

## Fruit Eating and Seed Dispersal by Howling Monkeys (*Alouatta palliata*) in the Tropical Rain Forest of Los Tuxtlas, Mexico

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The frugivory and ranging habits of howling monkeys living in the rain forest of Los Tuxtlas, Veracruz, Mexico, were studied for 5 consecutive years with the aim of investigating the role of seed dispersal agents played by the howling monkeys. The howling monkeys' consumption of fruit occupied half of their feeding time, and 80% of this time was spent feeding on mature fruit. Observations confirmed use of 19 tree species and a preference for a few species of Moraceae and Lauraceae. Fruit exploitation was very seasonal; only two species provided fruit year-round. Home range size was about 60 ha, and animals in the troop ( $N = 16$ ) showed a day range of 10-893 m. Monthly collection of fecal samples during 2 years indicated that 90% of the seeds ( $N = 7,928$ ) in the samples belonged to eight tree species and to one liana; the rest belonged to 15 unidentified species of vines. Germination success for the seeds in the feces was about 60% and for control seeds was 35%. Howling monkeys created diverse seed shadows in the vicinity of their leaf and fruit sources, and while they dispersed the seeds of some plant species, they also produced a great deal of fruit and seed waste for others.

**Key words:** howling monkeys; *Alouatta palliata*; seed dispersal; rain forest; Veracruz, Mexico

### INTRODUCTION

Most tropical tree species rely on animals as seed dispersal agents [Frankie et al, 1974; Howe, 1980]. Many factors interact to determine the density and dispersion patterns of plant populations; and frugivory, with associated seed dispersal by animals, is an important element in this process. The interactions between frugivores and plants are of particular value for understanding the dynamics of tropical rain forests, because seed and seedling mortality in various species is affected by density dependent factors in the vicinity of the parent tree [Janzen, 1969, 1970]. In

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addition, it has been reported recently that tropical frugivores play an important role in secondary succession and in maintaining the compositional heterogeneity of tropical forests [Fleming & Heithaus, 1981; Howe & Vande Kerckhove, 1979; McKey, 1975; Hartshorn, 1980].

The quantitative studies on seed dispersal in rain forest ecosystems have concentrated on frugivorous birds and bats [eg, Snow, 1971; Morton, 1973; Howe & Estabrook, 1977; McDiarmid et al, 1977; Cruz, 1980; Fleming & Heithaus, 1981; August, 1981; Morrison, 1980]. Many primates use fruit as an important element in their yearly diet, and troops range over variable distances; but, with a few exceptions [Hladik & Hladik, 1969; Lieberman et al, 1979; Cant, 1979; Howe, 1980; Muskin & Fischgrund, 1981; Mittermeir & van Roosmalen, 1981], studies of frugivory in primates have viewed the process of fruit eating as feeding behavior per se and not as a process involving the dispersal of seeds.

One of the most ubiquitous arboreal mammals in the Neotropical rain forest is the howling monkey. This primate, one of the largest arboreal mammals, lives in small permanent social groups and has a diet consisting primarily of leaves and fruit. Depending on locale, the howling monkey's diet may be dominated by leaves [Glander, 1975] or equal proportions of leaves and fruit [Milton, 1980; Estrada, 1983].

In the area of Los Tuxtlas, Veracruz, Mexico, we made observations during 5 consecutive years (1978-1982) of howling monkeys' fruit-eating habits. Specifically, we attempted to determine 1) fruit-eating preferences; 2) the diversity of the fruit diet; and 3) dispersal of the seeds of the tree species they exploit as fruit sources.

## METHODS

### Subjects and Observations

Direct field observations on the feeding behavior of a troop of howling monkeys (*Alouatta palliata*) consisting of 16 animals were carried out monthly for 5 years starting in September 1977. The feeding and ranging behavior of the howling monkeys was sampled an average of 12 days (range 10-15) per month, and the samples were distributed from 0600-1900 hr. The time spent feeding on various plant parts was recorded and measured with the aid of a wrist chronometer, and data were tape-recorded in the field. Randomized focal animal sampling was the observation technique employed [Altmann, 1974].

Home range was determined following the procedure described in Estrada [1982, 1983]. The distances travelled by the monkeys between food sources were measured with the aid of a pedometer attached to the observer's waist, and the readings were checked against daily tracings on maps. Since the quadrats into which the troop's home range was divided contained clusters of trees used by the howling monkeys, these were considered as equivalent to food patches in which food availability varied in time. With the data available from 1978-1982, an attempt was made to measure the recurrent use of food patches and of tree species by the monkeys year to year.

### Study Site

Research was carried out at the Estación de Biología "Los Tuxtlas," longitude 95° 04' W, latitude 18° 34' N, located in the eastern portion of the Sierra de Los Tuxtlas range, an area of volcanic origin dominated by the San Martin Volcano in the southern portion of the Mexican state of Veracruz. The reserve covers an area of 700 ha, which connects with 10,000 ha of rain forest extending toward and around the San Martin Volcano. The dominant vegetation type is the high evergreen rain forest [Miranda & Hernandez, 1963].

The climate of the area is hot and humid with a mean annual temperature of 27°C (range 17–29°C). Although it rains throughout the year, there is a "wet season" ( $\bar{X} = 486.25 \pm 87.0$  mm) from June to February and a "dry season" ( $\bar{X} = 111.70 \pm 11.7$  mm) from March to May; mean annual precipitation is 4,900 mm ( $N = 10$  years) [for further details see Estrada, 1982, 1983].

### Plant Resources

During our field observations, every tree used by *Alouatta* as a food source was marked, mapped, and identified. Trees belonging to the genus *Ficus* were grouped under *Ficus* spp. due to lack of adequate taxonomic information. Trees were located on a scale map (1:7,000), and a grid with quadrats 1 ha in size each was superimposed on it. Maps of each quadrat with details were made to obtain a more precise location of each tree and of the monkeys' movements within their home range.

The abundance of the tree species used by the animals of the focal troop was calculated by censusing all trees  $\geq 10$  m in height in three 1-ha belt transects (20  $\times$  500 m).

