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## Patterns of Foraging and Range Use by Three Species of Neotropical Primates

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**ABSTRACT.** This paper describes the diet and range use patterns of the three species of primates in Santa Rosa National Park, Costa Rica (*Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*) and examines the variation in these variables as they relate to seasonal changes and concomitant changes in food availability. These three primate species were studied over a four-year period for a total of 24 months in the field. Santa Rosa National Park is in an area that experiences a long severe dry season in which little if any rain falls and the majority of the non-riparian trees lose their leaves. However, even though the three species were very flexible in terms of diet and range use, the behavioural variability did not correspond to changes in food availability or season.

**Key Words:** Foraging; Range use; *Ateles*; *Alouatta*; *Cebus*.

### INTRODUCTION

A growing number of field studies have documented marked variation in the diet and range use patterns of primates. This variation is frequently suggested to be a response to varying environmental parameters, such as the abundance, distribution, or quality of food resources (CLUTTON-BROCK, 1974; HARRISON, 1983; KLEIN & KLEIN, 1975, 1977; MCKEY & WATERMAN, 1982; RAEMAEKERS, 1980; WRANGHAM, 1981). Variation in diet and movement patterns have also been attributed to the availability of safe resting sites (ALTMANN & ALTMANN, 1970; HAMILTON, 1982; KUMMER, 1968; RASMUSSEN, 1979), the digestive capabilities of the study species (MILTON, 1980), body size (CLUTTON-BROCK & HARVEY, 1977; MILTON & MAY, 1976; TERBORGH, 1983), disease control (FREELAND, 1976), and factors such as the availability of mates and the presence or absence of competitors and/or predators (RASMUSSEN, 1979; MITANI & RODMAN, 1979).

To understand interspecific variation in behavioural responses to dynamic environmental conditions, it is useful to study species inhabiting the same habitat, thereby eliminating variability between sites in potentially important, but unmeasured, variables. In addition, it is valuable to study synchronously all of the species for which comparisons will be made, since the density and distribution of shared food resources can change rapidly as a result of phenological changes in their food plant species. Different primate species are often studied at the same location (e.g., STRUHSAKER, 1978; TERBORGH, 1983), but rarely are all species studied synchronously (but see GAUTIER-HION, 1980; GAUTIER-HION et al., 1980; MACKINNON & MACKINNON, 1978, 1980).

The objective of this investigation was to describe the diet and range use patterns of the three species of primates found in Santa Rosa National Park, Costa Rica (spider monkeys, *Ateles geoffroyi*; mantled howling monkey, *Alouatta palliata*; and white-faced capuchin, *Cebus capucinus*) and to examine the variation in these variables as they relate to seasonal

changes and concomitant changes in food availability. Santa Rosa offers an excellent opportunity to determine if diet and range use patterns change in relation to season, since the climate of the region is highly seasonal. From mid-December until the end of May little if any rain falls in the park, and most of the non-riparian trees lose their leaves. Such environmental variation is likely to create situations where food availability differs markedly between seasons, as plants often synchronize fruiting, leaf flush, and flowering events to coincide with the rains.

## METHODS

The study was conducted at Santa Rosa National Park, Costa Rica during a total of 24 months in the field (July and August 1983, January to August 1984, January to July 1985, February to August 1986). During the final field season, only spider monkeys were studied. Santa Rosa is situated 35 km northwest of Liberia, Guanacaste, adjacent to the Pan-American highway. Rectangular in shape and covering approximately 10,800 ha, Santa Rosa consists of a series of stepped plateaus which start at an elevation of 300 m and drop to the ocean. The area was originally a dry deciduous forest dominated by clumps of oak forest (*Quercus oleoides*). Over the past 300 years, however, much of the upper plateau was cleared for cattle pastures. With the establishment of the park in 1971 and the removal of the cattle in 1978, some of the grassland areas have gradually reverted to woody vegetation, while others have been maintained by repeated burnings. The vegetation of the park is consequently a mosaic of grassland (*Hyparrheia rufa*), dry deciduous forest containing *Spondias mombin*, *Luehea candida*, *L. speciosa*, *Guazuma ulmifolia*, *Bursera simaruba*, and *Chlorophora tinctoria*, and semi-evergreen forest containing *Hymenaea courbaril*, *Mastichodendron capiri*, and *Manilkara chicle* (JANZEN, 1986). To facilitate access to remote areas, a system of approximately 20 km of trails was established in the area over the duration of the study.

The climate of the region is characterized by two distinct seasons: the dry season extends from approximately mid-December to late May, and the wet season encompasses the remainder of the year. Rainfall in Santa Rosa ranges between 900 and 2,400 mm annually, almost all of which falls in the wet season. During the dry season the majority of the non-riparian trees lose their leaves and remain bare until the rains.

Single groups of each of the three primate species, whose home ranges overlapped extensively, were chosen as study subjects. The howling monkey group had on average 40 individuals: 7-8 adult males, 16-18 adult females, 1-2 large immature males, 1 large immature female, 4-6 small immatures, and 6-9 infants (see FEDIGAN et al., 1985 for a description of the age-sex classes used). Howling monkeys have typically been described as living in relatively stable, cohesive, multimale multifemale social groups (CHIVERS, 1969; ESTRADA, 1984; GAULIN et al., 1980; GAULIN & GAULIN, 1982; GLANDER, 1980; MILTON, 1980; SMITH, 1977). The study group had a multimale multifemale type of social structure, but was neither stable nor cohesive. The group frequently divided into subgroups which were spatially separated for periods that lasted up to four weeks.

The cebus monkey group contained on average 26 individuals; 2-4 adult males, 9-10 adult females, 4-5 large immatures, 5-6 small immatures, and 0-4 infants. This was a large group for Santa Rosa: the mean cebus group size for the park was 14.0 individuals (FEDIGAN et al., 1985).

An exact count of the size of the spider monkey study group was not possible because of

the fission-fusion type of social organization possessed by spider monkeys (FEDIGAN & BAXTER, 1984). However, the minimum size of the community was obtained by summing the maximum counts of all age/sex classes seen in one year. Using this method the community was estimated to contain 42 individuals; 4 adult males, 17 adult females, 2 large immature males, 4 large immature females, 7 small immatures, and 8 infants.

#### BEHAVIOURAL OBSERVATIONS

Behavioural data were collected using a focal animal sampling regime to obtain the most complete record of not only what the subject did, but also of what was done to the subject. With this sampling procedure, 394 hr of focal animal data were collected on howling monkeys, 335 hr on the spider monkeys, and 171 hr on the cebus monkeys, for a total of 900 hr. Normally the species chosen to be sampled was alternated each day, although this depended somewhat on the ease with which each species could be located on a particular day. The length of the focal animal session was set at 10 min, and if the subject was lost prior to the end of the session, the session was terminated and the data discarded. When possible, the animal to be sampled was chosen according to a fixed rotation between age/sex classes (the identity of the individual was not always known). An attempt was made to obtain a complete record of each species' activity during a 3-week sample period so that at the end of this period approximately an equal number of observations were made in each hour of the day.

