

Comparison of Frugivory by Howling Monkeys (*Alouatta palliata*) and Bats (*Artibeus jamaicensis*) in the Tropical Rain Forest of Los Tuxtlas, Mexico

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Information on the fruit diets of howling monkeys and fruit-eating bats in the tropical rain forest of Los Tuxtlas, Mexico was collected for a year to compare the plant species used. Howling monkeys used 19 plant species whereas bats used 32 plant species as fruit sources. Eleven species were common in the diet of both mammals. A rank analysis at the plant species level showed that the fruit diets of *Alouatta* and *Artibeus* were very different. In contrast to bats, howling monkeys displayed a seasonal pattern in fruit consumption. Diet overlap between the two mammals was highest during the monkeys' fruit-eating season. Measures of fruit production in eight trees (four species) indicated marked variations in fruit biomass produced and in length of fruiting from tree to tree and species to species. Peaks in fruit production were typical both at the species and the individual tree levels, demonstrating the very patchy nature of the fruit available to the monkeys and the bats.

Key words: *Alouatta*, Howling monkeys, *Artibeus*, frugivory, resource partitioning

INTRODUCTION

One of the most conspicuous features of tropical rain forests is the great number of plants with fleshy fruits. These fruits serve as attractants to a wide variety of birds and mammals that use the fruit as an important part of their yearly diet [Frankie et al, 1974]. Quantitative studies on frugivory in tropical rain forests are concentrated primarily on the study of frugivorous birds and bats that (through the dispersal of seeds) are important contributors to the floristic and spatial heterogeneity of the ecosystem [Snow, 1971; Howe, 1977; Cruz, 1981; Fleming & Heithaus, 1981]. Many forest animals share food resources; thus, the study of dietary overlap among members of a community may help us understand community structure, flexibility in feeding adaptation, and ecological diversity [Schoener, 1974].

One of the most evident mammals inhabiting the forest canopy at Los Tuxtlas, Mexico, is the howling monkey. Our research on the behavioral ecology of *Alouatta*

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palliata at Los Tuxtlas has shown that *Alouatta* maintains the following types of relationships with the plants in the forest: 1) as herbivores consuming leaves and fruits of a particular group of tree species [Estrada, 1982; Estrada, 1984], they participate as primary consumers in the cycling of nutrients and energy in the ecosystem, and 2) as important dispersal agents of the seeds of several tree species, they participate in the natural process of rain forest regeneration and in the reproductive strategy of particular tree species [Estrada and Coates-Estrada, in press]. Another phase of this research concerns the ways in which howling monkeys share the resources with other animals in the forest, both as leaf-eaters and as fruit-eaters.

There are few comparative studies of frugivores and even fewer that consider the entire annual cycle; most focus on one section of the year or on one plant. Likewise, reports of interactions of Neotropical primates with nonprimate forest animals are scant, and only a few studies are available in the case of *Alouatta* [Glander, 1979; Rockwood & Glander, 1979; Young, 1982].

At Los Tuxtlas, howling monkeys display a particular preference for fleshy fruits with a sugary pulp when ripe. Data indicate that they spend about half their annual feeding time eating fruit, especially mature fruit [Estrada & Coates-Estrada, 1984]. In fact, for *Alouatta* fruit is more important than leaves during several months of the year, when it accounts for 80% of total feeding time per month [Estrada, unpublished manuscript].

The frugivorous niche of howling monkeys is shared with a wide array of birds and a small cluster of arboreal and volant mammals [Estrada & Coates-Estrada, unpublished manuscript]. The volant mammals are represented by about 40 species, of which 12 are frugivorous bats of the family Phyllostomatidae. They range in size from 14 to 176 gm, and most of them are gregarious, roosting in colonies varying in size from 50 to 500 individuals. At the study site, *Artibeus jamaicensis* (20–50 gm) is the most common of the Phyllostomatidae, as estimated from the number of colonies sighted in caves and tree hollows and from mist net trapping in the forest at night [Navarro, 1982, personal observations]. Morrison [1978] reports that, in Panama, this bat is mainly frugivorous although it supplements its diet with insects. Observations at Los Tuxtlas by Vasquez-Yanes et al [1975] show a predominance of fruit in its diet.

Because of the conspicuous presence of this bat species in forest inhabited by howling monkeys and its documented preference [Vasquez-Yanes et al, 1975] for the fruits of some of the same tree species exploited by the howling monkeys, we decided to investigate and compare the composition, diversity, and seasonality of the fruit diet of *Alouatta palliata* and of *Artibeus jamaicensis*.

