

A Preliminary Study of Resource Overlap Between Howling Monkeys (*Alouatta palliata*) and Other Arboreal Mammals in the Tropical Rain Forest of Los Tuxtlas, Mexico

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Potential resource overlap between howling monkeys and other arboreal mammals was studied in the rain forest of Los Tuxtlas, Veracruz, Mexico. Eight species of mammals belonging to the orders Primates, Carnivora, Rodentia, and Marsupialia were found to share the canopy and to overlap trophically with howling monkeys. These mammals made up 77% and *Alouatta* 23% of the arboreal mammalian biomass under consideration. The arboreal porcupine and spider monkey were the only mammals that also fed on leaves. However, in this feeding niche, *Alouatta* is the only important mammalian folivore in Los Tuxtlas, and resource depression derived from leaf-eating insects is more important. The eight arboreal mammals may exert more pressure upon fruit resources, for they consumed 75% of the estimated total dry weight of fruit/ha/yr consumed by arboreal mammals.

Key words: *Alouatta*, howling monkeys, arboreal mammals, resource overlap, tropical rain forest, neotropics, Mexico

INTRODUCTION

Neotropical primates share the forest canopy with a large array of insects, birds, reptiles, and other arboreal mammals, including other primate species. They may share vertical and horizontal space and, occasionally, food resources with some of these animals. Studies of interactions between neotropical primates and other non-primate animals are rare in the literature [but see Rockwood & Glander, 1979; Glander, 1979; Young, 1982; Estrada et al, 1984]. Comparative studies of interactions and ecological similarities between neotropical primates and nonprimate animals of similar habits (eg, arboreality, frugivory, etc) are necessary because we need to interpret how these aspects may also shape behavioral responses such as ranging patterns, vertical preferences, and resource utilization. On a more general level, questions about resource partitioning among tropical rain forest animals are of fundamental interest for understanding the dynamics and mosaic nature of animal-plant and animal-animal interactions.

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Background

Our long-term study of the behavioral ecology of howling monkeys in the tropical rain forest of southern Mexico is aimed at exploring two fundamental aspects: interactions of howling monkeys with the plants in the ecosystem and interactions with other animals at the level of resource utilization. Our continuous observations of *Alouatta* since September 1977 indicate that this primary consumer is species-selective in its diet, using approximately 51 plant species as sources of food. Leaf sources account for 31 species, and 34 species are used as sources of fruit [Estrada & Coates-Estrada, 1984]. These howling monkeys spend nearly equal proportions of time eating leaves and fruit and display a marked preference for young leaves and mature fruit. The troops' home ranges are about 60 ha in size, and they generally prefer trees that are above 10 m in height [Estrada, 1984]. Species of Moraceae (such as *Ficus* spp., *Poulsenia armata*, *Brosimum alicastrum*, *Pseudolmedia oxyphyllaria* and one species of Lauraceae (*Nectandra ambigens*) account for 92% of time feeding on mature fruit and 66% of time feeding on young leaves.

Objectives

Our aim here is to present the following preliminary information on the arboreal mammals with which howling monkeys share food resources: taxonomic identity, density and biomass, trophic level, vertical preferences, and home range size. We also examine demographic, chemical, and phenological aspects of food resources used by howling monkeys and some of these mammals.

METHODS

Study Site

Research was conducted 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. The reserve covers an area of 700 ha, which connects with 10,000 ha of rain forest extending toward and around the San Martín volcano. The dominant vegetation type is high evergreen rain forest [Miranda & Hernandez, 1963]. The climate is hot and humid, with a mean annual temperature of 27°C. Rainfall is seasonal, with a dry season ($\bar{X} = 111.7 \pm 11.7$ mm) from March to May and a wet season ($\bar{X} = 486.2 \pm 87.00$) from June to February. Mean annual precipitation is 4,900 mm [Estrada & Coates-Estrada, 1983].

