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RESEARCH ARTICLE

Foraging Ecology of Howler Monkeys in a Cacao (*Theobroma cacao*) Plantation in Comalcalco, Mexico

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Recent evidence indicates that primate populations may persist in neotropical fragmented landscapes by using arboreal agroecosystems, which may provide temporary habitats, increased areas of vegetation, and connectivity, among other benefits. However, limited data are available on how primates are able to sustain themselves in such manmade habitats. We report the results of a 9-month-long investigation of the feeding ecology of a troop of howler monkeys (n=24) that have lived for the past 25 years in a 12-ha cacao plantation in the lowlands of Tabasco, Mexico. A vegetation census indicated the presence of 630 trees ($\geq$20 cm diameter at breast height (DBH)) of 32 shade species in the plantation. The howlers used 16 plant species (13 of which were trees) as sources of leaves, fruits, and flowers. Five shade tree species (*Ficus cotinifolia*, *Pithecellobium saman*, *Gliricidia sepium*, *F. obtusifolia*, and *Ficus* sp.) accounted for slightly over 80% of the total feeding time and 78% of the total number trees (n=139) used by the howlers, and were consistently used by the howlers from month to month. The howlers spent an average of 51% of their monthly feeding time exploiting young leaves, 29% exploiting mature fruit, and 20% exploiting flowers and other plant items. Monthly consumption of young leaves varied from 23% to 67%, and monthly consumption of ripe fruit varied from 12% to 64%. Differences in the protein-to-fiber ratio of young vs. mature leaves influenced diet selection by the monkeys. The howlers used 8.3 ha of the plantation area, and on average traveled 388 m per day in each month. The howlers preferred tree species whose contribution to the total tree biomass and density was above average for the shade-tree population in the

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plantation. Given the right conditions of management and protection, shaded arboreal plantations in fragmented landscapes can sustain segments of howler monkey populations for many decades. Am. J. Primatol. 68:127–142, 2006.

Key words: howler monkeys; *A. palliata*; foraging ecology; agroecosystems; conservation; Tabasco, Mexico

INTRODUCTION

The pressures of land use have been implicated as the major cause of tropical rain forest loss and fragmentation throughout the world [Donald 2004; Henle et al., 2004a, b]. The resulting habitat destruction and fragmentation are believed to be the major cause of the increased rate of species extinction that has occurred in recent decades [Henle et al., 2004a,b]. Fragmentation of habitat and stochastic forces, and the increased loss of habitat play an important role in further declines of populations and species at the local level [Henle et al., 2004b, and references therein]. However, growing empirical evidence suggests that not all species decline toward extinction following fragmentation, and that certain species may be more resilient than expected [Estrada et al., in press, and references therein]. Similarly, the focus of landscape studies in the tropics has been the ''habitat'' rather than the ''matrix'' (the nonhabitat surrounding the native habitat patches of interest). This binary perspective has been applied to the study of the consequences of habitat fragmentation on biological communities in the neotropics, but is primarily based on a large body of research conducted in South America. Most of these studies examined the biological richness of forest fragments, and sought to determine how such richness is affected by isolation, edge effects, invasive species, and temporal isolation and management [Estrada et al., in press; Laurance et al., 2002].

Recently, attention has been focused on the value of matrix habitats for preserving large segments of biodiversity [Murphy & Lovett-Doust, 2004; Pimentel et al., 1992; Ricketts, 2001]. Evidence suggests that some agroecosystems may be important for sustaining vertebrate biodiversity in human-modified tropical landscapes by providing temporary habitats, functioning as stepping stones, increasing areas of vegetation and the availability of potential resources, and providing shelter and connectivity for isolated segments of populations in a broad spectrum of animal species [Daily et al., 2003; Greenberg et al., 2000; Harvey et al., 2004; Villaseñor & Hutto, 1995; Wunderle, 1999].

While extensive pasture land for cattle grazing dominates fragmented landscapes in Mesoamerica, some farming practices have resulted in highly heterogeneous landscapes in which patches of natural vegetation and agroecosystem coexist. Many of these landscapes harbor different types of arboreal and nonarboreal agroecosystems, such as forest- and tree-shaded (i.e., trees planted by humans) coffee (*Coffea arabica*), cacao (*Theobroma cacao*), and cardamom (*Elatteria cardamomum*; Zingiberaceae) plantations, as well as unshaded arboreal crops (e.g., allspice (*Pimienta dioica*) and citrus (*Citrus* spp.)), and nonarboreal cultivars such as bananas (*Musa* spp.) and corn, among others [Scroth et al., 2004]. Furthermore, throughout Mesoamerica farmers have planted linear strips of arboreal vegetation (known as live fences) to delimit land boundaries [Harvey et al., 2004].