### Fecal Samples

Between January 1980 and January 1982, samples of the monkeys' feces were collected from the forest floor and/or from the vegetation during each of the monthly sampling periods. The samples were examined under a microscope, and the seeds were counted, measured (length in millimeters), and most of them were identified. The seeds found in these samples were used in germination experiments. After January 1982, samples of feces were collected until December 1982. Some of these samples were used in germination experiments where the entire fecal specimen was planted. For all the fecal samples collected, a record was kept of the locality of the collection (ie, the tree used by the *Alouatta* when they defecated).

### Seed Germination Experiments

The seeds recovered intact from the feces were planted in plastic pots filled with forest soil. These pots were placed on a table, covered by a roof, at the forest edge and were watered daily. The number of seeds planted per pot ranged from 1–30 depending upon the seed size. Seeds of five Moraceae species were also separated from ripe fruits retrieved from the forest floor. These seeds were used as controls, planted under the same physical and light conditions as the defecated seeds.

In some cases the monkeys only removed the pulp from the fruit and dropped the seeds under the parent tree; germination of one such species was studied using, respectively, seeds handled by *Alouatta* and seeds without the pulp removed.

In a third experiment, entire fecal specimens from the samples collected between February and December 1982, with the seeds untouched, were planted under the same conditions. Weekly censuses were conducted to record germinations, and the seeds remaining in each pot were counted at the end of each experiment.

### Seed and Seedling Mortality of Selected Tree Species

Seed density, seed mortality, and seedling density and mortality under the shadow of the tree's crown were measured in two tree species in the monkey's fruit diet: *Brosimum alicastrum* and *Pseudolmedia oxyphyllaria*. These species were selected because 1) they produced fruits with one relatively large seed (10–20 mm) that allowed repeated censuses (something practically impossible to do with the seeds of *Ficus* spp. and of *Cecropia obtusifolia* that produced fruits with hundreds of small ( $\leq 1.0$  mm) seeds), and 2) they represented two of the most important tree species in the *Alouatta* fruit diet.

Five fruiting trees of each of these two species were selected at the beginning of the fruiting season. These trees were selected because they had been used by the howling monkeys as a source of fruit. Three plots of 1 m<sup>2</sup> each were randomly located under the crown of each tree. Fifteen square meters were censused monthly for each species. The censuses lasted 8 consecutive months, and in each 1-m<sup>2</sup> plot the number of seeds and of emerging seedlings were counted.

## RESULTS

### Plant Species Used

The howling monkeys used 19 tree species of the middle and upper levels of the forest as a source of fruit (Table I). Only two were secondary growth species (*Cecropia obtusifolia* and *Spondias mombin*). *Alouatta* spent 80% of their feeding time on mature rather than green fruit.

When the 19 species were ranked by the percentage of time they spent feeding on each species, it was found that five species accounted for 90% of fruit eating (Table I). These species belong to two families, Moraceae and Lauraceae. The Moraceae was the most important family for fruit; it was represented by five species (all of whose seeds were ingested), which accounted for 83% of the howling monkeys' feeding time on fruit, while the Lauraceae with one species accounted for 9%. However, seeds of *Nectandra ambigens* were never ingested.

The seeds recovered from the feces indicated that the howling monkeys used 15 additional plant species as a source of fruit. The majority, however, were vines and lianas, and the number of seeds representing them contributed to only 5% of the total number of seeds (N = 7,928) found in the fecal samples between January 1980 and January 1982.

TABLE I. Tree Species Used by the Howling Monkeys as Sources of Fruit Ranked in Order of Importance in Their Diet (% of Feeding Time)

Species	Family	Percentage of feeding time (Ft)	No. of months used (per year)	Relative density (Rd) (i/ha)	Selectivity index (Ft/Rd)	Seed size mm X (length)
<i>Ficus</i> spp. (N = 3)	Moraceae	49.23	12	1.4	34.18	1.5
<i>Poulsenia armata</i>	Moraceae	12.50	7	4.0	2.26	8.0
<i>Brosimum alicastrum</i>	Moraceae	10.10	3	4.0	3.13	17.5
<i>Nectandra ambigens</i>	Lauraceae	9.05	7	18.0	0.56	21.5
<i>Cecropia obtusifolia</i>	Moraceae	8.65	12	8.0	2.88	1.5
<i>Pseudolmedia oxyphyllaria</i>	Moraceae	2.85	2	15.0	0.19	10.9
<i>Cordia</i> sp.	Boraginaceae	1.95	5	1.0	1.95	5.0
<i>Dialium guianense</i>	Leguminosae	1.73	4	1.4	1.23	5.0
<i>Ampelocera hottlei</i>	Ulmaceae	1.48	2	3.2	0.46	—
<i>Spondias mombin</i>	Anacardiaceae	0.59	2	4.6	0.12	15.0
<i>Dipholis minutiflora</i>	Sapotaceae	0.45	1	0.3	1.50	15.0
"Olo zapote"		0.42	1	—	—	40.0
<i>Pouteria campechiana</i>	Sapotaceae	0.25	1	1.0	0.25	30.0
<i>Belotia mexicana</i>	Tiliaceae	0.20	1	1.0	0.18	2.0
<i>Guarea chichon</i>	Meliaceae	0.12	2	2.1	5.58	10.0
<i>Manilkara sapota</i>	Sapotaceae	0.12	1	—	—	20.0
<i>Bursera simaruba</i>	Burseraceae	0.12	1	0.3	0.34	8.0

### Seasonality in the Use of Fruit Sources

Only the species of the genera *Ficus* and *Cecropia* were used in every month of the year by the howling monkeys (Table I); four other species were used for  $\geq 4 \leq 7$  months of the year indicating seasonality in 90% of the plant species used as a source of fruit. The number of species used per month ranged from 2–10 ( $\bar{X} = 5.3 \pm 3.0$ ), and the number of months each was used ranged from 1–12.

While overall dietary diversity ( $H'$ ) measured by Shannon's function [Pielou, 1977] was 1.77, the intramonthly dietary diversity ranged from 0.69–2.20. The markedly higher value of  $H'$  for the period April–August (Fig. 1) stresses the marked seasonality in fruit eating.