Subjects and Observations

Arboreal mammals other than *Alouatta* at Los Tuxtlas include 12 species. Some of these share with howling monkeys anatomical adaptations for arboreality such as the prehensile tail. The social structure of the nonprimate species, however, contrasts with that of primates; individuals live alone or seasonally as male/female pairs, or temporarily as mother and offspring within a well-defined territory. Arboreal mammals represent five orders: Primates, Rodentia, Carnivora, Marsupialia, and Edentata. Three species are diurnal, and the remainder are nocturnal. The two anteaters (*Tamandua mexicana* and *Cyclopes didactylus*) and two marsupials (*Marmosa mexicana* and *Caluromys derbianus*) were excluded from this study because 1) the two anteaters occupy a very different ecological and dietary niche than that of *Alouatta*, and 2) the two marsupials are extremely rare and secretive, and only limited observations were possible.

Observations on the other arboreal mammals (*Coendou mexicanus*, *Ateles geoffroyi*, *Potos flavus*, *Bassariscus sumichrasti*, *Sciurus deppei*, *Sciurus aureogaster*, *Didelphis marsupialis*, and *Philander opossum*) were not carried out simultaneously in the same year but were spread through the period 1980-84. Behavioral records

were obtained, however, for each month of the year for individuals in each of these mammal species. All behavioral observations on these animals were carried out within the home range of howling monkey troop S ($n = 16$) [Estrada, 1984]. During this time, we also censused the vegetation and collected plant specimens.

Censuses of the Populations

Arboreal mammals were censused by "strip census" [Robinette et al, 1974; Cant, 1977]. The nonprimate arboreal mammals were censused within the home range area (60 ha) of troop S. The primates were censused throughout the entire reserve. The diurnal and nocturnal censuses were conducted along 35 km of trails that traverse the biological reserve. Data on body weights for each mammal were obtained from captured and captive individuals.

Determination of Trophic Level and Consumption Rates

Direct field observations of the foraging behavior of two *Sciurus deppei* and two *Sciurus aureogaster* and members of a small group of *Ateles geoffroyi* ($n = 6$) were carried out during the day with binoculars. At night, three *Coendou mexicanus*, five *Bassiriscus sumichrasti*, three *Potos flavus*, two *Didelphis marsupialis*, and three *Philander opossum* were observed with binoculars, flashlight, and, sometimes, a night vision scope (Javelin Electronics model 221). Focal animal sampling [Altmann, 1974] was employed for the above species and howling monkeys [Estrada, 1984; Estrada & Coates-Estrada, 1984]. The occurrence of behavioral events (eg, foraging for leaves, fruit, insects, or other food types; travel, and resting) was recorded onto a portable cassette tape recorder, and duration was timed with a stopwatch.

Food consumption by animals was calculated from their size and density following the procedure reported by Smythe et al [1982] and Leigh and Windsor [1982] for mammals of Barro Colorado Island in Panama. In this case, rate of basal metabolism was estimated with the standard formula $70 W^{.75}$ kcal/day, where W is the animal's weight in kilograms [Kleiber, 1961]. In the case of the arboreal porcupine, basal metabolic rate was assumed to be 63% of the value predicted from body weight [McNab, 1978]. Total energy expenditure was assumed to be twice the basal metabolic rate [Nagy & Milton, 1979]. Taking 1 g dry weight of fruit and seed to represent 5 kcal [Odum, 1970, in Leigh and Windsor, 1982] and 1 g dry weight of young leaves to represent 3 kcal [Golley, 1969; Estrada, 1984], it is possible to obtain an indirect and rough estimate of food consumption. Although these rough estimates do not take into account seasonal variations in animal activity and food input, they are nonetheless useful in producing a general picture of an animal's impact on energy flow in the ecosystem. Thus, a 2.5-kg *Potos flavus* eats 111 g dry weight of fruit per day, or 3.0 kg per month. A population of 0.12 adult individuals per hectare requires 400 g dry weight of fruit per hectare per month.

