



Use of Leaf Resources by Howling Monkeys (*Alouatta palliata*) and Leaf-cutting Ants (*Atta cephalotes*) in the Tropical Rain Forest of Los Tuxtlas, Mexico

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Use of leaf resources by a troop of howling monkeys and two colonies of leaf-cutting ants was studied for an annual cycle in the rain forest of Los Tuxtlas, Mexico. Howling monkeys spent half their annual foraging time feeding on leaves; leaf-cutting ants spent at least 80% of their recorded foraging time harvesting leaves. Both herbivores preferred young leaves over mature ones, and chemical analysis showed that the protein: fibre ratio of the leaves used was correlated with these preferences. Howling monkeys used 34 tree species as leaf sources. Leaf-cutting ants used 40 plant species of which 38 were trees. Eighteen species used by *Alouatta* were also used by *Atta*; species of Moraceae and Lauraceae were among the most important in their foraging preferences. The plant species used by monkeys and ants occurred at low densities (≤ 4.0 ind/ha). The seasonal production of leaves, the high density of leaf-cutting ant colonies at the study site, and the high amounts of young foliage harvested by the ants from tree species, and individual trees used by howling monkeys as sources of young leaves suggest that the foraging activities of *Atta* may represent a significant pressure upon leaf resources available to *Alouatta*.

Key words: *Atta*, *Alouatta*, herbivores, neotropical primates, Mexico

INTRODUCTION

Interactions of primates with organisms that constitute their sources of food have received more attention by field primatologists than interactions with other organisms with which space and resources are shared. This has led to the general impression that primates exist in an ecological vacuum, and much primate ecological behavior, such as ranging patterns, vertical preferences, and resource use, has been explained solely as a result of the features of exploited resources. This view is incomplete, as primates are members of very complex ecological matrices, in which other nonprimate primary consumers may occupy not only the same habitat but also the same (or overlapping) foraging niches. Primatologists must discard the assumption that the elemental interaction between primates and their food sources

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takes place in an environment where they are virtually the only inhabitants. That nonhuman primates of the tropical rain forest do not exist in an ecological vacuum but are a small component of the biotic community has been pointed out only recently [Bourlière, 1985].

More field evidence is available on interactions between sympatric species of primates than between primates and other animal taxa. In the case of herbivorous primates, a variety of coexisting organisms are relevant to the primate-plant interaction. Nonprimate organisms may interact with primates at the same trophic level, and this interaction may influence primate behavioral responses to resource availability, but empirical evidence documenting this situation is scanty and at best anecdotal [eg, Glander, 1979; Young, 1982]. A pioneer quantitative comparative study compared leaf-cutting ant (*Atta colombica*) and howling monkey (*A. palliata*) foraging preferences in a Costa Rican dry forest [Rockwood & Glander, 1979]. Recent attempts to detect the occurrence of potential interactions between primates and other vertebrates sharing the same resources have been reported for another neotropical forest [Estrada et al, 1984; Estrada & Coates-Estrada, 1985].

The leaves of tropical rain forest plants are a source of food for many organisms, especially phytophagous insects. Phytophagous insects and pathogens were present in the ecological scenario long before the first herbivorous mammals evolved [Scott & Taylor, 1983; Southwood, 1985], and certain features of leaves [eg, plant defensive compounds; Rosenthal & Janzen, 1979] are the consequence of an evolutionary interaction that rendered leaves differentially palatable to herbivores. It is usually recognized that young leaves are preferred by herbivorous animals over mature leaves because of their higher nitrogen and water content and because they are less tough and fibrous [Feeney, 1970; Milton, 1979; Coley, 1980; Glander, 1981]. Mature leaves may also contain substances that reduce digestibility such as tannins and resins [McKey, 1979; Rhoades, 1979]. Thus herbivores are confronted with a food source that is mechanically and/or chemically defended and that is produced seasonally.

Some arboreal mammalian species have nonetheless specialized, in a more recent evolutionary time, in the exploitation of leaves as an important complement in their yearly diet [Eisenberg, 1978]. In neotropical forests, the howling monkey is one of these mammals. This primate spends significant amounts of time feeding on leaves throughout the year [Glander, 1975; Milton, 1980; Gaulin & Gaulin, 1982; Estrada, 1984]. Although its digestive system does not show the specialized adaptations of some of the Old World leaf-eating primates [Bauchop, 1978; Milton, 1979, 1980], they are nevertheless capable of digesting large amounts of leaf material due to the fermentative action that takes place in their caecum, and by maintaining a way of life that is energetically conservative [Glander, 1975; Nagy & Milton, 1979]. Young leaves constitute a major source of protein in the diet of this primate and these monkeys move variable distances daily in search of particular plant species [Glander, 1975, 1981; Milton, 1980; Gaulin & Gaulin, 1982; Estrada, 1984].

Herbivory studies indicate that insects are major consumers of leaves in tropical forests and that young leaves are eaten much more rapidly than old leaves by herbivorous insects [Coley, 1982]. Of the great variety of insects that use young and mature leaves in the forest canopy, leaf-cutting ants may be one of the most important removers of foliage in tropical rain forests [Rockwood, 1976; Cherret, 1968]; they alone harvest more foliage than all vertebrates combined [Leigh & Windsor, 1982].