An index of dietary overlap between months was calculated using the coefficient of community "CC" [Pielou, 1975; Fleming, 1979], which ranges from 0 to 1.0 indicating null to 100% overlap. The monthly index for *Alouatta* preferences ranged from 0.50–1.0, with the least variation found in the period April–August (Fig. 1), which coincided with the time when fruit consumption of the Moraceae species was the most important feeding activity in the howling monkeys.

### Home Range and Ranging Patterns

The size of the home range of the troop was estimated at ca 60 ha [Estrada, 1983]. The ranging patterns of the *Alouatta* within their home range were strongly influenced by the availability, search, and exploitation of fruit (especially mature fruit). For example, a significant correlation was found between food patch (quadrat 1 ha in size), diversity ( $H'$ ), and time spent feeding on fruit ( $r_s = 0.56$ ,  $P < .05$ ;  $N = 12$ ), and between the total number of trees marked ( $N = 500$ ) per species between

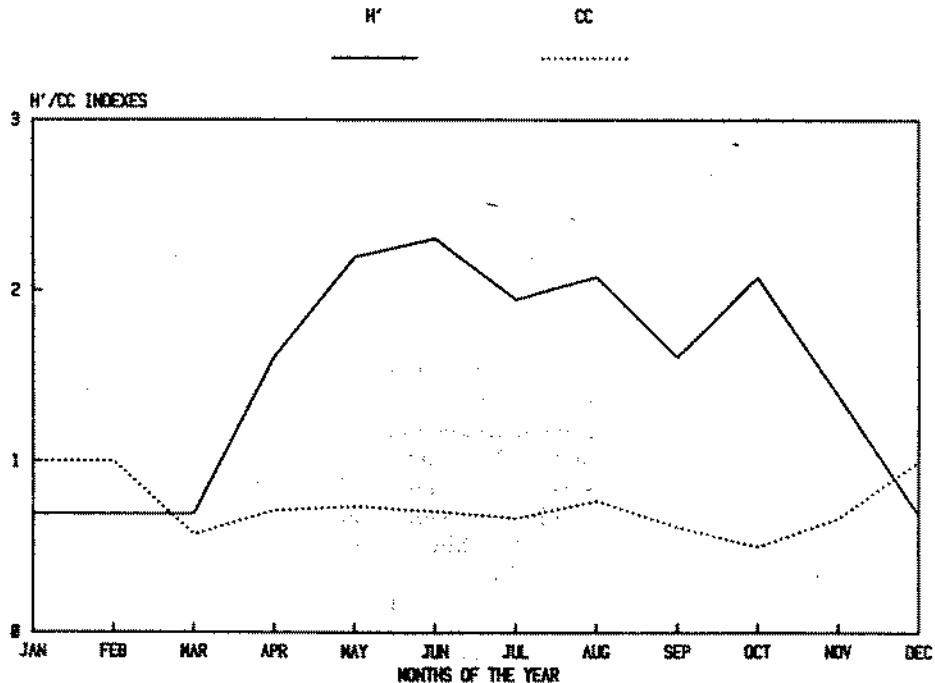


Fig. 1. Dietary diversity ( $H'$ ) and dietary overlap (CC) over the months of the year in the fruit diet of howling monkeys.

1978–1981 and percentage of time feeding on fruit ( $r_s = 0.76$ ,  $P < .005$ ), indicating that, over time, the addition of quadrats used and of trees exploited was intimately linked to the monkeys' search for fruiting trees. The data from the vegetation census indicated that localized exploitation of fruiting trees was usual; 90% of the tree species *Alouatta* used occurred at densities of 4.0 or less individuals per hectare. A tree species selectivity index (which weighs the relative density and relative utilization of the tree species by the monkeys) indicated a marked selection (values  $> 1.0$ ) for the most important species in their fruit diet (Table I). This preference was especially biased toward trees of *Ficus* spp. The howling monkeys responded to the spatial and temporal distribution of their sources of fruit by travelling distances that varied from day to day and that ranged from 10–893 m ( $\bar{X} = 147.80$ ;  $N = 650$  instances of travel scored).

### Year to Year Consistency in Use of Tree Species and Food Patches

When we examine the howling monkeys' preferences during the major fruit-eating season, we find a strong similarity ( $0.43 \leq CC \leq 1.0$ ) in each month from year to year (1972–1982) (Estrada, unpublished data). The mean overlap obtained for only the Moraceae species was  $0.87 \pm 0.09$ ,  $0.75 \leq CC \leq 1.0$ , while the remainder of the species showed a mean of 0.18 ( $SD \pm 0.28$ ,  $0 \leq CC \leq 0.67$ ).

The data on the ranging patterns of the *Alouatta* showed that the similarity (CC) in the use of particular food patches (quadrats 1 ha in size each) in specific areas within their home range ranged from 0 (August 1978 vs August 1979) to 0.86. The null overlap between August 1978 and August 1979 is due to the fact that the *Alouatta* used some patches 1 month earlier in 1979 as a result of an earlier production of fruit by the trees of some species.

### Seed Germination Experiments

From the fecal samples ( $N = 250$ ) collected between January 1980 and January 1982, 7,928 intact seeds were recovered and planted. Seed size ranged from  $< 1.0$  to 35.5 mm ( $\bar{X} = 8.0$ ) for all species together. Fifty-seven percent of the seeds from the feces ( $N = 7,928$ ) germinated, while only 35% of the control seeds ( $N = 750$ ) germinated.

Ninety-five percent of the intact seeds in the feces belonged to nine species and 5% to a cluster of unidentified species (Table II). Germination success ranged, for all of the identified species, from 9% (*Dialium quianense*) to 100% (*Brosimum alicastrum* and *Guarea chichon*). For the unidentified species, germination success was 40%.

A comparison of the control versus the treatment seeds indicated that in all species tested, except *Brosimum alicastrum*, germination success was significantly higher for seeds passed through the monkeys' digestive tract (Table II).

In the case of the feces planted ( $N = 100$ ), 77% showed some germination, ranging from 50–100% of the seeds present in each of the samples. The seeds of the liana *Abuta panamensis* whose pulp had been removed by the howling monkeys displayed 80% germination ( $N = 52$ ), while those planted with the pulp intact achieved only 33% germination ( $N = 50$ ).