Location of the group being followed was recorded every 10 min as a coordinate on a grid consisting of cells, 120 m by 120 m, superimposed on an aerial photograph of the study area. Since known individual trees could often be identified on the photograph, I felt that error in estimating location was small, and rarely resulted in the group being recorded in the wrong cell of the grid. Home ranges of the cebus and howling monkey groups were considered to be the sum of those cells of the grid that group members were seen using, or would have had to pass through to get from the location of one sighting to that of another sighting made on a subsequent day.

#### ECOLOGICAL SAMPLING

To quantify the size, density, and distribution of food resources, the most commonly used food plant species (see below) were identified for each primate species from the preceding three weeks of behavioural observation, and the location, size, and phenological status of all adult trees of these species were determined in three 4-ha grids. An adult tree was considered as any individual that had attained a diameter at breast height (DBH) greater than or equal to that of the smallest individual known to bear fruit. The three grids were 200 m by 200 m and each grid consisted of 400 cells that were 10 m by 10 m in size. Corners of the cell were marked with an individually labeled steel post. The three grids encompassed 9.0% of both the cebus and howling monkeys home ranges. Each grid was established in a different type of habitat, such that all major habitat types used by the monkeys were sampled. The phenological information recorded involved assessing the stage of leaf development (no leaves, leaf buds, young leaves, mature leaves) and noting the presence or absence of fruit and flowers. In 1984, phenological data were recorded on the plant species which the preceding three weeks of behavioural sampling had demonstrated to be important. In 1985 and 1986 the phenological status of all individuals of the major plant species used by the primates any

time during the study were determined. After January 1985 when a plant species was used which had not been eaten in the past, phenological data were recorded on it in all subsequent ecological sampling periods. Normally only four plant species were chosen to represent the ecological conditions for a 3-week period. The use of only four major plant species in each period seems appropriate since they always accounted for over 91% of all of the time spent feeding. The 3-week sampling period was chosen because within that time an adequate sample of each species behaviour could be obtained and because the phenological cycles of the majority of the food plants used by the monkeys changed little over that period. Individuals of the few species of plants that were exceptions to this (e.g., flowering *Tabebuia ochracea*) could be identified by looking for food items that had fallen to the ground. Thus, food resources were not so ephemeral that they could not be sampled accurately or that the primates could not respond to the changes.

To determine the distribution of the adult trees that were bearing food, the "Coefficient of Dispersion" (CD) was calculated (MILTON, 1980; PIELOU, 1969; SOKAL & ROHLF, 1981). The value of the CD is greater than one when the distribution pattern is clumped, less than one if the pattern is uniform, and equal to one if the pattern is random. The density of food trees was simply the number of food trees in the grids, divided by the area of the grids. The selectivity of a particular food item was measured as the proportion of the total time spent feeding on that food item, divided by the density of the adult trees that supplied that food item. Thus, high values indicated selection for an item. A food item was considered any unique combination of a plant species and part (e.g., *Mastichodendron capiri* fruit or *M. capiri* young leaves).

#### FOOD ABUNDANCE

The abundance of the food resources available to each of the three primate species was calculated separately for each sample period. Abundance would ideally be represented as the number of food items in all the patches available; however, because the large number of trees used by the monkeys precluded counting food items, the abundance within a tree was represented as diameter of the tree measured at breast height (DBH). For several tropical tree species, DBH has been shown to be a reasonably accurate reflection of the reproductive capacity of fruiting individuals (LEIGHTON, 1982; LEIGHTON & LEIGHTON, 1982; MCDIARMID et al., 1977; PETERS et al., 1988). To calculate a relative measure of food abundance for comparison between time periods, the size all of the food trees found in the gridded areas that were bearing food items was summed and this value was divided by the area of the grids.

By studying each of the three primate species simultaneously, it was hoped that more confidence could be placed in discussions of the significance of correlations. If strong similarities existed between the species in correlations of the same variables, then it is less likely that the results occurred by chance than would be the case if the relationships were found for only one primate species.

## RESULTS

### FORAGING STRATEGIES

Over the duration of the study the cebus and spider monkeys spent the greatest proportion

**Table 1.** Percentage of total feeding time spent eating different types of foods by the three species of primates found in Santa Rosa National Park, Costa Rica.

| Plant part | Cebus | Howler | Spider |
|------------|-------|--------|--------|
| Fruit      | 81.2  | 28.5   | 77.7   |
| Flower     | 0.2   | 22.5   | 9.8    |
| Leaves     |       |        |        |
| Mature     | 0.5   | 27.7   | 1.2    |
| Young      | 0.7   | 17.4   | 7.3    |
| Buds       | 0.1   | 3.9    | 2.6    |
| Insects    | 16.9  | 0.0    | 1.3    |

The data are derived from focal animal observations (cebus, *Cebus capucinus* 171 hr; spiders, *Ateles geoffroyi* 335 hr; and howlers, *Alouatta palliata* 393 hr).

of their feeding time eating fruit: 81.2% and 77.7%, respectively (Table 1). In contrast, the howling monkeys were more folivorous; they spent 49.0% of their feeding time eating leaves, and only 28.5% of their feeding time eating fruit. The cebus were the most insectivorous of the three species. They spent 16.9% of their feeding time eating insects. Unlike both of the other species, cebus monkeys virtually ignored both leaves and flowers. On a monthly scale, diet varied considerably. For instance, the diet of the cebus monkeys varied between sample periods from being entirely insectivorous (100% of their feeding time), to being primarily frugivorous (97.1% of their feeding time).

All three species fed on parts of a variety of plant species. Foods that constituted less than 1% of the observed feeding time represented feeding bouts of such short duration that the probability of observing them were largely a matter of chance. Using the 1% criterion, the howling monkeys had the most varied diet; they were observed eating 22 different food items from 11 species of trees. The spider monkeys ate 20 different food items, from 18 plant species and the cebus monkeys ate 14 different plant food items from 13 different species. Even though all three species ate many different food items, a few of them constituted the bulk of each species' feeding efforts. The cebus monkeys spent over 50% of their feeding time during the study eating only two different food items (*Sloanea terniflora* fruit, *Muntingia calabura* fruit). Spider monkeys spent more than 50% of their feeding efforts eating only three foods (*Muntingia calabura* fruit, *Ficus* spp. fruit, *Mastichodendron capiri* fruit), while howling monkeys spent over 50% of their feeding time eating six different food items (*Ficus* spp. fruit, *Brosimum alicastrum* leaves, *Manilkara chicle* flowers, *Pithecellobium saman* flowers, *Brosimum alicastrum* fruit, *Lonchocarpus costaricensis* flowers).

All three species tended to be selective in what they chose to eat, often relying heavily on tree species that occurred at low densities (Table 2). For instance, the heavy reliance of the spider monkey on the fruit of *Mastichodendron capiri*, which was the third most heavily used food item, constituting 6.6% of their feeding time, was almost exclusively the result of their feeding on two individual trees. Another similar example is the use of *Swartzia cubensis* fruit by all three of the primates. When this plant species was in fruit, all three primate species fed heavily on it, even when there was only one fruiting individual in the 12-ha gridded area, and only three individuals in the groups' home ranges. Since some of the most used food trees occurred at low density, it was concluded that the three primate species were relatively selective in their choice of food items. For all primate species the range in selectivity between food items was large (spiders 0.1–56.3, howlers 0.1–31.0, cebus 0.1–59.6). The average selectivity exhibited by the three primate species were: spiders 13.5, howlers 6.0, and cebus 8.1. This selectivity index did not differ significantly between the primate species ( $F = 1.26, p = 0.294$ ).