Studies of fungus-growing ants of the genus *Atta* at various sites indicate that they display a strong inclination to harvest the young leaves of many plant species, and that they are one of the most ubiquitous herbivorous insects in neotropical rain

forests [Rockwood, 1976; Cherret, 1983; Hubbell & Weiner, 1983 among others]. Some of these ants tend to forage during the day [eg, *Atta colombica*; Lugo et al, 1973] while others (*Atta cephalotes*) are basically active at night [Cherret, 1968].

In the rain forest of Los Tuxtlas in southern Mexico, howling monkeys (*Alouatta palliata*) share leaves as food with some vertebrates [Estrada & Coates-Estrada, 1985] and with many insects including leaf-cutting ants. The aim of this report is to present information on the use of leaf sources and preferred plant species by a troop of howling monkeys (*Alouatta palliata*) and by two mature colonies of leaf-cutting ants (*Atta cephalotes*).

METHODS

Study Site

Research was conducted at the Estacion de Biologia "Los Tuxtlas," longitude 95° 04' W, latitude 10° 34' N, located in the eastern portion of the Sierra de Los Tuxtlas in southern Veracruz. The dominant vegetation type is tall evergreen rain forest [Miranda & Hernandez, 1963]. Mean annual temperature and precipitation are 27°C and 4,900 mm, respectively [Estrada & Coates-Estrada, 1983].

Subjects and Observations

Howling monkeys. One troop (troop S) of howling monkeys (N = 16) with marked individuals was observed intensively in order to obtain monthly records on leaf-eating preferences. The feeding and ranging behaviors of the howling monkeys were sampled on an average of 12 days (range 10–15 days) per month and behavioral observations were evenly distributed from 0600–1900 hr. Focal animal sampling [Altmann, 1974] was the observation technique used. Focal samples were of variable duration (3–120 minutes; mean 28 minutes, N = 1450). These were evenly distributed among individuals representing the following age/sex classes: adult males, adult females, adult females with clinging infants, juveniles, and infants able to feed by themselves. In each focal sample the time spent feeding on leaves was recorded with a wrist chronometer. The relative age (ie, young or mature) of the leaves consumed was determined by their color, size (relative to other leaves) and texture (determined from leaves dropped by the monkeys) and was indicated in the record. The height at which the individual monkeys foraged on leaves was measured with a range finder. All trees used by *Alouatta* during observation were marked, measured (height, DBH, crown cover), mapped, and identified where possible to genus and species. During troop progression, the distances traveled were measured with a waist pedometer and checked against tracings on maps made from aerial photographs. The number of quadrats 1 ha in size entered by the troop in a year gave an estimation of home range size.

Removal rate (gm/dry weight) of foliage was calculated following food ingestion rate values provided by Milton et al [1979] and Nagy and Milton [1979] regarding basal metabolic rate requirements and energy metabolism and assimilation of *Alouatta palliata* in Panama. These constants were used along with data on biomass (kg/ha) of howling monkeys at Los Tuxtlas [Estrada, 1982]. Due to the great heights at which the animals frequently foraged, there was a logical difficulty in measuring (at least at our study site) the amounts of leaves ingested by howling monkeys. Monkeys often ingested clusters of leaves that very likely varied in the number of individual leaves. Thus, in view of this limitation, the constants provided by Nagy and Milton [1979] were used as the best approximation for calculating ingestion rates of leaves by the members of troop S.

Leaf-cutting ants. Mature colonies (surface area $\geq 20 \text{ m}^2$) of leaf-cutting ants were censused within an area 100 ha in size, which included the home range of

troop S, by walking along east to west lineal transects spaced 50 meters from north to south. When a colony was encountered, its surface area was measured (maximum length, maximum width and perimeter in meters) and its location was indicated on a map. Two active colonies (colonies 2 and 4) of leaf-cutting ants separated by a distance of 0.5 km were selected for intensive observations on foraging behavior.

Each month 8–10 consecutive nights (4–5 per colony) were spent conducting observations on plants used by the two colonies as sources of leaves. Although records of the ants' behavior were obtained between 0600–0100 hrs, observations were concentrated between 1900–0100 hr because this was the time of peak foraging activity. On each observation night, in both colonies, all foraging trails were followed to the plants from which leaves, flowers or fruits were being harvested. The plant was assigned a number and the foraging rate was calculated; all plants were identified when possible, measured (DBH, total height, and crown cover) and their location plotted on a map. Foraging rates were measured by counting with a hand-held tally counter the number of laden ants (an ant carrying a piece of leaf down the stem of the plant) per minute passing a fixed point on the plant. Flashlight, binoculars and a range finder were used to determine the height at which plant material was harvested by the ants. Also the length of the foraging trails was measured, and the direction of trails was determined with a compass.

For each plant used by the ants we collected 50 laden ants. The leaf fragments were weighed before and after drying them at constant temperature (60°C) for 12 hr. Dry weight of leaf material and the density (mature colonies/ha) of *Atta* were used to calculate the overall removal rates of leaves (gm per ha per year). Before drying, the area of each leaf fragment was measured with a Hewlett-Packard digitizing tablet (HP 9111A). The values obtained were expressed as square centimeters or as square meters. Removal rates for some individual trees were calculated following similar procedures.

