

Seasonal Variations in Diet and Foraging Behavior of *Ateles chamek* in a Southern Amazonian Tropical Forest

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*I present data regarding the diet and feeding ecology of a spider monkey community at Lago Caiman in northeastern Bolivia. The community was highly frugivorous, only consuming significant amounts of folivorous material during times of relative fruit resource scarcity. Spider monkeys fed on parts of 86 plant species, but the majority of the diet comprised a few dominant fleshy fruit species that were available at temporally distinct periods across the year. Accordingly, I identified candidate keystone resources for the region and discuss the results with reference to previous studies on *Ateles* and the importance of considering keystone fruit resources in the management of forestry concessions.*

KEY WORDS: Primates; frugivory; keystone resources; seasonality.

INTRODUCTION

Spider monkeys are highly frugivorous, spending 75–90% of their foraging time feeding on fruit (Castellanos, 1995; Chapman, 1987; Klein and Klein, 1977; McFarland Symington, 1988a; Nunes, 1995; Richard, 1970; van Roosmalen, 1985). Indeed, much of spider monkey anatomy is apparently designed either for soft fruit ingestion—enlarged incisors and reduced postcanine teeth and jaws—or effective foraging for patchy fruit

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resources, e.g., long limbs (Rosenberger and Strier, 1989). The predominantly frugivorous diet is supplemented by other food items particularly at times of low fruit availability: flowers, insects and leaves (Castellanos, 1995; Chapman, 1987; McFarland Symington, 1988a; van Roosmalen, 1985). Thus, previous researchers have described *Ateles* as displaying an energy maximizing foraging strategy (Nunes, 1995; Rosenberger and Strier, 1989; Strier, 1992), switching to an alternative diet when high energy resources are scarce. Dietary shifts usually lead to behavioural repercussions and changes in primate activity budgets (Oates, 1987).

The availability of food can be a significant limiting factor on wildlife population densities, though other factors such as access to water, climate, disease, and predation are certainly important (Dunbar, 1987). As Cant (1980) noted, populations are not generally constrained by the overall annual productivity of a habitat, which may far exceed the energetic requirements of the resident frugivore community (e.g., Coelho *et al.*, 1976; Terborgh, 1986a). Instead, populations are constrained by the availability of resources at times of relative food scarcity. These resources are probably critical in defining the carrying capacity of frugivore populations in tropical forests (McFarland Symington, 1988a). Terborgh (1986a) designated specific resources that are available during times of a general scarcity as keystone plant resources. Primate studies have also recorded a reduction in bodily conditions during periods of resource scarcity, e.g., in *Presbytis entellus* (Koenig *et al.*, 1997). Relative resource droughts may be seasonal, or products of rarer ecological crunch events (Wiens, 1977), such as the lack of fruiting in keystone resources, massive forest fruit failures, or severe climatic conditions (Cant, 1980; Dittus, 1977; Foster, 1982; Milton, 1982; Terborgh, 1986a).

METHODS

Study Area

I assessed seasonal variations in the diet and foraging behaviour of a community of black spider monkeys (*Ateles chamek*) in a southern Amazonian semideciduous tropical forest: Noel Kempff Mercado National Park (15,300 km²) in the northeastern corner of Department Santa Cruz, Bolivia (Fig. 1). The Itenez river defines the park's eastern and northern edges, and represents the border with the neighbouring Brazilian states of Rondonia and Mato Grosso. The region is situated on the Brazilian Shield geological formation that is characterized by poor kaolinitic clay and podsol soils (Peres, 1997; PLUS-CORDECRUZ, 1994).