All three monkey species used food resources that had a clumped distribution pattern

**Table 2.** A description of the pattern of feeding and selectivity of the three species of primates in Santa Rosa National Park, Costa Rica, depicting the five most used plant species for each primate species.

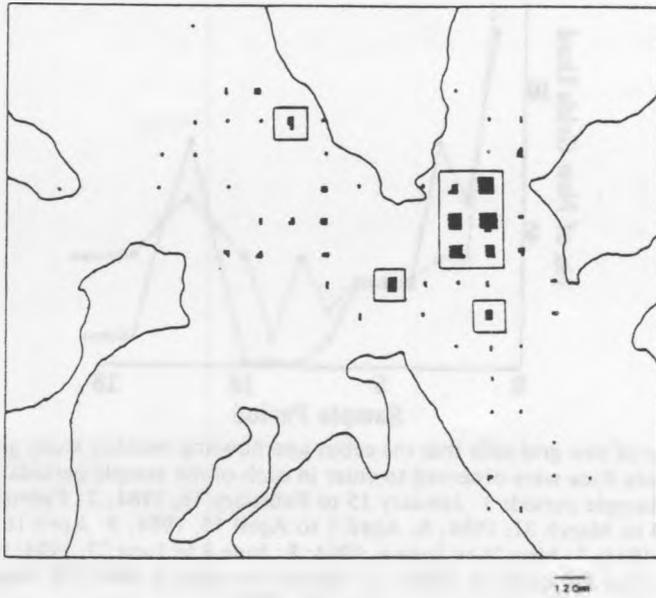
| Plant                                     | % of total feeding time | Density (ind./ha) | Selectivity |
|---|-------------------------|-------------------|-------------|
| Spider                                    |                         |                   |             |
| <i>Ficus</i> sp. Fruit                    | 29.2                    | 0.6               | 48.5        |
| <i>Muntingia calabura</i> Fruit           | 16.1                    | 0.3               | 53.7        |
| <i>Mastichodendron capiri</i> Fruit       | 6.6                     | 0.3               | 26.4        |
| <i>Dipterodendron costaricensis</i> Fruit | 6.3                     | 2.5               | 2.5         |
| <i>Pithecellobium saman</i> Flowers       | 2.9                     | 0.8               | 3.6         |
| Howler                                    |                         |                   |             |
| <i>Ficus</i> sp. Fruit                    | 15.5                    | 0.6               | 25.8        |
| <i>Brosimum alicastrum</i> Mature leaves  | 10.2                    | 0.8               | 12.8        |
| <i>Manilkara chicle</i> Flowers           | 7.4                     | 9.8               | 0.8         |
| <i>Pithecellobium saman</i> Flowers       | 6.8                     | 0.8               | 8.5         |
| <i>Brosimum alicastrum</i> Fruit          | 5.5                     | 0.8               | 6.9         |
| Cebus                                     |                         |                   |             |
| <i>Sloanea terniflora</i> Fruit           | 34.1                    | 2.3               | 14.8        |
| <i>Muntingia calabura</i> Fruit           | 17.9                    | 0.3               | 59.6        |
| <i>Luehea speciosa</i> Fruit              | 4.4                     | 19.9              | 0.2         |
| <i>Quercus oleoides</i> Fruit             | 3.5                     | 5.0               | 0.7         |
| <i>Sciadodendron excelsum</i> Fruit       | 2.5                     | 0.7               | 3.6         |

(CD = 1.25 cebus, 1.19 howlers, 1.18 spiders). No significant differences between the three species in the spatial distribution of their plant food resources ( $F = 0.454$ ,  $p = 0.638$ ). Similarly, all three primate species used plant food resources that occurred at a low density (cebus 6.46 individuals per ha, spiders 4.76 individuals per ha, howlers 7.96 individuals per ha: average density over all sample periods). There were no significant differences in the densities of the primates' plant food resources ( $F = 1.32$ ,  $p = 0.278$ ).

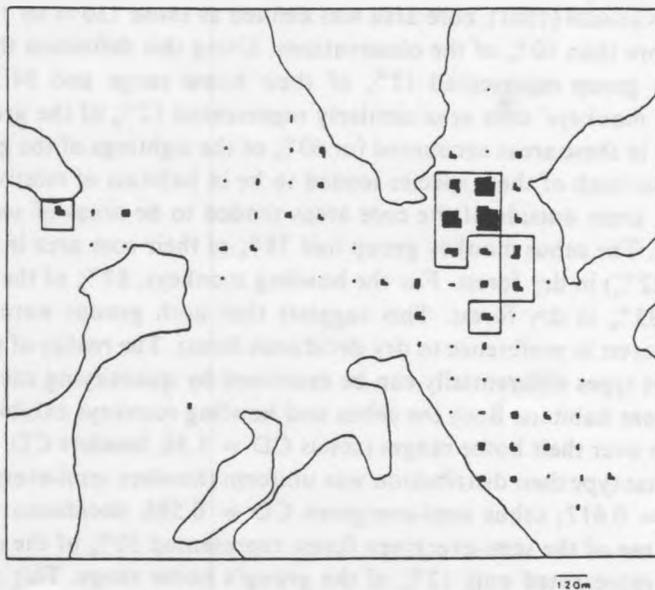
#### RANGE USE PATTERNS

The size of the cebus and howling monkey home ranges were calculated as the number of 120 m by 120 m grid cells that the groups were observed using, or would have had to pass through to get from one observation point to another (Figs. 1 & 2). Both groups had a 1.08-km<sup>2</sup> home range when observations from 1984 and 1985 were combined. Of the total area used by the cebus and howling monkey groups, 81% was used in common. The areas used by both cebus and howlers changed over the period of observation. In 1984 the howling monkey group used an area of 0.907 km<sup>2</sup>, while in 1985 it used 0.806 km<sup>2</sup>. In 1985 the group used 21 grid cells (36% of the total grid cells used) that they were not seen to use in 1984. The majority of the new cells entered (57%) were in areas on the periphery of the group's 1984 home range. The remainder of the new areas (43%) that were used in 1985 were cells within the 1984 home range and probably represent areas that were previously used but for which no record had been obtained. In 1984 the cebus monkey group had a home range of 0.89 km<sup>2</sup>, while in 1985 the group used an area of 0.78 km<sup>2</sup>. In the second year, the cebus monkey group used 18 new grid cells, 72% of which were in new areas on the periphery of their home range and 28% were cells that were within the 1984 home range, but for which no record of use had been obtained previously.

By plotting the number of new grid cells used by either of these two primate species in each of the sample periods against time, it is evident that there was a general decline in the



**Fig. 1.** The use of home range by the cebus monkey study group in Santa Rosa National Park, Costa Rica in the field seasons of the first three years of the study. The proportion of the cell that is dark represents the proportion of the total number of sightings for which the group was seen to use that area. Cells outlined in black represent the core area. Core area was defined as those 120 m by 120 m cells used by the group for more than 10% of the observations.