Home Range and Vertical Preferences

The distances traveled by animals were measured with the aid of a waist pedometer to the nearest meter, and the measurements were checked against tracings on maps made from aerial photographs. The total number of 1-ha quadrats entered by each mammal gave quantitative information on home range or territory size. The vertical position of the animal was measured with a range finder every 5 min during the focal sample. Some of the records reported are for several individuals within an annual cycle. For purposes of analysis, these records were grouped into three major height classes: lower level 0–10 m, middle level 10–20 m, and upper level ≥ 20 m.

Quality of Plant Food

Samples of young leaves of 11 species and of ripe fruit of 11 species were collected and weighted before and after drying them at 60°C for 48 h. The samples were subjected to chemical analysis in the Animal Nutrition Laboratory of the Veterinary Faculty of UNAM using standardized techniques. Crude protein content was determined by estimating total N by the macro-Kjeldahl technique and multiplying the results by 6.25. Crude Fiber was determined following the procedure described in Flores [1981], and soluble carbohydrate content of fruit was determined with the phenol-sulphuric acid method [Dubois et al, 1956]. Results of these analyses were used to assess food profitability by examining the protein:fiber ratio in the case of leaves and the soluble carbohydrate:fiber ratio in the case of fruit.

Relative Abundance of Resources

Data derived from censusing all trees ≥ 10.0 m in height in three 1-ha plots were used to assess relative abundance of tree species [Estrada, 1984]. Relative availability of food resources over time was estimated by phenological observations of trees of some of the most important species in the diet of howling monkeys, recorded twice a month for three consecutive years in the three 1-ha plots. Several tree species not used by the monkeys were also included in the phenological study.

RESULTS

Censuses

The censuses indicated that the eight species of mammals representing the orders Primates, Rodentia, Carnivora, and Marsupialia occurred at variable densities ranging from 0.01 ind/ha (*A. geoffroyi*) to 1.0 ind/ha (*S. deppoi*) and ranged in size from 190 g (*S. deppoi*) to 7,340 g (*A. geoffroyi*). Within the home range of the focal howling monkey troop, the most common of these mammals were the *Sciurus* species and the marsupials (Table I).

TABLE I. Arboreal Mammals With Which Howling Monkeys Share the Forest Canopy

Species	WT (g) \pm SD	ind/km ²	HR ^b	g/ha	TL/H ^c
<i>Alouatta palliata</i> (howling monkey)	7,000 \pm 250 (12) ^a	23.0	60	1,280	FFr/D
<i>Ateles geoffroyi</i> (spider monkey)	7,340 \pm 180 (6)	1.4	200	60	Fr/D
<i>Potos flavus</i> (kinkajou)	2,500 \pm 135 (4)	12.5	8	420	CFr/N
<i>Bassariscus sumichrasti</i> (ring-tailed cat)	1,035 \pm 80 (5)	20.2	12	207	CFr/N
<i>Coendou mexicanus</i> (arboreal porcupine)	3,500 \pm 350 (4)	15.0	10	525	GFr/N
<i>Sciurus deppoi</i> (deppe squirrel)	190 \pm 25 (6)	100.0	1.5	190	GFr/D
<i>Sciurus aureogaster</i> (gray squirrel)	350 \pm 55 (7)	70.0	2.0	318	GFr/D
<i>Didelphis marsupialis</i> (common opossum)	2,250 \pm 175 (10)	80.0	—	1,800	CFr/N
<i>Philander opossum</i> (four-eyed opossum)	320 \pm 37 (8)	54.0	—	173	CFr/N

^aParenthesis = number of animals from which weight was obtained.

^bHR = home range size (ha).

^cTL = trophic level (C = carnivore, Fr = frugivore, F = folivore, G = granivore); H = habits (N = nocturnal, D = diurnal).