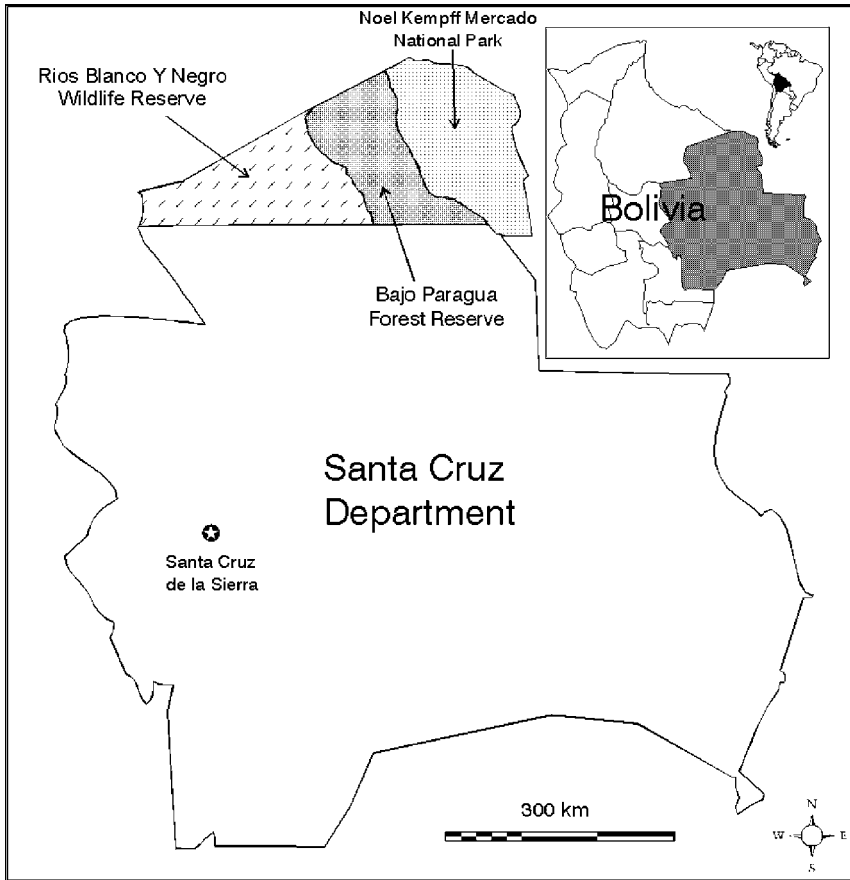


Fig. 1. Noel Kempff Mercado National Park, situated in the northeastern corner of Department Santa Cruz, Bolivia.

The park is dominated by the Serrania de Huanchaca, a Precambrian escarpment containing an array of markedly differing habitat types including open pampas, cerrado forest and gallery forest that rises 200–400 m above a broad swathe of humid forest of the Precambrian Shield (Killeen *et al.*, 1993). Between May 1996 and April 1997 Lago Caiman received 1636.9 mm of rainfall with a mean temperature for the period of 26°C (Fig. 2). Dry season months (April–September) have <100 mm of precipitation wet season months (October–March) have >100 mm of precipitation. The transitional phase between dry and wet seasons (September–October) is the warmest period of the year with temperatures

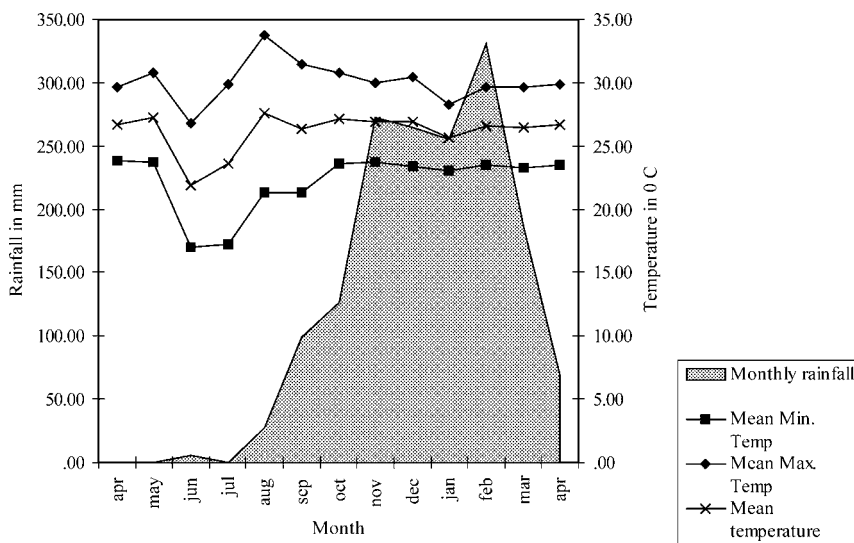


Fig. 2. Rainfall and temperature for Lago Caiman between April 1996 and April 1997.

up to 37°C. Between June and July strong southerly winds are common and temperatures may drop to 10°C. The winds are usually dry and accelerate evaporation rates in this region.

