

Diet of the Red Howler Monkey (*Alouatta seniculus*) in French Guiana

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We report the feeding behavior and food preferences of a troop of red howler monkeys (*Alouatta seniculus*) over two annual cycles in primary tropical rain forest in French Guiana. The monkeys used 195 plant species from 47 families as food. Major food categories were young leaves (54%), mature fruits (21.5%), and flowers (12.6%). Other food categories included old leaves, immature fruits, termitarium soil, bark, and moss. The monkeys were less selective than other howler groups, since 19 plant species contributed $\geq 1\%$ to their diet and accounted for only 35.7% of their total diet. The Sapotaceae was the most frequently eaten plant family and represented $>10\%$ of the total diet.

KEY WORDS: *Alouatta seniculus*; French Guiana; diet; selective feeding; termitarium consumption.

INTRODUCTION

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Since the pioneer work on *Alouatta palliata* (Carpenter, 1934), howler monkeys, especially *Alouatta palliata* and *Alouatta seniculus*, have been one of the most studied genera of Neotropical primates. Many aspects of *A. seniculus* have been studied: population structure (Neville, 1972a; Defler, 1981; Freese *et al.*, 1982; Crockett, 1985), social behavior (Neville, 1972b; Braza *et al.*, 1981; Crockett and Sekulic, 1984; Crockett and Pope, 1988), reproduction (Crockett and Sekulic, 1982; Crockett and Rudran, 1987a, b),

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vocalization (Sekulic, 1983; Sekulic and Chivers, 1986; Schön Ybarra, 1986, 1988), and locomotion (Schön Ybarra, 1984; Schön Ybarra and Schön, 1987); however, only one long-term study has been conducted on the diet of *A. seniculus* (Gaulin and Gaulin, 1982), in a very different habitat from ours. In addition, some observations on the diet of *A. seniculus* have been included in a number of multispecific studies (Izawa, 1975; Mittermeier and Roosmalen, 1981; Braza *et al.*, 1983).

Howler monkeys are principally vegetarian and probably the most folivorous of New World primates. Still, fruits and flowers can seasonally represent a large part of the diet. We report data on the diet of red howler monkeys during 2 years of observation in French Guiana, including the frequency of consumption of different food categories, and an analysis of consumed plant species and families.

STUDY SITE

Our study site is the Nourague Station in French Guiana, situated roughly 100 km from the coast (4°05'N, 52°40'W) in the middle of the Guiana forest block (Fig. 1). The study area is totally uninhabited by people and the forest has not sustained any human activity since the disappearance of the Nourague Indians >200 years ago. Thus, it can be considered a primary forest. The actual site consists of 160 ha broadly squared with pathways.

The equatorial climate of French Guiana is characterized by a very short dry season (mid-August to mid-November) and a wet season during the rest of the year. The wet season can be interrupted by a drier period between February and March, called "petit été de Mars," whose duration and intensity are very variable. Mean annual precipitation is between 3000 and 3250 mm, and mean annual temperature is around 26.5°C [climatic data of Régina in 1956–1975 (CEGET CNRS-ORSTOM, 1979)]. At the study site, the mean temperature was 26.1°C during the study period and the monthly precipitations were very different between the 2 calendar years (Fig. 2).

The forest, which covers 90% of the Guiana massif, is a tropical moist forest (Holdridge, 1964). In the study area, the canopy is continuous and generally 30–40 m high, with some trees emerging up to 65 m. The identification of trees and lianas, >10 cm DBH (diameter at breast height), in an area of 4.8 ha split into five transects, of 500 × 20 m for four transects and 400 × 20 m for the last one, has shown a high species richness, with 400 species and 59 families (Sabatier and Prévost, 1990). The most important families are Caesalpiniaceae, Lecythidaceae, Sapotaceae, Chrysobalanaceae, and Burseraceae, in order of population density, with 27, 28, 56, 33, and 20 species, respectively.

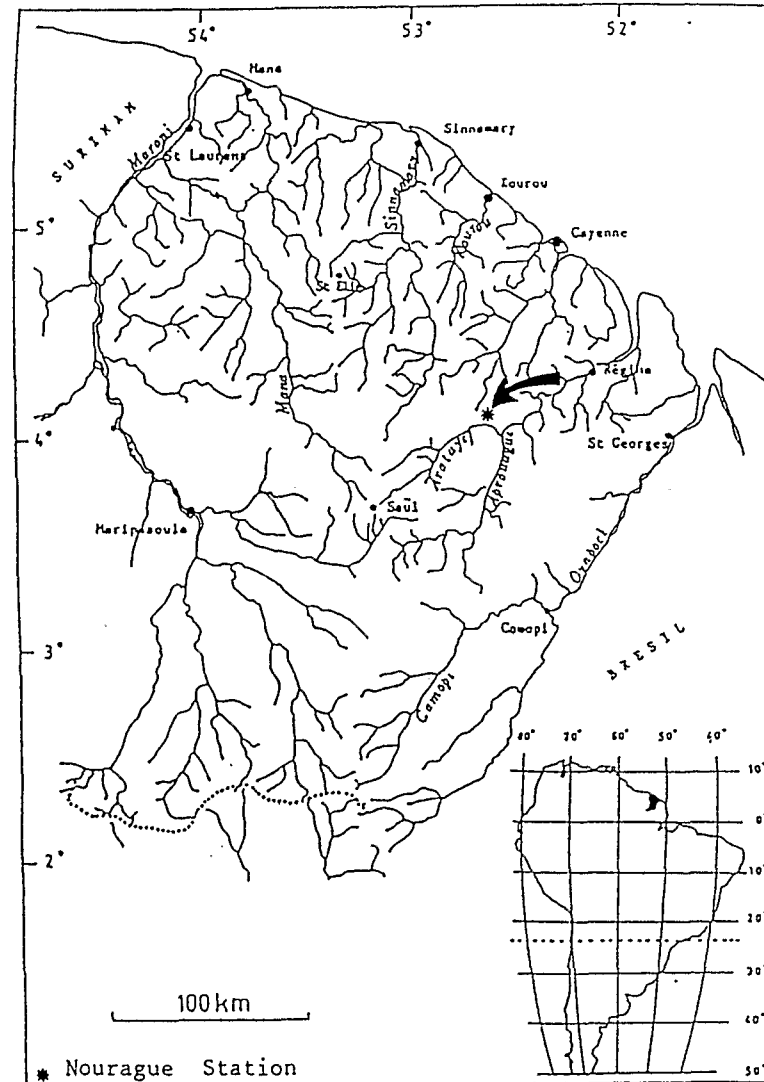


Fig. 1. Location of the Nourague Station in French Guiana.

Three of these five transects are included, to a great extent, in the home range of the monkey study troop (Fig. 3). These three transects showed the same principal families with nearly the same order of population density: Lecythidaceae, Caesalpiniaceae, Sapotaceae, Chrysobalanaceae, and Burseraceae, with 25, 22, 45, 28, and 12 species, respectively.