Home Range Size and Biomass

Estimated home range size based on observations of primate troops and of selected individuals in the case of the other mammals ranged from 1.5 ha (*S. deppei*) to 200 ha (*A. geoffroyi*) (Table I). Biomass estimates indicate that the most important contributors to the mammalian biomass on a per hectare basis were *D. marsupialis* followed by *A. palliata*. Other important contributors were *C. mexicanus*, *P. flavus*, and *S. aureogaster*. As a group, the eight arboreal mammals contributed 77% of the total arboreal mammalian biomass under consideration, while *Alouatta* contributed 23% (Table I).

Vertical Preferences

Data on vertical preferences by the arboreal mammals studied indicate that they displayed varying degrees of arboreality (Table II). Those strictly arboreal were *A. palliata*, *A. geoffroyi*, *C. mexicanus*, *P. flavus*, and *B. sumichrasti*. The data also showed that forest level preferences were variable but with some evident patterns. The two primate species were basically inhabitants of the middle and upper levels of the forest, displaying a preference for the latter which accounted for 70% of the records scored (Table II). *P. flavus*, *B. sumichrasti*, and *C. mexicanus* displayed evident preferences for the middle level of the forest. The two *Sciurus* species and the marsupials were more mobile vertically and spent 30–60% of the time on the ground (Table II).

Foraging Preferences

Leaf eating. Aside from *Alouatta*, only the spider monkey (*Ateles*) and the arboreal porcupine (*Coendou*) are consumers of foliage in the same vertical levels occupied by howling monkeys. However, leaf consumption by these two mammals represents only about 20% of their feeding time; the remaining 80% of the time is spent feeding on fruit (Table II). Our estimates of consumption rates of leaves by howling monkeys (with a biomass of 1.28 kg/ha) at Los Tuxtlas yielded 33.0 kg ha⁻¹yr⁻¹ whereas estimates for the arboreal porcupine (with a biomass of 0.53 kg/ha) and the spider monkey (with a biomass of 0.06 kg/ha) yielded 8.0 kg ha⁻¹ yr⁻¹ and 1.4 kg ha⁻¹ yr⁻¹, respectively.

A. geoffroyi and *C. mexicanus* displayed a marked preference for young leaves of several species of Moraceae, such as *Ficus* spp, *Brosimum alicastrum*, *Pseudol-*

TABLE II. Vertical and Feeding Preferences by Arboreal Mammals at Los Tuxtlas

Taxa	Forest ^a level			Food part			Hours ^d
	L (%)	M (%)	U (%)	Leaves (%)	Fruit (%)	Other ^b (%)	
<i>A. palliata</i>	—	30	70	48	50	2 ^c	950
<i>A. geoffroyi</i>	—	30	70	20	80	—	145
<i>P. flavus</i>	—	60	40	—	52	48	250
<i>B. sumichrasti</i>	—	60	40	—	40	60	300
<i>C. mexicanus</i>	—	75	25	18	82	—	220
<i>S. deppei</i>	30	40	30	5	95	—	150
<i>S. aureogaster</i>	30	40	30	10	90	—	150
<i>B. marsupialis</i>	60	25	15	—	38	62	130
<i>P. opossum</i>	50	30	20	—	52	48	140

^aL = lower (0–10 m), M = middle (10–20 m), U = upper (> 20 m).

^bFlowers, insects, small vertebrates.

^cFlowers.

^dHours of observation on each mammal during a 12-month period.

media oxyphyllaria, and *Cecropia obtusifolia*. Aside from these two mammals, the only other important vertebrate folivore in this forest is a reptile (*Iguana iguana*) that consumes mostly mature foliage of vines, lianas, and trees.

Fruit eating. Fruit eating is an important activity in *Alouatta* and the other arboreal mammals (Table II). Estimates of consumption rates of fruit indicate that arboreal mammals as a group consume 84 kg dry weight of fruit per hectare per year. Of this amount, 76% is consumed by the eight arboreal mammals under consideration (Table III). The eight species in question were observed to consume the ripe fruits of the above-mentioned plant species.