**Fig. 2.** The use of home range by the howling monkey study group in Santa Rosa National Park, Costa Rica in the field seasons of the first three years of the study. The proportion of the cell that is dark represents the proportion of the total number of sightings for which the group was seen to use that area. Cells outlined in black represent the core area. Core area was defined as those 120 m by 120 m cells used by the group for more than 10% of the observations.

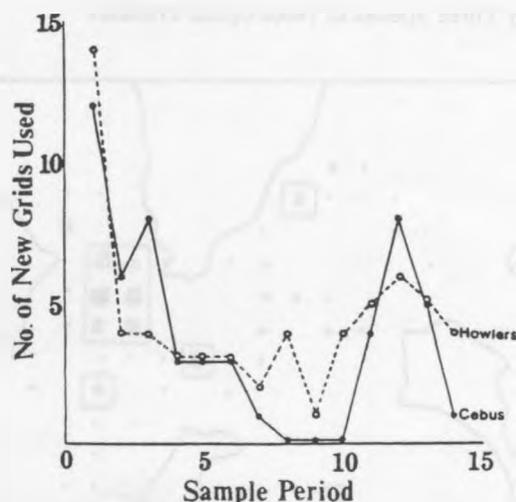


Fig. 3. The number of new grid cells that the cebus and howling monkey study groups of Santa Rosa National Park, Costa Rica were observed to enter in each of the sample periods. A grid cell is 120 m by 120 m in size (Sample periods 1: January 15 to February 16, 1984; 2: February 17 to March 13, 1984; 3: March 14 to March 31, 1984; 4: April 1 to April 15, 1984; 5: April 16 to May 3, 1984; 6: May 4 to May 20, 1984; 7: May 21 to June 6, 1984; 8: June 8 to June 27, 1984; 9: July 1 to July 26, 1984; 10: January 25 to February 23, 1985; 11: March 1 to April 3, 1985; 12: April 7 to May 3, 1985; 13: May 10 to May 31, 1985; 14: June 4 to June 21, 1985).

number of new cells that the groups were seen to enter in 1984 as the year progressed, but at the start of the 1985 season the number of new cells used increased sharply, only to decrease as the season continued (Fig. 3). This suggests that the home range of both the cebus and howling monkey groups shifted between years.

Following KAVANAGH (1981), core area was defined as those 120 m by 120 m cells used by the group for more than 10% of the observations. Using this definition the core area of the howling monkey group represented 12% of their home range and 54% of the observations. The cebus monkeys' core area similarly represented 12% of the group's home range, but observations in these areas accounted for 60% of the sightings of the group (Figs. 1 & 2). The core areas for both of these species tended to be in habitats of relatively wet semi-evergreen forest and areas outside of the core areas tended to be areas of seasonally dry semi-deciduous forest. The cebus monkey group had 78% of their core area in the wet forest and the remainder (22%) in dry forest. For the howling monkeys, 67% of their core area was in wet forest and 33% in dry forest. This suggests that both groups were selecting areas of semi-evergreen forest in preference to dry deciduous forest. The reality of the groups treating these two habitat types differentially can be examined by quantifying each group's distribution in the different habitats. Both the cebus and howling monkeys exhibited a clumped distribution pattern over their home ranges (cebus  $CD = 1.58$ , howlers  $CD = 1.76$ ). However, within each habitat type their distribution was uniform (howlers semi-evergreen  $CD = 0.987$ , deciduous  $CD = 0.617$ ; cebus semi-evergreen  $CD = 0.586$ , deciduous  $CD = 0.887$ ). For the howlers the use of the semi-evergreen forest represented 50% of the observations, while this forest type represented only 12% of the group's home range. This differs significantly from what would be expected if the group used the habitats in proportion to the area of each ( $\chi^2 = 71.2$ ,  $p < 0.01$ ). For the cebus monkeys the use of semi-evergreen forest represented

57% of the observations, but this type of habitat only accounted for 14% of their home range. Again, this differed significantly from what would be expected if the group used the habitats in proportion to the area of each ( $\chi^2 = 55.0, p < 0.01$ ).

There was considerable variability between sample periods in how each of the species used their home range. For instance, the percentage of their home range used by the cebus monkey group per sample period ranged from 8% to 27%. The howling monkey group's use of their home range varied from 5% to 32%. The number of grids that the groups fed in or passed through in a sample period ranged from 18 to 117 cells for cebus monkeys, and from 7 to 67 cells for the howlers.

The three species employed different foraging strategies which resulted in each species using their home range slightly differently. The howlers often stayed in close proximity to individual food trees for long periods of time (maximum 14 days). The group only left these food trees to make short excursions to feed nearby. When the group finally left such areas they tended to make long excursions to new feeding areas. This pattern of movement was reflected in the group's temporal use of their home range. On average 61% of the grids used in one sample period were used in the immediately subsequent period (range 0–89.4%).

In contrast to the howlers, the food trees that the cebus monkeys selected rarely became focal points of the group's activity. Rather, the group tended to move from one individual tree of a preferred species to another, or they would make foraging excursions away from large individual fruiting trees only to return several hours later. This type of movement pattern resulted in a temporal pattern of home range use that differed from the howling monkeys. On average, 57% of the grids used by the cebus monkey group in one sample period were used in the subsequent period; however, unlike the howlers, this value did not vary greatly among sample periods (range 47–88%).

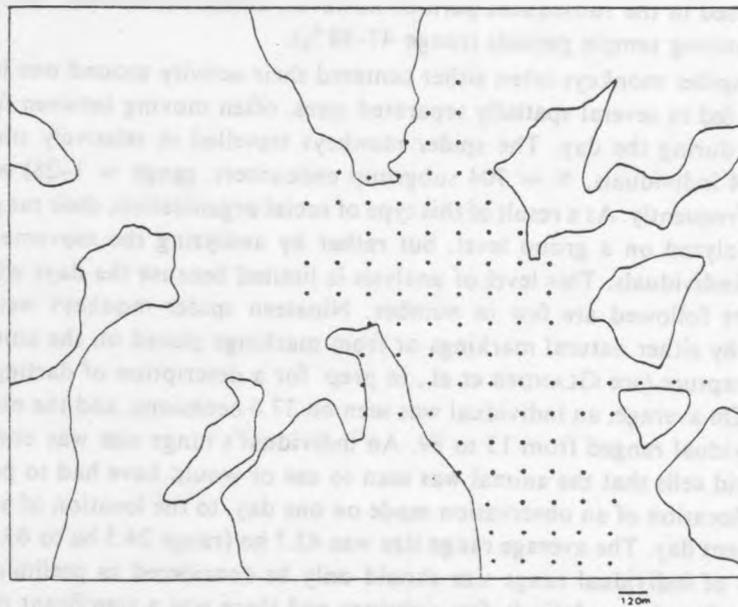
Individual spider monkeys often either centered their activity around one large food tree or repeatedly fed in several spatially separated trees, often moving between feeding sites in a set pattern during the day. The spider monkeys travelled in relatively small subgroups (mean = 4.54 individuals,  $N = 704$  subgroup encounters, range = 1–28) which changed composition frequently. As a result of this type of social organization, their range use patterns cannot be analyzed on a group level, but rather by analyzing the movement patterns of recognizable individuals. This level of analysis is limited because the days when known individuals were followed are few in number. Nineteen spider monkeys were individually recognizable by either natural markings or from markings placed on the animals following darting and capture (see GLANDER et al., in prep. for a description of darting and marking techniques). On average, an individual was seen on 37.6 occasions, and the number of sightings per individual ranged from 13 to 89. An individual's range size was considered as the number of grid cells that the animal was seen to use or would have had to pass through to get from the location of an observation made on one day, to the location of a sighting made on a subsequent day. The average range size was 43.7 ha (range 24.5 ha to 63.4 ha, Table 3). These values of individual range size should only be considered as preliminary estimates, since they are based on relatively few sightings and there was a significant relationship between the number of sightings of an individual and their range size ( $r = 0.654, p = 0.004$ ). That indicates that it is likely that as more sightings of individuals are obtained the estimate of their range size will increase.

