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Howling Monkey Feeding Behavior and Plant Secondary Compounds: A Study of Strategies

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Introduction

A long-term investigation of the relationship between the habitat and social organization of mantled howling monkeys (*Alouatta palliata* Gray) in Costa Rica was begun in June 1972. The data reported here are the result of a 14-month period between June 1972 and August 1973. During this time, 2071 hours of direct animal observation were accumulated on 172 days. The study group's composition (Group 1, herein) and the observation time for each animal is given in Table 1.

The study site was situated on Hacienda La Pacifica, Guanacaste Province, Costa Rica, at latitude 10°28'N, longitude 85°07'W. Hacienda La Pacifica is a 1330 ha cattle ranch located at the base of the Cordillera de Tilaran, 5 km northwest of Cañas. It is 45 m above sea level and lies within the lowland tropical dry-forest life zone (Holdridge, 1967). Approximately one-fourth of the ranch remains forested; the remainder has been cleared for farming. Total deforestation is not practiced. Instead, windbreak strips and riparian forests are left to protect the soil against wind and water erosion.

Table 1.—Name and age/sex class of each member of Group 1 at the beginning of the study, September 1, 1972. Also, the number of days each animal was the focal animal and the number of minutes each animal was observed.

Animal	*Age/Sex*	*Focal days*	*Time of observation minutes*
Scar	adult male	18	13218
Baker	adult male	19	13563
White/red	adult female	19	13631
Blue	adult female	18	13614
Yellow	adult female	19	13806
Green/red	adult female	19	14271
Dogcollar	adult female	20	14142
Green*	juvenile female	20	14917
Charlie	juvenile male	6	4021
Able	juvenile male	4	2423
Bonnie	juvenile female	5	3128
Shadow	infant male	3	2236
Blue's infant	infant male	2	1325

*Green was classified as an adult after she gave birth on 1/11/73.

The idea of viewing feeding strategies in terms of plant secondary compounds presented in this paper is not original nor of recent vintage (see McKey, 1978, for a similar study). The possible significance of plant produced chemicals was recognized as early as the late 19th-century (Stahl, 1888). For a long time, investigators working with nonprimate organisms—especially insects—have been concerned with the impact of plant secondary compounds (Fraenkel, 1959; Ehrlich and Raven, 1965; Whittaker, 1970; Feeny, 1970; Freeland and Janzen, 1974; and many others). On the other hand, primatologists have been derelict in considering the ramafications of these plant chemicals, especially since the expanding literature indicates that secondary compounds are widely distributed throughout the plant world (Willaman and Schubert, 1961; Watt and Breyer-Brandwijk, 1962; Kjaer, 1963; Shorland, 1963; Hegnauer, 1964; Moir, 1968; Feeny, 1970; Raffauf, 1970; Whittaker, 1970; Janzen, 1971; Whittaker and Feeny, 1971).

The presence of these chemicals does not mean that all secondary compounds are toxic to all organisms; even the very toxic ones can be and are ingested by some organisms (Janzen, 1978). However, the early work of Stahl (1888) in which he suggests that not everything that is green is palatable and the large volume of data since his time contain significant implications for investigators working with herbivorous primates, especially so since many investigators seem to feel that leaf-eating monkeys have an unlimited food resource.

Do leaf-eating monkeys utilize all of the available resources (leaves)? If not, which specific resources do they use and why? The objectives of this paper are to view the strategies of 1 group of folivorous primates for dealing with seasonal food availability and the chemical defenses of plants.

Methods

Details of the methods used to obtain a detailed description of the habitat and the capture and marking of the animals can be found elsewhere (Glander, 1975), but I will provide a brief résumé here in order to place the following data in perspective. Every tree in the home range of the study group was marked with a bright orange ordinal. The tree height, canopy depth, and distance between trees was measured. A map was constructed. Whenever possible the tree was identified as to species (Opler, personal communication). A weekly phenological record of the numbered trees was obtained. Climatological data were recorded at a government weather station located 600 m from the study area.

To collect durational data and overcome many of the problems unique to the study of arboreal primates, I employed the technique of focal animal observation (Altmann, 1974) plus a random method of preselecting the focal animal (Glander, 1975). This method provided a comprehensive record (durational) for all daily activities of a focal animal without sacrificing group dynamics. *Ad lib.* sampling (Altman, 1974) of nonfocal animals was done opportunistically. Durational information is necessary for determining energy budgets (Coelho, 1974), and energy budgets link the animal's social behavior with its environment; an explicit example of possible environmental impact on social structure (in preparation).

In order to insure unambiguoius individual recognition, individualized leather collars with colored metal tags were placed around the necks of all but 1 of the females in the study group. The uncollared female served as a behavioral control for the collared animals. The adult males were readily distinguished by physical markings and the infants and juveniles could be differentiated by their regular close association with particular tagged females. The capture of all animals (except infants) was effected by a CO_2 dart-gun. A large piece of canvas rigged with handles was used to catch the animals as they fell from the trees.

There were several other groups in areas around the study site but only one group (Group 2) had any contact with Group 1. Group 2 spent 69 of the 172 days of observation in the study area. At the beginning of the study, Group 2 contained 6 adult males, 15 adult females, 12 juveniles, and 2 infants. This group frequently split into subgroups of 27 and 8.

Results

Rainfall and temperature

On the basis of rainfall, the study site experienced 2 distinct and separate seasons, a 5-month dry season (December-April) and a 7-month wet season (May-November) (Figure 1). The total rainfall for the study period was 1431 mm.

The pattern of rainfall was somewhat unusual during the study period. Normally, a small dry season (*el veranillo*) occurs in June or July with most of the rain falling before and after the *veranillo*; however, June, July, and August were the wettest months with October being relatively drier (Figure 1).

The long dry season began in late December 1972 and continued until April 27, 1973. The onset of the dry season was gradual with very small amounts of rainfall after November 15, 1972 (ranging from 0.3 mm to 3.2 mm).The last rain fell on December 21, 1972 (3.2 mm). Following that day, no rain fell for 126 days. The first rain of the wet season fell on April 27, 1973 (110 mm). This was not only the beginning of the wet season, but also the day with the greatest amount of rainfall during the study. The sudden onset of the wet season is typical of the seasonal transition from dry to wet and contrasts with the gradual onset of the dry season.