Germination velocity in the control and treatment seeds ranged from 24 to 81 days and from 18 to 67 days, respectively. When the number of days to germination is considered in the case of the most important plant species in the *Alouatta* diet for the treatment and control seeds, we found in three species no significant differences (Table II). In the others there was a significant difference that ranged from less time (*Poulsenia armata*) to more time (*Cecropia obtusifolia*) to germination.

TABLE II. Results of the Germination Experiments in Seeds Ingested by the Howling Monkeys and in Control Seeds

Species	Percentage of seed germination from feces	(N)	Germination		Treatment Control		P
			control (%)	(N)	(days)	(days)	
<i>Ficus</i> spp.	60.1	(4,800)*	18.3	(200)	36	34	NS
<i>Cecropia obtusifolia</i>	57.6	(2,334)*	0.5	(200)	37	28	0.05
<i>Poulsenia armata</i>	22.0	( 100)*	0	(100)	66	—	0.05
<i>Pseudolmedia oxyphyllaria</i>	60.6	( 80)*	30.3	(100)	67	81	NS
<i>Dialium guianense</i>	9.0	( 30)	NA	—	78	—	—
<i>Brosimum alicastrum</i>	100.0	( 80)	94.5	(100)	18	24	NS
<i>Guarea chichon</i>	100.0	( 30)	NA	—	43	—	—
<i>Abuta panamensis</i>	80.8 <sup>a</sup>	( 52)*	33.3 <sup>b</sup>	( 50)	39	67	0.05
"Frijol negro"	39.0	( 57)	NA	—	20	—	—
"Unidentified"	40.3	( 365)	NA	—	—	—	—
Total X	56.9	(7,928)	35%	(750)			

\*Seeds dropped, not defecated.

<sup>b</sup>Pulp not removed.

\*Difference from control significant at  $P = 0.01$  or better.

NA, Control seeds not available; NS, not significant.

### Seed and Seedling Mortality Under the Parent Tree

The results of the census of the seeds and of emerging seedlings of the trees of *Brosimum alicastrum* and *Pseudolmedia oxyphyllaria* indicated, in general, that for both species there is a high mortality over time of seeds and seedlings under the crown of the parent tree (Fig. 2). In the case of *Pseudolmedia oxyphyllaria*, the censuses indicated that of a combined crop of 2,262 seeds recorded in the 15 m<sup>2</sup>-plots, only 4% ( $N = 98$ ) passed to the seedling stage; of these, only 16% ( $N = 16$ ) remained alive at the end of the eighth census. Of the remaining seeds ( $N = 2,164$ ), by the sixth census all had disappeared or were destroyed in situ by fungi and invertebrate predators (Fig. 2).

In the case of *Brosimum alicastrum*, while of a combined crop of 1,895 seeds where 63% passed to the seedling stage, at the end of the seventh census only 6% of the seedlings remained in the plots. Of the remaining seeds ( $N = 703$ ), at the end of the seventh census none remained (Fig. 2).

### Food Passage Rates and Distance Seeds Were Transported

Food passage rates were measured in two captive howling monkeys (male/female) using a mixed diet of figs and *Cecropia obtusifolia* to which an artificial colorant was added. The mixed leaf-fruit diet replicated their daily diet, which consists of leaves and fruits in varying proportions [Estrada, 1983; Milton, 1980]. Time of first appearance of colorant material in fecal matter ranged from 15–22 hr ( $\bar{X} = 18$  hr) [see Milton et al, 1980, for similar findings in Central America].

Since the howling monkeys of the study troop moved at least twice a day, early in the morning (0500–0900) and late in the afternoon (1700–1800), the distances they travelled after eating fruit could then be considered the distances they transported the seeds.

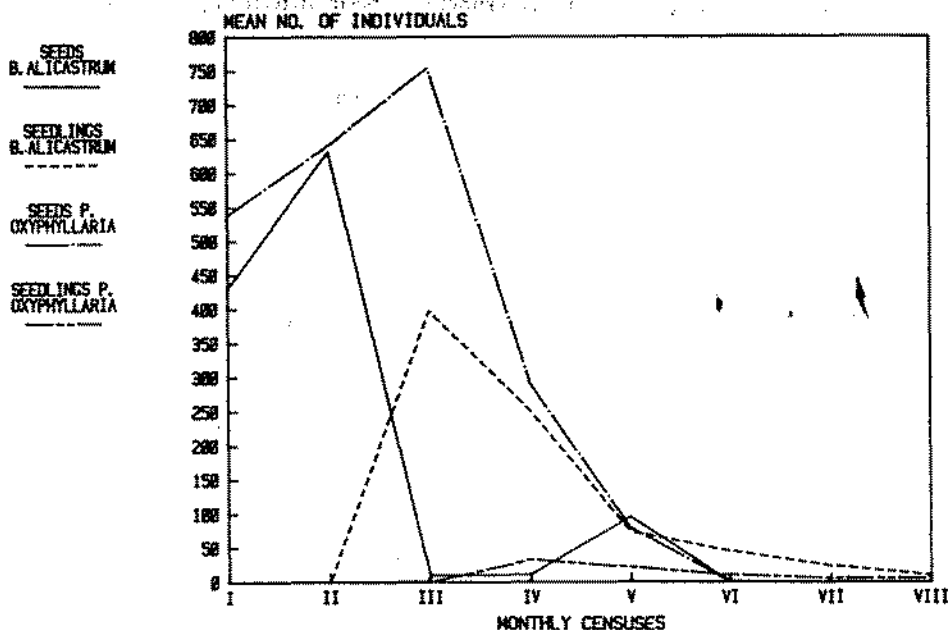


Fig. 2. Survival of seeds and seedlings of *Brosimum alicastrum* and *Pseudolmedia oxyphyllaria* under the crown of the parent tree. The total area sampled was 15 m<sup>2</sup> per species (5 trees per species).