Sampling of Vegetation

To assess the density of plant species used by both herbivores in the forest, all trees ≥ 5.0 cm DBH were censused in three 1 ha (500 \times 20 m) plots within the home range of troop S. In addition every two weeks, for a 12-month period, phenological censuses were conducted on every tree ≥ 10.0 m in height ($N = 312$, 59 species) in each of the three 1 ha plots. The presence or absence of leaves was scored, and, if present, the state of leaf maturation was noted.

Samples of young and mature leaves of 30 plant species used by the monkeys and of 24 plant species used by the ants were collected. Additional samples were obtained of 20 plant species not used by *Alouatta* and selected randomly from within the home range of troop S. A similar procedure was followed in the case of *Atta*: leaves of 21 randomly selected plant species not used by the ants were collected from within the territories of the two colonies. The collected samples were dried to a constant temperature (60°C) for 24 hr. These samples were subjected to chemical analysis at the Animal Nutrition Laboratory of the Veterinary School of UNAM to determine protein content ($N \times 6.25$) by the macro-Kjeldahl method and crude fibre following the procedure described in Flores [1981]. The results derived from four replicates for each species were expressed as means (\pm SD).

RESULTS

Vertical Foraging Preferences and Plant Species Used

Alouatta. All plants in which howling monkeys were observed feeding on leaves were trees (Table I). The height of these trees ranged from 10–43 m ($\bar{x} = 22.6 \pm$

TABLE I. Plant Species Used by *Alouatta* and *Atta**

Rank	<i>Alouatta</i>			<i>Atta</i>		
	Species	Months used	Density (ind/ha)	Species	Months used	Density (ind/ha)
1	<i>Nectandra ambigens</i> (Lauraceae)	11	11.6	<i>Nectandra ambigens</i> (Lauraceae)	11	11.6
2	<i>Ficus</i> spp. (Moraceae)	12	1.3	<i>Ficus</i> spp. (Moraceae)	12	1.3
3	<i>Brosimum alicastrum</i> (Moraceae)	9	4.3	<i>Pleuranthodendron mexicanum</i> (Flacourtiaceae)	12	1.0
4	<i>Poulsenia armata</i> (Moraceae)	8	3.6	<i>Bursera simaruba</i> (Burseraceae)	5	0.3
5	<i>Cordia megalantha</i> (Boraginaceae)	5	0.6	<i>Pseudolmedia oxyphyllaria</i> (Moraceae)	11	12.3
6	<i>Crataeva tapia</i> (Capparidaceae)	1	0.6	<i>Paullinia pinnata</i> ^a (Sapindaceae)	2	NA
7	<i>Pterocarpus rohrii</i> (Leguminosae)	7	3.3	<i>Brosimum alicastrum</i> (Moraceae)	9	4.3
8	<i>Cecropia obtusifolia</i> (Moraceae)	8	3.0	<i>Poulsenia armata</i> (Moraceae)	7	3.6
9	<i>Dussia mexicana</i> (Leguminosae)	3	0.6	<i>Turpinia occidentalis</i> (Staphyleaceae)	8	2.6
10	<i>Guarea glabra</i> (Meliaceae)	2	2.6	<i>Foramea occidentalis</i> (Rubiaceae)	10	0.3
11	<i>Pseudolmedia oxyphyllaria</i> (Moraceae)	3	12.3	<i>Mortoniadendron guatemalense</i> (Tiliaceae)	8	0.6
12	<i>Dendropanax arboreus</i> (Araliaceae)	1	5.0	<i>Omphalea oleifera</i> (Euphorbiaceae)	10	1.0
13	<i>Calatola laevigata</i> (Icacinaceae)	1	NA	<i>Dialium guianense</i> (Leguminosae)	4	1.3
14	<i>Dipholis minutiflora</i> (Sapotaceae)	2	0.3	<i>Robinsonella mirandae</i> (Malvaceae)	4	1.0
15	<i>Sapium nitidum</i> (Euphorbiaceae)	1	0.6	<i>Dendropanax arboreus</i> (Araliaceae)	5	5.0

(continued)

TABLE I. Plant Species Used by *Alouatta* and *Atta** (Continued)

Rank	<i>Alouatta</i>			<i>Atta</i>		
	Species	Months used	Density (ind/ha)	Species	Months used	Density (ind/ha)
16	<i>Omphalea oleifera</i> (Euphorbiaceae)	5	1.0	<i>Trichilia martiana</i> (Meliaceae)	3	0.3
17	<i>Mortoni dendron guatemalense</i> (Tiliaceae)	2	0.6	<i>Pterocarpus rohrii</i> (Leguminosae)	3	3.3
18	<i>Lonchocarpus guatemalensis</i> (Leguminosae)	2	1.3	<i>Quararibea funebris</i> (Bombacaceae)	4	2.0
19	<i>Spondias radlkoferi</i> (Anacardiaceae)	5	4.6	<i>Trophis mexicana</i> (Moraceae)	3	NA
20	<i>Robinsonella mirandae</i> (Malvaceae)	4	1.0	<i>Orthion oblanceolatum</i> (Violaceae)	6	0.6
21	<i>Cupania dentata</i> (Sapindaceae)	1	0.3	<i>Couepia polyandra</i> (Chrysobalanaceae)	2	0.3
22	<i>Lysiloma bahamensis</i> (Leguminosae)	1	NA	<i>Helicarpus appendiculatus</i> (Tiliaceae)	1	2.3
23	<i>Senna multijuga</i> (Leguminosae)	1	0.3	<i>Ocotea dendrodaphne</i> (Lauraceae)	2	NA
24	"Crespillo"	1	NA	<i>Pouteria zapota</i> (Sapotaceae)	2	0.6
25	<i>Coccoloba barbadensis</i> (Polygonaceae)	1	0.3	<i>Rheedia edulis</i> (Guttiferae)	1	NA
26	<i>Cymbopetalum baillonii</i> (Annonaceae)	1	4.6	<i>Guarea grandifolia</i> (Meliaceae)	1	2.0
27	<i>Tetrorchidium rotundatum</i> (Euphorbiaceae)	1	NA	<i>Ampelocera hottlei</i> (Ulmaceae)	1	2.9