Research was based at Lago Caiman (Lat. 13°, 36'S, Lon. 60°, 55'W), a large oxbow lake at the base of the northern tip of the Huanchaca escarpment. The Lago Caiman study plot (500 ha) contained several structurally and vegetatively distinct habitats; tall forest, low vine forest, sartenejal or swamp forest, piedmont forest, and cerrado forest (Wallace, 1998).

Data Collection

Ecological Parameters

I installed 50 vegetation plots (20 m × 50 m) along the study plot trails in a stratified random fashion with sampling effort distributed according to the relative abundance of each habitat. I divided each plot into two 20 m × 25 m subplots. In the first subplot I sampled all trees >20 cm dbh. In the second subplot I sampled all trees >10 cm in dbh. The arrangement sampled 1% of the study area. I used the plots to document phenological patterns in the forest. Because the diet of spider monkeys was largely unknown for the region, I considered this the most appropriate phenological sampling

design because individuals of all plant species within the sample area were monitored.

I collected phenological data for 1732 trees on a monthly basis. Following van Schaik (1986) and Kinnaird (1992) I used a 6-point linear scoring methodology to estimate the percentage of the total crown area of each tree for the various plant part categories considered, such that the total scores in each category pool could not exceed 5: 0 = 0%; 1 = 1–20%; 2 = 21–40%; 3 = 41–60%; 4 = 61–80%; 5 = 81–100%. For scoring purposes, I recognized combined leaf parts in one category pool, and flower buds, flowers, unripe fruit, and ripe fruit in a separate pool (Wallace and Painter, 2002). A potential problem with the scoring method is recognizing how much fruit a tree species is capable of producing, i.e., what exactly is 100%. In this case, the habituation period provided >1 yr of experience of crop sizes for the majority of feeding tree species at Lago Caiman.

Behavioral Parameters

Following habituation, I collected data on the behavioral ecology of a focal spider monkey community, made up of 55 individuals at the commencement of data collection, for 11 mo between June 1996 and April 1997. Because spider monkey subgroups frequently change in size and membership I made individual monkeys the focus of all day follows. Each month I attempted to follow 4 adult females (F), 4 adult males (M), and 1 subadult male (SAM) for a total of 9 days during 2 temporally distinct sessions of ≤ 5 days. I tried to randomize the data sampling regime; in the predawn, I randomly selected 1 of 5 radio-collared males (Karesh *et al.*, 1998) as the initial spider monkey contact and selected a focal-follow animal (FFA) from the monkeys at the sleeping site. Whenever possible I selected the age/sex class of the FFA from a randomly ordered list of the 9-day standard monthly sample.

I followed FFA from dawn (05:15–06:15 h) to dusk (17:45–18:45 h). If contact with a FFA was lost, I continued with another individual of the same age/sex class from the same or another subgroup: broken-day follows. When it was not possible to continue follows I considered the day a half or quarter day. If necessary I made up AM half or quarter days at a later stage with a PM follow on the same age/sex class. During follows I conducted 5-min point scan samples (Altmann, 1974; Dunbar, 1976) at 15-min intervals. I gathered data on activity budgets, diet and social behavior for as many individuals as possible. The total number of monkeys in a scan depended on subgroup size and ranged from 1 to 11 individuals.

In each scan, I collected data on climate, location and habitat type, subgroup size, spread, dominant activity, and the presence of other frugivorous species. For feeding individuals, I also recorded the dbh, crown shape (Synott, 1979) and phenology score of the feeding tree and the observed and estimated number of individuals feeding in the tree. I further documented the foraging behavior of the community of *Ateles chamek* by recording and collecting samples of food resources consumed during behavioral sampling sessions. I also mapped, measured the dbh and assessed crown shape and phenological scores of all trees in which *Ateles chamek* fed.

