

Flexibility in Diets of Three Species of Costa Rican Primates

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Abstract. Variability in diet and dietary overlap were documented for the three species of primates in Santa Rosa National Park, Costa Rica (*Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*). All three species exhibited great flexibility in their diets, such that in 1 month a monkey species could be considered as having one type of diet (e.g. frugivorous), while in a subsequent month it would be classified as having a different type of diet (e.g. folivorous or insectivorous). It is suggested that such variability in diet and dietary overlap make it unlikely that competition just between these primate species was a strong selective pressure determining their diets.

Introduction

Recent evidence from long-term studies of primates indicates that many species have highly varied diets and show considerable flexibility in the types of food items eaten [Hladik, 1977; Lindburg, 1977; MacKinnon and MacKinnon, 1978, 1980; Milton, 1980, 1984; Oates, 1977; Richard, 1977; Struhsaker, 1975; Waser, 1977]. For instance, MacKinnon and MacKinnon [1980] found that the percentage of fruit in the diet of *Presbytis obscura* varied between months from 13 to 80%.

Studies conducted over a number of years have discovered striking dietary differences

between years [Hladik, 1977; Kinzey, 1977; Struhsaker, 1975; Waser, 1975, 1977]. Waser [1977] provided a number of examples of annual variation in the dietary patterns of the mangabey *Cercocebus albigena*. For instance, he observed mangabeys feeding on the leaves of *Platyserium* in 1971 but not again until 1974, yet leaves were available in the intervening years. Similarly, Struhsaker [1975] found major differences in the foods eaten by *Colobus badius* in the same months in different years.

Intraspecific dietary differences between primate groups observed at different locations have been demonstrated in a number of field studies [Clutton-Brock, 1974, 1977;

Hladik, 1977; MacKinnon and MacKinnon, 1978, 1980; Oates, 1977; Richard, 1977; Struhsaker and Leland, 1979; Waser, 1977; Wrangham, 1977]. The majority of these dietary differences were probably a result of differences in the foods available at the study sites. However, dietary differences found between some populations cannot be explained by availability [Hladik, 1977; Kawamura, 1959; Azuma, 1973; Richard, 1977; Struhsaker, 1975; Waser, 1977]. Richard [1977] found that one population of *Propithecus verreauxi* fed extensively on the fruits of *Rothmannia decaryi*, while another population ignored the fruit. Such variability in diets could influence both how primates interact with their environment [e.g. seed dispersal; Herrera, 1985] and how they interact with other species [e.g. competitive interactions; Strong, 1983; Wiens, 1977].

The objective of this study was to examine the degree of flexibility in the diets of the three species of primates (spider monkeys: *Ateles geoffroyi*; capuchins: *Cebus capucinus*; howling monkeys: *Alouatta palliata*) living in Santa Rosa National Park, Costa Rica, by analyzing variation in their diets between months and between years. In addition, I attempted to discern the effect of this variation on the dietary overlap between the primate species to provide insights into how dietary overlap may have influenced the development of feeding strategies.

Methods

The study was conducted at Santa Rosa National Park, Costa Rica, during four field seasons: July and August 1983, January to August 1984, January to July 1985, and February to August 1986. In the last year only spider monkeys were observed. Santa Rosa is a 10,800-ha National Park, situated 35 km northwest of

Liberia, adjacent to the Pan-American Highway. The climate of the region is very seasonal, with a dry season beginning in mid-December and ending in late May and a wet season encompassing the rest of the year. Rainfall ranges between 900 and 2,400 mm annually. As a result of natural topography and past land-use practices, the vegetation of the park is a mosaic of grassland (*Hyparrhenia rufa*), dry deciduous forest containing *Spondias mombin*, *Luehea candida*, *L. speciosa*, *Guazuma ulmifolia*, *Bursera simaruba*, and *Chlorophora tinctoria*, and semi-evergreen forest containing trees such as *Hymenaea courbaril*, *Mastichodendron capiri*, *Castilla elastica*, and *Manilkara chicle* [Janzen, 1986; Chapman, unpublished data].

I concurrently studied one group of each primate species to maximize the temporal similarity of the available foods. The study groups occupied home ranges that overlapped extensively and included areas of both dry deciduous and semi-evergreen forest (fig. 1). The howling monkey group contained on average 40 individuals, and the capuchin monkey group comprised 26 individuals. Both groups were large for Santa Rosa, as the mean group size for the park in 1984 was 14.0 animals for capuchin monkeys and 13.7 individuals for howlers [Fedigan et al., 1985]. The fluid social structure of spider monkeys precluded an accurate estimate of community size. However, the minimum size of the community was estimated by summing the maximum counts of all age/sex classes seen in any one year. Using this method the community was estimated to contain 42 individuals [Chapman and Fedigan, in preparation].

Behavioral data were collected using a focal animal sampling regime which employed a session length of 10 min. If the subject was lost prior to the end of the session, the session was terminated and the data discarded. When the focal animal was observed feeding, the species of plant it was eating, the size of food plant (estimated as diameter at breast height, DBH), and the type of food eaten (i.e. fruit, flower, young leaves, etc.) were recorded. With this sampling procedure, 394 h of focal animal data were collected on howling monkeys, 335 h on spider monkeys, and 171 h on capuchin monkeys. Normally the species chosen to be sampled was alternated each day, although this varied somewhat depending on the ease with which each species could be located on a particular day. An attempt was made to obtain a complete record of the activity of each species during a 3-week