METHODS

Research was carried out at the Estacion de Biologia Tropical "Los Tuxtlas", located at 95°04' W longitude and 18°34' N latitude in the easter portion of the volcanic range Sierra de Los Tuxtlas in the southern portion of the state of Veracruz. The station's reserve covers an area of 700 ha, in which the dominant vegetation type is the "high evergreen rain forest" (*sensu* Miranda & Hernandez [1963]).

The climate 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 ± 87.0 mm) from June to February and a "dry season" (\bar{x} = 11.7 ± 11.7 mm) from March to May. Mean annual precipitation is 4,500 mm (N = 10 years) [see Estrada, 1982; Estrada, 1984, and Estrada et al, in press, for further details].

During a 12-month period (May 1980–May 1981), the fruit-eating preferences of troop S (N = 16), one of three howler groups with marked individuals, were observed. We obtained monthly records of their fruit-eating preferences (see Estrada & Coates-

Estrada, in press, for details). At the same time, a cave colony of *Artibeus jamaicensis* was sampled about 1.0 km from the forested area inhabited by the howling monkeys. The original rain forest around the cave has been destroyed and replaced by grass lands, and all that remains are a few trees [see Vasquez-Yanes et al, 1975; and Orozco-Segovia & Vasquez-Yanes, 1982 for detail]. The nearest area of undisturbed forest is that of the research station, and although no attempts were made to trap and mark the bats, we assumed that they tended to use the plant resources found in the reserve's land.

The roof of the cave is used by the bats for roosting. Our observations of the bats in the cave indicate that they feed on the fruits, brought from the forest, while hanging upside down. The seeds and uneaten pulp are dropped to the ground along with their excrement. To catch these remains, a nylon trap 3m² in size was placed about half a meter above the floor of the cave under the clusters of bats.

The debris was retrieved once a month during the 12-month period. The seeds were separated from the debris, identified as to genus and species, and weighed to determine the relative contribution of each species to the monthly sample [Vasquez-Yanes et al, 1975; Orozco-Segovia & Vasquez-Yanes, 1982]. Although the information on the bat's diet obtained from these samples was biased in the sense that large-seeded fruits were very likely excluded, the information is useful for several reasons. Alternative methods, such as visual observations (as in the case of howling monkeys) or mist net trapping of bats, could not include evidence of all of the species used by the animals unless the observer was with them 24 hours a day. If the use of species by monkeys and/or bats is frequent enough, partial sampling through observations and/or examination of feeding debris and fecal material should reflect the differential importance of species in their diet. Finally, it is important to point out that the data obtained on the feeding preferences of monkeys and bats are estimates; that the comparison of their fruit diets was done at the level of species used; and that no attempt was made to compare rates of use per species, as the original data were not recorded with comparable methods [see Orozco-Segovia & Vasquez-Yanes, 1982; Estrada & Coates-Estrada, 1984].

Availability of fruit in six of the most important tree species used by bats and howling monkeys was measured by conducting phenological censuses of 110 trees \geq 10 m in height along three belt transects (500 \times 20 m) located in the area of forest where the howling monkeys were studied. Every 15 days for 12 months, records were obtained of the presence or absence of fruit in each tree.

Fruit biomass available to the frugivores was measured by sampling the productivity of eight trees of four of the most important species in their diets. These trees had been used as fruit sources by *Alouatta* in other years as well as during the study period reported [Estrada, unpublished manuscript]. Fruit-traps, 0.50 m in diameter and 0.50 m above the ground (following the standards of the International Biological Programme), were placed under the shadow of the crown of the selected trees. The number of traps (16–200) placed under each tree was determined by the need to sample between 5 and 10% of the crown cover. The traps were placed before the beginning of fruiting in each tree, and their contents were removed every 2 days until the end of the fruiting period. The fruits collected in the traps were counted and weighed before and after drying at a constant temperature. Total fruit crop was estimated from the number of fruits counted and from the entire size of the tree crown. Fruit biomass was calculated as dry weight/gm from the dried fruit samples and extrapolated to the entire fruit crop. Although these calculations were not adjusted for the number of fruits removed by frugivores, we believe that the amounts of fruit measured reflect the general pulses of fruit production for each individual tree.

RESULTS

Plant Species Used

The results of the observations on the howling monkeys and of the examination of the contents of the trap in the bat cave indicate that the monkeys used 19 plant species representing ten families and that the bats used 32 plant species representing 14 families as sources of fruit. Only 11 of the species were shared by both mammals (Table I).