A few reports have described the presence of primates in agroecosystems. For example, cabruca cacao in Brazil has attracted attention because of its ability to harbor primates such as the golden-headed lion tamarin (*Leontopithecus chrysonelis*), an endangered species [Rice & Greenberg, 2000]. Similarly, in Gulung Palung National Park in Kalimantan, primates such as leaf monkeys (*Presbytes rubicunda*) and gibbons (*Hylopbates agilis*) are found in agroforests [Salafsky, 1993]. Michon and de Foresta [1995] reported the presence of macaques, leaf monkeys, gibbons, and siamangs (*Hylobates syndactilus*) in rubber (*Hevea brasiliensis*) and dammar (*Shorea javanica*) agroforests, and five species in durian (*Durio zibethinus*) agroforests in Sumatra. It was noted that the density of these primates was similar to that in primary forest. In Costa Rica and Nicaragua, howler monkeys (*Alouatta palliata*) have been found in shaded coffee plantations [McCann et al., 2003; Somarriba et al., 2004], and in Los Tuxtlas, Mexico, howler (*A. palliata*) and spider (*Ateles geoffroyi*) monkeys exploit forest-shaded cacao and coffee plantations [Estrada & Coates-Estrada, 1996].

More recently, a study conducted in human-modified landscapes in the lowlands of southern Mexico, Guatemala, and Costa Rica reported the presence of five (*Alouatta palliata*, *A. pigra*, *Ateles geoffroyi*, *Samiri oerstediii*, and *Cebus capucinus*) of the eight Mesoamerican primate species in 15 types of arboreal agroecosystems [Estrada et al., in press]. This study reports that the primates were permanently residing in eight of the agroecosystems investigated (e.g., cacao and coffee), while other agroecosystems were used as foraging or stop-over habitats. While the presence and residency of primates in particular arboreal agroecosystems is likely to reflect species-specific differences in behavioral and dietary flexibility, information on how primates sustain themselves in these habitats is extremely limited. A better understanding of the value of agroecosystems for conserving remnant primate populations in human-modified tropical landscapes has critical implications for ecological and restoration theory, and for assessing the conditions under which different primate taxa can persist in human-modified tropical landscapes [Henle et al., 2004b; Melbourne et al., 2004; Pimentel et al., 1992; Scroth et al., 2004]. In this paper we report the results of a 9-month-long investigation of the feeding ecology of a troop of howler monkeys (*Alouatta palliata*) living in a cacao plantation (*Theobroma cacao*) shaded by planted legume trees (mainly *Pithecelobium saman*), located in the lowlands of Tabasco, Mexico.

MATERIALS AND METHODS

Study Site

The study was conducted at a cacao plantation located 2.0 km from the town of Comalcalco (18°26′ N, 93°32′ W; altitude 10–40 m above sea level, mean annual precipitation=1,934 mm, mean temperature=26.4°) in the central lowlands of Tabasco, Mexico. Cattle ranching and cultivation of cacao are two major components of the local subsistence economy. Currently, about 24% of the municipal land is occupied by cacao plantations, about 1% is forest remnants, and the rest consists of pastures for cattle [INEGI, 2000]. The cacao plantation investigated in this study encompasses an area of 12 ha, and is part of a 28-ha cattle ranch. The plantation contains approximately 4,400 fruit-producing cacao trees. The shade required by these trees to grow is provided by tall, large crowned trees planted about 40 years ago by the plantation's owners. These consist mainly of Fabaceae species, such as *P. saman*, *Erythrina americana*, *Gliricidia sepium*, *Inga jinicuil*, and *I. vera*.

Primate Population

Surveys of the plantation indicated the existence of a single troop of howler monkeys. According to the owners of the plantation, the howlers are remnants of a once-larger population of *A. palliata* in the forests that covered the area about 40 years ago. At the time of the study, the howler troop consisted of 24 individuals (five adult males, 11 adult females, six juveniles, and two infants). Using mean weight values for *A. palliata* from Los Tuxtlas (400 km north of Comalcalco) [Estrada, 1982], we estimated the biomass represented by the troop of howler monkeys in the cacao plantation at 10.2 kg/ha.

Behavioral Observations

Between February and October 2003, we spent an average of 8 days (SD $\pm$1.8 days) each month conducting observations of the feeding behavior of the howler monkey troop. Observations were carried out between 0700 and 1900 hr by D.M. and a student assistant trained for 1 month prior to the start of systematic sampling. The observations consisted of focal samples [Altmann, 1974] of 10-min duration each on non-infant individuals in the troop. Individuals in the troop were identified by the presence of facial scars; patches of blonde fur on the tail, hand, or feet; or by association with others (i.e., mothers and clinging infants). The recorded behaviors were grouped into five broad categories: resting, feeding, locomotion, travel, and social interactions [Estrada et al., 1999].

In the case of feeding behavior, we measured the time the howlers spent feeding, and recorded the plant part being ingested, as well as its state of maturity (young/mature). The trees used by the howlers as sources of food were marked, identified as to species, and measured (height and diameter at breast height (DBH)), and their spatial position was recorded with a GPS device. These data were incorporated into a digital map of the plantation with the use of ArcView 3.1 software. When the activity was travel (i.e., synchronized movements by troop members from one tree or group of trees to another), we recorded the straight line distance between travel points. We quantified the howlers' use of space by dividing the 12-ha cacao plantation into 40×40 m quadrats, and recording for each observation day the time spent by the howlers in each quadrat. From this, we totaled the number of quadrats used per month, expressed their total accumulated area in ha, and calculated an index of diversity of quadrat use using Shannon's H' and an index of quadrat overlap between adjacent months using Sorensen's coefficient of similarity index [Brower et al., 1998].