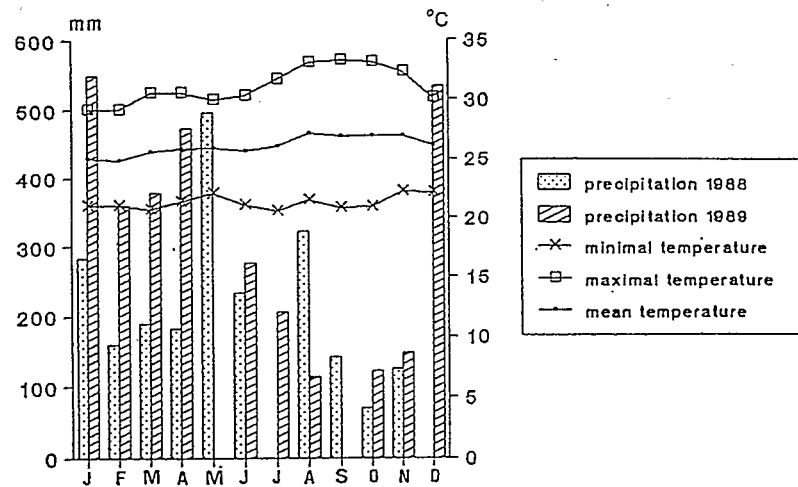


Fig. 2. Temperature means and precipitation by month at the Nourague Station for 1988 and 1989.

Most forest-living nonflying mammals of French Guiana (Charles-Dominique, 1993) have been observed at the study site. The other primate species present at the Nourague Station are *Ateles paniscus*, *Cebus apella*, *Cebus nigrivittatus*, *Sanguinus midas*, and *Pithecia pithecia*; only two of the eight primate species present in French Guiana (*Chiropotes satanas* and *Saimiri sciureus*) have never been observed.

MATERIALS AND METHODS

Monkey Focal Troop

At the beginning of this study, the monkey focal troop was composed of six members: one adult male, two adult females, two juvenile males, and one 11-month-old female. Its composition varied throughout the study due to birth, migration, and death (Table I). Individual animals could be easily identified by physiognomic characteristics (color, size, sex, etc.); the focal troop could be identified easily by the distinctive blond color of the adult male. The home range of the troop was 45 ha (Fig. 3), of which 9 ha overlapped with the home ranges of neighboring troops.

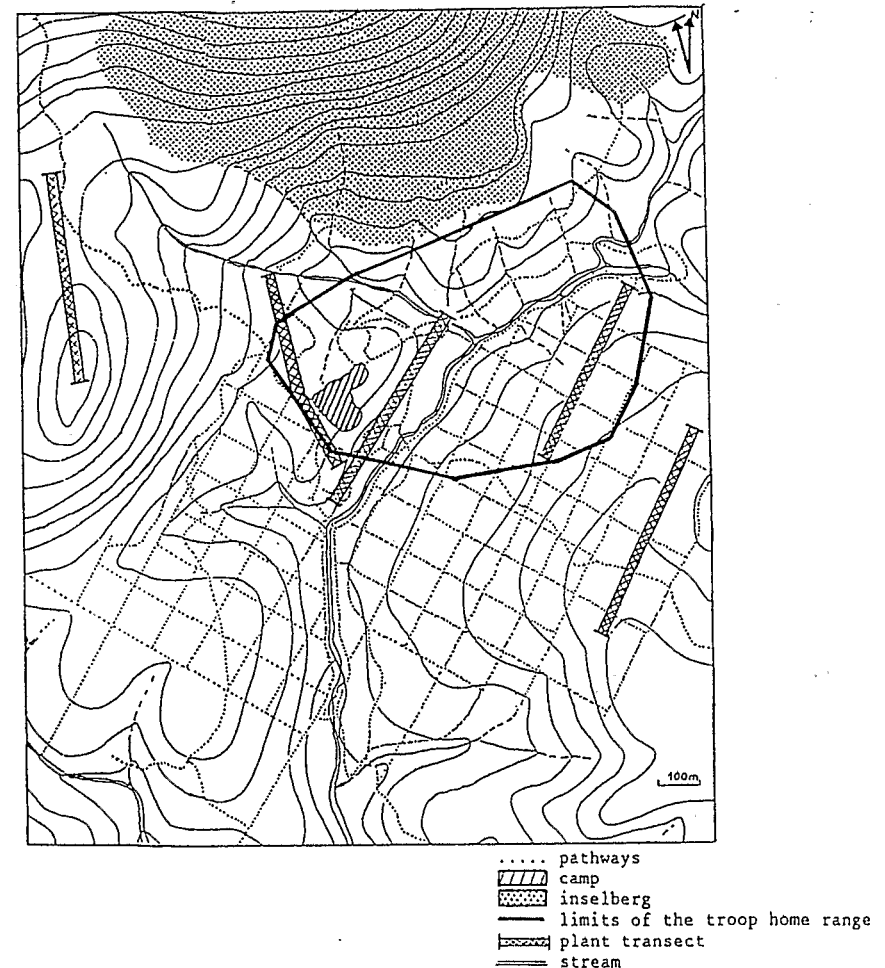


Fig. 3. Map of the study site, showing the home range of the focal troop and the five plant transects.

Feeding Observations

We conducted the field study in 2- to 4-month consecutive periods over 19 months between April 1988 and May 1990. We observed the monkey troop continuously, as far as possible, from 0600 to 1800 during 3–5 consecutive days every 2 weeks; the number of full days of observation per

Table I. Variation of the Focal Troop Composition from April 1988 to May 1990

May 1988:	troop composition (6 members) 1 adult male 2 adult females 2 juvenile males 1 young female
September 1988:	2 births—1 male and 1 female (8 members)
April–May 1989:	disappearance of 1 adult female and her infant (female) ^a (6 members)
March 1990:	1 birth—female (7 members)
April 1990:	emigration of 1 of the 2 subadult males (6 members)
May 1990:	troop composition (6 members) 1 adult male 1 adult female 1 subadult male 1 juvenile female 1 young male 1 infant (female)

^a Probably dead.

month fluctuated between 1 and 11, with a mean of 6 full days per month. In total, 1540 observation hr was accumulated over 168 days of observation, including 123 full days (Table II).

We collected feeding observations via the frequency method (Struhsaker, 1975; Harrison and Hladik, 1986). As soon as one member of the troop was seen eating something, an observer noted one feeding unit for the food category eaten. The different food categories are mature fruit, immature fruit, young leaves (leaf buds, sucker, and young leaves), mature leaves, flowers, termitaria, bark, and moss (wood, bark, moss, lichens, and any other vegetable food on a branch or trunk), and unknown (when it was not possible to identify the food item). A new feeding unit was noted for the same food resource if another member of the troop was observed to eat the same food resource or if the same member of the troop continued this feeding activity on the same food resource after 1 hr. If an individual ate successively the same food item in two different trees, two feeding units are noted. This method overestimates occasional consumption—food eaten only by one member of the troop—and short consumption (one feeding unit is noted equally for a bout of a few seconds as for one of 45 min. However, this method gives a good estimate of the diet of the red howler monkeys, which are not very active and have very high group coordination for any given activity. Moreover, Struhsaker (1975) and Clutton-Brock (1977) considered that this method gave results similar to those by time budget measurement.