Density of Plant Species and Phenology of Fruits and Leaves

Data from the census of three 1-ha vegetation plots within the home range of the howling monkey troop indicate that 92% of the tree species ($N = 53$; 312 trees ≥ 10 m in height) censused occur at densities ≤ 4.0 ind/ha. Phenological censuses of the same plots indicate that the production of leaves in the most important tree species used by howling monkeys is characterized by a seasonal pattern: young leaves are produced mainly from March to June. Fruit production is very seasonal at the species level and tends to be asynchronous among species. Of 20 species examined, only two appear to produce fruit in every month of the year: *Ficus* spp and *C. obtusifolia* (Fig. 1).

Nutritional Value of Leaves and Fruit

The young leaves consumed by howling monkeys, when contrasted with mature leaves, are a more important source of protein ($\bar{X} 16.7 \pm 5.2$ vs $\bar{X} = 12.6 \pm 4.2$; $N = 14$ spp). They contain less fiber ($\bar{X} = 17.2 \pm 1.8$ vs $\bar{X} = 26.8 \pm 0.6$; $N = 16$ spp), and they possess from moderate to low amounts of secondary compounds such as alkaloids [Estrada, 1984].

Although variations in the proportion of important nutrients in fruit pulp was found in 12 tree species examined, some patterns were evident in the case of the most popular species in the fruit diet. Fruit that are available year-round (eg, *Ficus* spp and *C. obtusifolia*) have low nutritional value (ie, soluble carbohydrates) and are rich in fiber. In contrast, fruits of species that are seasonally available (eg, *Brosimum alicastrum*) are more nutritionally valuable, thus offering higher rewards to frugivores (Fig. 2). While the fruits of species such as *Ficus* and *Cecropia* may be relatively undesirable in quality, they are available year-round in large quantities and thus constitute a more predictable or constant food source. On the other hand, the more nutritious fruit species are available only for a short period of time each year (Figs. 1, 2).

TABLE III. Removal Rates of Fruit by Arboreal Mammals as Calculated With the Formula $70 W^{.75}$ kcal/day (see text)

Taxa	Dry weight of fruit removed (kg/ha/yr)
<i>Alouatta palliata</i>	20
<i>Ateles geoffroyi</i>	5
<i>Potos flavus</i>	5
<i>Bassariscus sumichrasti</i>	4
<i>Coendou mexicanus</i>	5
<i>Sciurus deppei</i>	6
<i>Sciurus aureogaster</i>	6
<i>Didelphis marsupialis</i>	30
<i>Philander opossum</i>	3