Census of Trees in the Plantation

We conducted a complete count of all non-cacao trees $\geq$ 20 cm in DBH present in the 12-ha cacao plantation. The trees were identified as to species and measured (height and DBH), and the tree location was determined with the GPS device. For each tree species recorded in these counts, we calculated an importance value index (IVI). This index incorporates in a single measure the relative frequency and basal area of each species (IV(x)=100*BA(x)/BA(all species) + 100*NS(x)/NS(all species), where x is a particular species in a plot, BA is the basal area, and NS is the number of stems [Brower et al., 1998].

Protein and Fiber Content of Some Plant Foods

We collected samples of young and mature leaves from at least three individuals of each of eight species used by the monkeys as a source of food. The samples were dried at a constant temperature (60°C) for 48 hr and later analyzed with the use of procedures described in Lucas et al. [2003]. The proportions of crude protein and fiber were determined through laboratory analysis by ECOSUR in San Cristobal de las Casas, Chiapas, Mexico.

Data Processing and Analysis

The behavioral records were expressed as a percentage of the total recorded time spent on all activities, or as minutes per hour of focal observation [Estrada et al., 1999]. The total feeding time spent by individuals in the troop was divided by the total monthly feeding time spent on each plant part, and the results were expressed as minutes per hour of focal observation and as mean monthly feeding rates [Muñoz et al., 2002]. We estimated the total and monthly dietary diversity using Shannon's diversity index (H′), and used Sorensen's coefficient of similarity [Brower et al., 1998] to assess, at the species level, the degree of monthly overlap in the diet. A nonparametric analysis of variance (ANOVA; Kruskal-Wallis test) was used to determine monthly variations in the howlers' general activity pattern. Spearman's rank (r_s) correlation and Pearson's r coefficients were used to examine the relationship between pairs of variables (e.g., number of trees used per species and percentage of feeding time).

RESULTS

Plant Species Used

During the study period we completed 3,056 10-min focal samples totaling 509 hr of focal observations, or an average of 336 focal samples per month (range=267–397). We recorded the use by howler monkeys of 16 species of plants (10 botanical families) as sources of food. Species in the Moraceae and Fabaceae families accounted for 57% and 32% of feeding time, respectively. Species in seven additional plant families accounted for the remaining 11%. Thirteen of the 16 plant species used were trees, two were epiphytes, and one was a vine (Table I). The howlers used 139 trees as sources of food. These accounted for 22% of the non-cacao trees (≥20 cm in DBH; n=630) present in the plantation. The howlers concentrated 70% of their feeding time on three tree species (*Ficus cotinifolia*, *P. saman*, and *G. sepium*), which accounted for 67% of the trees used as sources of food. Another two tree species (*Ficus obtusifolia* and *Ficus* sp.) accounted for 16% of feeding time (Table I).

Quantitative Features of Vegetation

A count of non-cacao trees (>20 cm in DBH) in the 12-ha plantation resulted in a total of 630 trees belonging to 32 species. Of these, 66% were trees of species (n=13) used by the howlers as sources of food, and these (except for *P. saman* and *G. sepium*) were present at densities of <5 ind/ha (Table I). While the overall mean height and DBH of shade-providing trees in the plantation were 16.2±14.6 m and 59.9±48.7 cm, respectively, the trees used by the howlers as sources of food had a mean height of 19.2±4.6 m (range=6–28 m) and a mean DBH of 106±68.4 cm (range=17–365 cm). Shade trees and howler-used trees differed statistically

TABLE I. Plant Species Used by Howler Monkeys as Sources of Food in the Cacao Plantation for the Period February–October 2003*

Species	Family	Trees used	Trees in site	Density (ind/ha)	IVI	Months used	Percent of feeding time
Ficus cotinifolia	Moraceae	22	36	3.00	22.7	9	41.6
Pithecellobium saman	Fabaceae	41	99	8.25	98.2	9	15.6
Gliricidia sepium	Fabaceae	30	103	8.58	36.9	9	12.7
Ficus sp.	Moraceae	4	6	0.50	3.4	6	8.7
Ficus obtusifolia	Moraceae	11	18	1.50	7.7	8	7.1
Spondias mombin	Anacardiaceae	6	13	1.08	5.5	3	5.3
Diphysa robinioides	Fabaceae	13	35	2.92	14.0	8	3.5
Manikara zapota	Sapotaceae	1	1	0.08	0.5	2	2.1
Mangifira indica	Anacardiaceae	2	7	0.58	3.1	3	0.9
Bursera simaruba	Burseraceae	1	6	0.50	1.8	1	0.7
Erythrina americana	Fabaceae	6	55	4.58	16.7	3	0.5
Cecropia obtusifolia	Cecropiaceae	1	14	1.17	7.0	1	0.4
Selenicereus sp. (E)	Cactaceae	–	–	–	–	4	0.4
Terminalia amazonia	Combretaceae	1	3	0.25	1.3	2	0.3
Paullinia pinata (V)	Sapindaceae	–	–	–	–	1	0.2
Syngonium podophyllum (E)	Araceae	–	–	–	–	1	<0.01

*All species, except three (coded E epiphyte, V vine), were trees. Shown also is the number of trees ($\geq$20 cm DBH) of each species present in the plantation, their density and IVI index values, and the number of months that each was used by the howlers as a source of food.

in these two measures (height t-test=-3.68, $P<0.001$, df=406; DBH t-test=-5.97, $P<0.001$, df=97).