Table II. Monthly and Total Proportions of the Different Food Categories in the Howler Diet^a

Month	N	(n)	O.T. (hr:min)	F.U.	Diet (%)									
					F	f	I	L	R	T	B	U		
Apr. 88	10	(3)	45:25	204	44.1	29.4	26.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
May 88	12	(4)	55:25	436	40.6	12.4	44.0	0.0	0.0	0.0	0.0	0.0	3.0	3.0
June 88 ^b	5	(4)	35:15	199	21.1	3.0	51.8	0.5	0.0	0.0	3.5	12.1		
Aug. 88	13	(7)	106:00	313	11.2	3.9	60.4	0.0	14.0	0.0	2.2	8.3		
Sept. 88	13	(10)	143:05	1004	16.2	0.7	62.7	1.2	12.5	0.9	0.1	5.7		
Oct. 88	13	(10)	131:15	696	7.3	0.0	68.2	0.9	20.7	0.0	0.3	2.6		
Nov. 88	12	(9)	113:50	807	27.8	3.1	57.0	0.7	6.7	2.1	0.4	2.2		
Jan. 89	13	(9)	105:50	541	22.6	5.5	49.0	5.7	5.9	0.7	0.4	10.2		
Feb. 89	9	(6)	77:10	442	27.6	1.4	50.0	17.6	0.2	3.2	0.0	0.0		
June 89	11	(9)	102:45	513	1.7	4.7	77.4	1.6	9.4	2.3	0.0	2.9		
July 89	10	(9)	103:10	681	0.0	0.0	52.9	5.3	38.0	2.8	0.0	1.0		
Aug. 89	9	(8)	98:30	624	2.7	7.9	78.4	0.0	5.9	3.2	1.6	0.3		
Oct. 89	8	(7)	81:35	536	39.9	1.1	29.1	1.3	23.0	3.4	0.0	2.2		
Nov. 89	9	(9)	109:30	535	7.1	3.4	49.7	2.8	34.6	2.0	0.4	0.0		
Dec. 89 ^b	5	(4)	47:30	255	10.2	0.0	46.6	0.8	38.8	1.2	0.0	2.4		
Feb. 90 ^b	3	(3)	36:00	280	56.8	7.5	26.1	6.4	2.1	0.0	0.4	0.7		
Mar. 90	6	(6)	59:20	624	47.6	8.7	38.0	2.9	0.0	0.6	0.0	2.2		
Apr. 90	5	(3)	52:45	437	38.7	0.0	48.5	7.1	1.6	2.1	0.0	2.0		
May 90 ^b	3	(3)	37:00	129	25.6	0.0	65.9	3.9	0.0	2.3	0.0	2.3		
Total	168	(123)	1540:50	9256	21.5	4.0	54.0	3.0	12.6	1.5	0.4	3.0		

^a N, total number of observation days; (n), number of full observation days (including 2 complementary half-days); F.U., number of feeding units; O.T., observation time; F, mature fruit; f, immature fruit; I, young leaves; L, mature leaves; R, flowers; T, termitaria; B, bark and moss; U, unknown.

^b First or second 15 days of the month.

Each tree in which at least one member of the troop had eaten was marked with a numbered plastic label, upon which the date of the observation and the kind of food (fruit, leaf, flower) were noted. Each tree was given a unique number, which was recorded in later observations of the same tree.

Plant species identifications were done either directly from the tree characteristics or at the Cayenne Orstom Center with the help of samples collected in the field. Fruit and flower samples are deposited at the carpenterium of the Laboratoire d'Ecologie Générale du Muséum National d'Histoire Naturelle (Brunoy) and the herbarium samples at the Herbarium of the Cayenne Orstom Center. The localization of trees exploited by monkeys was not always easy, and it was more difficult for lianas. For fruit and flowers used as food resources, a sample could usually be collected on the ground, and in these cases identification was easier than for leaves, for which species identification was not always possible.

Fecal Sampling and Analysis

We collected fecal samples during daily troop observations. Feces of neighboring troops, particularly two of them, were also collected outside the main troop observation period. This was done either *ad libitum*, or in the morning at sleeping sites which were located the evening before. Fecal samples were analyzed to identify mature fruit whose seeds pass undamaged in feces and, thus, add supplementary data on mature fruit consumption to those obtained by direct observations. We retrieved seeds from feces by washing them through brass sieves of 2-, 1-, and 0.5-mm mesh; the 0.5-mm sieve was fine enough to catch the smallest (essentially *Ficus*) seeds ingested by the howler monkeys.

RESULTS

Quantitative Analysis of the Diet

Diet Composition

A total of 9256 observational feeding units was collected during the 19 months of observation. Young leaves, mature fruit, and flowers formed most of the feeding units—54, 21.5, and 12.6%, respectively (Table II). Immature fruit, mature leaves, termitaria, bark, and moss were only occasionally eaten—4, 3, 1.5, and 0.4%, respectively.

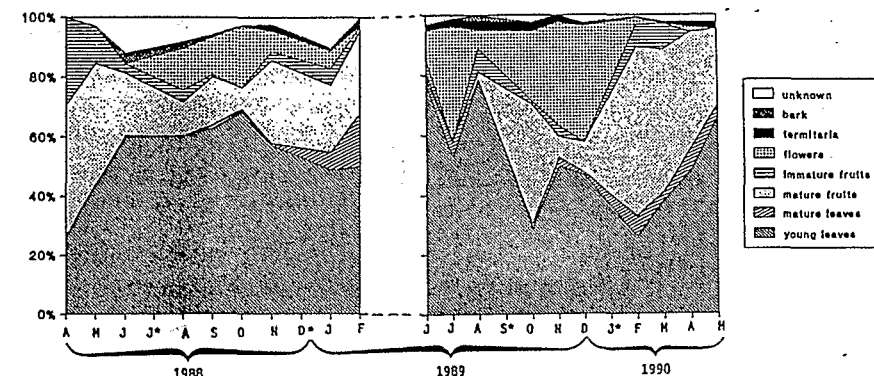


Fig. 4. Monthly variations of the different food categories in the howler diet (in percentage of feeding units). (*) Missing data (no observation; graph joins points of previous and following months).

Results obtained for the first 3 months showed the fewest food categories, but that was probably due to our difficulties in observing the monkey troop and distinguishing certain food categories as mature leaves or termitarium.

Seasonal Variations

Strong monthly variations in diet were observed (Table II, Fig. 4). Young leaves accounted for 29.5–77.7% of the monthly observations, mature leaves from 0 to 17.6%, mature fruit from 0 to 50.8%, immature fruit from 0 to 29.4%, and flowers from 0 to 39.4%.

On the whole, mature fruit attained their highest rates of consumption during the period of peak fruit production [from February to May (Sabatier, 1983, 1985)]. Nevertheless, we noted a peak of mature fruit consumption in October 1989. This peak preceded the normal peak by several months. According to Sabatier (1983), high rainfall could have induced earlier fruiting of some plant species. Thus, this peak of fruit consumption was probably due to the unusually high rainfall observed during the wet season in 1989. For instance, *Goupia glabra*, the principal food species during this month, with 13.6% of feeding units of identified plants, produced fruit 1 month earlier than in 1988. Moreover, 15 species were used as fruit resources in October 1989, compared with only 5 species in October 1988.

Immature fruit did not show a very pronounced seasonality, perhaps on account of their low consumption. The higher rate of immature fruit consumption observed in April and May 1988 is due to massive fruiting of *Vouacapoua americana*, from which immature fruit were consumed in large quantities by howler monkeys.