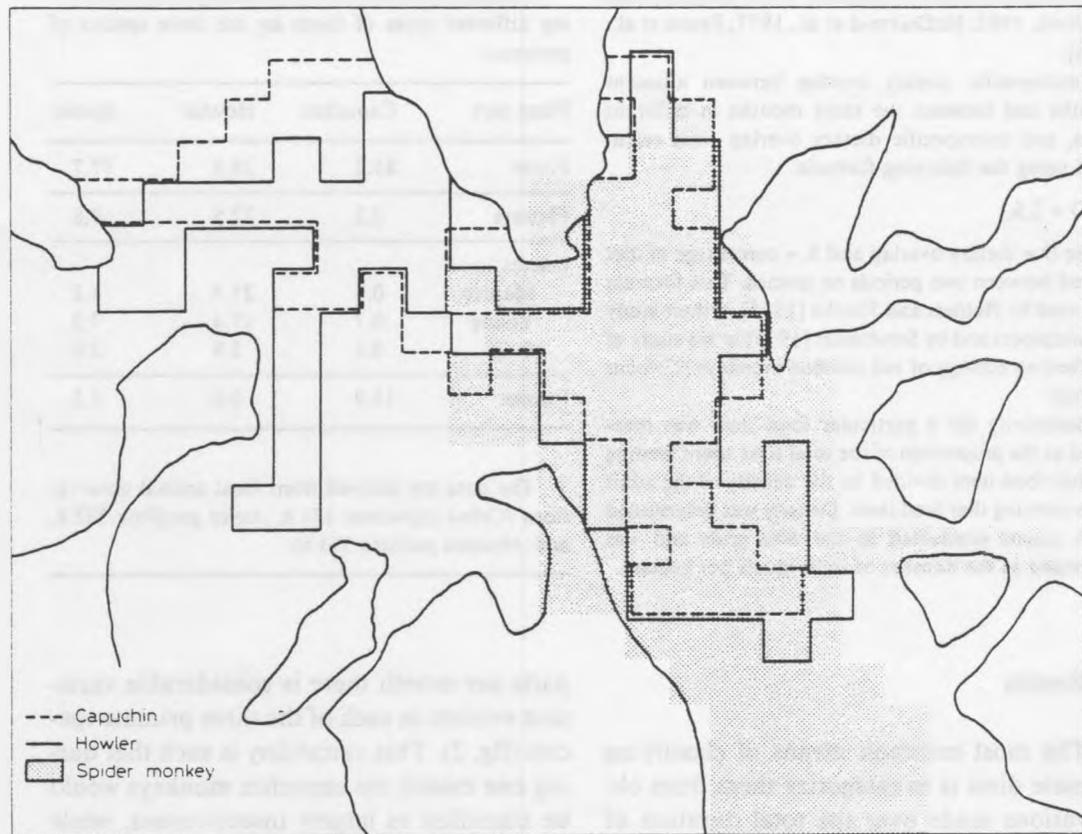


Fig. 1. Home range overlap for study groups of the three species of primates found in Santa Rosa National Park, Costa Rica.

sample period so that at the end of the period an equal number of observations had been made in each hour of the day. A scan sample was taken every half hour in 1984 and every 10 min in 1985 and 1986 to assess the group's activity, the tree species being used, the tree's size (DBH), the height of group members in the canopy, and the proximity of other primate species, and the group's location. Location was recorded as a coordinate on a grid (120 by 120 m) superimposed on an aerial photograph of the group's home range.

To describe the average size and density of the plant species being used by each of the three primates, the most commonly used food resources were identified for each primate species from the preceding 3 weeks of behavioral observation, and the location, size, and phenological status of all adult food trees

were determined in three 4-ha grids. These grids each contained 400 cells which were 10 by 10 m in size. Corners of the cells were marked with a steel post. The grids encompassed 9% of the home ranges of both the capuchins and the howling monkeys. Each grid was established in slightly different habitats, so that all the major habitats used by the monkeys were sampled. An adult tree was considered as any individual that had attained a DBH of the smallest individual known to bear fruit. The phenological data recorded involved assessing the stage of leaf development (i.e. no leaves, leaf buds, young leaves, mature leaves) and noting the presence or absence of fruit and flowers. The size of the trees was represented as DBH, which has been shown for a number of tropical plant species to accurately reflect the reproductive capacity

of fruiting individuals [Leighton, 1982; Leighton and Leighton, 1982; McDiarmid et al., 1977; Peters et al., 1988].

Intraspecific dietary overlap between adjacent months and between the same months in different years, and interspecific dietary overlap were calculated using the following formula:

$$D = \sum S_i$$

where D = dietary overlap and S_i = percentage of diet shared between two periods or species. This formula was used by Holmes and Pitelka [1968] in their study of sandpipers and by Struhsaker [1975] in his study of the feeding ecology of red colobus monkeys (*Colobus badius*).

Selectivity for 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 carrying that food item. Density was determined from counts conducted in the 4-ha grids and was expressed as the number of individuals per hectare.

Results

The most common means of classifying primate diets is to categorize them from observations made over the total duration of the study, in terms of the proportion of feeding time spent eating different plant parts (e.g. fruit, leaves, etc.). Using this classification system, both capuchin monkeys and spider monkeys were primarily frugivorous, and spent 81.2% and 77.7% of their total feeding time, respectively, eating fruit (table I). Howlers were more folivorous than the other two primate species. Leaves constituted 49.0% of their feeding time, whereas fruit accounted for only 28.5% of their feeding time. Capuchin monkeys were the most insectivorous of the three species, but the eating of insects constituted only 16.9% of their feeding time.