Plant Parts Used

The howlers in the cacao plantation spent 60% of their feeding time consuming leaves, and 35% consuming fruits. Flowers, shoots, and petioles accounted for the remaining 5% of feeding time. On a monthly basis, young leaves and mature fruits were the most important food items to the howlers, who spent an average of 51% of their monthly feeding time on young leaves, and 29% on mature fruit (Table II). The howlers used 11 species of plants as sources of young leaves. Among these, *F. cotinifolia*, *G. sepium*, and *Ficus* sp. accounted for 80% of feeding time on young leaves. In the case of mature leaves, species such as *P. saman* accounted for 60% of feeding time, and *F. cotinifolia* accounted for an additional 19%. The howlers used five and seven species of plants as sources of young and mature fruits, respectively. Species such as *F. cotinifolia* accounted for 70% of feeding time on young fruit, and *F. cotinifolia*, *Spondias mombin*, and *P. saman* accounted for 84% of feeding time on mature fruits. Two tree species–*P. saman* and *G. sepium*–accounted for 81% of the howlers' feeding time spent on flowers (Table II).

Monthly Variations in Feeding Patterns

The howlers used an average of 7.8 ($\pm$1.7) plant species per month as sources of food (range=5–11; Fig. 1a). The mean monthly dietary diversity, as measured by Shannon's diversity index, was $H'=1.55\pm0.29$. Dietary diversity was lowest value in July ($H'=0.97$) and greatest in August ($H'=1.95$; Fig. 1a). Sorensen's

TABLE II. Percent of Time Spent Feeding on Leaves, Fruits, Flowers, and Others for Each Plant Species Used by the Howler Monkeys in the Cacao Plantation*

Species	Young leaves	Mature leaves	Young fruit	Mature fruit	Flowers and other
Ficus cotinifolia	41.9	18.9	70.1	52.4	
Pithecellobium saman	6.9	60.0	9.0	12.9	42.5
Gliricidia sepium	20.9	8.9			38.8
Ficus sp.	17.2	2.6			
Ficus obtusifolia	3.6	4.3	6.8	10.0	
Spondias mombin			0.9	18.2	
Diphysa robinioides	5.9	5.4			
Manilkara zapota				5.3	15.5
Mangifera indica			13.1	0.3	3.0
Busera simaruba	1.3				
Erythrina americana	1.0				0.2
Cecropia obtusifolia	0.9				
Selenicereus sp. (E)					
Terminalia amazonia				0.9	
Paullinia pinata (V)	0.4				
Syngonium podophyllum (E)	0.1				
Number of species	11	6	5	7	5
Percent of monthly feeding time on plant parts					
Mean	49.6	10.5	4.6	30.5	4.8
±SD	14.9	7.2	6.1	18.0	5.5
Min	23.0	0.9	0.0	11.9	0.0
Max	69.9	22.1	17.6	63.6	14.0

*Also shown at the bottom of the table is the mean percent monthly time spent by howlers feeding on each plant part.

index of overlap between adjacent months in plant species used as a food source by the howlers ranged from 0.67 to 0.91 (average=0.76±0.08; Fig. 1a). The number of food trees used per month varied from 24 in September to 44 in October (mean 32±6.3), and was negatively associated with the mean monthly percentage of time spent resting (r_s=−0.66, P=0.02, n=9), and positively with the mean monthly percentage of time spent feeding (r_s=0.55, P=0.05, n=9). Leaves and fruits were consumed by howlers throughout the study period, but consumption varied from 23% in July to 67% in October for young leaves, and from 11.9% in February to 64% in July for mature fruits (Fig. 1b). The monthly feeding time spent by howlers feeding on young leaves was found to be positively associated with monthly dietary diversity (r_s=0.63, P=0.03, n=9). This relationship was negative and marginally significant in the case of mature leaves (r_s=−0.51, P=0.07, n=9).

Species Importance Value Index (IVI)

The tree species used by howler monkeys as a source of food had, on average, a greater mean IVI value (16.8±26.6) than other tree species (4.3±7.5) (Mann-Whitney test, P=0.0181). The three most important tree species in the monkeys' diet had the highest IVI values in the plantations: *P. saman* IVI=98.2, *G. sepium* IVI=36.9, and *F. cotinifolia* IVI=22.7. The rest of the species (except *E. americana*) had IVI values of <15.0 (Table I). *E. americana* had an IVI of 16.7,