While the distance travelled after eating fruit varied from 10–914 m for all species ( $\bar{X} = 214.47$  m;  $N = 650$ ), for those species whose seeds are in fact dispersed by the howling monkeys (ie, the five Moraceae), the distances ranged from 10–811 m (Table III). The smallest distances were obtained for the pioneer species *Cecropia obtusifolia* and the maximum in the range for *Poulsenia armata*. The figs, *Brosimum alicastrum*, and *Poulsenia armata* had similar average dispersal distances. However, the seeds of *Pseudolmedia oxyphyllaria* had the largest mean dispersal distances (Table III).

#### Seed Load Diversity

The number of fecal samples deposited per tree species ranged from 1–65 ( $\bar{X} = 16.5$ ). The number of species represented in each ranged from 1–11 ( $\bar{X} = 4.53$ ), and seed load diversity ( $H'$ ) ranged from 0–2.40 ( $\bar{X} = 1.24$ ) (Table III). In addition, data on all the fecal samples collected ( $N = 314$ ) between January 1978 and December 1982 show (Table IV) that the proportion of conspecific seeds deposited in the vicinity

TABLE III. Distances Seeds of Each Species Were Dispersed by the Howling Monkeys

Species	$\bar{X}$ (m)	SD	Min (m)	Max (m)	N
<i>Ficus</i> spp.	126.7	147.2	10	582.8	200
<i>Poulsenia armata</i>	102.4	177.9	12	811.2	100
<i>Brosimum alicastrum</i>	112.2	142.7	13	650.0	82
<i>Cecropia obtusifolia</i>	29.4	33.6	10	100.8	46
<i>Pseudolmedia oxyphyllaria</i>	186.9	113.2	30	320.0	20



of the trees in 79% of the cases ( $N = 19$  species) was 0 and in trees of only four species conspecific seeds were present in the feces but in very low proportions that ranged from 0.34 to 50% (Table IV) of the total number of seeds recovered in each case. That is, in very few cases were seeds deposited that corresponded to the identity of the trees where howling monkeys defecated; instead, the majority belonged to "foreign" species.

Some examples of the spatial distribution of trees of some of the most popular species in the howling monkeys' fruit diet and in the vicinity of which fecal samples were collected are shown in Figures 3 and 4, where it is very suggestive that the monkeys are contributing to the floristic heterogeneity of the forest.

## DISCUSSION

Our results showed that *Alouatta* displayed a marked preference for a particular group of plant species exploited for fruit. Among these species, those belonging to the Moraceae and Lauraceae plant families stand out both in the intensity with which they were used and in consistency of use year-to-year in the fruit-eating

TABLE IV. Parameters of Seed Loads (Feces) Deposited in the Vicinity of Trees of 21 Species by the Howling Monkeys

Species	No. of trees <sup>a</sup>	No. and type of species <sup>b</sup>	Percentage of seeds of same species	(N)	No. of fecal samples collected	Species diversity H'
<i>Ficus</i> spp.	10	10 (Ps, Ap, F, P, C, 15, 11, Fn, 4, 13)	53	( 2,347)	46	2.30
<i>Nectandra ambigens</i>	11	9 (F, P, 3, Ap, 15, 9, Ps, C, 4)	0	( 1,480)	40	2.20
<i>Poulsenia armata</i>	7	10 (Ap, Fn, 11, 1, P, F, Ps, 8, 6, C)	34	( 4,087)	42	2.30
<i>Brosimum alicastrum</i>	13	11 (B, F, P, C, 8, 9, Fn, Ps, D, 10, 15)	17	( 4,236)	65	2.40
<i>Cordia</i> sp.	5	5 (C, F, B, P, 1)	0	( 1,153)	19	1.61
<i>Cecropia obtusifolia</i>	1	3 (C, F, 2)	34	( 59)	5	1.10
<i>Pseudolmedia oxyphyllaria</i>	1	1 (F)	0	( 320)	3	0
<i>Pterocarpus hayessi</i>	2	2 (Ps, 12)	0	( 6)	2	0.69
<i>Dipholtis minutiflora</i>	1	4 (F, C, G, 1)	0	( 734)	17	1.39
<i>Ampelocera hottlei</i>	2	6 (P, C, 14, Ap, F, 4)	0	( 175)	9	1.79
<i>Robinsonella mirandae</i>	2	3 (5, Fn, 11)	0	( 20)	6	1.10
<i>Ulmus mexicana</i>	1	3 (F, C, P)	0	( 1,736)	9	1.10
<i>Coccoloba barbadensis</i>	1	6 (Ap, F, 2, C, P, 7)	0	( 2,013)	21	1.79
<i>Sapium lateriflorum</i>	1	4 (F, Fn, F, 6)	0	( 24)	6	1.39
<i>Spondias mombin</i>	1	2 (F, Ap)	0	( 11)	1	0.69
<i>Manilkara sapota</i>	1	3 (9, P, 3)	0	( 68)	14	1.10
<i>Dendropanax arboreus</i>	1	1 (F)	0	( 500)	5	0
<i>Zanthoxylum hellermanni</i>	1	2 (F, 7)	0	( 431)	3	0.69
"Crespillo"	1	2 (C, F)	0	( 900)	1	0.69
Total	63			(20,300)	314	
Means		4.53			16.5	1.24

<sup>a</sup>Under which fecal samples were collected.

<sup>b</sup>Species in fecal samples: Ps, *Pseudolmedia oxyphyllaria*; Ap, *Abuta panamensis*; F, *Ficus* spp.; P, *Poulsenia armata*; C, *Cecropia obtusifolia*; Fn, "Frjfol negro"; B, *Brosimum alicastrum*; D, *Dialium guianense*; G, *Guarea chichon*. Numbers indicate seeds of unidentified species.