It rained 108 of 358 days during the study. There was an average of 9 days of rain per month. The months of January, February, and March were without rain (Figure 1).

The maximum daily temperature experienced during the study was 37.0° C (Figure 2). The minimum daily temperature was 19.0° C. The mean monthly temperature for the study period was 27.7° C (range 26.1° C to 30.8° C) and the variation in the mean from month to month ranged from 0° C to 2.9° C. Both the hottest and coolest weather occurred during the dry season: April 1973 was the hottest month; December 1972 was the coolest. Strong winds contribute to the desiccation during the dry season.

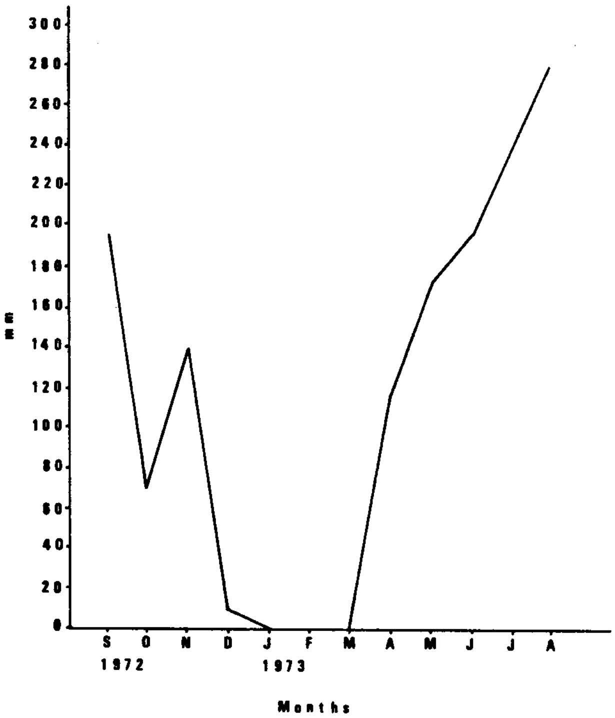

Figure 1. Rainfall for the study site.

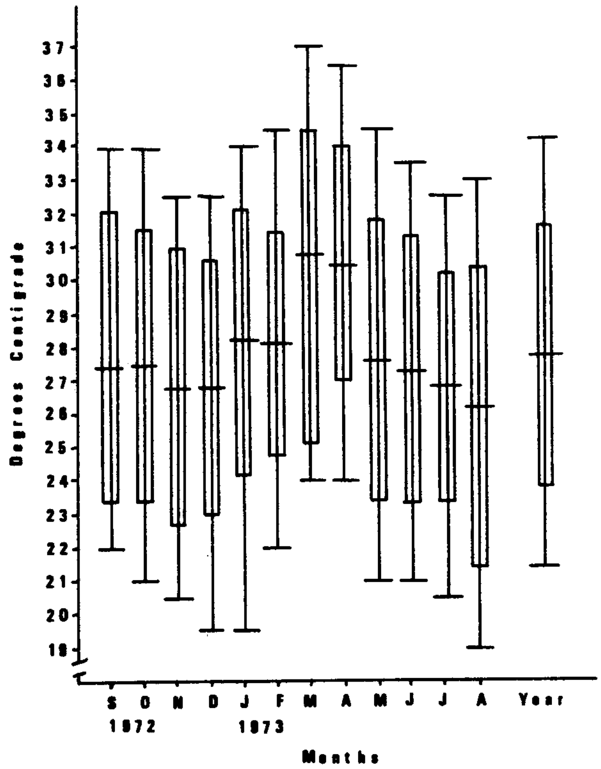

Figure 2. Monthly temperature averages and extremes. Single line represents the maximum-minimum temperature. Double lines represent the average maximum and average minimum temperatures. Mid-line represents the monthly average temperature.

Habitat description

The study site is a strip of remnant forest along the

Río Corobici. Utilizing naturally occurring lines of demarcation—tree phenophases—I conceived the study area as subdivided into 4 areas (Figure 3). Area 2 and Area 3 consisted of riparian forest on the left and right banks of the river, respectively; Area 1 and Area 4 were upland forest extensions connecting with the riparian forest of Areas 2 and 3, respectively. The distinction between riparian and upland forest was based on the phenology of the trees present in the areas. Most of the trees in the upland regions dropped their leaves and remained bare for much of the 5-month dry season. Trees in the riparian areas also were deciduous, but a majority flushed new leaves whenever leaf-fall occurred and maintained their leaves throughout the dry season. Only a few remained bare. The upland and riparian forest areas were markedly distinct during the dry season.

The riparian forest was composed of trees that formed a general canopy 15 to 20 m high. Emergents reached 33 to 37 m. The average tree height was 11.4 m (S.D. 5.6, N = 981); the average canopy depth was 7.3 m (S.D 4.8; N = 981). Stratification was apparent along the river. The understory in the riparian forest was variable due to browsing by cattle. Epiphytes were sparse with a few orchids and bromeliads present. Ten percent of the tree crowns contained lianas and vines.

The upland forest was composed of shorter trees that formed a canopy 10 to 15 m high. Emergents were rare. The average tree height was 8.3 m (S.D. 3.1, N = 696). The average canopy depth was 4.6 m (S.D. 2.2, N = 969). Stratification was not apparent in the upland forest. Epiphytes and lianas were rare. Vines were present in about 10 percent of the tree crowns in Area 1, but absent in Area 4.

The home range for Group 1 during the 12 months of the study contained 1699 trees, representing 96 species (Glander, 1975). Of these, 992 were tallied in the riparian forest, and 707 were found in the upland forest. The stand for the total area had a density of 172 trees/ha (69 trees/acre). The stand density was 207 trees/ha (84 trees/acre) for the riparian forest and 139 trees/ha (56 trees/acre) for the upland forest. The 96 species represented 79 genera and 37 families. Eight families (22 percent), Anacardiaceae, Bignoniaceae, Borginaceae, Caesalpinaceae, Mimosaceae, Myrtaceae, Papilionaceae, and Sterculiaceae, contained 76 percent of the trees. The family, Leguminosae, which is often divided into 3 families—Caesalpinaceae, Mimosaceae, and Papilionaceae—contained 29 percent (487) of the trees present. The family with the most representatives was Papilionaceae (341) although the 2 most common species were *Guazuma ulmifolia* (Sterculiaceae) and *Cordia dentata* (Boraginaceae). Thirteen families were represented by a single species and 4 by a single tree.