Flower consumption was also highly seasonal. Flowers were used as a food resource, especially from July to December, which is the main flowering period (Sabatier, 1983, 1985). The higher rates of flower consumption observed in 1989 were due, on one hand, to the massive flowering, from June to August 1989, of one species (*Micropholis cayennensis*), which did not bloom in 1988 and was heavily consumed by howler monkeys in 1989, and on the other hand, to a greater consumption of three other species, *Eperua falcata*, *Odontadenia* spp., and *Maripa scandens*, from October to December 1989.

Young leaves were always heavily consumed, but especially from June to August, during the times of least fruit consumption.

Seasonal variations in dietary composition were based on fruiting and flowering periods. Young leaves, always available, were consumed all year long, with a higher rate when the other kinds of food were less abundant.

Qualitative Analysis of Diet

Plant Food

A total of 195 plant species, representing 47 families, was used by the focal troop as a source of food, including 97, 96, and 36 different species for fruit, leaves, and flowers, respectively (Fig. 5).³ The analysis of fecal samples ($n = 236$) permits us to add 17 species of mature fruits consumed by the focal troop to the 73 species obtained by direct observations. However, these 17 species were observed in <1% of fecal samples, except *Ludovia lancifolia*, a nonligneous epiphyte, of which the consumption by monkeys could easily escape observation. Likewise, Estrada and Coates-Estrada (1984) obtained 15 supplementary species to the 19 species of mature fruit observed being eaten by howler monkeys at Los Tuxtlas Station in Mexico. They had noticed that supplementary species from feces were mostly lianas and vines and contributed only 5% to the total number of seeds found in fecal samples.

³A list of plant species that were eaten by the red howler monkeys at the Nourague Station and their months of consumption is available to the reader upon request addressed to C. Julliot.

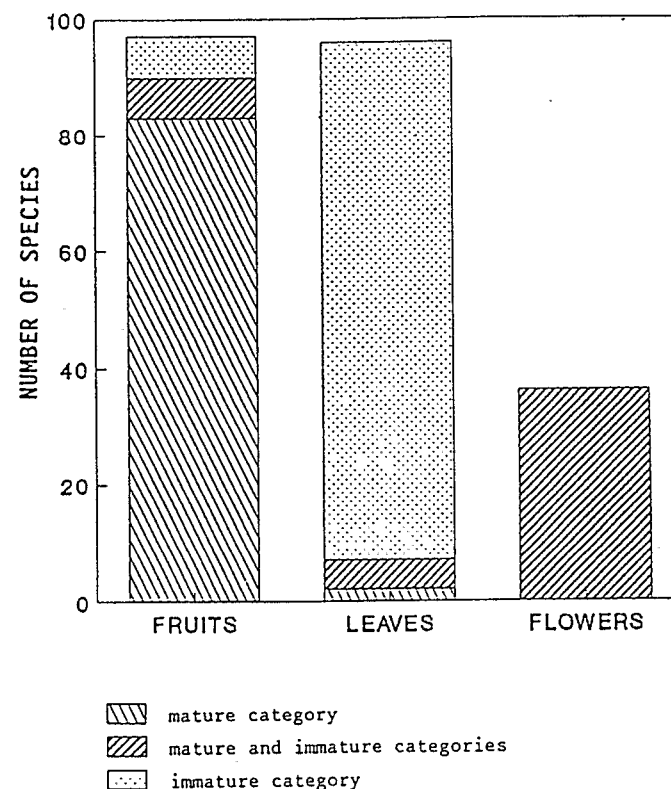


Fig. 5. Number of plant species eaten by the focal troop in the different food categories.

The analysis of fecal samples ($n = 79$) of neighboring troops give 68 plant species, including 24 additional species in five new families. Only 2 of the 24 supplementary mature fruit species were used by the focal troop as a leaf resource. Thus, a total of 217 species, representing 52 families, is known to be exploited by the howler monkey population; 114 of them provided mature fruit.

All plant species used for fruit and flower feeding may have been identified, but we identified only 50.9% of plant species that the howlers used as leaf resources. Accordingly, we identified $\leq 71.1\%$ of all feeding units.

Main Families

The proportions of feeding units per family for the three plant food categories—fruit, leaves, and flowers—and the number of species per family (Table III) showed that the principal families used as food are as follows:

- for fruit, Sapotaceae and Moraceae;
- for leaves, Fabaceae, Mimosaceae, and Caesalpiniaceae; and
- for flowers, Sapotaceae, Caesalpiniaceae, and Fabaceae.

The three principal families used as leaf sources are leguminous plants that are known to be rich in nitrogenous substances (Busson, 1965). In these families, 31 species were used, amounting to 43.9% of the feeding units on leaves of identified species (22.9% of leaf consumption). Only three leguminous species were used as a fruit resource. They are Caesalpiniaceae, which were exploited for immature fruit.

The family most frequently used as a food source was the Sapotaceae, which was the top-scoring family for fruit and flowers and one of the most important families for leaves.

Main Species

Only 19 species, representing 14 families (Table IV), accounted for $\geq 1\%$ each of the total diet. These 19 species made up 35.7% of the total diet and 52.8% of the feeding units of identified plant species. At least 40 species made up 50% of the total diet, which represent only 20.5% of identified species.

Main Species per Plant Food Category

Among the 195 species eaten by the focal troop, 83.6% were used for a single plant food category (78 for fruits, 67 for leaves, and 17 for flowers). The overlap rates of plant species for different plant food categories (number of mutual species for the two categories $\times 100$ /total number of species for the two categories) were 9, 5, and 14% for fruit-leaves, fruit-flowers, and leaves-flowers, respectively. It appears that there is a distinction between species used as fruit resources by howler monkeys and species used for leaves and flowers.

Table V shows that only 3 species made up $>50\%$ of flower feeding units, while 7 species accounted for 52.2% of fruit feeding and 14 species accounted for 51.3% of leaf feeding. Only 2 species accounted for 80.7% of immature fruit consumption (*Vouacapoua americana* and *Chrysophyllum lucentifolium*), and 2 species accounted for 79% of mature leaf consumption (*Pithecellobium jupumba* and *Strychnos* sp.).

Table III. Number of Plant Species per Family, and Composition of Diet (as Percentage of Feeding Units), for Each Plant Food Category and for All Identified Feeding Units on Plant Species^a