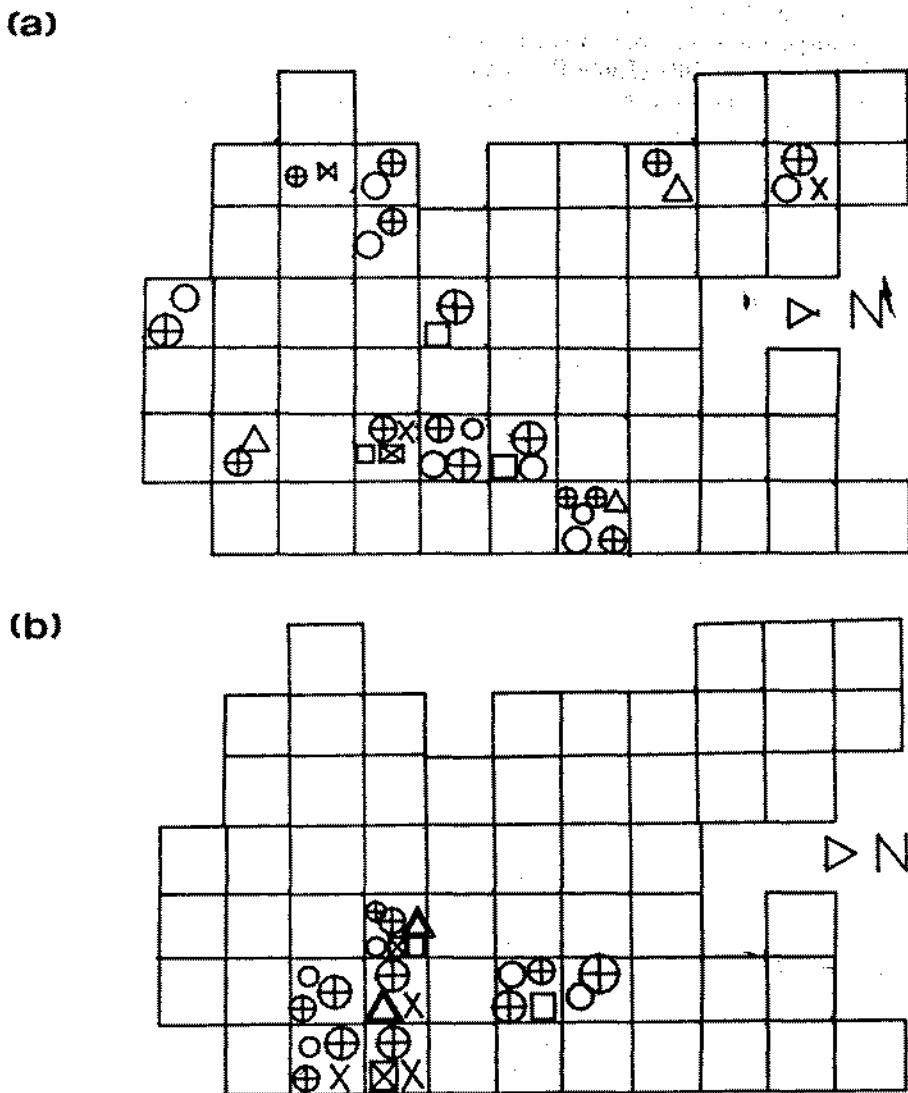


Fig. 3. a) Seeds of species defecated in the vicinity of trees of *Brosimum alicastrum* (⊕). The grid (quadrats 1 ha in size each) represents the howlers' home range (ca 60 ha). ○, *Ficus* spp.; △, *Poulsonia armata*; □, *Cecropia obtusifolia*; ⊗, *Pseudolmedia oxyphyllaria*; ⊗, *Dialium guianense*; △, *Abuta panamensis*; ×, "frijol negro". Note that not all of the species found in the fecal samples are included in these figures due to lack of space. b) Seeds of species defecated in the vicinity of trees of *Poulsonia armata*. Except for *Poulsonia armata* trees with the symbol (⊕) all other species indicated by symbols in a).

season (April–October). This indicates that these species very likely constitute *Alouatta*'s "primary" sources of fruit. With respect to the other species including the 15 unidentified species detected through the examination of the seeds in the fecal samples, the monkeys probably behaved more like opportunistic frugivores [sensu McKey, 1975], exploiting these species when they were encountered as the monkeys searched for their "primary" sources of fruit.

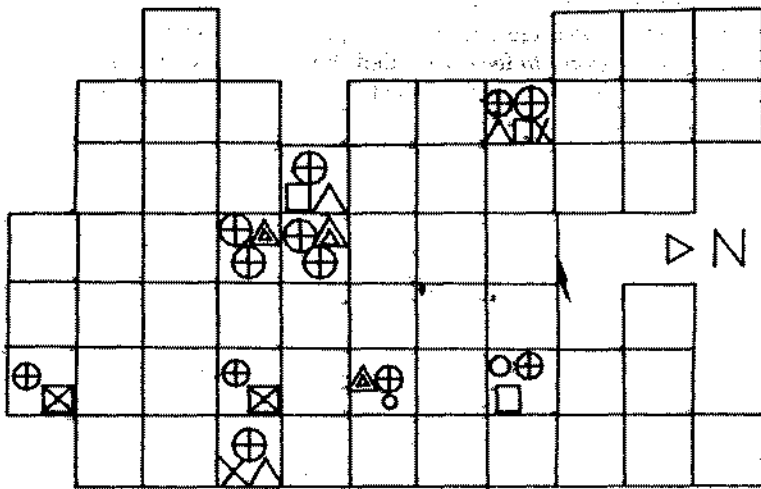


Fig. 4. Seeds of species defecated in the vicinity of trees of *Ficus* spp. Circles with cross and blank circles stand for *Ficus* trees. Rest of species see Figure 3 a) for key to symbols.

The fact that exploitation of the majority of the fruit sources by *Alouatta* is restricted to a few months in the year indicates the very seasonal nature of this type of food. This, plus the low relative densities of the tree species used, reflects the ability of howling monkeys to find individual trees of these species carrying fruit during the year and between years as suggested by the values of the dietary and foraging patch overlap indices.

A brief review of the fruiting strategies of tropical plants by Fleming [1979] indicated that fruit can occasionally be superabundant. At these times many species of frugivores can feed at the same tree, but the fruit is often produced at slow rates and in low quantities, a feature also observed in tree species at the study site. By selecting tree species that vary in relative density and in fruit producing strategies, *Alouatta* can face seasonality in fruit availability. For example, the species of the Moraceae used by the monkeys ranged in density, at the study site, from 1.33–13.67 individuals per hectare; and while some (eg, *Ficus* spp. and *Cecropia obtusifolia*) produced fruit year round, others (eg, *Poulsenia armata* and *Brosimum alicastrum*) were seasonal producers of fruit.