Data Analyses

I calculated monthly activity budgets for each of the following age/sex classes: adult and subadult females combined, adult males, subadult males, and noninfant juveniles. In order to provide information on diurnal activity budgets, I divided each age/sex class sample into hourly intervals and calculated as follows:

$$\frac{(\text{records for activity } i)}{(\text{records for all activities})} \times 100$$

in which i = feeding, resting, travelling or other behavior. I established an average activity budget for the spider monkey community by averaging the activity budget of the 4 age/sex classes, weighted by their proportion within the community.

In order to account for diurnal variations in feeding rates, I calculated diet on an hourly basis and then converted the scores for each tree species according to the percentage of total time spent feeding in each hour. For each sample month I calculated the spider monkey diet in hourly intervals as follows:

$$\frac{(\text{records for tree species } i)}{(\text{records for all tree species})} \times \% \text{ time spent feeding in hour } j$$

in which i = each documented food species, and j = each of the 12 sample hours. I then produced monthly values for each food species by averaging the hourly values. I produced a summary of the annual diet of the focal community by averaging monthly values for each documented food species.

I used the Electivity Index (Krebs, 1989) to determine resource species preferences within the spider monkey diet. Index values vary from -1 (not selected) to $+1$ (highly selected). The index is calculated as follows:

$$EI = \frac{(r_i - n_i)}{(r_i + n_i)}$$

in which r_i is the percentage of species i in the diet, and n_i is the relative availability of species i in the spider monkey home range (as derived from the production of ripe fruit known to be consumed by spider monkeys within the vegetation plots).

I also calculated a monthly measure of overall fruit abundance. Due to findings with respect to patch selection models (Wallace, 1998), I selected a dbh phenological score index as the most appropriate measure. I then used it to calculate monthly values for 4 subsets of fruit resources; availability of all ripe fleshy fruit species, availability of ripe fleshy fruit species consumed by the focal community, availability of fruit species constituting $>0.5\%$ of the overall spider monkey diet ($n = 20$), and availability of nonpalm fruit species constituting $>0.5\%$ of the overall spider monkey diet ($n = 18$). The third subset measures the abundance of resources that dominate the spider monkey diet, whilst the fourth subset is very similar but excludes palm species. Palm species show very little variation in dbh with increasing age due to a lack of secondary thickening (Gentry and Terborgh, 1990). Thus, dbh cannot be used in palm species to predict relative patch size or fruit crop size.

I analyzed the data via nonparametric statistical tests. The alpha level is $p < 0.05$, though nonsignificant trends are suggestive.

RESULTS

Seasonal Activity Patterns

Seasonal variations in spider monkey activity budgets occurred at Lago Caiman (Fig. 3). There is a significant negative relationship between the proportion of time moving and that spent resting ($R_s = -0.67$, $p = 0.01$, $n = 11$), whilst time in other activities remains at a relatively low but stable level throughout the year. The proportion of time feeding decreases significantly as moving time increases ($R_s = -0.56$, $p = 0.04$, $n = 11$). Another strong negative trend ($R_s = -0.61$, $p = 0.06$, $n = 10$; Fig. 4) is between time spent feeding and the average mass of the most dominant fruit species constituting 60% of the monthly diet.

Overall Dietary Composition

At Lago Caiman 85.8% of the diet of *Ateles chamek* consisted of fruit. More specifically, ripe fleshy fruit made up 78.4% of the overall diet. Nevertheless, I also observed them consuming unripe fleshy fruit (2.15%), ripe