A rank analysis similar to that used by Rockwood and Glander [1979] in their comparative study of leaf-cutting ants and howling monkeys was applied to our data. Analysis showed that the dietary preferences of *Artibeus* and *Alouatta* at the

TABLE I. Complete List of Plant Species Used (X) by *Artibeus jamaicensis* and *Alouatta palliata*: Also Indicated Are Those Species Shared by Both Mammals

| Species | Family | Artibeus | Alouatta |
|----------------------------------|------------------|----------|----------|
| <i>Ficus glabrata</i> | Moraceae | X | X |
| <i>Ficus hartwegii</i> | Moraceae | X | |
| <i>Ficus insipida</i> | Moraceae | X | X |
| <i>Ficus obtusifolia</i> | Moraceae | X | X |
| <i>Ficus</i> sp. (1) | Moraceae | X | |
| <i>Ficus</i> sp. (2) | Moraceae | X | |
| <i>Cecropia obtusifolia</i> | Moraceae | X | X |
| <i>Brosimum alicastrum</i> | Moraceae | X | X |
| <i>Poulsenia armata</i> | Moraceae | X | X |
| <i>Pseudolmedia oxyphyllaria</i> | Moraceae | X | X |
| <i>Nectandra ambigens</i> | Lauraceae | X | X |
| <i>Pouteria campechiana</i> | Sapotaceae | X | X |
| <i>Manilkara sapota</i> | Sapotaceae | X | X |
| <i>Pouteria unicularis</i> | Sapotaceae | X | |
| <i>Mastichodendrum capiri</i> | Sapotaceae | X | |
| <i>Dipholis minutiflora</i> | Sapotaceae | | X |
| #1 | Sapotaceae | | X |
| <i>Spondias mombin</i> | Anacardiaceae | X | X |
| <i>Cynometra retusa</i> | Leguminosae | X | |
| <i>Dialium guianense</i> | Leguminosae | | X |
| <i>Trema micrantha</i> | Ulmaceae | X | |
| <i>Ampelocera hottlei</i> | Ulmaceae | | X |
| <i>Cordia</i> sp. | Boraginaceae | | X |
| <i>Bellotia mexicana</i> | Tiliaceae | | X |
| <i>Guarea chichon</i> | Meliaceae | | X |
| <i>Bursera simaruba</i> | Burseraceae | | X |
| <i>Licania</i> sp. | Chrysobalanaceae | X | |
| <i>Calophyllum brasiliense</i> | Guttiferae | X | |
| <i>Quararibea funebris</i> | Bombacaceae | X | |
| <i>Diospiros digina</i> | Ebenaceae | X | |
| <i>Turpinia pinata</i> | Staphylaceae | X | |
| <i>Anthurium</i> sp. | Araceae | X | |
| <i>Solanum</i> sp. #1 | Solanaceae | X | |
| <i>Solanum</i> sp. #2 | Solanaceae | X | |
| <i>Solanum</i> sp. #3 | Solanaceae | X | |
| <i>Piper amalago</i> | Piperaceae | X | |
| <i>Piper hispidum</i> | Piperaceae | X | |
| <i>Piper lapathifolium</i> | Piperaceae | X | |
| <i>Piper sanctum</i> | Piperaceae | X | |
| <i>Piper auritum</i> | Piperaceae | X | |

plant species level were very different (Kendall's rank correlation coefficient = 0.166, n.s.). While *Alouatta* used only trees of the upper and middle canopy (≥ 10 m), *Artibeus* also exploited many plant species typical of the forest floor and of secondary growth (eg, *Piper* spp., *Solanum* spp.). In both mammals, however, there was a similar behavioral tendency to be species-selective. For example, seven species in the fruit diet of *Artibeus* and *Alouatta* accounted for 90% of the records in each case [Orozco-Segovia & Vasquez-Yanes, 1982; Estrada and Coates-Estrada, 1984]. Five of these fruit species (*Ficus glabrata*, *Ficus insipida*, *Ficus obtusifolia*, *Brosimum alicastrum*, *Cecropia obtusifolia*) were common in the fruit diet of both bats and howling monkeys. At the family level, we found 70% overlap in the case of the Moraceae, 100% in the case of the Lauraceae and Anacardiaceae, and 50% in the case of the Sapotaceae.