FIGURE 3

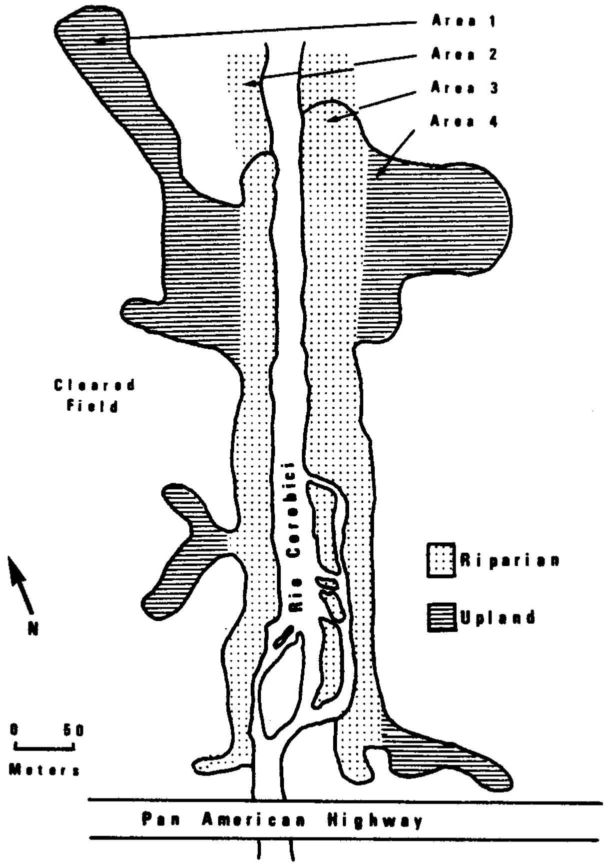

Figure 3. Diagrammatic representation of the study site. The study area was surrounded on all sides by cleared fields except up-river where the riparian forest was continuous.

There were 20 dioecious tree species comprising 10 percent (170) of the total trees in the area. An attempt was made to determine the sex of each dioecious tree. Group 1 fed on the fruit of the following dioecious species: *Chlorophora tinctoria, Cecropia peltata, Coccoloba caracasana, Simarouba glauca, Spondias mombin, S. nigrescens.* The individuals of *C. tinctoria* (3 of 6) were equally divided between males and females, but *C. peltata* (1 of 3), *C. caracasana* (1 of 9), and *S. glauca* (1 of 4) had only 1 female each. *S. mombin* (9 of 12) and *S. nigrescens* (7 of 9) had more females than males.

Habitat utilization and day range

In two-dimensional terms the home range of Group 1 consisted of 98,850 sq m (9.9 ha). The upland forest

Table 2.—All tree species used as food sources by Group I listed by family (alphabetical order). The number of individuals of each species and family is indicated.

No.	Family	Species
75	ANACARDIACEAE	
48		*Anacardium excelsum*
10		*Astronium graveolens*
8		*Spondias mombin*
7		*S. nigrescens*
2		*S. purpurea*
12	BIGNONIACEAE	
6		*Tabebuia neochrysantha*
6		*T. rosea*
1	BOMBACACEAE	
1		*Ceiba pentandra*
9	BORGINACEAE	
1		*Bourreria quirosii*
1		*Cordia alliodora*
1		*C. collococca*
5		*C. dentata*
1		*C. panamensis*
8	BURSERACEAE	
8		*Bursera simaruba*
16	CAESALPINACEAE	
11		*Hymenaea courbarill*
5		*Schizolobium parahybum*
1	CARICACEAE	
1		*Cariaca papaya*
2	COCHLOSPERMACEAE	
2		*Cochlospermum vitifolium*
2	EBENACEAE	
2		*Diospyros nicaraguensis*
8	ELAEOCARPACEAE	
4		*Muntingia calabura*
4		*Sloanea terniflora*
1	FLACOURTIACEAE	
1		*Casearia arborea*
2	MALPIGHIACEAE	
2		*Byrsonima crassifolia*
8	MELIACEAE	
1		*Cedrela mexicana*
2		*Trichilia cuneata*
5		*Trichilia* sp.
40	MIMOSACEAE	
1		*Albizzia adinocephala*
6		*Enterolobium cyclocarpum*
2		*Inga vera* var. *spuria*
7		*Lysiloma seemannii*
14		*Pithecolobium longifolium*
10		*P. saman*
8	MORACEAE	
3		*Cecropia peltata*
2		*Chlorophora tinctoria*
2		*Ficus glabrata*
1		*F. ovalis*
2	MYRTACEAE	
2		*Eugenia salamensis*
76	PAPILIONACEAE	
22		*Andira inermis*
6		*Dalbergia retusa*
15		*Gliricidia sepium*
1		*Lonchocarpus costaricensis*
2		*L. hondurensis*
24		*L. minimiflorus*
1		*Myrospermum frutescens*
4		*Pterocarpus hayesii*
1		*Sweetia panamensis*
2	POLYGONACEAE	
2		*Coccoloba caracasana*
16	ROSACEAE	
16		*Licania arborea*
5	RUBIACEAE	
2		*Calycophyllum candidissimum*
1		*Chomelia spinosa*
1		*Genipa caruto*
1		*Guettarda macrosperma*
2	RUTACEAE	
2		*Zanthoxylum procerum*
1	SAPINDACEAE	
1		*Thouinidium decandrum*
11	SAPOTACEAE	
6		*Manilkara achras*
5		*Mastichodendron tempisque*
2	SIMAROUBACEAE	
2		*Simarouba glauca*
5	STERCULIACEAE	
2		*Guazuma tomentosa*
3		*Sterculia apetala*
16	TILIACEAE	
15		*Luehea candida*
1		*L. speciosa*

contained 50,900 sq m (5.1 ha) and the riparian forest, 47,950 sq m (4.8 ha). However, since Group 1 came to the ground only 3 times, all in the same place, I believe a more realistic estimation of the area used by Group 1 can be obtained by using the average canopy depth for the trees in the study site. Thus, the 3-dimensional area—tree crowns—utilized by Group 1 was 234,140 cu m of upland forest and 350,035 cu m of riparian forest. Further, they spent 160 of the 172 observation days (93 percent) in the riparian forest. Therefore, 93 percent of their time was spent in 60 percent of their home range.