Family	Species number				Dietary composition			
	T	F	L	R	F	L	R	PR
Anacardiaceae	4	2	3	0	0.25	1.00	—	0.54
Annonaceae	2	1	1	0	0.50	0.60	—	0.30
Apocynaceae	4	2	1	1	0.50	0.67	13.19	3.00
Araceae	4	1	3	1	0.17	3.72	0.25	1.72
Araliaceae	1	1	0	0	3.53	—	—	1.34
Bignoniaceae	6	1	2	3	0.25	5.32	2.83	2.83
Bombacaceae	1	0	1	0	—	0.45	—	0.19
Boraginaceae	2	2	0	0	1.85	—	—	0.71
Burseraceae	6	3	5	1	2.10	9.45	0.50	4.95
Caesalpiniaceae	9	3	9	3	9.21	12.69	15.97	11.99
Caricaceae	1	1	0	0	—	—	—	—
Caryocaraceae	1	1	0	0	0.08	—	—	0.03
Cecropiaceae	10	9	2	1	3.45	5.99	0.50	3.99
Celastraceae	1	1	0	0	8.41	—	—	3.20
Chrysobalanaceae	6	3	4	1	2.35	1.64	0.50	1.70
Convolvulaceae	1	0	0	1	—	—	9.58	1.82
Cucurbitaceae	2	2	0	0	0.29	—	—	0.12
Cyclanthaceae	1	1	0	0	—	—	—	—
Dilleniaceae	2	2	0	0	0.25	—	—	0.10
Euphorbiaceae	1	1	1	0	3.99	0.30	—	1.65
Fabaceae	16	0	13	7	—	14.48	13.77	8.83
Gnetaceae	1	1	0	0	2.57	—	—	0.98
Hippocrateaceae	7	6	1	0	1.30	0.22	—	0.59
Icacinaeae	1	1	0	0	0.25	—	—	0.10
Lauraceae	4	0	4	0	—	1.60	—	0.69
Lecythidaceae	6	0	6	0	—	3.35	—	1.45
Loganiaceae	1	0	1	0	—	1.34	—	0.58
Loranthaceae	3	1	2	0	0.76	0.89	—	0.68
Malpighiaceae	1	0	1	0	—	0.22	—	0.10
Melastomataceae	2	1	1	0	0.88	0.22	—	0.44
Menispermaceae	3	1	2	0	—	0.37	—	0.16
Mimosaceae	10	0	9	2	—	16.71	2.52	7.66
Moraceae	20	12	7	3	14.55	2.75	4.45	7.59
Myristicaceae	4	4	2	0	3.41	0.67	—	1.59
Nyctaginaceae	3	1	2	1	—	5.28	0.50	2.37
Ochnaceae	1	1	0	0	1.26	—	—	0.48
Oleaceae	1	1	0	0	2.82	—	—	1.07
Polygalaceae	2	1	0	2	2.40	—	1.68	1.23
Polygonaceae	1	1	0	0	0.76	—	—	0.29
Quiinaceae	1	1	0	0	0.71	—	—	0.27
Rhamnaceae	1	1	0	0	—	—	—	—
Rubiaceae	2	2	0	0	6.56	—	—	2.49
Sapindaceae	2	1	1	0	0.67	0.45	—	0.45
Sapotaceae	28	21	9	5	18.80	8.45	30.75	16.66
Solanaceae	2	1	1	0	5.09	0.22	0.43	2.03
Tiliaceae	1	0	1	0	—	0.22	—	0.10
Verbenaceae	1	0	1	0	—	0.67	—	0.29
Indet	5	1	0	4	—	—	3.53	0.67

^a F, fruit; L, leaves; R, flowers; T, total number of species; PR, proportion of the feeding

Table IV. Species that Represented at Least 1% Each of the Diet^a

Family	Species	Cons	PI	PD
Sapotaceae	<i>Micropholis cayannensis</i>	F,R,l	6.46	4.36
Sapotaceae	<i>Chrysophyllum lucentifolium</i>	F,f,l	4.64	3.13
Moraceae	<i>Bagassa guianensis</i>	F,R	4.45	3.00
Caesalpiniaceae	<i>Eperua falcata</i>	f,R,l	3.82	3.58
Caesalpiniaceae	<i>Vouacapoua americana</i>	f,l	3.66	2.47
Mimosaceae	<i>Pithecellobium jupumba</i>	l,L	3.41	2.30
Celastraceae	<i>Goupia glabra</i>	F	3.20	2.16
Apocynaceae	<i>Odontadenia</i> sp.	R	2.51	1.70
Burseraceae	<i>Tetragastris altissima</i>	F,l	2.46	1.66
Rubiaceae	<i>Psychotria</i> cf. <i>carthaginensis</i>	F	2.46	1.66
Caesalpiniaceae	<i>Dicorynia guianensis</i>	l	1.95	1.32
Fabaceae	<i>Bocoa guianensis</i>	l	1.93	1.31
Solanaceae	<i>Solanum</i> sp. 1	F	1.93	1.31
Convolvulaceae	<i>Maripa scandens</i>	R	1.82	1.23
Bignoniaceae	<i>Tabebuia serratifolia</i>	l	1.79	1.21
Euphorbiaceae	<i>Drypetes variabilis</i>	F,l	1.65	1.11
Mimosaceae	<i>Inga bourgoni</i>	l,R	1.63	1.10
Cecropiaceae	<i>Pourouma minor</i>	f,l,L	1.58	1.07
Cecropiaceae	<i>Pourouma villosa</i>	F,l	1.52	1.03
Total			52.87	35.71

^a Cons, food categories (F, mature fruit; f, immature fruit; l, young leaves; L, mature leaves; R, flowers); PI, proportion of identified plant species (%); PD, proportion of the total diet (%).

Seasonal Variations

The monthly distribution of the species' consumption showed that the exploitation of one part of a plant of a particular species was generally localized in time. Exceptions were a few species — *Philodendron linnaei*, *Bocoa prouaensis*, and *Pithecellobium jupumba* — that were exploited as sources of leaves year-round. The first species was an abundant epiphyte in which each individual produced a few young leaves year-round. In the case of *Bocoa prouaensis*, many trees ($n = 14$) with an asynchronous pattern of leaf production among individuals were used as a young leaf source by the monkey troop. *Pithecellobium jupumba* was used by the monkeys for both young and mature leaves.

Table V. List of Species Making Up $\leq 50\%$ of the Feeding Units in Each Plant Food Category

Family	Species	Pr ^a
Fruit		
Moraceae	<i>Bagassa guianensis</i>	10.20
Sapotaceae	<i>Chrysophyllum lucentifolium</i>	9.53
Caesalpiniaceae	<i>Vouacapoua americana</i>	8.43
Celastraceae	<i>Goupia glabra</i>	8.39
Rubiaceae	<i>Psychotria</i> cf. <i>carthaginensis</i>	6.46
Solanaceae	<i>Solanum</i> sp.	5.08
Euphorbiaceae	<i>Drypetes variabilis</i>	3.99
Leaves		
Mimosaceae	<i>Pithecellobium jupumba</i>	7.94
Caesalpiniaceae	<i>Dicorynia guianensis</i>	4.55
Fabaceae	<i>Bocoa prouaensis</i>	4.51
Burseraceae	<i>Tetragastris altissima</i>	4.40
Bignoniaceae	<i>Tabebuia serratifolia</i>	4.18
Cecropiaceae	<i>Pourouma minor</i>	3.47
Mimosaceae	<i>Inga bourgoni</i>	3.13
Mimosaceae	<i>Inga</i> spp.	3.13
Araceae	<i>Philodendron linnaei</i>	3.10
Nyctaginaceae	<i>Neea</i> sp.2	2.69
Nyctaginaceae	<i>Neea</i> sp.1	2.61
Fabaceae	<i>Swartzia panacoco</i>	2.54
Caesalpiniaceae	<i>Eperua falcata</i>	2.50
Sapotaceae	<i>Pouteria filipes</i>	2.42
Flowers		
Sapotaceae	<i>Micropholis cayannensis</i>	26.55
Caesalpiniaceae	<i>Eperua falcata</i>	13.45
Apocynaceae	<i>Odontadenia</i> sp.	13.19

^a Proportion of feeding units of the plant category (%).