Seasonality in the Use of Fruit Sources

Monthly species diversity in the diet of *Artibeus* and *Alouatta* plotted against the months of the year indicate a more seasonal exploitation of fruit by *Alouatta* (Fig. 1). Monthly overlap at the plant species level was measured by a simple index of similarity. The index range from zero to 1.0, indicating null to 100% overlap between *Alouatta* and *Artibeus*, ($CC = 2(S_{xy}/S_x + S_y)$, where S_{xy} stands for the number of species common to the two frugivores in 1 month and S_x and S_y are the total number of species used by each frugivore in that same month; [Pielou, 1977]). The values ranged from 0.20 to 0.57 with the highest values between April and August (range 0.30 to 0.57), when fruit-eating was an important activity in *Alouatta*.

The phenological records obtained on trees of six of the most important species in the diet of *Alouatta* and *Artibeus* indicated a marked seasonality in fruit produc-

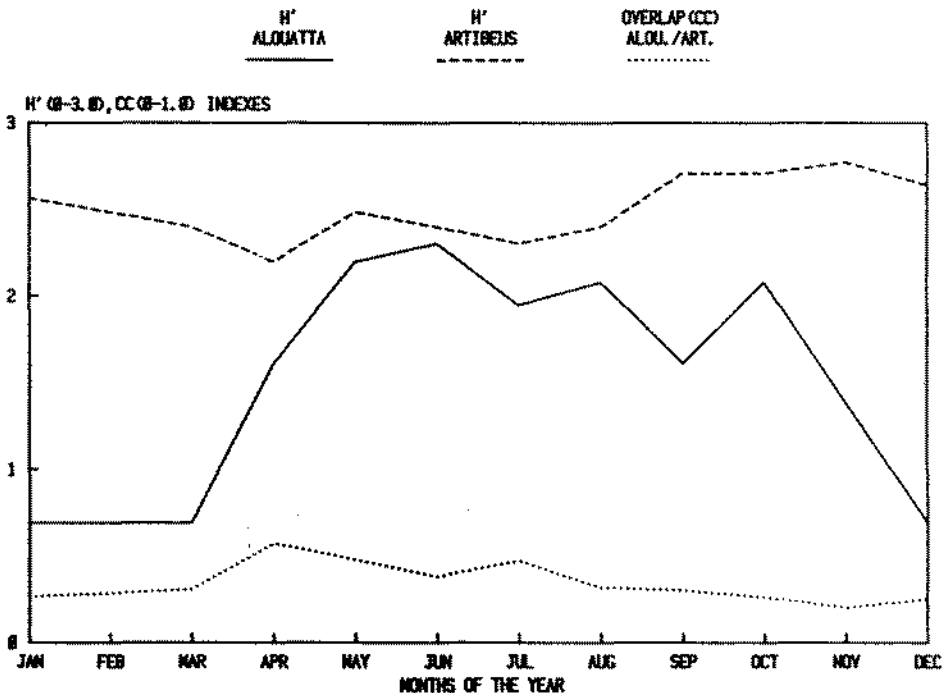


Fig. 1. Monthly species diversity (H') in the fruit diet of *Alouatta* and *Artibeus* and monthly overlap (CC) in their diet. Note the marked seasonality in fruit-eating in *Alouatta*.

tion (Fig. 2). Particularly important was the production of fruit between April and October, which coincided with the marked increase of fruit-eating in *Alouatta*. Further, the tree species were characterized by unimodal (eg, *Nectandra ambigens*) or bimodal (eg, *Poulsenia armata*) patterns in fruiting. Even "year-round" producers of fruit (eg, *Cecropia obtusifolia*) displayed some seasonality (Fig. 2).

Fruit Productivity in Selected Species

The results of the fruit productivity estimates (eight trees representing four tree species) indicated that, when total fruit biomass was considered, there was an apparent abundance of fruit (Table II). However, a careful examination of these data shows great variation in fruit biomass produced from species to species and from tree to tree in one species (Table II). In addition, the duration of fruiting was also very variable, ranging from six days in the case of a *Poulsenia armata* tree to 52 days in the case of a *Ficus* tree, and trees of different species did not fruit at the same time (Fig. 2).