28	<i>Licania platypus</i> (Chrysobalanaceae)	1	0.3	<i>Spondias radlkhoferi</i> (Anacardiaceae)	1	4.6
29	<i>Busera simaruba</i> (Burseraceae)	1	0.3	<i>Myriocarpa longipes</i> (Urticaceae)	1	NA
30	<i>Ampelocera hottlei</i> (Ulmaceae)	1	2.9	<i>Manilkara zapota</i> (Sapotaceae)	1	NA
31	<i>Zanthoxylum hellermanii</i> (Rutaceae)	1	1.3	<i>Cymbopetalum baillonii</i> (Annonaceae)	4	4.6
32	<i>Couepia polyandra</i> (Chrysobalanaceae)	1	0.3	<i>Mappia longipes</i> (Icacinaceae)	2	0.3
33	<i>Pouteria zapota</i> (Sapotaceae)	2	0.6	<i>Lunania mexicana</i> (Flacourtiaceae)	1	NA
34	<i>Eugenia sp.</i> (Myrtaceae)	1	NA	<i>Guarea glabra</i> (Meliaceae)	2	2.6
35				<i>Rollinia jimenezii</i> (Annonaceae)	1	1.3
36				<i>Randia alaticarpa</i> (Rubiaceae)	1	NA
37				<i>Salacia megistophylla</i> ^a (Hippocrataceae)	1	NA
38				<i>Inga sp.</i> (Leguminosae)	1	0.6
39				<i>Eugenia sp.</i> (Myrtaceae)	1	NA
40				<i>Clarisia biflora</i> (Moraceae)	1	1.6

*The importance rank of each species, determined by percent of feeding time for howling monkeys and by the mean number of laden ants per minute for leaf-cutting ants (see text), is indicated. Species densities obtained from vegetation censuses in three 1 ha plots and the number of months each species was used as a source of leaves by each herbivore are also indicated.

^aLianas.

6.1) and DBH was 10–250 cm (47.6 ± 28.6). Foraging heights ranged from 10–40 m, but 83% of the records ($N = 575$) were scored between 16 and 30 m. Howling monkeys spent almost equal portions of their feeding time eating leaves (46%) and fruit (53%). Young leaves were preferred over mature leaves (36% versus 10%) and accounted for 78% of *Alouatta*'s leaf feeding time. The monkeys were species-selective in their leaf diet, using 34 species representing 21 plant families (Table D). When percent of total feeding time was considered, the most important plant families in their leaf diet were: Lauraceae (one species), Moraceae (five species), Leguminosae (five species), and Boraginaceae (one species). The mean number (\pm SD) of species used per month by *Alouatta* was $8.5 (\pm 2.3)$; range 5–12). Five species could be considered constant sources of leaves throughout the year since they were used ≥ 8.0 months. Seventeen species were used only one month and the remainder were used from 2.0 to 7.0 months (Table D).

Vegetation censuses indicated that 95% of the species used by howling monkeys occurred at densities ≤ 4 individuals/ha. In only 3 months (May, July, and December) did the monkeys use (percent of feeding time eating young leaves) species in the proportion in which they occurred in their home range (May $r = 0.60$ $P < .05$ $N = 12$; July $r = 0.75$ $P < .05$ $N = 12$; December $r = 0.96$ $P < .05$ $N = 7$). The home range of troop S was 60 ha in size and the troop moved from 50 to 1500 m when foraging on leaves.

Atta. Censuses of mature colonies of leaf-cutting ants yielded densities of 1.13 colonies/ha. Within the home range of *Alouatta* troop S, we detected the presence of 26 mature colonies of *Atta cephalotes* (Fig. 1). Two colonies selected for intensive observations covered areas of 32 m² (colony 2) and 40 m² (colony 4), and the sizes of their foraging territories were 1 ha and 2 ha, respectively.