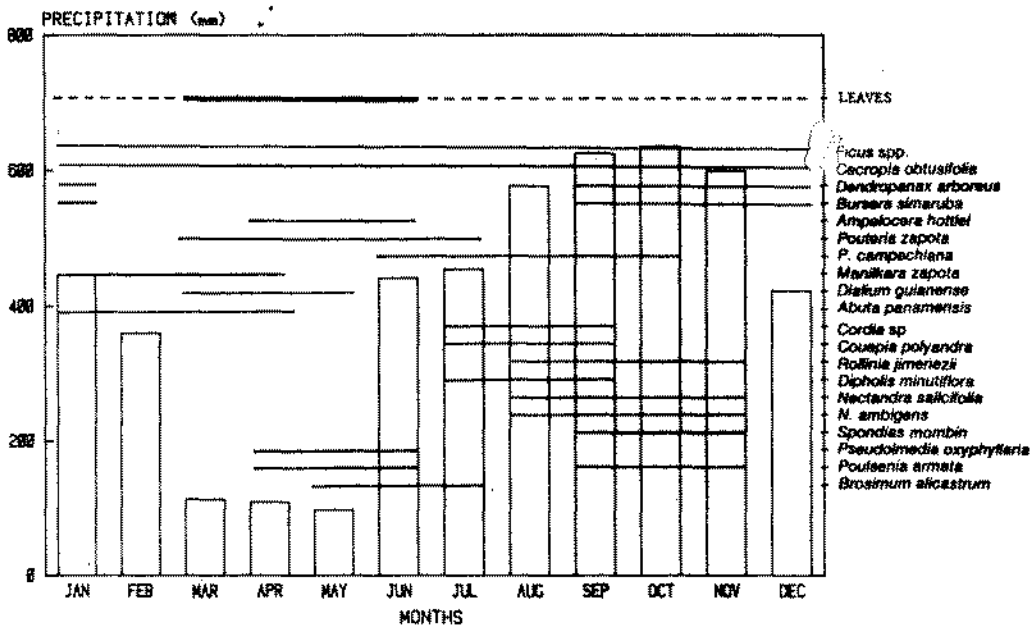


Fig. 1. Monthly precipitation (bars) and phenological patterns (horizontal lines) for leaf and fruit production of selected tree species at Los Tuxtlas. The continuous line in leaf production indicates major synchrony (leaf flush and new leaves) among the majority of the middle and upper canopy tree species; the broken line indicates a lower number of species producing new leaves in the rest of the months. Fruit-producing months are indicated by the continuous lines for each of the species listed.

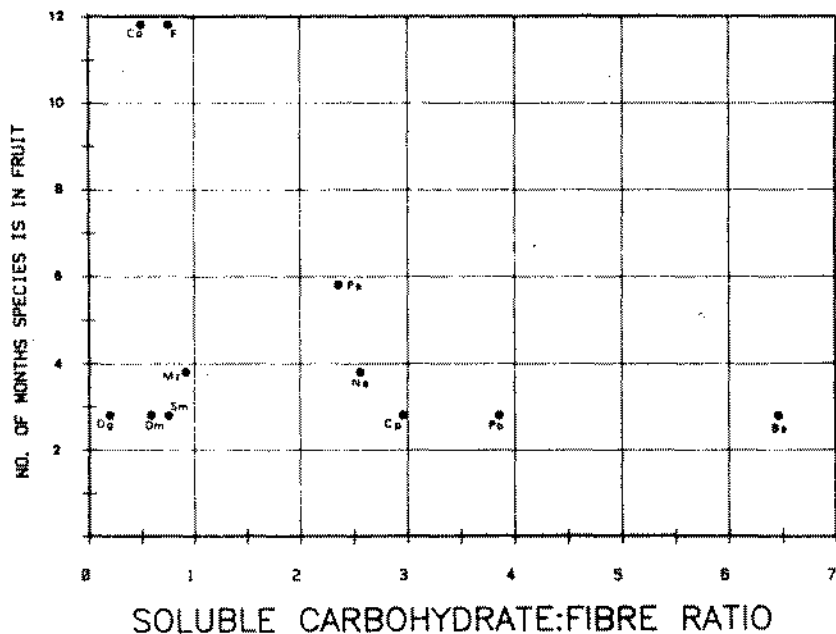


Fig. 2. Soluble carbohydrate:fibre ratio of fruit and number of months in which the species is in fruit in selected tree species. High values in the X axis indicate low fiber content. F = *Ficus* spp (Moraceae), Na = *Nectandra ambigens* (Lauraceae), Pa = *Poulsenia armata* (Moraceae), Ba = *Brosimum alicastrum* (Moraceae), Po = *Pseudoimedia oxyphyllaria* (Moraceae), Co = *Cecropia obtusifolia* (Moraceae), Sm = *Spondias mombin* (Anacardiaceae), Dg = *Dialium guianense* (Leguminosae), Cp = *Couepia polyandra* (Rosaceae), As = *Manilkara zapota* (Sapotaceae), Dm = *Dipholis minutiflora* (Sapotaceae).

DISCUSSION

It is evident from the data reported here that arboreal mammals other than *Alouatta*, despite some marked differences in habits (eg, diurnality versus nocturnality), contribute to resource depression. This suggests that the leaves and fruits of the plant species used by these mammals have morphological and chemical components that these animals are capable of processing to satisfy nutritional requirements. These components are, evidently, recognized and sought out by animals in distantly related taxa and these animals thus converge on specific subsets of species and/or individual plants.