For fruit and flowers, feeding periods rarely exceeded 1 or 2 months, except for a few species in the following categories.

- (1) Successive fruiting of two or three trees, more or less overlaps, and each tree bears a lot of fruit for a long time: *Schefflera paraensis*, *Bagassa guianensis*, and *Gnetum paniculatum*,

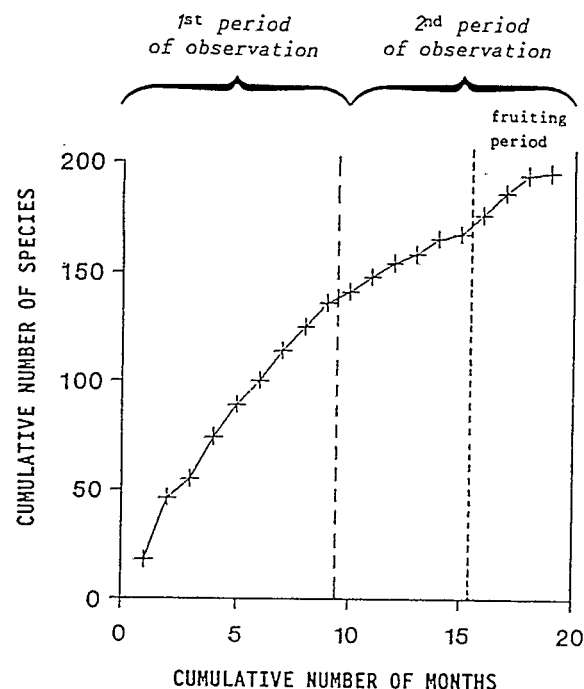


Fig. 6. Cumulative number of plant species eaten by the focal troop per month.

- (2) Massive fruiting occurs, in which many trees bear fruit, more or less successively, although the fruiting period of each tree is relatively short: *Tetragastris altissima*, *Drypetes variabilis*, and *Moutabea guianensis*. The same explanation applies to the long feeding periods on flowers of *Micropholis cayennensis* and on immature fruit of *Vouacapoua americana* and *Chrysophyllum lucentifolium*. Immature fruit were generally available for a longer period than mature fruit or flowers were.

The graph of the cumulative number of plant species that were used as foods by monkeys (Fig. 6), obtained by summing each month the number of new species, is an asymmetrical S-curve. The increased slope of the curve in the 16th month corresponds with a new peak of fruiting (February to May). Among the 28 supplementary species consumed in the last 4 months, 22 were used by howlers as a fruit source, 1 as a flower source, and 5 as

leaf sources. In spite of insufficient phenological data, the majority of tropical plant species seems to have a fruiting recurrence frequency between 2 and 4 years (Sabatier 1983, 1985). We hypothesize that the slope of the cumulative curve must decline each fruiting period for 3 or 4 years, before reaching a plateau.

Other Food Categories

Termitaria

Howler monkeys were observed eating material from arboreal termite nest in 1.5% of the feeding units (39 observations). They generally fed directly with their mouths or used their hands to tear up pieces of termitarium wall. Most of the time, many troop members ate from the same termitarium; either several individuals fed together or they took turns. Most of the termitaria were exploited several times, and one of them was used until it disappeared. It was common for the troop to travel a long way to exploit a termitarium site.

Except on one occasion, when termite galleries at the base of the tree revealed the presence of termites, it was impossible to ascertain if termitaria were occupied. Considering that termite remains have never been found in our howler fecal samples, and that they generally bit the walls of termitaria, it is unlikely that the searching food was termites, even if they might have ingested some termites with the walls. Our examination of fragments on the ground showed that the monkeys ate the nests of at least two termite genera. One kind of termitarium is constituted principally of organic material, and the second principally of soil. The latter, which was the most frequently eaten by monkeys, probably belongs to the genus *Constrictotermes*, the only South American genus to have arboreal nests made principally of soil (Grassé, 1983).

Bark and Moss

Consumption of bark, moss, lichens, and other vegetable food on branches and trunks was very rare. The higher rates obtained in June and August 1988 for this food category were probably due partly to a confusion with termitarium consumption.

DISCUSSION

The principal studies of howler monkey diet are presented in Table VI. With 57 and 25.5% of the feeding units for leaves and fruit, respectively, the red howler monkeys of our study site ate more leaves and fewer fruit than other red howler populations. However, these proportions are not very different from those observed for all species of *Alouatta*. Moreover, the rate of mature leaves (3%) is much lower than that generally noted, which is $\geq 10\%$. It is usually considered that howler monkeys prefer young leaves to mature leaves. Many studies have shown that young leaves contain more protein and less fiber than mature leaves do and have a higher digestibility since mature leaves are often rich in secondary compounds (Hladik, 1978; Milton, 1979; Glander, 1982). The great plant species diversity of our habitat (400 plant species for 4.8 ha), which may induce a greater availability of young leaf species for monkeys, could explain the low rate of mature leaf consumption. This may also explain the high number of plant species used as young leaf sources.

The consumption of soil, processed by termites, has been observed for red howler monkeys in Colombia (Izawa and Lozano, 1990). Geophagy is a well-known behavior for several Old World primates: gibbon, gorilla, black-and-white colobus, red colobus, indris (Hladik and Guegen, 1974), black colobus (Harrison and Hladik, 1986), and red leaf monkeys in Borneo (Davies and Baillie, 1988). It is usually suggested that monkeys eat soil for supplemental minerals. On the contrary, Hladik and Gueguen (1974) and Harrison and Hladik (1986) consider that the mineral elements in soils are trifling in comparison with those contained in plant foods. They noted that geophagy is a common behavior of folivorous primates and is associated with the consumption of mature leaves with a high tannin content, to facilitate the adsorption of polyphenols. We are inclined to agree with the second hypothesis, though a detailed analysis of diet and digestive physiology of the monkeys and studies on the nutritive advantage and adsorptive capacity of termitaria soils are needed to test the two hypotheses and to reveal which is the more important factor in soil-eating by howler monkeys at our study site.

The singularity of our study lies in the large number of plant species eaten (195 species) and, more particularly, the large number of fruit species consumed (97 species). Milton (1978) recorded 105 species eaten for two troops of *Alouatta palliata* on Barro Colorado Island in Panama, from which 70 species were used by each troop: 54–55 for leaves, 17–14 for flowers, and only 20 for fruit. With only 34 plant species consumed in the study by Gaulin and Gaulin (1982) in Colombia, and 40 plant species noted by Braza *et al.* (1983) in Venezuela, the diversity of the diet of red howler monkeys is much lower than that obtained in our study. However, the duration of the two

other studies was only 1 year, while ours covered 2 years. But the total number of plant species eaten in our initial 11-month period of observation (April 1988 to February 1989) is 136 species. This difference may be due to the habitats where the other two studies were conducted; they are very different from Nourague station: high-altitude forest with a discontinuous canopy and patches of secondary vegetation in the study by Gaulin and Gaulin (1982) and gallery forest, with canopy 15–20 m high and isolated patches of forest in savanna, in the study by Braza *et al.* (1983). Our study was the first long-term study on the diet of *Alouatta seniculus* in an old, intact forest of low altitude. Moreover, the 22 supplementary species used as mature fruit sources by neighboring troops suggest that there may be large intergroup differences in diet even within the same habitat, which may be due to the heterogeneity of the environment. Thus, the total number of plant species used as food sources by the howler population in our study area might have been > 217 species if the study have been made on several monkey troops.