All plants but two (lianas *Paullinia pinnata* and *Salacia megistophylla*) used by the leaf-cutting ants were trees. The trees used by *Atta* ranged in height from 3–36 m ($\bar{x} = 15.0 \pm 7.78$) and in DBH from 5–200 cm ($\bar{x} = 57.6 \pm 56.0$). The heights at which leaves were harvested ranged from 2.3–34m, but 78% ($N = 3800$) of the

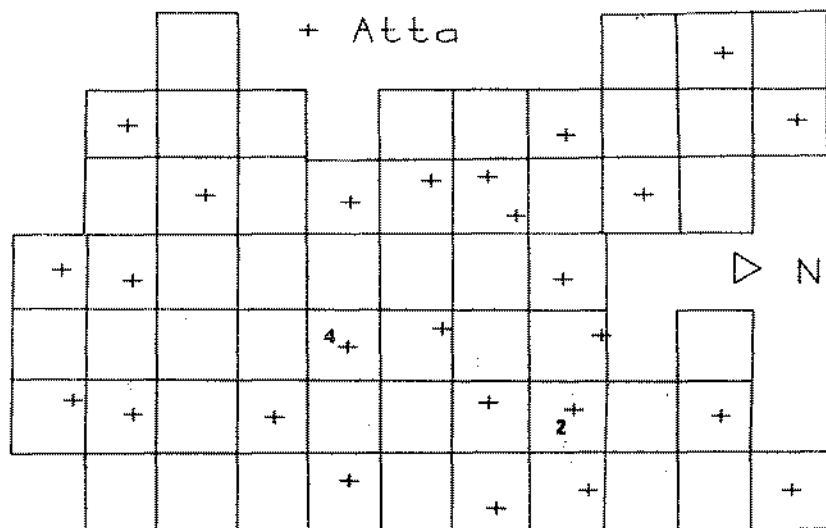


Fig. 1. Home range of troop S (about 60 ha) and location of mature colonies of *Atta cephalotes*. Colonies 2 and 4 were selected for intensive observations. Each square = 1 ha.

records occurred between 6 and 20 m. The harvesting of young leaves accounted for 90% of foraging records and that of mature leaves for only 6% (fruits 3% and flowers 1%). Leaf-cutting ants harvested leaves from 40 species of plants representing 25 families (Table I). In terms of number of laden ants, the most important plant families were Moraceae (six species), Lauraceae (two species), Flacourtiaceae (two species), and Burseraceae (one species).

Nine species were used by the two colonies for at least 8.0 months. Thirty-three percent of all species were used for only 1 month of the year; the remaining species were used for 2.0 to 7.0 months. The mean (\pm SD) number of species used per month by colonies 2 and 4 were 9.8 (\pm 3.5) and 6.0 (\pm 0.8), respectively. On a monthly basis, the harvesting of young leaves accounted for more than 80% of the foraging records. Vegetation censuses indicated that 95% of the tree species used by the ants occurred at densities \leq 4 individuals/ha and no significant correlation was found for any month of the year between the number of laden ants per tree species and the densities of tree species. The highest correlation value was found in the month of March ($r = 0.45$ $N = 15$), but it was not significantly different from zero.

These results demonstrate the following salient points: 1) howling monkeys and leaf-cutting ants used a limited number of species as sources of leaves, 2) both displayed a preference for young leaves over mature leaves, 3) species of Moraceae and Lauraceae were among the most important sources of leaves to both herbivores, 4) there was no strong evidence that species were used in the proportion in which they occurred in the forest; in fact, many of the most frequently attacked plant species were those which are rarest in the forest, and 5) although use of species was mainly seasonal, harvesting of young leaves was consistently more important over time than the harvesting of mature leaves in the foraging preferences of both herbivores.

Plant Species and Plant Part Overlap Between *Atta* and *Alouatta*

Eighteen (53%) of the thirty-four species used by *Alouatta* as sources of young leaves were also used by *Atta* (data from both colonies combined). Colony 2 shared 10 plant species with the monkeys, and colony 4 shared 12. In comparison, colonies 2 and 4 shared nine species. Ranking the species used by howling monkeys according to percent of feeding time and those used by *Atta* according to the number of laden ants resulted in significant Kendall Coefficients of Rank Correlation when data from both colonies were considered separately and when they were combined (Table II). For comparison, the Kendall Coefficient of Rank Correlation between colonies 2 and 4 was also significantly different from zero.

The ranking analysis and the observed overlap at the plant species level leads us to infer that monkey and ant foraging preferences were not very different. An overlap between ants and monkeys was also evident at foraging heights between 11

TABLE II. Kendall Rank Correlation Coefficients Between *Atta* and *Alouatta* When Species Used as Sources of Leaves Were Ranked According to Number of Laden Ants per Minute and Percent of Feeding Time, Respectively

Comparison	Coefficient of rank correlation (T)	Probability (P)
Colony 2/Troop S	0.381	0.0505
Colony 4/Troop S	0.393	0.0375
Colony 2 and 4/Troop S	0.477	0.0030
Colony 2 vs colony 4	0.571	0.0239

TABLE III. Convergence at Foraging Heights by Howling Monkeys and Leaf-cutting Ants

Height class (m)	<i>Atta</i> (N = 3,800) (Percent)	<i>Alouatta</i> (N = 575) (Percent)
3-5	7	0
6-10	27	0
11-15	29	7
16-20	24	36
21-25	5	31
26-30	4	16
31-35	4	6
36-40	0	4

and 20 m. Fifty-one percent of the foraging records for ants and 43% of those for monkeys were scored at this height interval (Table III).