There was considerable variability in the distance covered each day, ranging from 207 to 1261 meters. The average day range for the year was 596 meters, but based on the extreme daily variability the yearly average is all but meaningless. The average daily difference (distance covered on 1 day compared to distance covered on the day immediately before or after the focal day, 76 such records) was 234 meters (range 0 to 742 m). There were only 19 days when the difference between daily distances traveled was less than 100 m; only 1 record where the distance covered was identical. There was a seasonal difference in the average daily distance covered, i.e., 592 m during the wet season and 552 m during the dry season. The seasonal average difference was 246 m for the wet season and 227 m for the dry season.

Resource use

A total of 331 trees, 51 vines, and the mistletoe in 2 trees were utilized as food sources by Group 1 (Table 2). Only the trees will be considered here. Many of the individual trees were used very few times, i.e., 104 were used only once. Based on the time spent feeding in the various trees, Group 1 obtained a majority of their food from only 5.2 percent of the trees available (88 of 1699). They spent 20,074 minutes of their feeding time (75.7 percent) in those 88 trees and only 6461 minutes feeding in the other 243 resource trees.

Additional information about the howlers' feeding pattern can be garnered by returning to the 104 trees used only once. The howlers fed in the 104 trees for 719 minutes. Of the 104, 78 are of the same species as the 88 used for a major part of the food. Those 78 trees were utilized for a total of 569 minutes (7.3 minutes/tree) as compared to 20,074 minutes (288 minutes/tree) for the 88 trees. Apparently sampling of new individuals of a major resource species was occurring as well as sampling of new tree species, e.g., 26 of the 104 trees utilized once represented 18 new species not previously utilized. These trees were used by Group 1 for 150 minutes (5.8 minutes/tree). The 18 sampled species represented 12 families. As further evidence for sampling of new tree species, eight species were used for only 82 minutes (Table 3). In 2 cases, Rubiaceae and Sterculiaceae, Group 1 members sampled at least 1 tree of each species in the family. The sampling was always done by an adult and only 1 animal at a time.

The 331 individual food trees represent 61 species from 26 families. The food species were not utilized with equal frequency. Twenty-four species were visited 5 times or less. There were 8 species that were visited 100 or more times. In many cases, only a few trees from any 1 species were used for food (Table 3). For example, only 2 percent of the *Cordia alliodora*, 3 percent of *C. dentata*, 1 percent of the *Guazuma ulmifolia*, and 4 percent of the *Myrospermum frutescens* individuals were utilized for food. Also, many of the higher percentages of utilization occurred

Table 3.—Alphabetical listing of every tree species used as a food source by Group I.

Species	*Number of trees present*	*Number of trees used*	*% used*	*Total time species used min*	*Number of visits*	*Average length of visit min*	*Part eaten*
Albizzia adenocephala	1	1	100	173	17	10	Nl,Fl
Anacardium excelsum	68	48	71	1855	302	6	NlPe,Nl,Pe,FlPe
Andira inermis	28	22	79	3118	217	14	Nl
Astronium graveolens	18	10	56	1401	113	12	Le,Nl,NlPe,Pe
Bourreria quirosii	2	1	50	2	1	—	Fl
Bursera simaruba	19	8	42	694	66	10.5	Le,Nl,Fl
Byrsonima crassifolia	2	2	100	83	5	17	Fr
Calycophyllum candidissimum	17	2	12	15	4	4	Le
Carica papaya	1	1	100	7	2	3.5	Le
Casearia arborea	7	1	14	1	1	—	Nl
Cecropia peltata	4	3	75	286	30	9.5	NlPe,Nl,Fr
Cedrela mexicana	8	1	13	1	1	—	NlPe
Ceiba pentandra	6	1	17	9	2	4.5	Nl,NlPe
Chlorophora tinctoria	7	2	29	24	4	6	Le,Fl,Fr
Chomelia spinosa	5	1	20	6	1	—	Le
Coccoloba caracasana	9	2	22	92	3	30	Fr,Nl
Cochlospermum vitifolium	30	2	7	16	5	3	Fl,NlPe
Cordia alliodora	42	1	2	23	4	6	Le
Cordia collococca	23	1	4	3	2	1.5	Nl
Cordia dentata	197	5	3	107	12	9	Fr
Cordia panamensis	6	1	17	10	3	3	Nl,Fl,Le
Dalbergia retusa	20	6	30	224	13	17	Fl
Diospyros nicaraguensis	2	2	100	35	3	12	Le,Nl,Fl

Table 3.—Alphabetical listing of every tree species used as a food source by Group I.

Species	*Number of trees present*	*Number of trees used*	*% used*	*Total time species used min*	*Number of visits*	*Average length of visit min*	*Part eaten*
Enterolobium cyclocarpum	13	6	46	389	59	6.5	Fl,Le,Nl
Eugenia salamensis	75	2	3	167	13	13	Fr
Ficus glabrata	2	2	100	910	74	12	Nl
Ficus ovalis	1	1	100	28	1	—	Nl
Genipa caruto	5	1	20	1	1	—	Nl
Gliricidia sepium	149	15	10	336	60	5.5	Le,Nl,Fl
Guazuma ulmifolia	201	2	1	13	2	6.5	Le
Guettarda macrosperma	2	1	50	9	2	4.5	Le
Hymenaea courbarill	64	11	17	139	23	6	Nl,Fl
Inga vera var. *spuria*	5	2	40	168	24	7	Nl,Fl,Le
Licania arborea	29	16	55	1812	186	9	Nl,Le
Lonchocarpus costaricensis	7	1	14	26	1	—	Fl
Lonchocarpus hondurensis	2	2	100	118	12	10	Fl,Nl
Lonchocarpus minimiflorus	97	24	25	821	59	15	Nl,Fl
Luehea candida	54	17	31	423	69	6	Fl
Luehea speciosa	2	1	50	231	24	9.5	Fl
Lysiloma seemannii	24	7	29	69	15	4.5	Nl,Tw,Fl
Manilkara achras	7	6	86	1587	103	15	Fr,Nl
Mastichodendron tempisque	6	5	83	523	40	13	LePe,Fr,NlPe,Fl
Mungingia calabura	9	4	44	967	87	11	Fr,Nl,Fl,Le
Myrospermum frutescens	24	1	4	311	21	15	Le,Nl,Fl
Pithecolobium longifolium	16	13	81	2033	169	11	Nl,Fl
Pithecolobium saman	11	10	91	2577	260	10	Le,Nl,Fl,Fr
Pterocarpus hayesii	4	4	100	1209	117	10	Nl
Schizolobium parahybum	6	5	83	370	42	8.5	Fl,Fr
Simarouba glauca	6	2	33	2	2	1	Fr,Le
Sloanea terniflora	16	4	25	23	4	5.5	NlPe
Spondias mombin	20	8	40	843	76	11	Fr,Nl,Fl,Le,Pu
Spondias nigrescens	10	7	70	428	56	8	Pu,Fl,Nl,Fl
Spondias purpurea	31	2	6	112	15	7	Nl,Le,Fr
Sterculia apetala	4	3	75	18	3	6	Nl,Pu,Pe
Sweetia panamensis	5	1	20	33	6	5.5	Le,Nl
Tabebuia neochrysantha	32	6	19	240	23	10	Fl
Tabebuia rosea	34	6	19	115	23	5	Nl,Fl,Fr
Thouinidium decandrum	26	1	4	5	1	—	NlPe
Trichilia cuneata	3	2	67	124	17	7	Le
Trichilia sp.	12	5	42	69	9	7.5	Fl,NlPe,Nl,Le
Zanthoxylum procerum	4	2	50	73	9	8	Nl,Fl,Le

