et al., 2003; Silver and Marsh, 2003]. Even if trees were the most eaten plant form, we suggest that the high population density and increased rate of depletion of primary food sources are forcing howler monkeys in AGA to forage on alternative resources, such as vines, lianas, shrubs and herbs (which individually do not provide the large quantities of food present in trees). Feeding on shrubs and herbs is uncommon for an arboreal primate; it forces howlers to descend to the lower levels of the canopy and sometimes to the ground. It seems that the food availability in their ecological niche (high canopy and emergents [Mendel, 1976]) is so reduced due to high density and large group size that the howlers are being forced to exploit alternate food sources.

Although ranging patterns were not studied, time spent travelling can be a good indicator of distances covered and the associated energy expenditure. In AGA, time spent travelling was significantly higher than at the other 2 sites; furthermore, howler monkeys here were never observed foraging in a single tree, groups of several small trees or other non-arboreal forms for a complete day, but they fed on many different species during feeding episodes. Lianas and vines are widely dispersed resources that require intense searching; thus, howler monkeys in AGA need to travel more and spend more time feeding to maintain food intake ('feed to move and move to feed' [Napier and Napier, 1985]).

Fission-fusion patterns appear to be a complementary adaptation to improve foraging efficiency and reduce competition for resources [Symington, 1990]. Although howler monkeys in AGA initially foraged cohesively, after the population had grown from 10 to 57 individuals over 8 years, they began to split into subgroups [Rodriguez-Luna, 2000], which varied in size depending on seasonal changes in food availability [Dias, 2002]. The shift to a fission-fusion pattern allowed howlers at AGA to remain in a single social unit, reducing resource competition and maximizing foraging efficiency, while exploiting small food patches such as herbs, shrubs and lianas.

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Given the high population density (4.6 individuals/ha), the small size (1.3 ha) and the degree of degradation in vegetation in LIZ [Gómez-Marín et al., 2001], we expected this group to adopt some of the strategies the howler monkeys in AGA implemented to cope with the reduction in food availability: a mainly folivorous diet, consumption of uncommon food items, increased travelling time, reduction of resting time and group fragmentation during feeding.

Although howler monkeys in LIZ consumed less fruit (51.18% of total feeding time) than in PLA (57.34%), they still maintained a mainly frugivorous diet compared to AGA (21.78%). Two population traits could explain this last difference. First, even if the population density at LIZ is much higher than the mean value reported by Chapman and Balcomb [1998] for the species, it is still half the density of that in AGA. Second, contrary to AGA, the small group size in LIZ would allow all group members to feed simultaneously from fruiting trees. These demographic differences could also explain why howlers did not forage more frequently on vines, epiphytes and lianas.

Howler monkeys in the LIZ fragment spent more time resting and less time travelling and feeding compared to AGA and PLA. The reduction of the total travelling time [Juan et al., 2000] on the one hand and the increase in resting time and reduction of feeding time [Silver and Marsh, 2003] on the other have been described as energy-minimizing strategies. The little time spent moving at LIZ could be a consequence of 2 main effects: (1) the small area limits troop movements, and (2) better knowledge of the location and phenological status of feeding resources maximizes direct travelling and minimizes travelling effort.

Therefore, our results from LIZ suggest that the small group size allowed these howler monkeys to eat high-quality food items (fruits and young leaves, 40 and 33.52% of total feeding time, respectively) while compensating for the presumably low year-long availability of these resources (imposed by the small size of the fragment) by using energy-minimizing strategies.

Although our study showed that howler monkeys cope well with the restrictions imposed by habitat fragmentation, further studies on food availability, demographic evolution and physiological health (i.e. cortisol) are needed to assure that the adaptations shown are sufficient to guarantee the long-term survival for these populations.

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