Fruit produced per tree was not produced in the same quantities from day to day during the fruiting season. All the trees examined were characterized by peaks

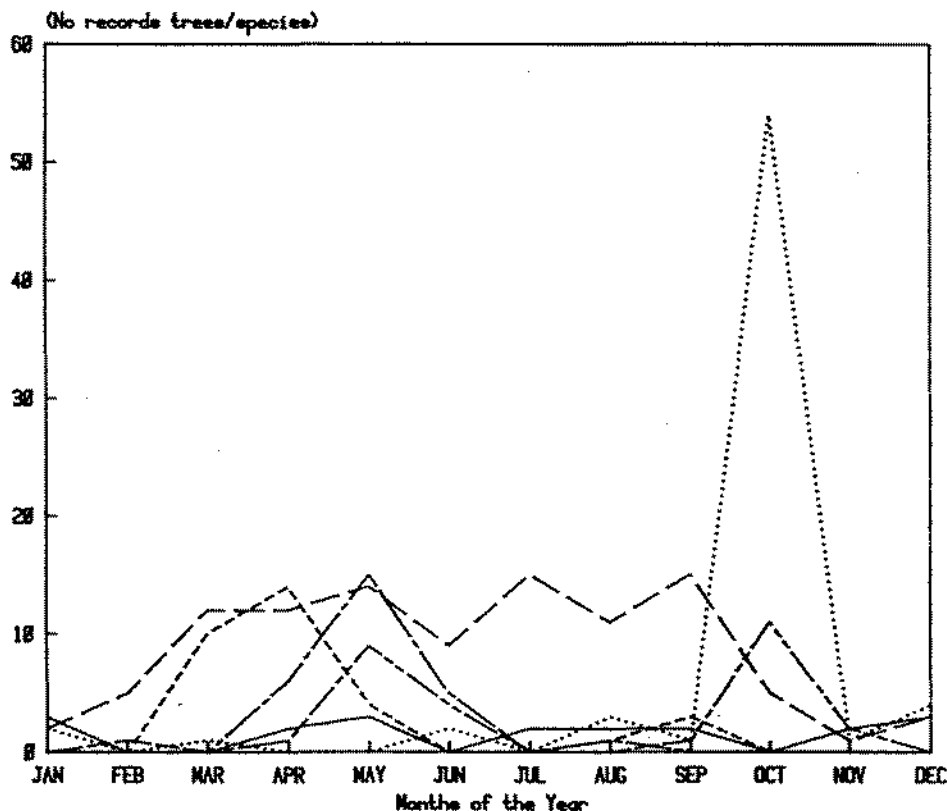


Fig. 2. Fruit phenology of trees of eight of the most popular species in the diet of *Artibeus* and *Alouatta*. Note marked seasonality and brief duration of fruit production per species. Number of records trees/species refers to presence of fruit in trees for each phenological census (see text). *Ficus* spp., — (N = 3); *Cecropia obtusifolia*, — — — (N = 8); *Brosimum alicastrum*, — — — (N = 11); *Poulsenia armata*, — — — (N = 10); *Pseudolmedia oxyphyllaria*, - - - - (N = 39); *Nectandra ambigens*, . . . (N = 39).

of fruit production, in some cases one (Fig. 3) and in others more than one (Fig. 4). For example, in the case of the *Ficus* sp. tree we examined, a peak in fruit production responsible for 43% of the total crop was recorded 18 days after the initiation of fruiting (Fig. 3). In spite of the fact that the total fruit crop was enormous and that total fruit production was 52 days long, the availability of about half the fruit crop

TABLE II. Results of Fruit Productivity Estimates in Eight Trees of the Most Popular Species in the Diet of Bats and Howling Monkeys: Note Great Variation in Duration of Fruiting, Total Crop, and Fruit Biomass Produced

| Tree species | Total crop ^a | Crop duration (days) | Crop biomass ^c (dry wt/gm) | Crown cover (m ²) |
|-------------------------------------|-------------------------|----------------------|---------------------------------------|-------------------------------|
| <i>Ficus</i> sp. | 76,888 | 52 | 9,995.51 | 1,345 |
| <i>Pseudolmedia oxyphyllaria</i> #1 | — ^b | — | — | 271 |
| <i>Pseudolmedia oxyphyllaria</i> #2 | 4,032 | 30 | 1,330.56 | 128 |
| <i>Pseudolmedia oxyphyllaria</i> #3 | 13,060 | 30 | 4,766.90 | 180 |
| <i>Poulsenia armata</i> #1 | 3,040 | 17 | 10,396.80 | 240 |
| <i>Poulsenia armata</i> #2 | 2,560 | 6 | 8,038.80 | 256 |
| <i>Brosimum alicastrum</i> #1 | 9,190 | 14 | 4,000.00 | 216 |
| <i>Brosimum alicastrum</i> #2 | — ^b | — | — | 300 |

^aTotal number of fruits produced.