A minimum home range for the community was calculated by summing the number of grid cells used by all of the identifiable spider monkeys, and those that had to have passed

**Table 3.** A description of the individual home ranges of identifiable spider monkeys (*Ateles geoffroyi*) in Santa Rosa National Park, Costa Rica.

| Animal                                     | Age:sex class         | No. of sightings | Home range size in ha | Index of central tendency |
|--|-----------------------|------------------|-----------------------|---------------------------|
| 1  | Adult female          | 14               | 24.5                  | 2.33                      |
| 2  | Adult female          | 30               | 53.3                  | 1.58                      |
| 3  | Adult female          | 13               | 34.6                  | 2.17                      |
| 4  | Adult female - Dep    | 54               | 37.4                  | 3.60                      |
| 5  | Large immature        | 26               | 49.0                  | 1.63                      |
| 6  | Adult male            | 29               | 51.8                  | 1.71                      |
| 7  | Adult female          | 38               | 57.6                  | 2.00                      |
| 8  | Adult female - Dep    | 34               | 36.0                  | 2.27                      |
| 9  | Small immature        | 32               | 38.9                  | 2.13                      |
| 10   | Large immature Dep    | 30               | 31.7                  | 2.00                      |
| 11   | Adult female - Dep    | 33               | 41.8                  | 1.94                      |
| 12   | Adult female - Dep    | 30               | 31.7                  | 2.00                      |
| 13   | Adult female          | 27               | 43.2                  | 1.93                      |
|  | With dependent No. 14 | 62               | 44.6                  | 2.95                      |
|  | Total                 | 89               | 63.4                  | 3.40                      |
| 14   | Large immature        | 12               | 36.0                  | 2.40                      |
|  | When dependent on 13  | 62               | 44.6                  | 2.95                      |
|  | Total                 | 74               | 60.5                  | 3.08                      |
| Average                                    |                       | 37.6             | 43.7                  | 2.27                      |
| Only totals for numbers 13 and 14 included |                       |                  |                       |                           |

Index of central tendency = the number of sightings divided by the number of 120 m by 120 m grid cells that were used by that individual (Dep = dependent infant).



**Fig. 4.** The use of the study area by the individually recognizable spider monkeys of Santa Rosa National Park, Costa Rica over the entire study period. The dots are at the center of a 120 m by 120 m grid cell.

through. Considering home range in this fashion, the spider monkey community used an area of 1.47 km<sup>2</sup> (Fig. 4). Individuals seemed to use their range differently: some were seen frequently in a relatively restricted area (approximately 8 ha) and only infrequently outside that area, while other individuals were more widely dispersed across their range. This was quantified by using the Coefficient of Dispersion (CD, standard deviation of the number of sightings per cell divided by the mean). This index averaged 1.71 for all animals, and ranged from 0.6 to 5.2 (Table 3). This indicates that the location of the sightings tended to occur in a clumped distribution pattern. The adult females with either infants or small immatures tended to be seen frequently in a central area and thus have a more clumped pattern of distribution (CD = 2.2), whereas females without immatures were more evenly dispersed in the use of their range (CD = 1.5). This was not always true for all individuals. In one instance a female with a clinging infant had a CD lower than the average CD for females without an infant or small immature.

One identifiable adult female was accompanied by her offspring in 1984 and 1985, while in 1986 this offspring was primarily ranging independent of his mother. Between these two periods the distribution of sightings made of this female became relatively less clumped (CD without an infant = 1.8, CD with an infant = 2.2). This observation suggests that when a female is accompanied by an offspring she tends to concentrate her activity in a small area, only rarely making excursions away from this area. In contrast, when a female is not accompanied by an offspring, she tends to range more widely. Observations suggest that when females with accompanying offspring leave their central area, they become members of a large subgroup, often containing males.

#### USE OF WATER RESOURCES

Santa Rosa experiences a long, severe, dry season, during which most of the non-riparian trees lose their leaves. It seems likely that during the dry season, particularly near the end of May, the availability of water influences the ranging patterns and diet of the three primate species. During the early dry season, water was available to primates from three sources: arboreal water holes, standing water that remained in creek beds, and water contained in their food resources. In the study area both the arboreal water holes and the standing water sources in creek beds dried up before the end of the dry seasons. For approximately the last two months of the dry season, the only water that was available to the monkeys was contained in the foods they ate. Behavioural responses to this restricted access to water were most evident in the cebus monkeys. By the end of February, when most of the non-riparian trees had lost their leaves, the cebus monkey group started to center their activity around the few remaining water holes in a creek bed in the dry forest part of their range. The group made repeated foraging excursions away from the water holes, only to return every 3–6 hr to drink. In essence they became central place foragers, centering their activity around the few remaining water holes. Once these water holes became dry, the group left the area of the creek bed almost entirely and tended to center their activity in an area of semi-evergreen forest where a large proportion of the trees kept their leaves throughout the dry season.

During the 1985 field season, eight maximum-minimum thermometers were placed in semi-evergreen and dry deciduous sections of forest. The maximum daily temperature in the areas

of semi-evergreen forest was on average 1.7°C cooler than the maximum daily temperature in the dry forest. The area of semi-evergreen forest was used extensively in the dry season by both the cebus and howling monkey groups. That may have been a response by the monkeys to the differences in temperature between the forest types and the availability of water in the two areas. Yet, in the wet season, when water was readily available and the maximum daily temperature had decreased, both species still used the area of semi-evergreen forest frequently. By the end of the dry season the only water available to the cebus group came from the foods they ate. This may have influenced the group's choice of foods. For instance, near the end of the 1984 and 1985 dry seasons the cebus monkey group was eating primarily the fruits of *Muntingia calabura*, a fruit with a high water content (FLEMING et al., 1985). However, with the start of the wet season, the group stopped feeding on *Muntingia calabura*, fruit almost entirely and switched to eating dry acorns of *Quercus oleodites*, even though the abundance of *M. calabura* increased.

Although responses to the availability of water were most evident in observations of the cebus monkeys, spiders were also seen coming to the ground to drink from standing water holes. While howlers were never seen to come to the ground to drink, they were frequently seen using arboreal water holes early in the dry season when they were available.