If diets are depicted as the amount of time spent feeding on the different food

Table I. Percentage of total feeding time spent eating different types of foods by the three species of primates

Plant part	Capuchin	Howler	Spider
Fruits	81.2	28.5	77.7
Flowers	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 capucinus* 171 h, *Ateles geoffroyi* 335 h, and *Alouatta palliata* 393 h).

parts per month there is considerable variation evident in each of the three primate species (fig. 2). This variability is such that during one month the capuchin monkeys would be classified as largely insectivorous, while in other months they were almost entirely frugivorous. Similarly, the spider monkey's diet varied from being exclusively composed of fruit to consisting primarily of foliage. As shown in figure 2, the monthly patterns of variation in diet do not appear to be highly synchronized between the species. This was tested statistically for the three types of plant foods using Kendall's test of concordance and in no instance did the three species appear to synchronize their feeding (fruit $W = 0.21$, $p > 0.05$; leaves $W = 0.19$, $p > 0.05$; flowers $W = 0.07$, $p > 0.05$).

A more precise means of classifying primate diets is to categorize them in terms of the food items eaten, including the plant species used and the part taken. If the plant

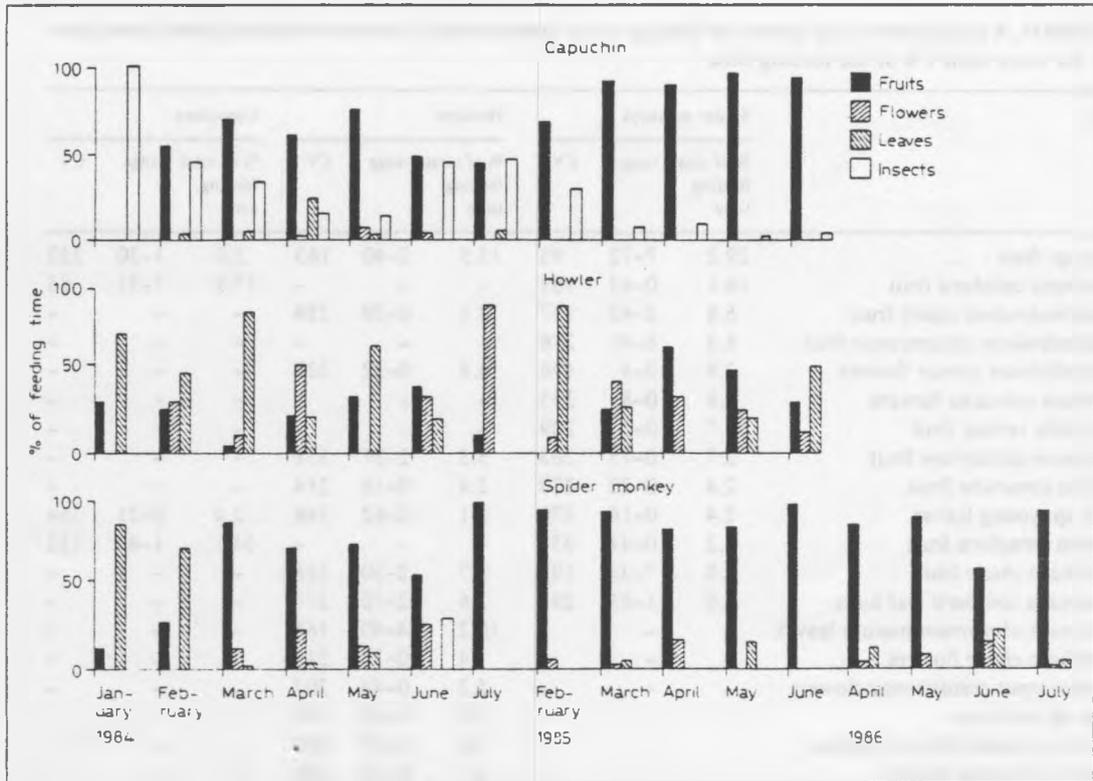


Fig. 2. Percentages of observed feeding time that the three species of primates spent eating different type of foods in each month of the study.

diets of the three primate species studied here are classified in these terms, again there is a large amount of temporal variability in use (table II). Variability in the use of different plant species when there are appreciable differences in the mean values can be indicated by the coefficient of variation (CV) [Sokal and Rohlf, 1981]. For all three primate species, the CV ranges widely among plant species (capuchin 83–354, mean = 222; howler 163–355, mean = 239; spider monkey 95–370, mean = 227). Plant items with the lowest CV tended to be those items available for a longer proportion of the study period. However, a number of food items had high

CV's even when they were available for the duration of the study, suggesting that the monkeys were not using these plant species in proportion to their availability. Overall, no relationship existed between the variability in use of a plant species (CV) and the length of time the resource was available (spider monkeys: $r = -0.41$, $p = 0.16$; howlers: $r = -0.20$, $p = 0.44$; capuchins: $r = -0.49$, $p = 0.27$). Nor was it related to the density of the plant species (spider monkeys: $r = 0.26$, $p > 0.10$; capuchins: $r = 0.18$, $p > 0.10$; howlers: $r = 0.14$, $p > 0.10$) or the density of the plant species weighted by their size (DBH; spider monkeys: $r = 0.16$, $p > 0.10$;

Table II. A description of the pattern of feeding of the three species of primates depicting those plant parts used for more than 1% of the feeding time