Leaf Eating

While *Alouatta* is not a true folivore in the strict sense of the term, it is the only arboreal mammalian folivore in the forest of Los Tuxtlas that depends on leaves for a significant proportion of its diet. The sloths (genus *Bradypus* and *Choloepus*), the most important mammalian arboreal folivores in the forests of Central and South America [Eisenberg & Thorington, 1973], do not occur in Mexico. Their northernmost extension in the neotropics is found, apparently, in Honduras [Novak & Paradiso, 1983]. On Barro Colorado Island (BCI) in Panama, the sloths eat about 160 kg dry weight of leaves per hectare per year versus 41 kg dry weight of leaves per hectare per year consumed by *Alouatta* [Leigh & Windsor, 1982]. Sloths, then, may be important in the foraging ecology of howling monkeys on BCI. At Los Tuxtlas, *Alouatta* faces no pressure from sloths, and while the arboreal porcupine consumes more leaves than spider monkeys, our observations indicate that this plant part constitutes a minor element in the porcupine diet. However, it is important to note that these mammalian herbivores recognize the same palatable species (eg, *Cecropia obtusifolia*, *Ficus* spp, etc). The predominance of young leaves in the diet confirms that this plant is the major source of protein for howling monkeys [Milton, 1980; Estrada, 1984] and a complementary source of protein for *A. geoffroyi* and *C. mexicanus*.

Alouatta apparently faces little feeding overlap with other leaf-eating vertebrates in this forest. Feeding overlap with the reptile *I. iguana* is probably minimal, as consumption by the primate is concentrated on young leaves whereas *I. iguana* seems to prefer mature foliage [Estrada, unpublished data; see Rand, 1978, for a review of feeding habits of iguanas]. Insect herbivores, however, are major consumers of leaves. Herbivory studies on BCI indicate that young leaves are eaten much more rapidly than are old leaves by herbivorous insects [Coley, 1982]. Of the great variety of insects that use young and mature foliage in the forest canopy, leaf-cutting ants may be one of the most important removers of foliage in tropical rain forests [Cherret, 1968; Rockwood, 1976], and they alone may consume more foliage than all vertebrates combined [Leigh & Windsor, 1982].

Our observations during 12 months on the foraging behavior of two mature colonies of leaf-cutting ants (*Atta*) in the forest of Los Tuxtlas indicate that 80% (N = 150) of the trees from which they harvest young leaves intensively belong to the upper and middle forest levels. Among the ten most important tree species used as sources of young leaves by *Atta* are the most important tree species used by howling monkeys as sources of the same plant part. Our estimates of removal rates of leaves by leaf-cutting ants (which at Los Tuxtlas occur at a density of 1.13 mature nests per hectare) yield from 90 to 120 kg ha⁻¹ yr⁻¹, as contrasted with 33.0 ha⁻¹ yr⁻¹ removed by howling monkeys [Estrada & Coates-Estrada, unpublished data]. In Panama, leaf-cutting ants take from 90 to 300 kg of leaves per hectare per year versus 41 kg taken by howling monkeys represented by a biomass of 4.2 kg/ha [Leigh & Windsor, 1982]. The contrasting rates of removal of foliage by *Alouatta*

and leaf-cutting ants attest to the important impact of insect herbivores upon the availability of leaf resources for *Alouatta* [see Rockwood & Glander, 1979, for a comparative study of leaf-cutting ants and howling monkeys in Costa Rica].

Fruit Eating

Fruit production in tropical forests is seasonal [Frankie et al, 1974; Foster, 1982a] and, on occasion, erratic. This contributes to the convergence of frugivores and at times to a general condition of famine [see Foster, 1982b, for an example on BCI, Panama]. Under these circumstances, frugivores may compete with one another for food. At Los Tuxtlas, both the arboreal seed eaters (the rodents) and the arboreal fruit pulp eaters (*A. geoffroyi*, *P. flavus*, etc), together with birds and bats, remove fruit, making it unavailable to howling monkeys and other fruit-eating animals. For example, our observations of one fig tree showed that while fruit production lasted 52 days, 43% of the entire crop was shed in a brief period of 6 days. Further, while *Alouatta* consumed 12.0% of figs eaten by frugivores, the remaining 88.0% of the fruit was consumed by birds (49.0%) and by bats and other mammals (39.0%) [Estrada & Coates-Estrada, unpublished data].