#### THE INFLUENCE OF SEASON ON DIET AND RANGE USE PATTERNS

Based on the extremely seasonal climate in the region of Santa Rosa, and on previously conducted studies of the phenological cycles of many tropical plant species (BAKER et al., 1982; DAUBENMIRE, 1972; FRANKIE et al., 1974a, b; OPLER et al., 1976, 1980; SMYTHE, 1970), I expected that all three primate species would exhibit marked differences in diet and range use between seasons. However, when the diet and range use patterns exhibited by each of the primates in sample periods in the wet season were compared to those in the dry season, few differences were evident (Table 4). It seemed reasonable to speculate that the failure of these relationships to reach significance might have been because the cessation of the rains was not what influenced the animal's behaviour, but rather the monkeys responded to the phenological status of their plant food resources. The plants respond to seasonal changes

**Table 4.** Seasonal differences in the diet and range use of the three species of primates living in Santa Rosa National Park.

|                            | Cebus |         | Howlers |       | Spiders |      |
|----------------------------|-------|---------|---------|-------|---------|------|
|                            | Wet   | Dry     | Wet     | Dry   | Wet     | Dry  |
| % of time feeding          | 25.3  | 28.9    | 17.6    | 13.8  | 29.4    | 26.7 |
| % of time travelling       | 47.8  | 25.3*** | 8.4     | 6.7   | 25.6    | 18.7 |
| Density of food trees      | 5.4   | 6.9     | 8.5     | 7.8   | 4.8     | 4.7  |
| Distribution of food trees | 1.4   | 1.2     | 1.2     | 1.2   | 1.2     | 1.2  |
| % fruit                    | 67.1  | 79.7    | 26.9    | 26.4  | 75.1    | 70.3 |
| % leaves                   | 4.2   | 2.2     | 55.3    | 46.9  | 12.1    | 17.0 |
| % flowers                  | 0.0   | 0.8     | 21.0    | 26.7  | 7.4     | 10.8 |
| Food abundance             | 104.0 | 74.4    | 566.6   | 245.5 | 109.9   | 87.6 |
| No. of grids used          | 9.8   | 10.8    | 11.3    | 10.1  | —       | —    |
| % of home range            | 4.0   | 7.0     | 15.3    | 13.5  | —       | —    |
| % of time in core area     | 60.1  | 52.0    | 61.5    | 46.4  | —       | —    |
| Distribution in range use  | 0.6   | 0.6     | 0.9     | 0.8   | —       | —    |
| % insects                  | 30.3  | 18.4    | —       | —     | —       | —    |

Presented are the mean values for dry season and wet season. (\*\*\*)  $p < 0.01$

**Table 5.** Seasonal differences in the diet and range use of the three species of primates living in Santa Rosa National Park.

|                            | Cebus |          | Howlers |          | Spiders |          |
|----------------------------|-------|----------|---------|----------|---------|----------|
|                            | Water | No water | Water   | No water | Water   | No water |
| % of time feeding          | 38.4  | 22.0***  | 14.2    | 16.2     | 24.6    | 31.7     |
| % of time travelling       | 35.9  | 24.0     | 8.0     | 5.7      | 22.6    | 12.5*    |
| Density of food trees      | 6.9   | 5.7      | 7.0     | 9.7      | 5.2     | 6.2      |
| Distribution of food trees | 1.2   | 1.2      | 1.4     | 1.2      | 1.2     | 1.2      |
| % fruit                    | 71.1  | 85.1     | 24.3    | 30.6     | 71.4    | 73.5     |
| % leaves                   | 1.9   | 4.3      | 51.6    | 45.1     | 18.7    | 6.8      |
| % flowers                  | 0.1   | 1.5***   | 25.5    | 24.9     | 6.6     | 17.0     |
| Food abundance             | 59.7  | 104.0    | 290.2   | 339.0    | 131.4   | 52.0     |
| No. of grids used          | 9.7   | 12.0     | 10.4    | 10.4     | —       | —        |
| % of home range            | 12.9  | 16.0     | 14.0    | 13.9     | —       | —        |
| % of time in core area     | 48.8  | 64.9     | 57.1    | 39.1     | —       | —        |
| Distribution in range use  | 0.5   | 0.6      | 1.0     | 0.6      | —       | —        |
| % insects                  | 28.1  | 10.4**   | —       | —        | —       | —        |

Presented are the mean values when water is available and when water is not available. \* 0.1; \*\* 0.05; \*\*\* < 0.01.

in rainfall only after a lag period. Perhaps primates also did not exhibit seasonal changes in behaviour until they did not have access to arboreal water holes or standing water in the creek beds. That normally occurred two months after the cessation of the rains. To test these ideas, the range use characteristics and diet of each of the three primate species expressed in the sample periods when standing water was available, was compared to when standing water was not available. These two periods corresponded closely to the periods when the majority of the trees that lose their leaves in the dry season have done so, and the time when the majority of trees have leaves. When comparisons were made in this manner, some differences in diet were evident (Table 5). Cebus ate flowers more when standing water was not available than when it was. Yet, flowers were not more available during these periods. In fact the total density of trees bearing flowers that were eaten by the monkeys was 16.3 individuals/ha in the wet season and 0.92 individuals/ha in the dry season. The cebus monkeys also fed more on insects during the period when standing water was available, than when it was not available. That would have been predicted based on the fact that insect availability is greater in the wet season (BUSKIRK & BUSKIRK, 1976; JANZEN, 1973). Also, the cebus group spent more time feeding when water was not available to them, than when it was available. None of the range use variables varied significantly between the two periods for any of the three primate species.

#### THE INFLUENCE OF FOOD ABUNDANCE ON DIET AND RANGE USE PATTERNS

Table 6 presents correlations between range use variables, diet, and food abundance for each of the primate species. There were significant correlations between the dietary composition of the three primate species per sample period and the overall abundance of their plant food resources. For instance, the use of insects by the cebus monkeys was negatively related to plant food abundance, suggesting that they fed on insects during periods when other food resources were scarce. Similarly, both spider and howling monkeys tended to eat flowers when other plant food resources were not abundant. The range use variables did not relate to the abundance of food resources for any of the primate species.

**Table 6.** The relationship between food abundance and diet and range use variables for the three species of primates in Santa Rosa National Park, Costa Rica (Pearson  $r$  values reported).

|                   | Cebus<br>Food abundance | Howlers<br>Food abundance | Spiders<br>Food Abundance |
|-------------------|-------------------------|---------------------------|---------------------------|
| Feeding time      | 0.64                    | 0.68                      | -0.62                     |
| Travel time       | 0.41                    | 0.15                      | 0.51                      |
| % fruit in diet   | 0.61                    | 0.27                      | 0.54                      |
| % leaves in diet  | 0.36                    | 0.19                      | 0.96**                    |
| % flowers in diet | 0.36                    | -0.18                     | 0.41                      |
| No. of grids used | 0.32                    | 0.22                      |                           |
| % home range used | 0.37                    | 0.23                      |                           |
| Use of core area  | 0.04                    | -0.28                     |                           |
| % insects in diet | -0.92**                 |                           |                           |

\*\* &lt; 0.05.