Plant	Spider monkeys			Howlers			Capuchins		
	% of total feeding time	range	CV	% of total feeding time	range	CV	% of total feeding time	range	CV
<i>Ficus</i> sp. fruit	29.2	7-72	95	15.5	2-40	163	2.0	1-30	232
<i>Muntingia calabura</i> fruit	16.1	0-45	169	-	-	-	17.9	7-31	83
<i>Mastichodendron capiri</i> fruit	6.6	2-42	147	3.1	0-30	259	-	-	-
<i>Dipterodendron costaricensis</i> fruit	6.3	8-41	216	-	-	-	-	-	-
<i>Pithecellobium saman</i> flowers	2.9	0-4	196	6.8	0-52	228	-	-	-
<i>Tabebuia ochracea</i> flowers	2.8	0-8	235	-	-	-	-	-	-
<i>Coccoloba venosa</i> fruit	2.7	0-3	209	-	-	-	-	-	-
<i>Brosimum alicastrum</i> fruit	2.7	0-15	203	5.5	2-37	331	-	-	-
<i>Bursera simaruba</i> fruit	2.4	0-22	270	2.4	0-16	214	-	-	-
<i>Ficus</i> sp. young leaves	2.4	0-16	370	5.1	0-62	346	2.4	0-21	354
<i>Sloanea terniflora</i> fruit	2.2	0-41	354	-	-	-	34.1	1-87	152
<i>Manilkara chicle</i> fruit	2.0	7-32	198	2.7	2-30	216	-	-	-
<i>Hymenaea courbaril</i> leaf buds	2.0	1-86	289	2.6	2-70	277	-	-	-
<i>Brosimum alicastrum</i> mature leaves	-	-	-	10.2	4-40	168	-	-	-
<i>Manilkara chicle</i> flowers	-	-	-	7.4	0-33	214	-	-	-
<i>Lonchocarpus costaricensis</i> flowers	-	-	-	5.2	0-44	207	-	-	-
<i>Ficus</i> sp. leaf buds	-	-	-	2.0	0-22	219	-	-	-
<i>Bursera simaruba</i> mature leaves	-	-	-	3.8	0-39	225	-	-	-
<i>Bursera simaruba</i> flowers	-	-	-	2.7	0-14	355	-	-	-
<i>Castilla elastica</i> leaf buds	-	-	-	2.4	0-11	193	-	-	-
<i>Brosimum alicastrum</i> leaf buds	-	-	-	2.3	0-16	214	-	-	-
<i>Brosimum alicastrum</i> young leaves	-	-	-	2.2	0-14	235	-	-	-
<i>Luehea speciosa</i> fruit	-	-	-	-	-	-	4.4	0-56	286
<i>Quercus oleoides</i> fruit	-	-	-	-	-	-	3.5	0-32	213
<i>Sciadodendron excelsum</i> fruit	-	-	-	-	-	-	2.5	0-28	312

capuchins: $r = 0.09$, $p > 0.10$; howlers: $r = 0.05$, $p > 0.10$).

Much of the variability in use of food sources was probably due to the changing availability of particular food resources. However, that was not the case in a number of instances. For example, the use of fruits of *Muntingia calabura* was not related to its availability. Fleming et al. [1985], in a study conducted over 10 years in Santa Rosa, demonstrated that, although *M. calabura* pro-

duces fruits year round, there is a peak in production following the onset of the rainy season. However, in 1984 and 1985 both spider and capuchin monkeys fed heavily on *M. calabura* in the months preceding the rains and greatly decreased the amount of time spent eating this fruit in the months following the rains, the time of the year when the fruits were most abundant. In contrast, preceding the onset of the wet season in 1986, spider monkeys rarely fed on *M. cala-*

bura fruits, but they fed on this fruit heavily immediately following the onset of the rains, and continued to use the fruits well after their availability had declined. The consumption of acorns of *Quercus oleoides* by capuchin monkeys and the use of certain mature leaves by howling monkeys are similar examples [Chapman and Chapman, 1988].

It is possible that the recorded variability in the use of resources by the primates is attributable to a sampling problem, since the probability of the monkeys finding plants occurring at low densities was largely a matter of chance. If this were the case, CV values for use should be negatively related to the densities of plant species. However, contrary to expectation, for none of the primate species was the variability in use related to the density of the plant species (spider monkeys: $r = 0.24$, $p = 0.44$; howlers: $r = 0.17$, $p = 0.53$; capuchins: $r = 0.21$, $p = 0.76$). Thus, overall variability in resource use was probably not caused by an inability of any of the three primate species to sample their environment effectively.

A means of examining variability in diet, which reduces the effect of availability, is to quantify the dietary overlap between adjacent months (e.g. May vs. June and May vs. April), since directly adjacent months are likely to have the most similar levels of abundance of particular types of foods [Struhsaker, 1975, 1978]. For some pairs of months diets were similar, while at other times diets were very dissimilar (table III). On average, the diets of the three species tended to overlap by only 31% with a neighboring month. Monthly dietary overlap differed significantly between the species ($F = 4.02$, $p = 0.03$). An a posteriori comparison demonstrated that the diet of spider monkeys overlapped more between adjacent

months than did the diet of howling monkeys (Scheffe's $p < 0.05$); capuchins were intermediate, but closer to spider monkeys than to howlers. These analyses illustrate that the diets of these monkeys were highly variable, both in terms of the plant parts eaten and in terms of the food items (i.e. species part, e.g. fig fruit) used. They also suggest that variability in use was not simply due to the monkeys tracking a variable resource base.

Even though the monthly variability in diet for all three primate species was high, there could be annual consistency in their diets as these three species exploited food resources that became available at roughly the same time each year. When dietary overlap values were calculated for the same month in each of the years that data were available for all three species, little annual consistency in diet between years was apparent (table IV). In fact, dietary overlap calculated between adjacent months was not significantly different from dietary overlap calculated on an annual basis for any of the three species (capuchins: $t = -0.69$, $p = 0.50$; spider monkeys: $t = 0.40$, $p = 0.69$; howlers: $t = -0.67$, $p = 0.52$). As the time of onset of the rains differed between years (May 22, 1984 and May 9, 1985), an examination was made of whether or not there was a significant change in dietary overlap if the time frame used for the comparison was shifted by ± 1 month (e.g. March 1984 vs. April 1985 and March 1984 vs. February 1985). This analysis demonstrated that the dietary overlap values obtained from comparisons of the same months in different years were not significantly different from either of the two shifted scales ($F = 0.76$, $p = 0.39$).