Pu = pulvinus, Pe = pedicel, Tw= twig, N1Pe = new leaf petiole, F1Pe = flower petiole, LePe= leaf petiole because only 1 or 2 trees of that species were present in the range.

In fact, the most common tree species were utilized very little. The 5 most common trees were used for only 5.1 percent of the feeding time and more than 50 percent of that was the ingestion of the flowers of *Lonchocarpus minimiflorus*, the fourth most common tree (Table 4). Of the 15 most important food species (based on feeding time), only 4 rank in the top 15 most common trees, with 2 of those being fourteenth and fifteenth (Table 5). The second most important food species rank thirty-second in frequency of occurrence in the study area. The tenth most important food species ranks seventy-second. The 15 most common tree species were utilized for 35.6 percent of the total feeding time and three-quarters of that time was spent in the sixth, fourteenth, and fifteenth ranked tree species (Table 4).

The species utilized most for food (in terms of time) was *Andira inermis*, 3118 minutes. An individual *A. inermis* (tree 38) also was the tree in which the howlers spent the most time feeding, 924 minutes. The species used most on a per tree basis was *Lonchocarpus hondurensis*: 118 minutes for 2 trees. Many species were utilized for less than 10 minutes and 3 for only 1 minute (Table 3).

The longest average feeding bout of 30 minutes occurred in *Coccoloba caracasana* (Table 3). The average length of feeding bouts in *A. inermis*, the species utilized most, was 14 minutes. *Byrsonima crassifolia* and *Dalbergia retusa* each were used for an average of 17 minutes per feeding visit.

The species with the most feeding visits was *Anacardium excelsum* (Table 3). It was also the species with the most individuals (48 trees) visited for food.

Several species, *Muntingia calabura*, *Ficus glabrata*, and *Gliricidia sepium*, merit special comment. *M. calabura* was the only species to produce flowers, fruit, and new leaves throughout the year. It ranked thirty-fourth in frequency of occurrence and ninth in minutes of utilization (Table 5). The howlers spent 967 minutes feeding, primarily on fruit, in trees of this species.

The 2 individuals of *F. glabrata* produced new leaves during all months of the year with a large burst of new leaves at the beginning of the wet season. These 2 trees were utilized for 910 minutes of feeding.

There were 149 *G. sepium* trees present in the range of Group 1. Although Table 4 shows that 15 trees were used as food sources, new leaves were ingested from only 5 trees (#49, 50, 593, 599, 659) and mature leaves from only 3 trees (#49, 50, 593). Flowers were the only part eaten from the other 10 and nothing was taken from the remaining 134 trees. Phenophase for all 149 individuals was identical. The total feeding time of Group 1 for *G. sepium* was 343 minutes. Group 2 utilized the same tree parts from the same *G. sepium* individuals.

The families Anacardiaceae, Mimosaceae, and Papilionaceae are very important as food sources. Fifty-seven percent of the trees utilized as food sources by the howlers were members of these 3 families. In addition, the group fed in these families for 16,214 minutes or 61 percent of all feeding time (N = 26,535 minutes). All 3 families were utilized about equally—Papilionaceae was used for 6053 minutes. In each of these 3 families, 2 species received a majority of the feeding pressure.

Moraceae constituted another important food source. In fact, on a per tree comparison, Moraceae was more important than Anacardiaceae, Mimosaceae, or Papilionaceae. Individual trees of Moraceae were utilized for a total of 1230 minutes. There were 14 trees of this family in the range. Eight of them served as a food source during the study. The average feeding bout in these 8 trees was 154 minutes as compared to an average bout of 85 minutes for trees of Anacardiaceae, Mimosaceae, and Papilionaceae. Also, the group utilized more individuals of Moreceae (57 percent, 8 of 14 trees) than they did Anacardiaceae, Mimosaceae, and Papilionaceae (33 percent, 190 of 569 trees).

Two more families deserve mention: Rosaceae (1 species) and Tiliaceae (2 species). Group 1 utilized the 3 species in these families for a total of 2486 minutes (9 percent of 26,535 minutes total).

The importance of the 6 families profiled above—Anacardiaceae, Mimosaceae, Moraceae, Papilionaceae, Rosaceae, and Tiliaceae—can be further documented by noting that Group 1 spent 19,930 (75 percent) minutes feeding in species of these 6 families, while feeding for only 6605 minutes in all of the remaining 20 resource families.

Not all parts of an individual tree or tree species were utilized. The parts that were used varied with the time of year, the phenology of the tree, and the tree species. The average daily diet composition, based on the amount of time spent feeding on each tree part, consisted of 19.4 percent mature leaves, 44.2 percent new leaves, 12.5 percent fruit, 18.2 percent flowers, and 5.7 percent petioles and pulvinus (Figure 4). There was a distinct seasonal difference in the apportionment of feeding time for the various tree parts (Figure 5). The utilization of mature and new leaves was closely linked (Figure 6).