Another interesting point of our study is the division between species used as fruit sources and those used as leaf or flower sources. Estrada and Coates-Estrada (1986) suggested that *plant species used as leaf resources may be trading of some damage to its foliage for seed dispersal services by howler monkeys*. They noticed that 33% of trees in which monkeys fed on fruit were also used as sources of leaves. Most of them (80%) belonged to the Moraceae. In our study, 20 species of the Moraceae were eaten by monkeys, but none of them was used by the focal troop for both fruit and leaves.

Like many other primates (Hladik, 1981), howler monkeys appeared to be very selective in their food choices and use a very small number of plant species as principal food sources (Hladik and Hladik, 1969; Milton, 1978; Glander, 1978; Gaulin and Gaulin, 1982; Chapman, 1988). Our results seem to differ from this pattern, since ≥ 40 plant species are necessary to reach 50% of the total diet, and the most consumed species accounts for only 4.36% of the total diet. Nevertheless, the 19 main species, which accounted for 35.7% of the diet, represent only 9.7% of plant species used as food plant sources by the study troop. Thus, this large number of main species must be related to the greater plant species diversity of monkey diet and their greater availability in the habitat, in comparison with other study sites.

In the majority of studies (Hladik and Hladik, 1969; Milton, 1978; Mittermeier and Roosmalen, 1981; Gaulin and Gaulin, 1982; Estrada, 1984; Rumiz *et al.*, 1986; Chapman, 1988), Moraceae constituted the favorite family of howler monkey food plants. At Nourague Station, howler monkeys displayed a marked preference for the Sapotaceae ($\approx 17\%$ of total diet), though the Moraceae was also important. This preference for Sapotaceae could be due partly to the domination of this family at the study site.

Table VI. Characteristics of Diet Found in Principal Studies of Howler Monkeys Compared with Results of this Study^a

Species	Location	Number of plant species						Diet					Method
		F	f	L	l	R	Total	F	f	L	l	R	
Al.s	Surinam	— ^b	—	—	—	—	—	69	—	14.3	14.3	2.4	F
Al.s	Colombia	12	2	9	24	4	34	28.4	13.9	7.5	44.5	5.4	FT,FA
Al.s	Venezuela	—	—	—	—	—	40	—	—	—	—	—	FS,SC
Al.p	Costa Rica	—	13	—	26	42	30	13	—	19	50	18	FT
Al.p	Costa Rica	—	—	—	—	—	11	28.5	—	27.7	21.3	22.5	FT,FS
Al.p	Mexico	12	5	16	19	1	27	41.4	8.5	10	39.3	0.2	FT,FS
Al.p	Panama (BCI)	19	4	—	10	—	7	34.5	28.3	6.2	21.2	5.9	FA
Al.p	Panama (BCI)	—	—	—	—	—	—	38.8	—	55.6	—	5.6	FT
Al.p	Panama (BCI)	—	32	—	80	—	28	42	—	10	38	10	FT
Al.c	Argentina	13	—	—	24	—	4	29 ^c	—	71	—	—	FT
Al.f	Brazil	—	—	—	—	—	30	10	—	80	—	10	FT
Al.s	French Guiana	90	14	7	94	36	195	21.5	4	3	54	12.6	F,FS

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Table VI. Continued

Species	Location	Duration of observations (months)	Habitat	Reference
Al.s	Surinam	11	F	Mittermeier and Roosmalen (1981)
Al.s	Colombia	10	HAF	Gaulin and Gaulin (1982)
Al.s	Venezuela	12	GF,S	Braza <i>et al.</i> (1983)
Al.p	Costa Rica	12	GF	Glander (1978)
Al.p	Costa Rica	24	DF,S	Chapman (1988)
Al.p	Mexico	12	F	Estrada (1984)
Al.p	Panama (BCI)	14	F,SF	Hladik and Hladik (1969)
Al.p	Panama (BCI)	10	F,SF	Smith (1977)
Al.p	Panama (BCI)	8	F,SF	Milton (1978)
Al.c	Argentina	15	DF	Rumiz <i>et al.</i> (1986)
Al.f	Brazil	9	DF	Galetti (1987)
Al.s	French Guiana	19	F	This study

^a Species: Al.s, *Alouatta seniculus*; Al.p, *Alouatta palliata*; Al.c, *Alouatta caraya*; Al.f, *Alouatta fusca*. Habitat: F, old forest; HAF, high-altitude forest; GF, gallery forest; DF, degraded forest; SF, secondary forest; S, savanna. Method (of dietary measurement): F, frequency of consumption; FT, feeding time; FA, feeding amounts; FS, analysis of fecal samples; SC, analysis of stomach contents. Food categories: F, mature fruit; f, immature fruit; L, mature leaves; l, young leaves; R, flowers.

^b Missing data.

^c Fruit and flowers.

Diet of *Alouatta seniculus* in French Guiana

Sapotaceae is the most abundant family in species number (45 species for the three transects included in the home range of the troop) and the third one in population density (Sabatier and Prévost, 1990).

The composition and the diversity of the diet of howler monkeys are obviously related to the availability of food in their habitat. The usual preference of howler monkeys for Moraceae is probably due to the fact that most previous studies have been conducted in more or less secondary environments, where the Moraceae is very abundant. Similarly, the small number of plant species used as food sources by howler monkeys may be due not only to the high density of Moraceae species, especially species of the genera *Ficus* and *Cecropia*, which characterizes secondary habitats (Milton 1978; Gaulin and Gaulin, 1982; Estrada, 1984; Rumiz *et al.*, 1986) but also to the low diversity of plant species in the study areas, for instance, that of Glander (1978), with only 96 species in 37 families.

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REFERENCES

- Braza, F., Alvarez, F., and Azcarate, T. (1983). Feeding habits of the red howler monkeys (*Alouatta seniculus*) in the Llanos of Venezuela. *Mammalia* 47: 205-214.
- Braza, F., Alvarez, F., and Azcarate, T. (1981). Behaviour of the red howler monkeys (*Alouatta seniculus*) in the Llanos of Venezuela. *Primates* 22: 459-473.
- Busson, F. (1965). *Plantes alimentaires de l'Ouest africain. Etude botanique, biologique et chimique*, Leconte, Marseille.
- Carpenter, C. R. (1934). A field study of the behavior and social relations of howling monkeys. *Comp. Psychol. Mongr.* 10: 1-168.
- CEGET CNRS-ORSTOM (1979). *Atlas des départements français d'Outre-Mer. IV—La Guyane*. Lassere, G. (ed.), CNRS-ORSTOM, Paris.
- Chapman, C. A. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates* 29: 177-194.
- Charles-Dominique, P. (1993). Ecologie des mammifères forestiers de Guyane française: origines biogéographiques et organisation du peuplement. Actes du IIème Congrès Ecosystèmes forestiers et Aménagement de l'espace régional, Cayenne, Février 1990 (in press).
- Clutton-Brock, T. H. (1977). Appendix I. Methodology and measurement. In Clutton-Brock, T. H. (ed.), *Primate Ecology*, Academic Press, London, pp. 585-601.
- Crockett, C. M. (1985). Population studies of red howler monkeys (*Alouatta seniculus*). *Natl. Geog. Res.* 1: 264-273.