Some of the annual variability in diet was directly related to food resources that were

Table III. Intraspecific dietary overlap between adjacent months for the three primate species

Month	Capuchins	Howlers	Spider monkeys
1984			
January/February	0.0	40.3	46.2
February/March	36.3	26.7	31.5
March/April	48.6	6.5	28.5
April/May	32.3	9.1	45.3
May/June	21.2	5.9	48.9
June/July	51.9	2.3	45.3
1985			
February/March	19.6	23.3	40.1
March/April	36.7	0.0	44.2
April/May	45.7	45.1	34.9
May/June	61.9	41.1	19.4
Average	35.4	20.0	38.4

available on a supra-annual basis, such as *Mastichodendron capiri* and *Swartzia cubensis*. *S. cubensis* bears fruit on a supra-annual basis in which several years lapse between fruiting events [D.H. Janzen, personal commun.]. When it fruited in 1985, *S. cubensis* was used heavily in the months it was available (% of feeding time when available: spider monkeys 6.9%, howlers 11.7%, capuchins 9.5%). *Mastichodendron capiri* bears fruit on a biennial basis, and it constituted as much as 42.2% of the spider monkeys' feeding time in a month. When foods such as *M. capiri* and *S. cubensis* are not available, the monkeys must make alternate dietary selections. Such supra-annual fruiting events induce variability in the diet of these three primate species. However, it seems likely that a large proportion of the annual variability in diet cannot be related directly to the supra-annual fruiting of specific plants. A number of food items were equally available in all years, but were used heavily in one year and

Table IV. Intraspecific dietary overlap between the same months in two different years (1984 and 1985) for the three species of primates

Month	Capuchins	Howlers	Spider monkeys
February	42.9	21.5	20.0
March	46.6	18.5	28.9
April	51.9	44.4	49.3
May	62.3	37.1	53.7
June	9.2	20.9	27.5
Average	42.6	28.5	31.9

used little if at all in a subsequent year. For example, the capuchin monkey group fed on *Quercus oleoides* acorns heavily in 1984, while in 1985 no group member was seen eating acorns; yet acorns were abundant in both years (density of *Quercus oleoides* = 5 individuals/ha, mean DBH = 57.3 cm). A similar example concerns the use of *Bursera simaruba* by spider monkeys. *B. simaruba* is a common tree in areas of dry deciduous forest. In 1984 and 1985, spider monkeys were rarely seen eating this fruit (0.10% of their total feeding time); but in 1986 it constituted 21.8% of their diet in one sample period and 2.4% of their total feeding time that year. This amounted to a 25-fold increase in the use of *B. simaruba* between years. The difference in the amount of time spent feeding on *B. simaruba* cannot be attributed to a change in the availability of the species, since the density of fruiting individuals was similar in each year (individuals/ha: 1984 and 1985 = 20.8, 1986 = 19.7).

Interspecific Dietary Overlap

To assess the consequences of the variability in diets for interspecific dietary overlap, it is necessary to calculate overlap in terms of the plant species used and the parts

taken. Calculating dietary overlap in this fashion revealed considerable variability in monthly dietary overlap between each pair of the species (range: 0–83.7%, table V). The average monthly overlap was high for capuchin-spider monkeys (mean = 23.6%) and howlers-spider monkeys (mean = 22.9%). However, the range in overlap for howlers-spider monkeys (0–83.7%) was larger than the range for capuchin-spider monkeys (0–43.0%). Both the average monthly overlap (\bar{x} = 4.95%, F = 4.39, p = 0.02, Scheffe's p < 0.05) and the range in monthly overlap values (0–30.1%) were lower for the capuchin-howler pair than for the other species pairs.

To examine the relationship between the diets of the three primate species, a cluster analysis was conducted in two fashions: first using the proportion of the feeding time that each species spent eating the different plant parts (e.g. fruit, young leaves, etc., fig. 3) and secondly using the six most commonly eaten food items (i.e. species, part) and each primate species (fig. 4). In the first analysis, the major clusters were not exclusively formed from the diets of a single species. On four occasions the monthly dietary samples of the spider monkeys were most closely related to a monthly dietary sample of the capuchin monkeys. In one instance a dietary sample of the spider monkeys was more similar to that of howling monkeys than to a different spider monkey dietary sample collected at another time. The monthly dietary samples of the howling monkeys clustered together separate from the monthly dietary samples of the other two primates in all but one case.

The second level of analysis, using the plant species and part, is a more precise level of examining dietary overlap than examining the different plant parts eaten. The dendrogram produced from this analysis shows

Table V. Interspecific dietary overlap per month for the three species of primates

	Month	Howlers/ spider monkeys	Capuchins/ spider monkeys	Capuchins/ howlers
1984	January	83.7	0.0	0.0
	February	30.3	0.0	0.0
	March	0.0	34.9	0.2
	April	13.1	43.0	30.1
	May	29.1	21.5	19.0
	June	31.9	36.0	7.0
	July	0.7	38.0	0.0
1985	February	0.0	12.4	0.0
	March	0.0	29.1	0.0
	April	39.4	12.4	3.2
	May	25.8	13.5	0.0
	June	20.7	42.5	0.0
Average		22.9	23.6	5.0

little clustering of monthly dietary samples in terms of either monkey species or sample period. Contrary to the first analysis, most dietary samples of howling monkeys were not closely associated. Also, as in the previous analysis, there was no clear seasonal or annual structuring to the dendrogram.