New leaves were the only part eaten from *Andira inermis*, *Casearia arborea*, *Ceiba pentandra*, *Ficus glabrata*, and *Hymenaea courbarill*. Mature leaves

Table 4.—The 15 most common tree species ranked by number of individuals present in the study area.

Rank	*Species*	*Number present*	*Percentage of total present*	*Feeding time minutes*
1.	Guazuma ulmifolia	201	11.8	13
2.	Cordia dentata	197	11.6	107
3.	Gliricidia sepium	149	8.8	336
4.	Lonchocarpus minimiflorus	97	5.7	725
5.	Eugenis salamensis	75	4.4	167
6.	Anacardium excelsum	68	4.0	2112
7.	Hymenaea courbarill	64	3.8	139
8.	Luehea candida	54	3.2	423
9.	Cordia alliodora	42	2.5	23
10.	Tabebuia rosea	34	2.0	115
11.	Tabebuia neochrysantha	32	1.9	240
12.	Spondias purpurea	31	1.8	112
13.	Cochlospermum vitifolium	30	1.8	16
14.	Licania arborea	29	1.7	1832
15.	Andira inermis	28	1.6	3077
	Totals	1131	66.6	9437

Table 5.—The 15 top resource tree species ranked by the amount of total time spent feeding in each species. The rank of each species by number present in the study site also is given.

Rank	*Species*	*Feeding time min.*	*Percentage of total feeding time*	*Rank by number present*
1.	Andira inermis	3077	11.6	15th
2.	Pithecolobium saman	2566	9.7	29th
3.	Anacardium excelsum	2112	8.0	6th
4.	Pithecolobium longifolium	1945	7.3	26th
5.	Licania arborea	1832	6.9	14th
6.	Manilkara achras	1584	6.0	34th
7.	Astronium graveolens	1379	5.2	23rd
8.	Pterocarpus hayesii	1203	4.5	48th
9.	Muntingia calabura	967	3.6	32th
10.	Ficus glabrata	910	3.4	55th
11.	Spondias mombin	814	3.1	21st
12.	Lonchocarpus minimiflorus	725	2.7	4th
13.	Burera simaruba	692	2.6	22nd
14.	Mastichodendron tempisque	523	2.0	40th
15.	Spondias nigrescens	434	1.6	30th
	Totals	20763	78.2	

were never eaten from these tree species. In fact, when the leaves reached a certain stage of development, signaled to me by a color change, the howlers stopped feeding from those tree species until new leaves were again produced.

Mature leaves of 24 species were eaten, but the quantity eaten from many of these species was very small. Relatively larger amounts of mature leaves, based on feeding time, were taken from *Bursera simaruba*, *Pithecolobium saman*, *Trichilia cuneata*, and *Myrospermum frutescens*.

On those occasions when Group 2 was observed in the study area, their feeding behavior was recorded. The feeding of a solitary young male and a solitary female were also noted. In all cases, these monkeys fed on the same kinds of food that Group 1 members ate. They utilized the same parts from the same trees as Group 1 used. Frequently, it appeared that they moved into the range expressly to utilize a particular food item such as the fruit of *Spondias mombin*, the new leaves of *Pithecolobium longifolium*, or the new leaves of *Andira inermis*.

Discussion

At first glance, the results reported here (i.e., a very small percentage of the available resources were used) seem to support the suggestion of other investigators that howlers have more food available than they could ever use (Carpenter, 1934; Altmann, 1959; Chivers, 1969). However, the resource utilization was not random as should be expected if all trees were equally valuable resources. In almost all cases, the resources selected were not the most abundant (Tables 4 and 5). Why did Group 1 avoid the leaves of almost all of the most common trees even though 63.6 percent of their feeding time was spent eating leaves? (See McKey, 1978, for similar results for another primate). On some days leaf-eating comprised as much as 99 percent of the feeding time. Group 1 demonstrated a high degree of selectivity between the parts of a tree, between individuals of a tree species, between tree species, and between tree families.

It might be argued that these feeding patterns are simply adventitious or fortuitous and once established have remained fixed in the group. If that were the case, then another group inhabiting an area with the same or similar tree composition should not have the same feeding pattern. As was mentioned above, when Group 2 came into the study area they utilized the same tree families, tree species, and tree parts for food. The duplication of food resources even went so far as the use of exactly the same 3 individual trees (widely separated) of *Gliricidia sepium* for mature leaves.

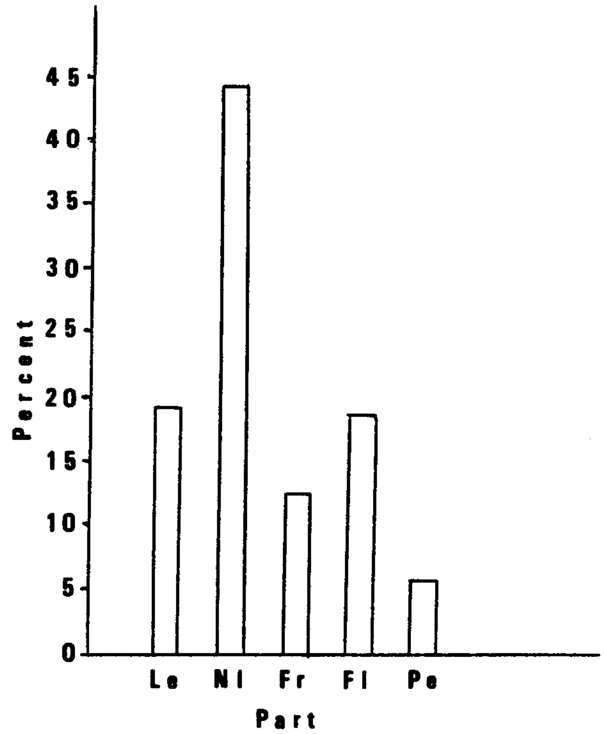

Figure 4. Diet composition. Based on the number of minutes spent feeding on each tree part. Results given as percent of total daily feeding time. Le = mature leaves; Nl = new leaves; Fr = fruit; Fl = flowers; Pe = petioles and pulvinus.