^bFruit production aborted (see text).

^cWeight of seeds excluded.

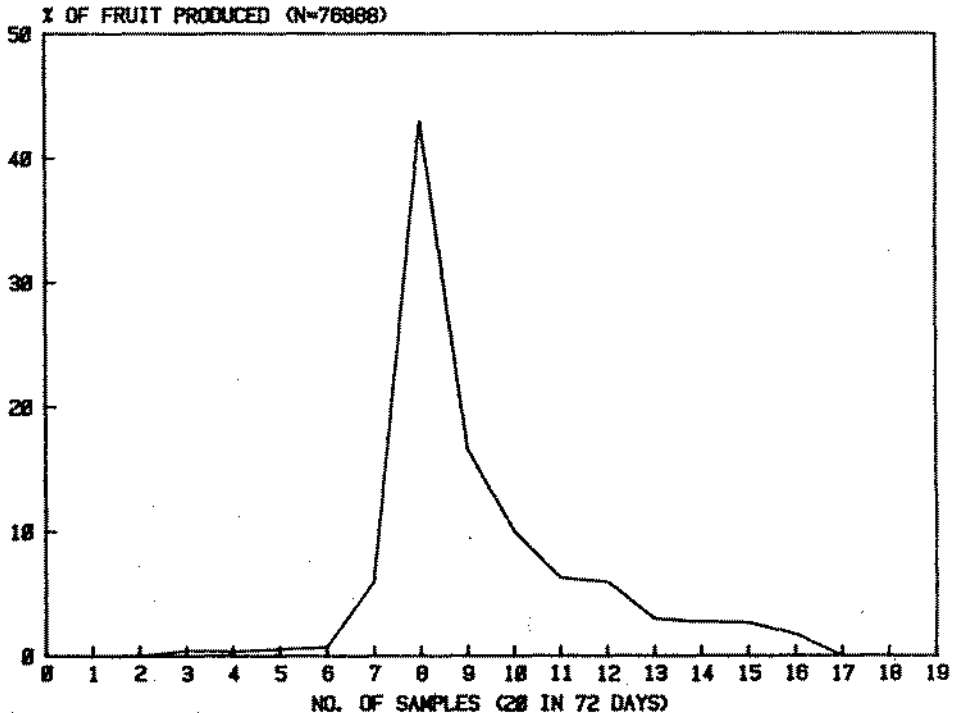


Fig. 3. Fruit production in a *Ficus* sp. tree. Peak responsible for 43% of total fruit crop occurred at 18 days after the initiation of fruiting. Availability of 43% of the fruit crop only lasted 6 days.