In order for the three primate species to be in a position where competition for resources might occur, they must overlap spatially and use areas at the same time, or at some time interval after one another that is shorter than the time required for the resources to be replenished. The home ranges of the capuchin monkeys and howling monkeys overlapped considerably (fig. 1). There was an 81.3% overlap in the home ranges of these two primate species (areas of overlap were considered as those 120 by 120 m grid cells used by both primate species). Their core areas overlapped by 66.7%, and the core area of each of the primate species was

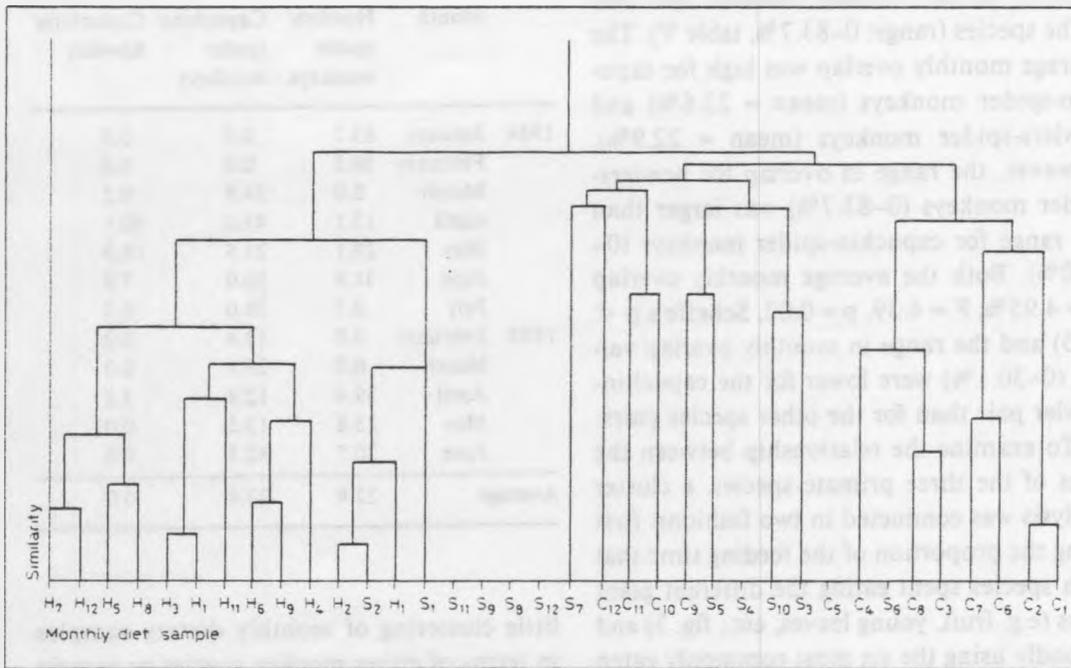


Fig. 3. A dendrogram depicting the similarity in the diets of the three species of primates. The unit of comparison was the type of foods eaten (i.e. fruit, flowers, leaves, insects). For the monthly dietary sample, C represents *Cebus capucinus*, S the spider monkey *Ateles geoffroyi*, and H the howling monkey *Alouatta palliata*. The numbers in the monthly diet sample represent the consecutive months of the study, i.e. 1 = January 1984, 2 = February 1984, 3 = March 1984, 4 = April 1984, 5 = May 1984, 6 = June 1984, 7 = July 1984, 8 = February 1985, 9 = March 1985, 10 = April 1985, 11 = May 1985, 12 = June 1985.

used by the other species at some time during the study. For capuchin monkeys only 13.7% of the total number of sightings ($n = 225$) were in one of the 120 by 120 m cells not used by the howling monkey group. Conversely, 19.7% of the total number of sightings ($n = 314$) of howlers were in cells not used by the capuchin monkey group. The likelihood of howlers having exclusive use of an area is probably lower than is represented here, because they also overlap considerably with neighboring groups of capuchin monkeys. The area that the howling monkey study group used but that was not used by the capuchin monkey study group was in an

area where a neighboring capuchin monkey group was frequently seen (22 occasions).

Since the spider monkeys do not form cohesive groups, home range parameters cannot be calculated in the same fashion as for the capuchin and howling monkey study groups. To calculate a minimum home range size for the community, the number of grid cells that were used by all of the identifiable spider monkeys, or which they had to pass through were summed. Considering home range in this fashion, the spider monkey community used an area of 1.47 km² (fig. 1). The spider monkeys that were well habituated to the presence of an observer were pri-