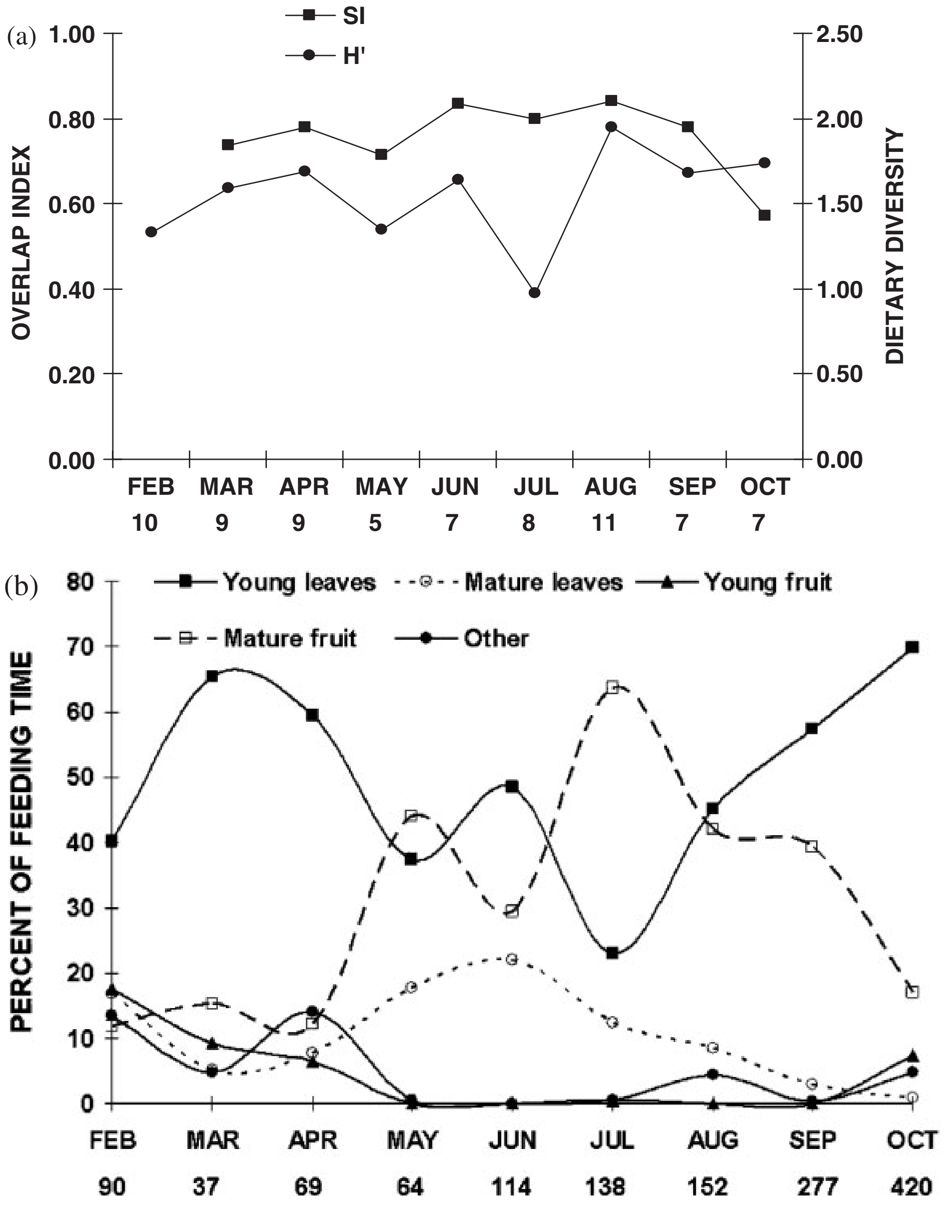

Fig. 1. **a**: Monthly dietary diversity (H′) and dietary overlap (SI), at the species level, between adjacent months. The number below the initial for each month refers to the number of plant species used as a source of food by the howlers. **b**: Seasonality in the use of plant parts by the howlers. Note the marked peaks and valleys in the use of young leaves, mature fruit, and mature leaves. The number below the initial for each month indicates the mean monthly precipitation in millimeters.

but it was the 11th ranking tree species based on feeding time in the overall howlers' diet. The tree species' IVI was a significant predictor of the actual number of trees used by the howlers to feed ($r=0.89$, $r^2=79.7\%$, $P<0.001$, $n=13$), but not of feeding time ($r=0.36$ n.s.).