Resource Overlap or Potential Competition?

The forest of Los Tuxtlas is characterized, as are other tropical forests, by a high species diversity with low densities for individual species. Seasonal production of leaves, flowers, and fruits during the year and year-to-year irregularities in phenological patterns are common in many plant species. This variability places arboreal mammals on unpredictable grounds regarding availability of resources [Foster, 1982b; Smythe et al, 1982]. One could argue that direct and indirect competition might exist between *Alouatta* and other diurnal and nocturnal arboreal mammals, since the selection of a fruit either for pulp or seeds by animals other than howling monkeys results in its loss to the latter [see Gautier-Hion et al, 1980 for an example of potential competition in primates, ruminants, and squirrels; see Kantak, 1981, for avian frugivores]. Similar arguments could be made regarding the use of young leaves as a source of food by howling monkeys. Leaves are young for a very short period of time, after which they undergo mechanical and chemical changes and lose some of their nutritional and energetic value to herbivores [Milton, 1980; Coley, 1982]. Thus, removal of young leaves by animals other than *Alouatta* may also influence the ability of howling monkeys to find enough resources in the forest to satisfy protein requirements.

Resource overlap, however, does not necessarily indicate competition. Factors that tend to reduce levels of potential competition among species include differences in diet, foraging techniques, habitat preferences, and general habits [Fleming, 1979; Pianka, 1974]. In the case of frugivory and folivory, differences in fruit and leaf morphology and chemistry may also reduce potential competition. It is thus important to emphasize that while *Alouatta* shares the canopy with other arboreal mammals, these differ markedly in body size, group size, ranging patterns, population density, and activity cycles. Further, for the majority, fruit and/or leaves are only complementary to their diets, plant material other than leaves and fruit pulp (eg, seeds) and nonplant material (eg, insects and small vertebrates) being important constituents.

While competition among tropical vertebrates is difficult to measure, it is clear that resources are removed during the day and at night by an assemblage of folivores and frugivores. Howling monkeys therefore have to adapt not only to the patchy nature of leaf and fruit production in a particular set of tree species, but also to resource depression caused by other herbivores in the forest canopy. They may

respond to these pressures by shifting preferences for particular species in a nonrandom opportunistic fashion and by traveling long distances in the search of resources [Estrada, 1984; Estrada & Coates-Estrada, 1984]. Although living in a permanent social group has advantages for individuals through the sharing of a bank of information on the location (in time and space) of food [see Hamilton, 1981], unpredictable environmental variables such as resource depression by other forest canopy animals, coupled with irregularities in the phenology of plants, may offset the success with which food is procured. Most studies of foraging behavior of neotropical primates have looked at such aspects as the selection, quality, size, location, and availability, in time and space, of food patches; our study suggests that resource overlap with other animals with which the canopy is shared may be another important variable influencing foraging behavior.

CONCLUSIONS

1. Howling monkeys in Los Tuxtlas overlap in vertical preferences and trophic level with eight arboreal mammals.
2. The arboreal porcupine and the spider monkey are the only other mammalian folivores, but their competitive potential for *Alouatta* is very low as a result of the minor role played by leaves in their diets.
3. Insect herbivores (eg, leaf-cutting ants) may inflict a greater impact upon howling monkey leaf sources than that exerted by other arboreal mammals.
4. Arboreal mammals other than *Alouatta* account for 77% of the arboreal mammalian biomass under consideration, and they consume five times as much fruit as howling monkeys per hectare per month, contributing, therefore, with frugivorous birds and bats, to resource depression in the canopy.

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