Overlap at the Individual Plant Level Between *Alouatta* and *Atta*

A total of 12 individual trees (5 in colony 2 and 7 in colony 4) used by howling monkeys as sources of young leaves were harvested for the same plant part by leaf-cutting ants (Table IV; Fig. 2). These trees belonged to nine species, of which some ranked highest in the foraging preferences of both herbivores (Table I). Harvesting rates of leaves by *Atta* at each of these 12 trees showed that the ants removed significant amounts of young leaves during the total number of days in which they were used. These rates varied from 0.02 kg dry weight (*Poulsenia armata*) to 7.78 kg dry weight (*Ficus* sp.) (Table IV).

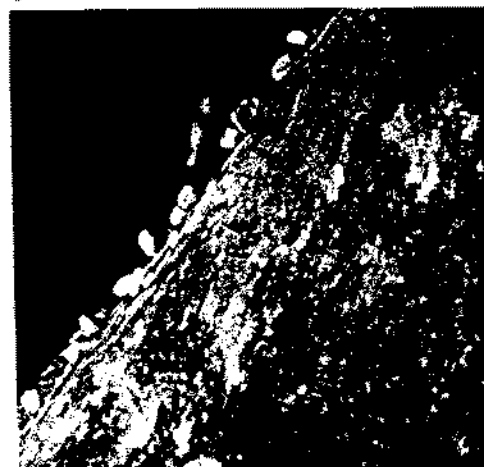
The analyses to this point have dealt with only the yearly totals of leaf parts harvested and have ignored the seasonal variations in overlap in the use of species sources of leaves. The mean (\pm SD) number of species per month shared by the ants of both colonies and howling monkeys was 4.3 [\pm 1.8; range 2 (December) to 7 (May)], but the number of species shared in the period March to July was significantly greater ($t = 2.12$, $df = 10$ $P < .05$) than that shared during the rest of the year. Phenological records indicated that the number of species producing new leaves was significantly greater between March and July ($\bar{x} = 46.8 \pm 1.4$) than in all other months ($\bar{x} = 28.8 \pm 6.4$; $t = 5.05$, $df = 10$ $P < .002$). An index of foraging overlap at the species level between howling monkeys and the two colonies of leaf-cutting ants indicated higher overlap values between March and July than in other months (Fig. 3).

Leaf Chemistry

Chemical analysis of the leaves used by howling monkeys showed that young leaves contained significantly higher proportions of protein (dry weight) and significantly lower fibre (dry weight) than mature leaves of the same species (Table V). When these "positive" (protein) and "negative" (fibre) attributes of the leaves used by *Alouatta* were contrasted against those of leaves not used by the monkeys, we found that while they did not differ in protein content, the former had significantly less fibre than the latter (Table V).

Young leaves harvested by *Atta* had significantly higher protein content and less fibre than mature leaves (Table V). The analysis showed no significant differences in protein and fibre content between young leaves of species used and young leaves of species not used by the leaf-cutting ants. However, mature leaves of species

a)



b)

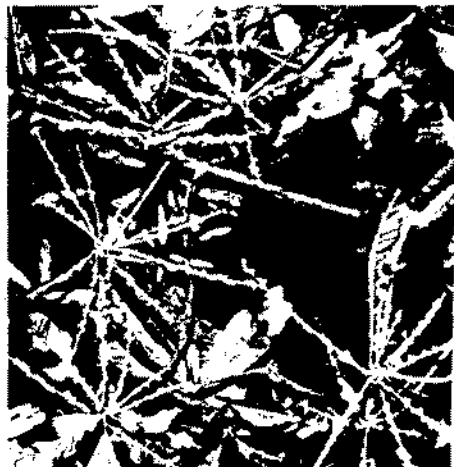


Fig. 2. (a) Leaf-cutting ants laden with fragments of young leaves of *Ficus* sp. coming down the trunk of the tree; (b) damage to young leaves by leaf-cutting ants in a section of the crown of the same tree. This tree was also used as a source of young leaves by howling monkeys.

TABLE IV. Individual Trees Used by Howling Monkeys as Sources of Young Leaves and in Which Leaf-cutting Ants Were Observed Harvesting the Same Plant Part

Species/tree	Crown (m ²)	Colony	Days ^a	kg ^b	m ^{2c}	Months ^d
<i>Ficus</i> sp.	176	4	26	7.4	33.2	5
<i>Poulsenia armata</i>	277	4	6	1.7	7.7	3
<i>Poulsenia armata</i>	19	4	1	0.02	0.08	1
<i>Brosimum alicastrum</i>	177	4	4	0.28	1.2	1
<i>Nectandra ambigens</i>	133	4	8	1.6	7.2	4
<i>Mortoniendron guatemalense</i>	95	4	4	0.6	2.9	2
<i>Pterocarpus rohrii</i>	154	4	5	0.2	1.1	1
<i>Pterocarpus rohrii</i>	133	2	6	0.8	3.8	3
<i>Nectandra ambigens</i>	133	2	5	2.7	12.1	2
<i>Bursera simaruba</i>	50	2	12	7.4	32.9	4
<i>Dialium guianense</i>	133	2	10	5.6	24.9	4
<i>Manilkara sapota</i>	133	2	4	0.2	1.2	1

^aTotal number of days in which the ants were observed foraging on the tree.