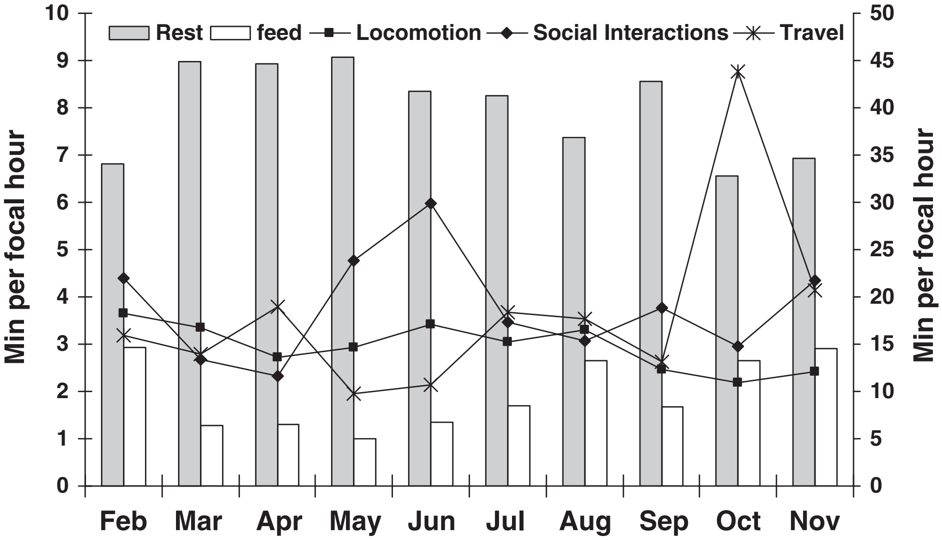

Fig. 2. Monthly general activity patterns of howler monkeys living in the cacao plantation. While the pattern is consistent from month to month, there is some variation in the distribution of behavior patterns recorded. The scale to the right refers to values for resting and feeding, illustrated by the bars. The scale to the left refers to values for travel, locomotion, and social interactions.

Protein and Fiber Content of Leaves

Chemical analysis of the plant parts in the howlers' diet showed that the mean content (% dry matter/g) of crude protein was higher in young leaves (19.87 ± 10.38) than in mature leaves (11.59 ± 5.56; T=1.96, P=0.039, df=10). The mean fiber content, on the other hand, was higher in mature leaves (6.35 ± 3.83) than in young leaves (3.15 ± 0.94; T=−2.16, P=0.037, df=6). Young leaves also had a higher mean protein-to-fiber ratio (7.02 ± 4.54) than mature leaves (1.39 ± 0.33; T=3.09, P=0.018, df=7). We used a partial correlation analysis to determine whether the protein-to-fiber ratio was a significant predictor of foraging effort (after we controlled for the effects of food tree density), but did not find a significant association (r=−0.57, P=0.06, n=8).

Distance Traveled per Month, Use of Space, and Dietary Diversity

The mean monthly distance traveled by the howlers per day was 388 ± 153.3 m (range=175 m in February to 651 m in October). The shortest and longest travel distances recorded on a daily basis were 20 m and 1,057 m in February and August, respectively. The index of monthly dietary diversity was found to be positively correlated to the average distance traveled per month by the howlers (r_s=0.75, P=0.009, n=9), and the mean distance traveled per month was negatively associated with consumption of mature leaves (r=−0.66, P=0.04, n=9).

Monthly Use of Space and Dietary Diversity

The howler monkeys used 52 40×40 m quadrats or 8.32 ha of the plantation's land. On a monthly basis, the howlers used an average of 25.1 ± 4.7 quadrats or 4.0 ha per month in which they were able to acquire resources.

The number of quadrats used per month ranged from 18 (2.88 ha) in March to 32 (5.12 ha) in October. Sorensen's index of overlap between adjacent months in quadrat use ranged from 0.38 in July to 0.71 in March (mean=0.57 ± 0.13). The monthly index of quadrat diversity (H′) ranged from 0.95 in July to 1.26 in October (mean=1.1 ± 0.1), and this was positively associated with the monthly index of dietary diversity (r=0.71, P=0.03, n=9). This suggests that monthly increases in diet breadth were paralleled by an increase in the area used to harvest food resources.

General Activity Patterns

Resting accounted for 68% of the time howlers spent on the five general activities recorded, and it occurred at a rate of 40.6 min per focal hour of observation. Feeding was the next most common activity, accounting for 15.2% of the time (9.1 min per focal hour of observation). Social interactions contributed to 6.4% of the time recorded (3.8 min/focal hr), and locomotion and travel accounted for 6% and 5% of the time, respectively (Fig. 2). We found no differences among months in the general activity pattern displayed by howlers (H=3.34, df=8, P=0.91). A calculation of a simple index of activity vs. inactivity, in which we subtracted for each month the time howlers spent resting from all other activities, yielded a numerical value indicating when the howlers invested more time (= energy) in maintenance activities, such as feeding, locomotion, social activities, and travel. The monthly values of this index were found to be positively related to Sorensens' index of dietary overlap (r_s=0.66, P=0.2, n=9), and negatively associated with the number of 40×40 m quadrats and number of food trees used per month by the howlers (r_s=−0.70, P=0.1, n=9, r_s=−0.78, P=0.005, n=9, respectively). Monthly dietary diversity was not closely related to the monthly values of the index (r_s=0.16, P=0.33, n=9).

DISCUSSION

Consistency in Use of Plant Species Used As a Source of Food

Our study shows that the howlers were able to sustain themselves in the cacao plantation by exploiting the leaves, fruits, flowers, and other items of a small coterie of plant species, 80% of which were trees. Of these, five species (*F. cotinifolia*, *P. saman*, *G. sepium*, *F. obtusifolia*, and *Ficus* sp.) accounted for slightly over 80% of the total feeding time recorded. The same five species contributed to 78% of the total number of trees used by the howlers, and were consistently used by the howlers from month to month. These tree species could thus be considered as primary sources of food for the howlers in the cacao plantation. The five tree species mentioned above belong to the Fabaceae and Moraceae plant families. Tree species in these families have been reported to be important sources of food for *Alouatta* at other sites in Mexico [Estrada, 1984; Estrada et al., 1999; García del Valle et al., 2001; Rivera & Calme, in press; Serio-Silva & Rico-Gray, 2002], Belize [Pavelka & Knopff, 2004; Silver et al., 1998], Costa Rica [Glander, 1975], Panamá [Milton, 1980], and Colombia [Gaulin & Gaulin, 1982].