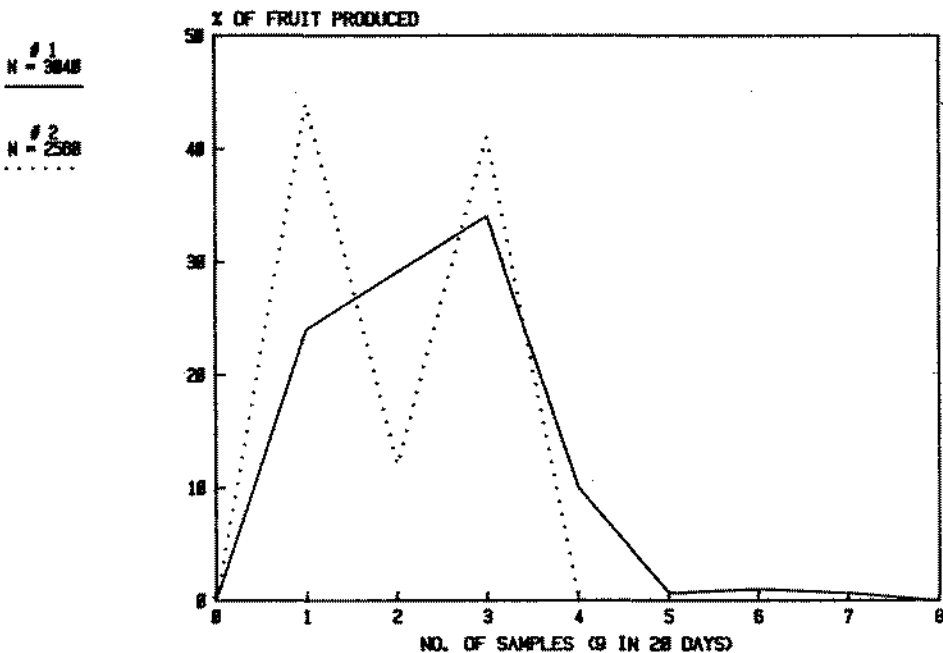


Fig. 4. Fruit production in two trees of *Poulsenia armata*. Note variation in total amount of fruit produced and shape of curves as well as differences in duration of fruit production between the two trees. In tree #2 the two peaks accounted for 85% of total fruit crop. Total fruiting time for tree #1 = 17 days and for tree #2 = 6 days (other parameters shown in Table II).

to frugivores was brief (about six days) and the rest was produced at a very slow rate and in a declining fashion after the major peak.

In the case of two additional trees representing the species *Pseudolmedia oxyphyllaria* and *Brosimum alicastrum*, fruit production was completely aborted as a result of strong southerly winds that blew away all their flowers.

DISCUSSION

The data showed that *Alouatta* and *Artibeus* used a small number of plant species as sources of fruit. The majority of the species used, 69% by *Artibeus* and 90% by *Alouatta*, were mature forest species, indicating the importance of this habitat to both mammals. Secondary growth species (eg, *Cecropia obtusifolia*, *Piper* spp.) are found in rain forest gaps produced by tree falls and at the man-produced forest edge, both of which habitats were visited by *Alouatta* and, apparently, more often by *Artibeus*.

The lower number of plant species used by *Alouatta* reflects the fact that howling monkeys also spend about half their annual feeding time eating leaves [Estrada, 1984] whereas fruit is the most important element in the diet of *Artibeus* [Morrison, 1978; this study].

The seasonality observed in *Alouatta* is apparently related to the exploitation of fruit of species of the Moraceae and of other families (eg, Lauraceae) that fruit during April to October. For example, the sharp increase in fruit consumption by howling monkeys in the early part of the year coincided with the production of fruit by species such as *Pseudolmedia oxyphyllaria*, *Brosimum alicastrum*, and *Poulsenia armata* and in the later part of the year (August to October) with the production of fruit by *Poulsenia armata* and *Nectandra ambigua*. Individuals of the genus *Ficus*

and *Cecropia* tend to fruit "year-round" and their use by *Alouatta* [Estrada & Coates-Estrada, 1984] and *Artibeus* [Orozco-Segovia & Vasquez-Yanes, 1982] throughout the year reflects the continuous availability of these fruits.

The high values of the overlap index found between April and August corresponded to the months of intensive fruit consumption by *Alouatta* of the Moraceae species that are seasonal fruit producers (eg, *Poulsenia armata*). This indicates that though the bats used a greater number of fruit sources than the howling monkeys, they also displayed a particular preference for the fruits of a small set of tree species used by the monkeys during some months of the year.

Does the ability to share these resources reflect an abundant food supply? Fleming [1979], in a brief review of the fruiting strategies of tropical plants, indicated that fruit can occasionally be superabundant, at which time many species of frugivores can feed at the same tree. However, our results showed that fruit is often produced at slow rates, in low quantities, in an asynchronous pattern between tree species, and that sometimes fruit production may be aborted altogether.

Fruit production, at least by some of the species popular in the diet of the two mammals under comparison, was also: 1) very seasonal; 2) varied greatly in amount from tree to tree within one species and from species to species; and 3) was not necessarily related in duration to total biomass of fruit produced by the tree. In spite of the foraging problems that these features of fruit productivity represented to howling monkeys and fruit-eating bats, it is interesting that the monkeys and bats tended to choose, nevertheless, the same subset of species as fruit sources in some months of the year.

Is plant taxonomy relevant to relative and specialized frugivores when searching for fruit? What is relevant in the selection of plant species as fruit sources is finding those plant species that produce the most nutritionally rewarding fruit (see Wheelwright & Orians [1982] and Herrera [1982] for a discussion of this aspect in avian frugivores). This means that different frugivores, even those that are in distant taxa, may converge at fruit sources that have nutritionally rewarding fruits suited to their requirements, simultaneously depleting the available food.