## DISCUSSION

The diet and range use patterns of the three species of primates found in Santa Rosa National Park, Costa Rica exhibited few clear changes in relation to the shift in season or differing levels of food availability. A review of the literature for relationships between such variables indicates little consistency. For example, CLUTTON-BROCK (1977) found no consistent trend across a broad range of primate species with respect to whether or not they responded to changes in food abundance by altering the distance they travelled. There are a number of theoretical and methodological reasons why we should not expect consistent, significant relationships between gross measures of range use or diet and food abundance and season.

(1) It is likely that many species can deal with a specific situation in a number of different fashions. For instance, if food availability decreased, a group could respond either by increasing travel time to locate more food trees, or they could travel less to decrease costs, so as to conserve energy. Another example, illustrated by this study, deals with the ability of primates to respond to environmental conditions by forming subgroups. In response to a change in food availability or conditions associated with season, the howlers or spider monkeys of Santa Rosa could change their behaviour, their subgroup size, or some combination of both. When a mixed strategy such as that is used, the question of interest becomes: what determines the strategy to be used?

(2) Primates likely respond to subtle changes in the environment, and measures such as season and overall food abundance do not accurately reflect the situation experienced by the animals. I suggest that monkeys are more likely to respond to the phenological cycles of specific food plants than to season, as defined by the presence or absence of rain. Many plants have coevolved with the animals that disperse their seeds (HERRERA, 1985). This coevolution often has resulted in single species or group of species staggering their fruiting periods to support a population of dispersers (HOWE & ESTABROOK, 1977). Such coevolution may have favoured plants which produce fruit not when it would be physiologically easiest (i.e., when water is available), but when dispersal was likely to be most successful. An example of how season may have little influence on phenology is illustrated by the fruiting schedule of *Ficus* spp. and the monkey's use of fig fruit. One of the three species of primates in Santa Rosa ate fig fruit in 94% of the sample periods, reflecting the seasonal fruiting cycle of figs (see MILTON et al., 1982).

Observations made in this study suggest that range use is likely situation-dependent. A single fruiting tree can strongly influence the range use patterns of any of the primate species. This was illustrated in the example provided previously which suggested that the presence of a fruiting *Ficus* spp. or *Swartzia cubensis* tree in an area was strongly related to that area's use.

Another example of how range use can be situation-dependent is evident when comparisons between this and other studies are made. For instance, MCKEY and WATERMAN (1982) found that when food resources were scarce, their study group of black colobus (*Colobus satanas*) used peripheral areas of their home range. In this study no relationship existed between the use of the cebus and howling monkey's core areas and food abundance.

(3) Defining what food resources are available for primate consumption is a difficult task. For instance, in 1986 the fruits of *Bursera simaruba* were used heavily by spider monkeys (22.8% of their feeding time in one monthly period), but in the preceding years that food item was almost totally ignored (0.10% of the spider monkeys feeding time in 1984 and 1985). The availability of this food resource changed only slightly between the years (mean density in 1984 and 1985 = 20.8 individuals per ha, mean density in 1986 = 19.7 individuals per ha). If the observations of feeding on *B. simaruba* fruit had not been made in 1986, the 1984 and 1985 data would have suggested that it was not a food source.

(4) Many of the traditional measurements used to identify relationships examined here may be inadequate. For instance, tree species likely differ in the abundance of food they carry relative to their DBH. Home range has proven difficult to define conceptually (BURT, 1943; CLUTTON-BROCK, 1975), as well as operationally. The size of a group's home range is likely more closely related to observer sampling effort than to many ecological variables. In this study, the cebus and howling monkey groups were still entering new areas at the end of the study, and there was a positive relationship with the number of sightings of an individual spider monkey and the size of its home range.

(5) Since primates live in an environment that is unpredictable (inevitable when feeding on plant species that fruit asynchronously or species with many years between fruit crops), they must sample their environment by moving through their home range. Movement conducted when feeding on superabundant patches may reflect their need to sample the environment, or a need to patrol their territory.

(6) All three primate species studied here exhibited changes in diet, then returned to feeding on the original food resources that they ate prior to the change, even when the abundance of the foods remained constant. This suggests that changes in diet may in some instances simply reflect attempts to obtain a varied diet (MCKEY & WATERMAN, 1982).

In conclusion, the description of the diets and range use patterns of the three species of primates in Santa Rosa National Park and the examination of the expectation that diet and range use would be related to season and food availability, illustrated that these primate species were flexible in their response to the environment. Their behaviour was not stereotyped, but rather flexible to individual events, such as individual asynchronous fruiting trees, or the availability and location of standing water. Behavioural flexibility was also apparent in their diet. For all three species it was inadequate to classify their diet in terms of one simple category (e.g., frugivore), as is often done (RICHARD, 1985). Over the entire study each of the species observed showed foraging preferences which would allow them to be classified in categories such as insectivore, frugivore, or folivore. However, often for any

one sampling period their diet could be classified in a different category than the total sample period would suggest. Such behavioural flexibility would be advantageous in unpredictable environments.

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## REFERENCES

- ALTMANN, S. A. & J. ALTMANN, 1970. *Baboon Ecology*. Univ. of Chicago Press, Chicago.
- BAKER, H. G., K. S. BAWA, G. W. FRANKIE, & P. A. OPLER, 1982. Reproductive biology of plants in tropical forests. In: *Ecosystems of the World: Tropical Forests*, F. B. GOLLY & H. LEIGH (eds.), Elsevier, Amsterdam, pp. 183-215.
- BURT, W. H., 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.*, 24: 346-352.
- BUSKIRK, R. E. & W. H. BUSKIRK, 1976. Changes in arthropod abundance in a highland Costa Rica forest. *Amer. Midland Natur.*, 95: 288-298.
- CHIVERS, D. J., 1969. On the daily behaviour and spacing of howling monkey groups. *Folia Primatol.*, 10: 48-102.
- CLUTTON-BROCK, T. H., 1974. Primate social organization and ecology. *Nature*, 250: 539-542.
- , 1975. Ranging behaviour of red colobus (*Colobus badius tephrosceles*) in the Gombe National Park. *Anim. Behav.*, 23: 706-722.
- , 1977. Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London, pp. 539-556.
- & P. H. HARVEY, 1977. Species differences in feeding and ranging behaviour in primates. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London, pp. 557-579.
- DAUBENMIRE, R., 1972. Phenology and other characteristics of tropical semi-deciduous forests in Northwestern Costa Rica. *J. Ecol.*, 60: 147-170.
- ESTRADA, A., 1984. Resource use by the howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. *Int. J. Primatol.*, 5: 105-131.
- FEDIGAN, L. M. & M. J. BAXTER, 1984. Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates*, 25: 279-294.
- , L. FEDIGAN, & C. A. CHAPMAN, 1985. A census of *Alouatta palliata* and *Cebus capucinus* monkeys in Santa Rosa National Park, Costa Rica. *Brenesia*, 23: 309-322.
- FLEMING, T. H., C. F. WILLIAMS, F. J. BONACCORSO, & L. H. HERBST, 1985. Phenology, seed dispersal, and colonization in *Muntingia calabura* a neotropical pioneer tree. *Amer. J. Bot.*, 72: 383-391.
- FRANKIE, G. W., H. G. BAKER, & P. A. OPLER, 1974a. Comparative phenological studies of trees in tropical wet and dry forest in the lowlands of Costa Rica. *J. Ecol.*, 62: 881-919.
- , ———, & ———, 1974b. Tropical phenology: Applications for studies in community ecology. In: *Phenology and Seasonality Modelling*, H. LEIGH (ed.), Springer-Verlag, Berlin, pp. 287-297.
- FREELAND, W. J., 1976. Pathogens and the evolution of primate sociality. *Biotrop.*, 8: 12-24.
- GAULIN, S. J. C. & C. K. GAULIN, 1982. Behavioural ecology of *Alouatta seniculus* in Andean cloud forest. *Int. J. Primatol.*, 3: 1-32.
- , D. H. KNIGHT, & C. K. GAULIN, 1980. Local variance in *Alouatta* group size and food availability on Barro Colorado Island. *Biotrop.*, 12: 137-143.
- GAUTIER-HION, A., 1980. Seasonal variation of diet related to species and sex in a community of *Cercopithecus* monkeys. *J. Anim. Ecol.*, 49: 237-269.