Fig trees were especially important in the howlers' diet, contributing to 58% of their total feeding time, and were used by the monkeys in all months as a source of leaves and fruit. Fig trees $\geq$ 20 cm in DBH occur at densities of <3 ind/ha in the plantation, which suggests that much of the howlers' travel bouts and use of different areas of the cacao plantation was probably related to the harvesting of leaves and fruit from fig trees. Another important tree for the howlers was the shade tree *P. saman*, the most dominant tree species (i.e., with the highest IVI value) in the plantation. Adult individuals of this tree species had a higher mean height (mean height *P. saman*=21.0±2.4 m; other trees=14.3±3.8 m; t-test=27.74, $P<0.001$, df=163) and DBH (mean DBH *P. saman*=115.8±28.0 cm; other trees=54.9±51.9 cm; t-test=20.00, $P<0.001$, df=169) than other shade trees in the plantation. These features, together with the fact that *P. saman* has large crowns and robust branches, probably explain why the howlers' spent so much time resting and feeding on this tree.

Consistency in Use of Plant Parts

On a monthly basis, the most important food items in the howlers' diet in the cacao plantation were young leaves and mature fruit. Mature leaves, and young fruits and flowers complemented their monthly diet. Species such as *F. cotinifolia*, *G. sepium*, and *Ficus* sp. were their principal source of young leaves, while *P. saman* was their principal source of mature leaves. Fig trees were the howlers' principal source of ripe fruit, and species such as *P. saman* and *S. mombin* complemented their ripe-fruit diet. The howlers in the cacao plantation displayed dietary patterns and preferences (i.e., a preponderance of young leaves and ripe fruit) similar to those reported for howler monkeys in forest fragments and continuous forest tracts in other localities in southern Mexico [Estrada, 1984; Estrada et al., 1999; Fuentes et al., 2003; García del Valle, 2001] and the neotropics [Glander, 1975; Milton, 1980; Rivera & Calme, in press; Silver et al., 1998]. The young leaves consumed by the howlers had a higher protein-to-fiber ratio than mature leaves, which suggests that the howlers respond, as do other leaf-eating primates [Chapman et al., 2002; Wasserman & Chapman, 2003], to that feature when they select leaves. The preference by the howlers for the mature leaves of *P. saman* may be related as well to their higher protein content (23.3±3.5% g/dry weight, n=10 samples) compared to the mature leaves of other tree species also consumed by the howlers (mean=9.6±2.3% g/dry weight, n=6 species; three samples per species) in the plantation.

The howlers exploited only 22% of the trees (630 trees ≥20 cm in DBH) present in the plantation, and concentrated their activities on trees of the species they favored in their diet. These trees accounted for only 35% of existing trees (≥20 cm in DBH) of these species, which suggests that there may be additional potential resources available to the howlers. However, tree-to-tree variations in nutritional quality and presence, and in concentrations of secondary compounds may also explain the howlers' selectivity of leaves of particular sets of trees within their home range, as has been reported for other primate populations [Chapman & Chapman, 2002; Chapman et al., 2003; Wasserman & Chapman, 2003].

Monthly Variations in Feeding and Activity Patterns

The howlers shifted species in their diet from month to month, probably in response to changes in the availability of leaves and fruit. Apparently such shifts, as suggested by the relatively high range of values dietary overlap index (SI=0.67–0.91), focused around travel to trees belonging to a small coterie of tree species (n=13) from which the howlers derive most of their nutrition. The howlers' diet was more diverse when young leaves dominated their monthly diet, and less diverse when time spent consuming mature leaves increased. Although this may be opposite to general expectations, given the presumed higher levels of secondary compounds in mature leaves, it is possible that the temporal availability of young leaves of several tree species present at the study site may help explain these findings.

The general activity pattern of the howler monkeys in the cacao plantation is consistent with that reported for howlers in other localities in the neotropics, with resting accounting for >50–60% of their activity budget, followed by feeding. The data also suggest that the howlers rest more after periods of increased travel (as required to reach dispersed resources), and rest less when resources are aggregated. Increases in howler dietary diversity were paralleled by an increase in distance traveled, suggesting that the monkeys were actively searching for alternative sources of food in addition to those represented by the primary plant species in their diet. However, when mature leaf consumption predominated in their diet, the howlers traveled less.

Quantitative Features of Vegetation

The howlers preferred trees of species whose contribution to the total tree biomass and density (IVI index values) are above average for the shade-tree population. The three dominant species in their diet were the highest ranking in IVI values, and the monkeys consistently used these species from month to month as a source of food and for other maintenance activities. The trees used by howlers to feed on, as well as for other activities, were usually larger and taller than the rest of the tree population in the plantation. These large trees may not only provide howlers with significant amounts of food (leaves, fruit, and flowers), but may also provide them with robust physical strates upon which they carry out other maintenance activities. The stature of these trees suggests that howlers may also prefer them because they offer greater ventilation and visibility of the contiguous canopy.