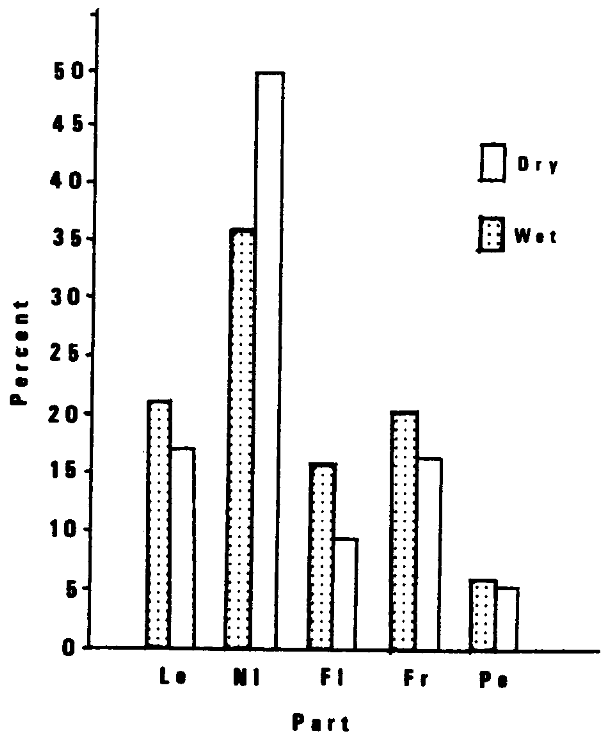

Figure 5. A comparison of wet-season and dry-season diet based on feeding time. Symbols and method of reporting results are the same as Figure 4.

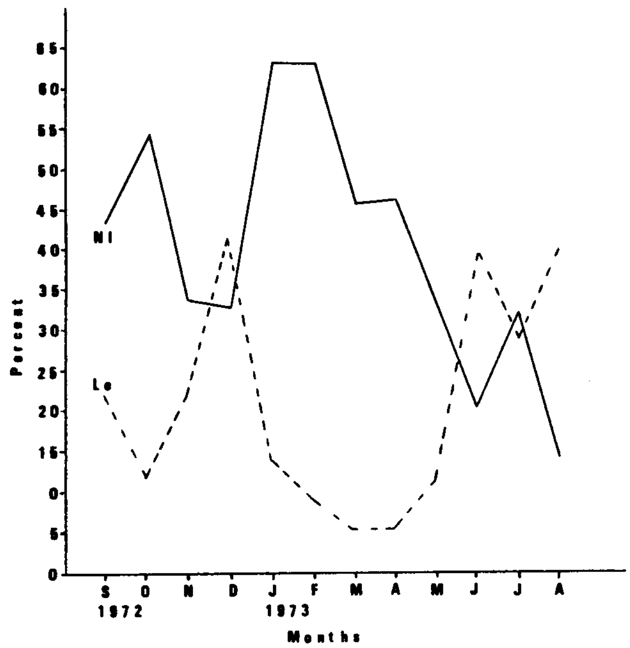

Figure 6. A monthly comparison of the percent of feeding time spent ingesting mature leaves and new leaves.

Another explanation for the selectivity demonstrated by Group 1 might be based on nutrition; however, as described below, plant secondary compounds may bind the nutrients. Even if they do not interfere with nutrition in this manner, secondary compounds are ubiquitous and must be dealt with by folivores.

I propose that the high degree of resource selectivity demonstrated by Group 1 is in response to the presence of secondary compounds in their food. The results reported here support Janzen's (1973) suggestion that animals do not feed on all of the plants available in their habitat, but do feed as though the plant's secondary compounds occur in definite and predictable patterns.

Secondary compounds do not have to kill to serve their purpose. They may serve as repellants (unpalatable or toxic), attractants (attracting pollinators), phytoncides (protecting against bacteria and fungi), or allelopathics (inhibiting other plant growth) (Whittaker, 1970). The ubiquitous presence of secondary compounds, produced by the plants as a chemical defense against predators (Stahl, 1888; Dethier, 1954; Fraenkel, 1959; Ehrlich and Raven, 1965; Whittaker, 1970; Freeland and Janzen, 1974), present folivores with a nonuniform food supply (Dethier, 1970). To counteract this defense certain folivores have evolved the capability of detoxifying ingested toxins but not all toxins can be detoxified by any one species (Whittaker and Feeny, 1971).

Plant secondary compounds directly and indirectly affect what is available as food. These compounds can prevent the animals from realizing the full nutritional benefits of a plant by binding some of the available nutrients (Feeny, 1970). In response, the animal must ingest more of the food to derive the same nutritional benefits from a similar food without the secondary compounds. However, the increased consumption results in the increased ingestion of associated toxins placing a heavier load on the animal's detoxification system. Thus the preference of new leaves by Group 1 is highly adaptive since plants concentrate nutrients in young leaves and stems (Fraenkel, 1953) and trees may have evolved the strategy of concentrating their toxins in mature leaves, leaving the new leaves relatively free of toxins (McKey, 1974).

Similarly, a knowledge of some of the selection pressures operating on plants can help to explain howler feeding strategies. Many investigators comment on the "wasteful" feeding habits of howlers, especially when feeding in *Cecropia* spp. Upon close inspection, I found Group 1 was eating the new leaves and the long petioles of the mature leaves and dropping the mature leaf blades of *Cecropia peltata*. This method of feeding also was used for *Sterculia apetala* and *Anacardium excelsum* leaves. Usually, only one part of a plant contains the secondary compound (Sim, 1965). Since the leaf blade is subjected to predator pressure first, it seems reasonable to assume that the trees concentrate the toxins in the leaf blades with very little in the petioles or pulvinus. As Freeland and Janzen (1974) suggest, herbivores should preferentially select that plant part with the least amount of toxin. The howlers are eating the petioles and new leaves, the parts with little or no toxins, and dropping the leaf blades, the part containing the concentrated toxins.

A similar feeding behavior was observed when the howlers fed on the fruit of *A. excelsum* and the pulvinus of *Spondias mombin* and *S. nigrescens*. An awareness of the location of the toxins can help to explain this feeding strategy. The howlers picked the *A. excelsum* fruit, but ate only the pedicel, a fleshy appendage which attaches the fruit to the tree. The fruit was dropped intact. The rind around the fruit of the closely related *A. occidentale* contains a poisonous oil: cardol oil (Little and Wadsworth, 1964), but the greatly enlarged pedicel is eaten by many humans (personal observation). Anacardiaceae is the poison ivy family. *S. mombin* and *S. nigrescens* are members of the family Anacardiaceae. The dropping of large amounts of *S. mombin* and *S. nigrescens* leaves occurs because the howlers ate only the pulvinus, the enlarged node at the base of the petiole.