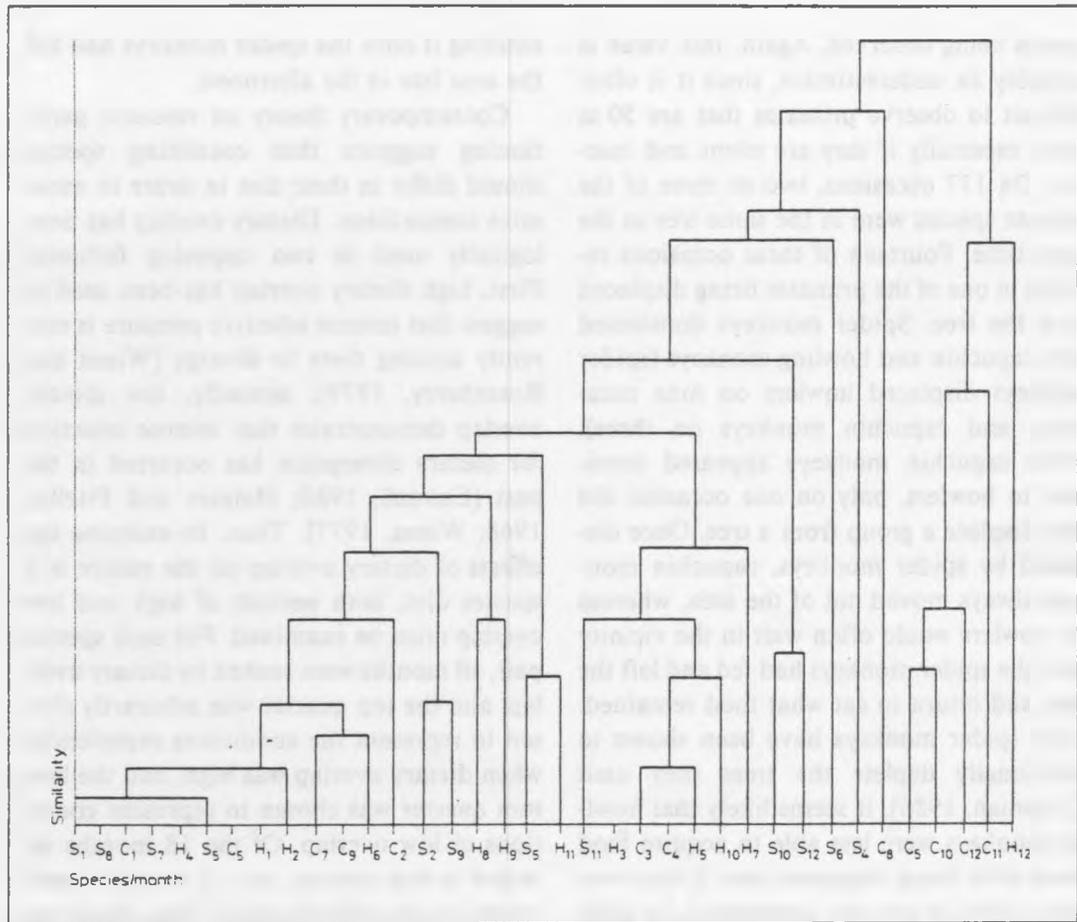


Fig. 4. A dendrogram depicting the similarity in the diets of the three species of primates. The unit of comparison was the six most commonly eaten food items (i.e. species, part) consumed by each primate species. For the monthly dietary sample, C represents *Cebus capucinus*, S the spider monkey *Ateles geoffroyi*, and H the howling monkey *Alouatta palliata*. The numbers in the monthly diet sample represent the consecutive months of the study, as in figure 3.

marily studied in one section of forest which was separated from a second block of forest by a narrow corridor. The second block of forest was rarely used by identifiable spider monkeys, and I believe that the spider monkeys using this area belong to a second community. If interspecific home range overlap is calculated within the section of forest in

which spider monkeys were primarily studied, 95% of the area used by the capuchin monkey study group and 96% of the area used by the howling monkey group were also used by identifiable spider monkeys.

Scan samples indicated that during 15.4% of the observation time another primate species was within 50 m of the primate

species being observed. Again, this value is probably an underestimate, since it is often difficult to observe primates that are 50 m away, especially if they are silent and inactive. On 177 occasions, two or three of the primate species were in the same tree at the same time. Fourteen of these occasions resulted in one of the primates being displaced from the tree. Spider monkeys dominated both capuchin and howling monkeys (spider monkeys displaced howlers on nine occasions, and capuchin monkeys on three). While capuchin monkeys appeared dominant to howlers, only on one occasion did they displace a group from a tree. Once displaced by spider monkeys, capuchin monkeys always moved out of the area, whereas the howlers would often wait in the vicinity until the spider monkeys had fed and left the tree, and return to eat what food remained. Since spider monkeys have been shown to functionally deplete the trees they used [Chapman, 1986], it seems likely that howling monkeys were less able to acquire food items after being displaced than if they were able to feed in the tree unmolested. In addition, by being displaced howlers were probably forced to take food items of lower quality (e.g. less ripe fruit) than they would have if they were not displaced by spider monkeys.

In a number of cases this type of interaction probably altered the dietary choices of the primates. In particular, for a number of fruiting trees such as *Swartzia cubensis* and *Ficus* sp. that occurred at low density, it was possible for one primate species to monopolize the resource. Once spider monkeys located such a food source, they often excluded howlers from it for the major part of the day. On a number of occasions, howlers were seen foraging in the vicinity of a fruiting fig tree that was being used by spider monkeys, only

entering it once the spider monkeys had left the area late in the afternoon.

Contemporary theory on resource partitioning suggests that coexisting species should differ in their diet in order to minimize competition. Dietary overlap has been logically used in two opposing fashions: First, high dietary overlap has been used to suggest that intense selective pressure is currently causing diets to diverge [Wiens and Rotenberry, 1979]; secondly, low dietary overlap demonstrates that intense selection for dietary divergence has occurred in the past [Connell, 1980; Holmes and Pitelka, 1968; Wiens, 1977]. Thus, to examine the effects of dietary overlap on the nature of a species diet, both periods of high and low overlap must be examined. For each species pair, all months were ranked by dietary overlap, and the top quarter was arbitrarily chosen to represent the conditions experienced when dietary overlap was high, and the bottom quarter was chosen to represent conditions of low overlap. Of the 18 months selected in this fashion, only 3 were the same month in the different years. Thus, there was little consistency between years in terms of which months had either high or low dietary overlap. At the time of high dietary overlap, the monkeys were primarily eating fruit; however, there were also instances involving high overlap for flowers and leaf buds. The trees for which a high level of overlap occurred varied from being common (34.4 individuals/ha) to rare (0.50 individuals/ha). Some of these plant species were preferred foods, while others were not (selectivity ranged from 0.04 to 31.7). Some of the species for which overlap was high bore food items for a short period (> 1 month), while others bore food items for extended periods (maximum 12 months). Similarly, when di-