The possibility that *Alouatta* were seen using these species because our sampling took place in a highly productive year (as has been reported for the preference for *Tetragastis panamensis* by howling monkeys in Panama [Howe, 1980]) is not supported by our observations of howling monkey feeding behavior over 5 consecutive years and by the values of the overlap index. Instead, our data indicate that the use of these species is not occasional. The consistency over time of this selectivity at the species and individual tree level is an important aspect of the degree to which a frugivore can be a reliable dispersal agent for a particular group of plants [McKey, 1975; Howe & Estabrook, 1977].

### Survival of Ingested Seeds

The marked preference for mature fruit implies that mostly mature seeds are ingested by *Alouatta*. The germination experiments clearly showed that the monkeys did not harm many of the seeds they ingested. They ingested seeds of various

sizes representing several species, and in some cases germination velocity was apparently affected by passage through the primate's digestive tract. The microscopic examination of *Alouatta* feces revealed that the seeds were usually "trapped" in undigested fiber. The slow transit of food through their digestive tract suggested that the seeds were subjected to a long mechanical and chemical treatment that apparently was beneficial to seed survival and germination.

Experiments in Central America by Hladik & Hladik [1969] also indicated that passage through the howling monkey digestive tract produced faster germination in seeds of some tree species. Similar findings have been reported for birds [McDiarmid et al, 1977] ingesting the seeds of *Stemmadenia donnel-smithii* and *Caesaria corymbosa* [Howe, 1977; Howe & Vande Kerckhove, 1979] and for bats [Fleming & Heithaus, 1981] ingesting the seeds of *Cecropia peltata* and *Solanum hazenii*.

### Seed Dispersal and Seed Shadows

The physiological feature of the slow passage rate of food through the monkeys' digestive systems and the behavioral feature that they move daily over variable distances between leaf and fruit sources strongly suggest that the seeds ingested are likely to be deposited away from the parent tree, thus escaping high density dependent mortality, and reach a habitat suitable for germination and growth [Denslow, 1980]. This in turn suggests that *Alouatta* do not create dense seed shadows like some sedentary bird species do [Howe & Primack, 1975] when feeding at the tree. Instead, like the more mobile bats and mobile bird species, they contribute to the creation of large seed shadows for some species of tree.

Since howling monkeys feed on several sources of fruit per day or on consecutive days, they seem to bring a substantial number of "foreign" seeds to the vicinity of other fruit and leaf sources, a feature also reported for frugivorous birds, bats, and mammals in Central America [Fleming & Heithaus, 1981; Fleming, 1979; Smythe, 1970; Janzen et al, 1976; Howe & Primack, 1975; Howe & Estabrook, 1977], thus creating "diverse" seed shadows [sensu Fleming & Heithaus, 1981] around these trees.

### Mutual Benefits in the Interaction Between *Alouatta* and Plants

Howling monkeys at Los Tuxtlas are apparently acting as true dispersers for some tree species as they ingest the whole fruit and defecate the seeds in conditions suitable for germination. They also obtain a nutritious reward in the form of carbohydrates, lipids, some protein, and minerals as a consequence of ingesting the pulp. In this situation there is mutual benefit.

The selection of fruit by frugivores has been suggested to depend, as in the case of foliage-eating, not only on purely nutritional attributes [McKey, 1975; Howe & Estabrook, 1977] but also on specific taste preferences, presence and concentration of secondary compounds, and digestibility [Herrera, 1982]. It is possible that the selection of species whose fruits are consumed by *Alouatta* is probably closely related to finding the best match to their requirements favoring those plant species that produce the most nutritionally rewarding fruit.

There may be some disadvantages to howling monkeys due to the ingestion of nutritionally irrelevant seeds, as it occurs in frugivorous birds where additional ingested seeds represent undesirable ballast. However, our observations and the large size of *Alouatta* suggest the following assumptions reasonable: 1) the seeds ingested may not represent a significant part of the nutritionally irrelevant matter more importantly represented in their diet by the undigestible fiber of fruits and leaves [Milton, 1979]; 2) the additional ballast represented by the small seeds has no apparent effect on their movements; 3) they are capable of ingesting more fruit/

seeds in a single meal than a bird or a bat; 4) they have a slow food passage rate that ensures that the seeds undergo a treatment that our data indicate is beneficial for survival and germination; and 5) the seeds are deposited away from their source of origin. These features may make howling monkeys more "efficient" dispersal agents than the smaller volant vertebrates.

### Fruit Waste

While the howling monkeys are in effect dispersing the seeds of some species, in other cases the removal of the pulp without ingestion of the seed may have a positive

effect on seed survival and germination. Our data for *Brosimum alicastrum* and *Pseudolmedia oxyphyllaria* suggest, however, that the act of dropping the seed beneath the parent tree may not be enough to eliminate the density dependent factors affecting seed and seedling survival unless the seed is dispersed by terrestrial agents.

A great deal of fruit waste is caused by *Alouatta* for large seeded species and for others whose seeds they disperse. *Alouatta* is one of the largest arboreal mammals (mean weight = 7.5 kg) at Los Tuxtlas. Due to its movements while foraging in a particular tree crown laden with mature fruits, howling monkeys produce a "light" or a "heavy" rain of ripe fruit to the ground, therefore making fewer seeds available for dispersal not only by them but also by birds, bats, and other mammals that may

4. The exploitation of fruit is very seasonal, and the troop's home range was ca 60 ha. *Alouatta* travelled distances between fruit sources that ranged from 10–893 m.
5. Fifty-seven percent of the seeds recovered from the fecal samples germinated, while only 35% of the control seeds ( $N = 750$ ) germinated.
6. Food passage rate measured in two adult howling monkeys was 18 hr, and dispersal distances for seeds ranged 10–811 m.
7. Howling monkeys displayed a recurrent use of tree species and food patches year-to-year (1978–1982), indicating reliability of visitation at fruiting trees from season to season.
8. Seeds dispersed were deposited in the vicinity of trees of 21 tree species that howling monkeys used as sources of leaves and/or fruit, thus contributing to the surrounding floristic heterogeneity.
9. Assumptions about primates acting as seed dispersal agents should be supported with field data demonstrating seed viability after ingestion, animal movement away from the fruit source, and data on food passage rates.