^bkg dry wt of leaves estimated as follows: *Ficus* sp 2598 (laden ants) × .02 (gm/fragment) = 51.9 gm/130 (minutes of sampling) = 0.39 gm × 60 (gm per hour) = 23.9 gm × 12 (12 hour activity per 24 hours) = 287 gm × 26 (number of days of records on ants using this tree) = 7.4 kg.

^cArea removed from the tree estimated as follows: 7.4 kg × 1,000 = 7,480 gm/.02 (gm per fragment) = 374,000 × .89 cm² (mean area of each fragment) = 332,860 cm²/10,000 cm² (one square meter) = 33.2 m².

^dNumber of months tree was used.

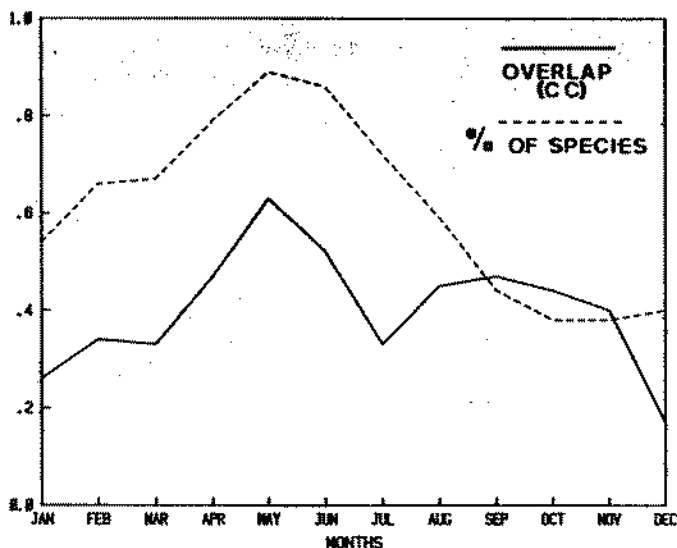


Fig. 3. Seasonality in overlap (CC) at the species level between howling monkey troop S and leaf-cutting ant colonies 2 and 4 in the use of leaf sources [CC = index of foraging overlap at the species level = $2Sx_y$ (species in common between two subsequent months)/ $S_x + S_y$ (species in month A) + S_y (species in month B)]. A value of zero and of 1.0 for the index indicates no overlap and 100% overlap respectively. Also shown is the leaf phenology (broken line) of 59 tree species in the forest of Los Tuxtlas. The values for this curve refer to the percent of species, out of a total 59, recorded every month in three one-hectare transects, which had young leaves ($.6 \times 100 = 60\%$).

TABLE V. Results of Chemical Analyses in Which Protein ($N \times 6.25$) and Crude Fibre Content Were Determined in Leaves of Plant Species Used and Not Used by *Alouatta* and *Atta*

	N	Protein ($N \times 6.25$)		Fibre (percent)	
<i>Alouatta</i>					
Young leaves					
Used	30	17.1	} $t=.67$ $P=.25$	21.4	} $t=2.1$ $P<.01$
Not used	20	18.4		26.4	
} $t=3.2$ $P<.005$					
Mature leaves					
Used	30	12.9	} $t=.74$ $P=.22$	26.6	} $t=.24$ $P=.40$
Not used	20	14.3		27.1	
<i>Atta</i>					
Young leaves					
Used	24	16.4	} $t=1.4$ $P=.07$	22.3	} $t=.88$ $P=.19$
Not used	21	18.5		25.0	
} $t=2.6$ $P<.005$					
Mature leaves					
Used	24	13.3	} $t=.11$ $P=.45$	29.3	} $t=1.9$ $P<.02$
Not used	21	13.5		23.6	
} $t=2.1$ $P<.01$					

not used by *Atta* had significantly lower fibre content than that of mature leaves they harvested (Table IV).

A higher content of protein and a lower content of fibre in leaves was, apparently, a factor contributing to their selection by both herbivores.

DISCUSSION

Although leaf-cutting ants exploited some leaf resources in the forest understory (≤ 10 m in height) which the monkeys ignored, they also intensely harvested the leaves of tree species of the mid and upper canopy (≥ 10 m in height). Although some of these species were not used by *Alouatta* (eg, *Pleuranthodendron mexicanum*) others (eg, *Ficus* spp., *Nectandra ambigens*) were among those ranked highest in their leaf diet. These findings disagree somewhat with those of Rockwood and Glander [1979] in a Costa Rican dry forest, where they found that *Atta colombica* and *Alouatta palliata* differed significantly in plant species used and plant parts exploited. These contrasts could be attributed to differences between *Atta colombica* and *Atta cephalotes* in the requirements of the fungi cultured and/or to differences in structure and species composition between the two forests.

At Los Tuxtlas there are approximately 250 species of trees (M. Martinez, personal communication) of which 14% were used by leaf-cutting ants and howling monkeys, indicating foraging selectivity by these two herbivores. These species represented a broad spectrum ($\pm 30\%$) of 75 families of trees known to occur in this forest. Although species of the ubiquitous families Moraceae and Lauraceae were particularly important in foraging preferences of howling monkeys and leaf-cutting ants, these herbivores shared species of other families. Species differed, however, in their relative importance (percent of feeding time or mean number of laden ants). For example, *Bursera simaruba*, a low-ranking species in the leaf diet of howling monkeys, ranked fourth in the foraging preferences of *Atta*.