etary overlap was low, there was little consistency in the types of food being used by any of the three primate species. For instance, during the months of the lowest dietary overlap for spider and capuchin monkeys, spider monkeys fed primarily on leaves in one month, on a combination of flowers and fruit in the next month, and primarily on fruit in the third month, while the capuchin monkeys fed primarily on fruit (of different species) and insects in all months. Since the climate of Santa Rosa is highly seasonal, and many plants exhibit similar phenological cycles, one might expect some synchronization in dietary overlap between the species pairs. No consistent period of either high or low overlap existed for all species pairs, and there was no temporal synchronization in the degrees of dietary overlap (Kendall's test of concordance, $W = 0.31$, $p > 0.05$).

Discussion

While the major emphasis in primate ecology has been on the identification of consistent patterns, rather than on examination of variability, a large body of evidence suggests that variability, such as was found here, commonly occurs in primates [Clutton-Brock, 1977; Struhsaker, 1975; Waser, 1977]. By simultaneously examining the diets of the three primate species found in Santa Rosa, it was possible to quantify the extent of the variability in diet and its influence on interspecific dietary overlap. The diets of all three species varied considerably on a monthly and annual basis. Variability occurred both in terms of the types of foods consumed (fruit vs. leaves, etc.) and in what plant species were exploited. This variation in diet contributed to the variability in inter-

specific dietary overlap between the three primate species. There was little consistency between years in when dietary overlap was likely to be high or low, or in the types of trees that were the source of the overlap. A number of other studies on a variety of animal species have demonstrated great variability in diet similar to the results obtained in this study [Feinsinger, 1976; Gautier-Hion, 1980; MacKinnon and MacKinnon, 1978, 1980; Wiens, 1977; Wiens and Rotenberry, 1979; Rotenberry, 1980].

If primates commonly have flexible diets, this will influence how they interact with other species in their community. The view that primate communities exist in balanced coexistence, where each species exploits a different combination of resources, has been shaped by studies which have not examined variability and its consequences. Variability in diet will influence the relative importance of dietary overlap as a selective pressure favoring the divergence of diets. For the species studied here, high variability in diet, in overlap, and in the plants over which overlap occurs, are likely to result in dietary overlap only acting as a selective pressure determining diet choice on an intermittent basis [Strong, 1983; Wiens, 1977]. In fact, overlap may only be a significant force on a supra-annual basis, possibly being associated with periods of atypical conditions [e.g. fruit crop failure, Foster, 1982, or cyclone destruction, Dittus, 1985]. Thus, dietary separation may occur only at a few critical times and involve only certain food items. However, if these periods of 'significant' overlap occurred on a periodic basis which was much greater than the study species' generation time, or if the strategy which was most profitably used during these periods varied, the predictability of success of a given genotype is probably low.

Thus, heritability of a specific diet favored by dietary overlap will also be low. For primates, it seems probable that the profitability of a specific diet will vary between periods of 'significant' overlap. Not only do primates have diverse diets, and thus many options as to which types of foods to eat during any period, but also the diet will probably differ in different regions between which gene flow is possible. The particular conditions favoring dietary divergence may be site-dependent. Given the level of variability shown between neighboring groups or populations in other studies (cited above), the diet used to deal with the periods of 'significant' overlap will probably vary between sites.

Another factor that probably decreases the importance of competitive interactions in determining diet is that each species of monkey is not responding just to the pressures exerted on it by other primates, but to all of the species with which it overlaps in diet. In tropical communities, many species often feed on the same food resource. For example, Beebe [1916] observed 51 tropical bird species entering a single fruit tree, and Willis [1966] lists 28 species of birds using the berries of one species of small tree. Rockwood and Glander [1979] documented an example of dietary overlap between two phylogenetically unrelated species when they observed overlap between howling monkeys and leaf cutter ants [see also Emmons, 1980; Estrada and Coates-Estrada, 1985; Estrada et al., 1984; Fleming, 1979; Gautier-Hion et al., 1980; Glander, 1979; Terborgh, 1983]. These arguments suggest that although behavioral interactions, such as the displacement from food trees, do occur, it is unlikely that interactions occurring between just the primate species represent a strong force determining their diets.

Summary

A 4-year study of the three species of primates living in Santa Rosa National Park, Costa Rica (spider monkeys: *Ateles geoffroyi*; howling monkeys: *Alouatta palliata*; capuchin monkeys: *Cebus capucinus*), revealed that these species employed highly flexible dietary strategies. When dietary patterns of these three species were depicted as the percentage of time spent feeding on different food parts per month (i.e. leaves, flowers, fruit, insects), variability was such that the capuchin monkey was classified as primarily insectivorous in one, while in other months it was largely frugivorous. Similarly, the diet of the spider monkeys varied from being composed of exclusively fruit to consisting of primarily of leaves, and the howlers changed from being primarily folivorous to being primarily frugivorous. The patterns in which diet varied were not synchronized between species. Much of the variability in diet was due to changes in the availability of particular food resources, but a number of instances are documented in which the use of a food resource was not related to its availability. In addition to demonstrating dietary variability on a monthly scale, it was shown that there was little annual consistency in the diets of these three species even though they used resources that became available at roughly the same time each year. This level of dietary variability resulted in great differences in the level of interspecific dietary overlap. It is suggested that the extent of this variability in diet and dietary overlap will make it unlikely that competition between these primate species is an important pressure determining diet in these species.

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