Ecological Impact of Howlers in the Plantation

Our observations of the howlers in the cacao plantation, and interviews with the plantation's owners indicated that the monkeys do not feed on the cacao fruit pods. Instead, the howlers concentrate their feeding on leaves and fruits of the trees that provide the shade for the cacao trees. In fact, the presence and activities of howler monkeys may be beneficial to the plantation. For example, the feeding activities of howlers at these habitats may favor (via a pruning effect and the dislodging of branches and other organic matter in the canopy) primary productivity by accelerating the flow of nutrients and the conversion of matter and energy [Estrada & Coates-Estrada, 1993]. Howler monkey dispersal of seeds may contribute to the persistence of trees of species that are their sources of fruit in the plantation, and to the recruitment of seedlings harvested by humans for reforestation activities in the plantation and the surrounding land [Estrada et al., in press].

Defecation by the monkeys also may add important nutrients to the soil. It has been reported that the waste excreta of howlers tend to be very nutrient-rich [Milton et al., 1980; Nagy & Milton, 1979], and that their dung contains 1.8–2.1% nitrogen (N) and 0.3–0.4% phosphorus (P) (based on dry mass measurements) [Milton et al., 1980]. In contrast, concentrations of nutrients in leaf litter are $\sim$1% N and 0.04% P for tropical moist forests [Feeley, 2005]. In a study conducted in Venezuelan forests, the total soil N concentration under the trees in which howlers defecated was 1.6 to 1.7 times greater than that in control sites (test plots in surrounding soil), and the P concentration was 3.8 to 6 times greater under the resting or resting/feeding trees than in the surrounding soil, which probably enriched the soil and nutrient uptake of these trees [Feeley, 2005]. High dispersal of nutrients via howler feces in the plantation may result from the howlers' daily movements, benefiting not only the shade trees used for resting and/or feeding, but also the cacao and other cultivated plants that grow directly underneath.

Final Considerations

The howlers in the cacao plantation investigated are living in a habitat that was made completely by humans. The shade trees (e.g., *P. saman* and *G. sepium*) were planted about 40 years ago, along with other trees (e.g., the exotic avocado) of interest to the owners. Over time, other trees, such as strangler figs (e.g., *F. cotinifolia*) colonized the plantations, probably via the dispersal of their seeds by birds and/or bats residing in nearby forest patches. The howlers immigrated into the plantation about 25 years ago, probably escaping deforestation in the surrounding land. The diversity of tree species in the plantation is low (2.9 tree species/ha, based on a count of all trees $\geq$20 cm in DBH) and the canopy of the plantation is strongly dominated (IVI index) by a few tree species. Our study suggests that the howlers have been able to sustain themselves in the cacao plantation by consuming the leaves, fruits, and flowers of these tree species. The howlers' diet in the cacao plantation is not as diverse as those of howlers living in small forest fragments [Bicca-Marques, 2003; Estrada et al., 1999; Juan et al., 2000], but resources in the plantation seem to be sufficient to sustain a relatively high howler monkey biomass (10.2 kg/ha). This biomass exceeds that reported for populations of the same species existing in continuous forests (1.8 kg/ha) north of the study site [Estrada 1982], and in areas in which tree species diversity is $\sim$80 tree species/ha (DBH $\geq$20 cm (A. Estrada, unpublished data)).

While our study suggests that certain types of agroecosystems may have a potential to contribute to the persistence of primate populations, we also need to consider that dispersal of individuals and/or groups through manmade habitats may place migrants in a perilous matrix in which they are more exposed to humans, dogs, parasites, and diseases. Moreover, arboreal agroecosystems in which primates may be able to reside may also act as ecological sinks and traps for primate populations, as is the case with isolated forest fragments [Kristan, 2003; Laurance & Vasconcelos, 2004; Murphy & Lovett-Doust, 2004]. Changes in regional and world market demands may result in important changes in the local and regional distribution of agroecosystems, such as shaded cacao and coffee plantations, in which primate populations can exist. For example, the current trend to switch from forest-shade-grown to sun-grown coffee in many Mesoamerican countries [Perfecto & Armbrecht, 2003] may mean an important loss of habitats in which primate populations could persist. The trend to expand cultivation of sun-grown coffee at the expense of areas dedicated to the cultivation of forest-shaded cacao [Rice & Greenberg, 2000] may have similar consequences. In other instances, cacao agroforestry systems may be abandoned due to disease problems, and converted to other land uses (such as pastures, and banana or plantain production) that lower their value for primate conservation.

Considering our results and the above caveats, our investigation indicates that given the right conditions of management, shaded arboreal plantations (e.g., cacao plantations) can sustain segments of howler monkey populations for many decades in fragmented landscapes [Estrada & Coates-Estrada, 1996; Estrada et al., in press]. To avoid isolation of the populations and its negative consequences, the managers of such populations need to contemplate the establishment and/or protection of corridors of arboreal vegetation between manmade and natural arboreal vegetation units in the landscape [Harvey et al., 2004; Mandujano et al., in press].

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