- Crockett, C. M., and Pope, T. (1988). Inferring patterns of aggression from red howler monkey injuries. *Am. J. Primatol.* 15: 289-308.
- Crockett, C. M., and Rudran, R. (1987a). Red howler monkey birth data. I. Seasonal variation. *Am. J. Primatol.* 13: 347-368.
- Crockett, C. M., and Rudran, R. (1987b). Red howler monkey birth data. II. Interannual, habitat, and sex comparisons. *Am. J. Primatol.* 13: 369-384.
- Crockett, C. M., and Sekulic, R. (1982). Gestation length in red howler monkeys. *Am. J. Primatol.* 3: 291-294.
- Crockett, C. M., and Sekulic, R. (1984). Infanticide in red howler monkeys (*Alouatta seniculus*). In Hausfater, G., and Blaffer Hrdy, S. (eds.), *Infanticide*, Aldine, New York, pp. 173-191.
- Davies, A. G., and Baillie, I. C. (1988). Soil-eating by red leaf monkeys (*Presbytis rubicunda*) in Sabah, Northern Borneo. *Biotropica* 20: 252-258.
- Defler, T. R. (1981). The density of *Alouatta seniculus* in the eastern Llanos of Colombia. *Primates* 22: 564-569.
- 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. (1984). Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *Am. J. Primatol.* 6: 77-91.
- Estrada, A., and Coates-Estrada, R. (1986). Frugivory by howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: Dispersal and fate of seed. In Estrada, A., and Fleming, T. H. (eds.), *Frugivores and Seed Dispersal*, Dr. W. Junk, Dordrecht, The Netherlands, pp. 93-104.
- Freese, C. H., Heltne, P. G., Castro, N. R., and Whitesides, G. (1982). Patterns and determinants of monkeys densities in Peru and Bolivia, with notes on distributions. *Int. J. Primatol.* 3: 53-90.
- Galetti, M., Laps, R., and Pedroni, F. (1987). Feeding behavior of the brown howler monkey (*Alouatta fusca clamitans*) in a forest fragment in state of Sao Paulo, Brazil. *Int. J. Primatol.* 8: 542.
- Gaulin, S. J. K., and Gaulin, C. K. (1982). Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. *Int. J. Primatol.* 3: 1-32.
- Glander, K. E. (1982). The impact of plant secondary compounds on primate feeding behavior. *Yb. Phys. Anthropol.* 25: 1-18.
- Glander, K. E. (1978). Howling monkey feeding behavior and plant secondary compounds: A study of strategies. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, DC, pp. 561-574.
- Grassé, P. P. (1983). *Termitologie. Tome II: Fondation des sociétés, Construction*, Masson Ed, Paris.
- Harrison, M. J. S., and Hladik, C. M. (1986). Un primate granivore: Le Colobe noir dans la forêt du Gabon; Potentialité d'évolution du comportement. *Terre Vie* 41: 281-298.
- Hladik, C. M. (1981). Diet and the evolution of feeding strategies among forest primates. In Harding, R. S. O., and Teleki, G. (eds.), *Omnivorous Primates*, Columbia University Press, New York, pp. 215-254.
- Hladik, C. M. (1978). Adaptive strategies of primates in relation to leaf-eating. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, DC, pp. 373-395.
- Hladik, C. M., and Gueguen, L. (1974). Géophagie et nutrition minérale chez les Primates sauvages. *C.R. Acad. Sci. Paris Ser. D* 279: 1393-1396.
- Hladik, A., and Hladik, C. M. (1969). Rapports trophiques entre végétation et Primates dans la forêt de Barro Colorado (Panama). *Terre Vie* 1: 25-117.
- Holdridge, L. R. (1964). *Life Zone Ecology*, Trop. Sci. Center, San José, Costa Rica.
- Izawa, K. (1975). Foods and feeding behavior of monkeys in the upper Amazon basin. *Primates* 16: 295-316.
- Izawa, K., and Lozano, H. M. (1990). Frequency of soil-eating by group of wild howler monkeys (*Alouatta seniculus*) in La Macarena, Colombia. *Field Stud. New World Monkeys, La Macarena, Colombia* 4: 47-56.

- Milton, K. (1978). Behavioral adaptation to leaf-eating by the mantled howler monkey (*Alouatta palliata*). In Montgomery, G. G. (ed.), *The Ecology of Arboreal-Folivores*, Smithsonian Institution Press, Washington, DC, pp. 535-549.
- Milton, K. (1979). Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *Am. Nat.* 114: 362-378.
- Mittermeier, R. A., and van Roosmalen, M. G. M. (1981). Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatol.* 36: 1-39.
- Neville, M. K. (1972a). The population structure of red howler monkeys (*Alouatta seniculus*) in Trinidad and Venezuela. *Folia Primatol.* 17: 56-86.
- Neville, M. K. (1972b). Social relations within troops of red howler monkeys (*Alouatta seniculus*). *Folia Primatol.* 18: 47-77.
- Rumiz, D. I., Zunino, G. E., Obregozo, M. L., and Ruiz, J. C. (1986). *Alouatta caraya*: Habitat and resource utilization in northern Argentina. In Taub, D. M., and Kine, F. A. (eds.), *Current Perspective in Primate Social Dynamics*, Van Nostrand Reinhold, New York, pp. 175-193.
- Sabatier, D. (1983). *Fructification et dissémination en forêt guyanaise. L'exemple de quelques espèces ligneuses*, Thèse de 3^{ème} Cycle, Université des Sciences et Techniques du Languedoc, Montpellier.
- Sabatier, D. (1985). Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Terre Vie* 40: 298-320.
- Sabatier, D., and Prévost, M.-F. (1990). Variations du peuplements forestier à l'échelle stationnelle: Le cas de la station des Nouragues en Guyane française. Actes de l'Atelier MAB-UNESCO sur "l'aménagement et la conservation de l'écosystème forestier tropical humide," Mars 1990, pp. 169-187.
- Schön Ybarra, M. A. (1984). Locomotion and postures of red howlers in a deciduous forest-savanna interface. *Am. J. Phys. Anthropol.* 63: 65-76.
- Schön Ybarra, M. A. (1986). Loud calls of adult male red howling monkeys (*Alouatta seniculus*). *Folia Primatol.* 47: 204-216.
- Schön Ybarra, M. A. (1988). Morphological adaptation for loud phontions in the vocal organ of howling monkeys. *Primate Rep.* 22: 19-24.
- Schön Ybarra, M. A., and Schön, M. A. (1987). Positional behavior and limb bone adaptations in red howling monkeys (*Alouatta seniculus*). *Folia Primatol.* 49: 70-89.
- Sekulic, R. (1983). The effect of female call on male howling in red howler monkeys (*Alouatta seniculus*). *Int. J. Primatol.* 4: 291-305.
- Sekulic, R., and Chivers, D. J. (1986). The significance of call duration in howler monkeys. *Int. J. Primatol.* 7: 183-190.
- Smith, C. C. (1977). Feeding behaviour and social organization in howling monkeys. In Clutton-Brock, T. H. (ed.), *Primate Ecology*, Academic Pres, London, pp. 97-126.
- Struhsaker, T. T. (1975). *The Red Colobus Monkey*, University of Chicago Press, Chicago.