These examples of dropping what appears to be food should be evaluated carefully in terms of feeding strategies. I do not consider this to be wasteful or careless feeding by the howlers. Rather, these are examples of highly selective feeding: a behavioral adaptation to counteract the tree's defensive strategy. From a cost-benefit point of view, the howlers may be maximizing their nutritional benefits while minimizing the amount of toxins being ingested. Ingestion of large amounts of toxins or certain toxins could be physiologically debilitating if not fatal. A physiological adaptation to the presence of these chemicals may be to reduce basal rates, thereby decreasing the intake of toxic substances (McNab, 1978). In terms of an energy budget, the functioning of a detoxification mechanism requires energy and specific nutrients at the expense of an animal's normal synthetic and maintenance processes (Williams, 1959).

Basically there are 2 feeding strategies that can be adapted by herbivores faced with the problems of secondary compounds, i.e., become a specialist (restricted diet) and feed on only one or two food species or become a generalist (broad diet) and feed on a wide variety of plant species (Cody, 1974). Cody further concludes that high resource abundance or renewal rate is favorable for specialists while a mixture of similar resources would favor a generalist. In terms of herbivory, a high resource abundance provides the specialist with a plentiful food supply. Howlers cannot be classified as specialists because, as pointed out by my data the home range of Group 1 does not contain the resource trees in sufficient density to permit adapting the strategy of a specialist. Not only are there not enough individuals of any 1 food species present in the home range, but the added factors of seasonality and secondary compounds further limit resource availability. Preferred food items such as new leaves are short-term occurrences. And, as the feeding behavior of Group 1 suggests, the diet must be diversified due to limited amounts of toxins which can be detoxified at any 1 time.

A specialist need only detoxify 1, or at most only a few toxins, thus diverting less energy and nutrients than the generalist who ingests a wide variety of toxic compounds. Even with a detoxification system, herbivores are limited in the amount of any food item they can safely ingest. The amount ingested is controlled by the concentration of the toxins in the food item and the quantity of that toxin the system is capable of processing.

The content and concentration of toxins present in a plant varies with environmental conditions. There are marked fluctuations of alkaloid content during the growing season as well as a circadian fluctuation (Huges and Genest, 1973). Many secondary compounds are increased when the plant is in full sunlight (Swain, 1972). Alkaloids are higher in actively growing tissue while slow growth enhances concentrations of hydrocyanic acid (Huges and Genest, 1973; Willaman and West, 1916). Also, geographical variations, edaphic conditions, and climatic factors affect secondary compounds (Swain, 1972).

Rainfall had little effect on the howler's activity, except during heavy downpours when they were inactive. In terms of food availability, however, rainfall is extremely important. As with most tropical forests, the distribution and not the amount of rainfall is the critical factor. Rainfall, in one way or another, appears to provide the trees with a cue as to when to begin leaf-drop, flower production, or new leaf production. A majority of the flower and new leaf production occurred during the dry season. There was almost no new leaf production during the wet season. As a result, there was more productivity, in terms of preferred food, during the dry season than during the wet season. Thus, even though the wet season appears to be a time of food abundance, it may actually be a time of stress since most of what is available are mature leaves, a tree part with large amounts of toxins. As pointed out, the consumption of mature leaves went down dramatically whenever new leaves were available (Figure 6).

The seasonal difference in average-day ranges can be explained in terms of food dispersion and toxin content. The consumption of new leaves (with little or no secondary compounds) does not require the animals to move very far (dry season). Most of the daily food intake can be obtained from one part of their home range, individual trees of *Pithecolobium longifolium* and *Andira inermis* on one side of the river had synchronous production of new leaves. Additionally, more flowers appear in the dry season and provide a localized resource. The consumption of mature leaves (with high toxin content) requires ingesting a small amount of leaves from many different tree species or several different trees of the same species which are widely dispersed (wet season). Also, fruit ingestion is high during the wet season and contributes to the increased day range since many tree species ripen only a few fruit each day. To harvest these, the howlers must travel greater distances.

The home range of any group of forest primate contains many trees, but, because of high tree-species diversity and low conspecific density, there may be very few individual trees of any one tree species available to the animals. Even though there may be several trees of a species present, utilization of all individuals may not occur because of different levels of toxin content within a tree species. This may help to explain why Group I moved through individuals of a species without feeding to feed in other members of the same tree species, e.g., they fed on mature leaves of only the same three *Gliricidia sepium* trees. [The mature leaves and fruit of *G. sepium* are crushed in water and used as an effective rat poison (Little and Wadsworth, 1964; Altschul, 1973)]. In some instances, the distance covered between feeding bouts in individuals of the same tree species exceeded 600 m, but there were individuals of that species much closer.

Any investigation of primate feeding behavior, especially folivorous primates, must consider the impact of plant produced secondary compounds. A few comparative studies of howlers and studies of other primate species have been done or are now in process (see McKey, 1978; Milton, 1978; and Rudran, 1978) but much work remains to be accomplished. Of immediate concern should be the biochemical and nutritional analysis of the food eaten by the animals. Equally important is the biochemical and nutritional analysis of the resources available but not consumed. Also needed are studies of the digestive mechanism of these leaf-eating monkeys.

These kinds of studies and continued quantitative investigations of free-ranging primates may provide an insight into the coevolutionary race between the predator (folivores such as howlers) and the prey (trees). The prey may react to predation by developing new secondary compounds or slightly altering old ones. The predator must either change to other resources or develop approximate detoxification mechanisms. That this is a dynamic system is of critical importance in the evaluation of the relationship between primate social structure and the environment.

Summary

Quantitative data collected during a 14-month field study of mantled howling monkeys (*Alouatta palliata* Gray) in Costa Rica indicates that the study group fed as though plant secondary compounds occur in a predictable manner. The study site was 9.9 ha of riparian forest containing 1699 trees over 4 m tall. The 13-member study group utilized 331 different trees, 51 vines, and the mistletoe in 2 trees. They spent 75.7 percent of their feeding time in only 88 trees and demonstrated a high degree of selectivity within and between tree species. Their daily diet consisted of 19.4 percent mature leaves, 44.2 percent new leaves, 12.5 percent fruit, 18.2 percent flowers, and 5.7 percent petioles and pulvinus.

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