While both herbivores selected leaves with high protein and low fibre content there are other elements, such as plant secondary metabolites [McKey, 1979; Rosenthal & Janzen, 1979; Milton, 1979], that are known to contribute to the selection of foliage by herbivores. Our preliminary analyses of alkaloids in the leaves of plants used by *Alouatta* at Los Tuxtlas showed that the majority of the species examined ($N = 17$) had only moderate to low amounts of the compounds [Estrada, 1984]. Selectivity in species used and the action of gut microorganisms in detoxification of secondary metabolites have been suggested as measures that circumvent the problem of secondary compounds in plant parts eaten by leaf-eating mammals [Janzen, 1978]. It has been proposed that this is also an important reason why leaf-cutting ants culture fungus [Cherret, 1980] and could explain why leaf-cutting ants at Los Tuxtlas preferred mature leaves of species containing a high fibre content.

Both monkeys and ants displayed a seasonal convergence in the use of species as sources of leaves. The observed "peak" in overlap corresponded with the production of new leaves by many species in the forest (March–July). Since leaf flushing may last only days to a few weeks for many species, this narrows the opportunities for a herbivore to locate these new leaves. Furthermore, leaves remain young for only a short time after which they undergo morphological and mechanical changes that modify their palatability [Milton, 1979; Coley, 1980]. The low density of plant species and the temporal patchiness of young leaves may prompt leaf-cutting ants to harvest leaves assiduously from selected trees and to switch trees and species within a few days and/or weeks. These same factors may induce howling monkeys to display a similar behavior in their leaf diet over short and long time periods and to travel variable distances daily to encounter new leaves.

Resource Depression by *Atta*

In the evergreen forest canopy of Los Tuxtlas there are many more insects that, together with leaf-cutting ants, use leaves as food sources, causing complete or nearly complete defoliation of individual plants. These insects most commonly are moth larvae (Lepidoptera), adult beetles (Coleoptera), Orthoptera, and various groups of Homoptera. A great deal of foliage is taken by thousands of species of herbivorous insects. Insects make holes and notches in leaves, mine in leaves, scrape epidermis off leaf surfaces, cut leaves off, etc. [Janzen, 1983]. The majority of these insects are characterized by populations that fluctuate significantly on a seasonal basis (eg, Sphinx moth larvae, *Urania fulgens* larvae, etc.), and most are host-specific with respect to the species attacked. These insects represent a large biomass with a much higher turnover rate than vertebrate folivores and which extract more from the ecosystem per gram of animal biomass [Janzen, 1983]. In contrast, leaf-cutting ants are not host-specific and are active all year round; they hence conduct a more sustained defoliating activity than do some other insects and monkeys. Mature colonies of leaf-cutting ants may have from 650,000 to 5,000,000 ants [Lewis et al, 1974; Martin et al, 1967; Weber, 1982]. Conservative estimates from Panama report that these insects take from 90–300 kg of leaves per hectare per year [Leigh & Windsor, 1982]. At Los Tuxtlas we have estimated that *Atta cephalotes* harvests from 90–140 kg (dry weight) of leaves per ha per year, whereas *Alouatta palliata* consumes from 12–33 kg (dry weight) of leaves/ha/yr [Estrada & Coates-Estrada, 1985; unpublished data].

Leaf-cutting ants may affect, through their defoliating activities, the availability of another very important food item to howlers: fruit. Among the most important impacts of defoliation in tropical trees is that it results in failure to produce fruit (and seeds) or failure to sexually reproduce in the following cycle [Rockwood, 1973]. Among the eleven species ranked most important in the howling monkey leaf diet are six of the most important in their fruit diet [Estrada & Coates-Estrada, 1984]. The leaves of several of these species were harvested by leaf-cutting ants, causing a significant loss of foliage to the trees.

At Los Tuxtlas *A. palliata* is the most important arboreal mammalian folivore. The sloths (*Bradypus* and *Choelopus*) do not occur in Mexico. Their northernmost extension in the neotropics is in Honduras. Therefore, at Los Tuxtlas, howling monkeys face very little feeding overlap with other leaf-eating vertebrates, including *Iguana iguana* [Estrada & Coates-Estrada, 1985]. Feeding overlap with leaf-eating invertebrates is evidently a more important attribute of the ecological scenario in which *A. palliata* occurs in southern Mexico.

At a broader level, our results suggest that not only phenological and demographic aspects of the plants have an important effect upon the ranging and foraging behaviors of leaf-eating primates, but that the spatial and temporal predictability of palatable immature leaves may be lowered by the foraging activities of other leaf-eating organisms.

CONCLUSIONS

- 1) Leaf-cutting ants are a conspicuous element in the habitat occupied by howling monkeys at Los Tuxtlas.
- 2) Since they harvest young leaves of plant species and individual plants used by *Alouatta*, leaf-cutting ants may exert important pressures upon leaf resources available to howling monkeys.
- 3) Resource depression by other leaf-eating organisms in the forest canopy, coupled with plant attributes such as density, leaf phenology, and leaf chemistry,

may contribute to spatial and temporal variations in foraging preferences and ranging behavior of leaf-eating primates.

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