For example, at the study site, systematic observations of trees of *Cecropia obtusifolia*, one of the five most important species in the diet of *Alouatta* and *Artibeus*, indicated that not only did howling monkeys and *Artibeus jamaicensis* consume the fruit, but that five other nonvolant arboreal mammals (another bat species, 31 species of birds, a reptile (*Iguana iguana*), leaf-cutting ants, and four terrestrial mammals), also made use of the fruit [Estrada & Coates-Estrada, unpublished manuscript]. Similar data are available in the case of species of the genus *Ficus* in Central America [August, 1981; Jordano, 1983].

Howling monkeys not only have to develop food-search strategies to adapt to the phenological features of their fruit sources but, in addition, are faced with the condition that these food supplies also are used by other forest canopy animals. Monkeys seem to respond to these pressures by 1) maintaining a reservoir of knowledge about the location in time and space of other seasonal fruit sources and by traveling directly to them [Glander, 1975; Milton, 1980; Estrada, 1984] and 2) exploiting species that are "year-round" producers of fruit (eg, *Ficus* spp., and *Cecropia obtusifolia*). Our field observations indicated that species of the genus *Ficus* and *Cecropia* were used as complementary fruit sources when the howling monkeys exploited seasonally produced fruit. These species became primary sources of fruit when the preferred seasonal species were not producing fruit [Estrada, unpublished manuscript]. Species of the genus *Ficus* have been reported to be very important sources of fruit for *Alouatta* and *Artibeus* at other localities [Morrison, 1978; Milton, 1980; Milton et al, 1982].

Fleming [1979] has pointed out that the trend is for different species of neotropical mammalian frugivores to have dissimilar diets. The comparison between the diets of *Artibeus* and *Alouatta* at Los Tuxtlas supports this idea, but it also suggests the possibility of important ecological interactions between distantly related taxa, especially when important ecological parameters such as fruit phenology, fruit biomass production, and length of fruiting are examined at the species and individual tree level.

Do *Alouatta* and *Artibeus* compete for food? Unless it is demonstrated that resources are in short supply, dietary overlap need not necessarily indicate the existence of competition [Pianka, 1974; Fleming, 1979]. Likewise, factors that tend to reduce levels of potential competition among species include differences in diet, foraging techniques, habitat preferences, and general habits [Pianka, 1974]. These general arguments can be applied to frugivores, with the addition that even differences in fruit morphology may reduce potential competition [Pijl, 1969; Snow, 1971; Janson, 1983]. At Los Tuxtlas, however, the following ideas may approach ecological reality. *Alouatta* apparently can be classified as a "generalized" fruit feeder because it exploits fruit that, morphologically, can be classified as "bird fruit" (eg, *Pseudolmedia oxyphyllaria*, *Nectandra ambigens*) and as "bat fruit" (eg, *Poulsenia armata*, *Ficus*). Like *Artibeus*, *Alouatta* forages in the upper canopy and uses the same habitat (eg, mature and secondary forest). Fruit availability at Los Tuxtlas is very patchy. It is necessary to consider that, for animals that feed on fruit, once a fruit is removed, it is gone; it is not replenished or replaced during the day (or night) (see Kantak [1981] for a discussion of this aspect among avian frugivores).

The ability to fly probably allows the bats to cover greater distances and to screen more trees of the preferred species per unit of time than would be possible for howling monkeys. This may complicate the task of finding fruit for the monkeys. Due to the large size of howlers (about 7.5 kg) and their continuous movements when sampling for fruits in different parts of the tree crown, they cause a large number of fruits to fall to the ground. Added to the amounts they eat, this may cause a reduction in the fruit available to night volant frugivores.

While the question of competition between *Alouatta* and *Artibeus* remains unanswered, their comparison is illuminating in that it places howling monkeys in the proper ecological scenario, including not only the plants that they use, but also other animals with whom they partition the existing resources in the rain forest.

CONCLUSIONS

1. A small set of plant species were used by bats ($N = 32$) and by howling monkeys ($N = 19$) as sources of fruit, and only 11 of the plant species were eaten by both animal species.
2. The fruit diet of bats and howling monkeys was very different. Bats exploited many species of the lower level (≤ 10 m) of the forest and of secondary growth, whereas howling monkeys used species of the middle and upper canopy (≥ 10 m) mainly in primary vegetation.
3. The use of fruit was very seasonal in *Alouatta*, but not so in *Artibeus*. The seasonality of fruit eating by howling monkeys was related to the fruit phenology of plant species of the Moraceae and Lauraceae families.
4. Fruit production in trees of four of the most important species in the diet of bats and howling monkeys showed great variation in fruit biomass produced, length of fruiting, and in day-to-day fruit production from tree to tree and from species to species.

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