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### REFERENCES

- Altmann, J. Observational study of behavior: Sampling methods. *BEHAVIOUR* 69:227–267, 1974.
- August, P.V. Fig fruit consumption and seed dispersal by *Artibeus jamaicensis* in the llanos of Venezuela. *BIOTROPICA* 13:70–76, 1981.
- Cant, J. Dispersal of *Stemmadenia donnell-smithii* by birds and monkeys. *BIOTROPICA* 11:122, 1979.
- Cruz, A. Bird activity and seed dispersal of a montane forest tree (*Dunalia arborescens*) in Jamaica. *BIOTROPICA* 13:34–44, 1981.
- Denslow, J.S. Gap partitioning among rain-forest tropical trees. *BIOTROPICA* 12:47–55, 1980.
- Estrada, A. Survey and census of howler monkeys *Alouatta palliata* in the rain forest of Los Tuxtlas, Veracruz, Mexico. *AMERICAN JOURNAL OF PRIMATOLOGY* 2:363–372, 1982.
- Estrada, A. Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. *INTERNATIONAL JOURNAL OF PRIMATOLOGY*, in press, 1983.
- Fleming, T.H. Do tropical frugivores compete for food? *AMERICAN ZOOLOGISTS* 19:1157–1172, 1979.
- Fleming, T.H.; Heithaus, E.R. Frugivorous bats, seed shadows, and the structure of tropical forests. *BIOTROPICA* 13:45–53, 1981.
- Frankie, G.W.; Baker, H.G.; Opler, P.A. Comparative phenological studies of trees in tropical Wet and Dry forests in the lowlands of Costa Rica. *THE JOURNAL OF ECOLOGY* 62:861–919, 1974.
- Glander, K. Habitat and Resource Utilization: An Ecological View of Social Organization in Mantled Howling Monkeys. Ph.D Thesis, University of Chicago, 1975.
- Hartshorn, G. Neotropical forest dynamics. *BIOTROPICA* 12:23–30, 1980.
- Herrera, C.M. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *ECOLOGY* 63:773–784, 1982.
- Hladik, A.; Hladik, C.M. Rapports tropiques entre végétation et primates dans la forêt de Barro Colorado (Panama). *TERRE VIE* 116:25–117, 1969.
- Howe, H.H. Monkey dispersal and waste of a Neotropical fruit. *ECOLOGY* 61:944–959, 1980.
- Howe, H.H.; Estabrook, G.F. On intraspecific competition for avian dispersers in tropical trees. *AMERICAN NATURALIST* 111:817–832, 1977.
- Howe, H.H.; Primack, R. Differential seed dispersal by birds of the tree *Caesaria nitida* (Flacourtiaceae). *BIOTROPICA* 7:278–283, 1975.
- Howe, H.H.; Vande Kerckhove, G.A. Seed dispersal by birds and the fecundity of a tropical tree. *ECOLOGY* 60:180–189, 1979.

- Janzen, D. Seed eaters versus seed size, number, toxicity and dispersal. *EVOLUTION* 23:1-27, 1969.
- Janzen, D. Herbivores and the number of tree species in tropical forests. *AMERICAN NATURALIST* 104:501-528, 1970.
- Janzen, D.; Miller, G.A.; Hackforth Jones, J.; Pond, C.M.; Hooper, K.; Janos, D.P. Two Costa Rican bat generated seed shadows of *Andira inermis* (Leguminosae). *ECOLOGY* 57:1068-1075, 1976.
- Lieberman, D.; Hall, J.B.; Swaine, M.D.; Lieberman, M. Seed dispersal by baboons in the Shai Hills, Ghana. *ECOLOGY* 60:65-75, 1979.
- McDiarmid, R.M.; Ricklefs, R.E.; Foster, M.S. Dispersal of *Stemmadenia donnel-smithii* (Apocynaceae) by birds. *BIOTROPICA* 9:9-25, 1977.
- McKey, D. The ecology of coevolved seed dispersal systems, pp. 159-191 in *COEVOLUTION OF ANIMALS AND PLANTS*, L. Gilbert, P. Raven, eds. Austin, University of Texas Press, 1975.
- Milton, K. Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *AMERICAN NATURALIST* 114:362-378, 1979.
- Milton, K. *THE FORAGING STRATEGY OF HOWLER MONKEYS*. New York, Columbia University Press, 1980.
- Milton, K.; Van Soest, P.J.; Robertson, B. Digestive efficiencies of wild howler monkeys. *PHYSIOLOGICAL ZOOLOGY* 53:402-409, 1980.
- Miranda, F.; Hernandez, E. Los tipos de vegetacion de Mexico y su clasificacion. *BOLETIN DE LA SOCIEDAD BOTANICA DE MEXICO* 29:29-179, 1963.
- Mittermeier, R.A.; van Roosmalen, M.G.M. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *FOLIA PRIMATOLOGICA* 36:1-39, 1981.
- Morrison, D.W. Efficiency of food utilization of fruit bats. *OECOLOGIA* 45:270-275, 1980.
- Morton, E. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *AMERICAN NATURALIST* 107:8-22, 1973.
- Muskin, A.; Fischgrund, A.J. Seed dispersal of *Stemmadenia* (Apocynaceae) and sexually dimorphic feeding strategies by *Ateles* in Tikal, Guatemala. *BIOTROPICA* 13:78-80, 1981.
- Pielou, E.C. *ECOLOGICAL DIVERSITY*. New York, John Wiley and Sons, 1975.
- Pielou, E.C. *MATHEMATICAL ECOLOGY*. New York, John Wiley and Sons, 1977.
- Smythe, N. Relationship between fruiting seasons and seed dispersal methods in a Ne-tropical forest. *AMERICAN NATURALIST* 104:25-35, 1970.
- Snow, D.W. Evolutionary aspects of fruit eating by birds. *OIKOS* 113:194-202, 1971.