- , L. H. EMMONS, & G. DUBOST, 1980. A comparison of the diets of three major groups of primary consumers of Gabon (primates, rodents, and ruminants). *Oecologia*, 45: 182-189.
- GLANDER, K., 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *Amer. J. Phys. Anthropol.*, 53: 25-36.
- , L. M. FEDIGAN, L. FEDIGAN, & C. A. CHAPMAN, in prep. Capture and marking monkeys in Santa Rosa National Park, Costa Rica.
- HAMILTON, W. J., 1982. Baboon sleeping site preferences and relationships to primate grouping patterns. *Amer. J. Primatol.*, 3: 41-53.
- HARRISON, M. J. S., 1983. Patterns of range use by the green monkey *Cercopithecus sabaues*, at Mt. Assirik, Senegal. *Folia Primatol.*, 41: 157-179.
- HERRERA, C. M., 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos*, 44: 132-141.
- HOWE, H. F. & G. A. ESTABROOK, 1977. On interspecific competition for avian dispersers in tropical trees. *Amer. Naturalist*, 111: 817-832.
- JANZEN, D. H., 1973. Sweep samples of tropical foliage insects: effects of season, vegetation types, time of the day, and insularity. *Ecology*, 54: 687-708.
- , 1986. Guanacaste National Park: Tropical, ecological, and cultural restoration. Editorial Univ. Estatal a Distancia, San Jose.
- KAVANAGH, M., 1981. Variable territoriality among tanzania monkeys in Cameroon. *Folia Primatol.*, 36: 76-98.
- KLEIN, L. L. & D. J. KLEIN, 1975. Social and ecological contrasts between four taxa of neotropical primates. In: *Socioecology and Psychology of Primates*, R. H. TUTTLE (ed.), Mouton, Hague, pp. 59-85.
- & ———, 1977. Feeding behaviour of the Colombian spider monkey. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London, pp. 153-181.
- KUMMER, H., 1968. *Social Organization of Hamadryas Baboons*. Univ. of Chicago Press, Chicago.
- LEIGHTON, M., 1982. Fruit resources and patterns of feeding, spacing, and grouping among sympatric Bornean hornbills (Bucerotidae). Unpubl. Ph.D. Dissertation, Univ. of California, Davis.
- & D. R. LEIGHTON, 1982. The relationship of size of feeding aggregate to size of food patch: Howler monkey (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotrop.*, 14: 81-90.
- MACKINNON, J. R. & K. S. MACKINNON, 1978. Comparative feeding ecology of six sympatric primates in West Malaysia. *Rec. Adv. Primatol.*, 1: 305-321.
- & ———, 1980. Niche differentiation in a primate community. In: *Malayan Forest Primates*, D. J. CHIVERS (ed.), Plenum Press, New York, pp. 167-190.
- MCDIARMID, R. W., R. E. RICKLEFS, & M. S. FOSTER, 1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. *Biotrop.*, 9: 9-25.
- MCKEY, D. & P. G. WATERMAN, 1982. Ranging behaviour of a group of black colobus (*Colobus satanas*) in the Douala-Eden Reserve, Cameroon. *Folia Primatol.*, 39: 264-304.
- MILTON, K., 1980. *The Foraging Strategy of Howler Monkeys*. Columbia Univ. Press, New York.
- & M. L. MAY, 1976. Body weight, diet and home range area in primates. *Nature*, 259: 459-462.
- , D. WINDSOR, D. MORRISON, & M. ESTRIBI, 1982. Fruiting phenologies of two neotropical *Ficus* species. *Ecology*, 63: 752-762.
- MITANI, J. C. & P. S. RODMAN, 1979. Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav. Ecol. Sociobiol.*, 5: 241-251.
- OPLER, P. A., G. W. FRANKIE, & H. G. BAKER, 1976. Rainfall as a factor in the release, timing and synchronization of anthesis by tropical trees and shrubs. *J. Biogeog.*, 3: 231-236.
- & ———, 1980. Comparative phenological studies of shrubs and treelets in wet and dry forests in the lowlands of Costa Rica. *J. Ecol.*, 68: 167-188.
- PETERS, R. H., S. CLOUTIER, D. DUBE, E. EVANS, P. HASTINGS, H. KAISER, D. KOHN, & B. SARWERFONER, 1988. The allometry of the weight of fruit on trees and shrubs in Barbados. *Oecologia*, 74: 612-616.
- PIELOU, E. C., 1969. *An Introduction to Mathematical Ecology*. Wiley, New York.
- RAEMAEKERS, J., 1980. Causes of variation between months in the distance traveled daily by gibbons. *Folia Primatol.*, 34: 46-60.
- RASMUSSEN, D. R., 1979. Correlates of patterns of range use of a troop of yellow baboons (*Papio*

*cynocephalus*). I. Sleeping sites, impregnable females, births, and male emigrations and immigrations. *Anim. Behav.*, 27: 1098-1112.

RICHARD A. F., 1985. *Primates in Nature*. W. H. Freeman & Co., New York.

SMITH, C. C., 1977. Feeding behaviour and social organization in howling monkeys. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London, pp. 97-126.

SMYTHE, N., 1970. Relationships between fruiting seasons and seed dispersal methods in a Neotropical forest. *Amer. Naturalist*, 104: 25-35.

SOKAL, R. R. & F. J. ROHLF, 1981. *Biometry*. W. H. Freeman & Co., San Francisco.

STRUHSAKER, T. T., 1978. Food habits of five monkey species in the Kibale forest, Uganda. In: *Recent Advances in Primatology*, D. J. CHIVERS & J. HERBERT (eds.), Academic Press, New York, pp. 225-248.

TERBORGH, J., 1983. *Five New World Primates. A Study in Comparative Ecology*. Princeton Univ. Press, Princeton.

WRANGHAM, R. W., 1981. Drinking competition in vervet monkeys. *Anim. Behav.*, 29: 904-910.

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