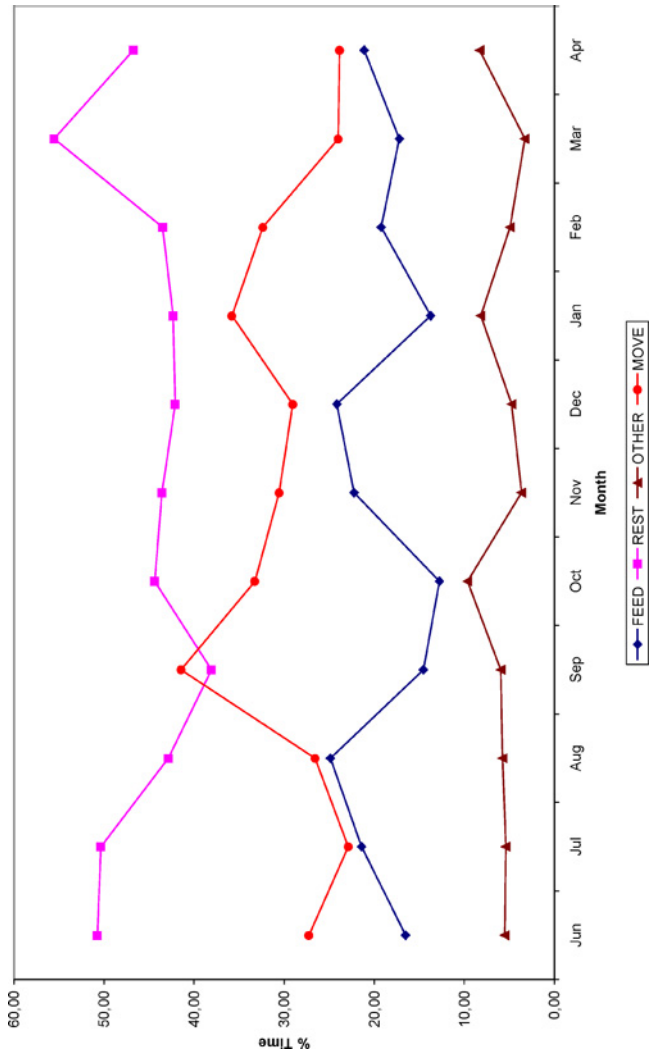


Fig. 3. Seasonal variations in activity budgets of black spider monkey (*Ateles chamek*) at Lago Caiman.

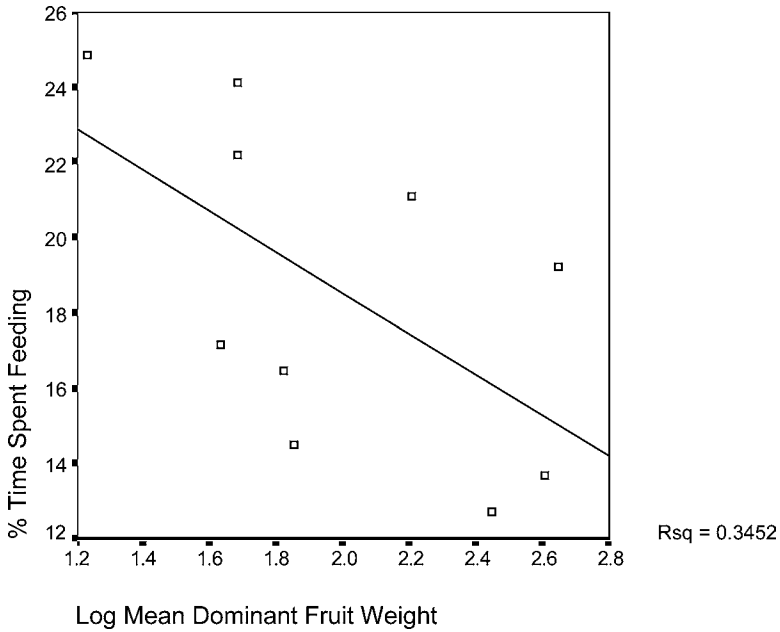


Fig. 4. Log-normal regression of monthly mean dominant fruit mass and percentage time spent feeding for black spider monkeys (*Ateles chamek*) at Lago Caiman.

and unripe nonfleshy fruit (2.7% and 2.5% respectively), flower buds and flowers (2.9%), leaf buds, young and mature leaves (10.7%), and a variety of other items: invertebrates, leaf galls, bark, and fungi (0.6%). *Ateles chamek* consumed at least part of the fruit of 75 plant species from ≥ 31 families, of which 68 also provided nonfruit vegetative parts such as flowers or leaves, and at least another 11 species also provided these foods.

Seasonal Variations in Overall Diet

Fruit was over $>70\%$ of the diet in 10 of 11 sample mo, though there were monthly variations in the degree of frugivory and the number of fruit species in the diet (Table I). Monthly dietary diversity is not a function of fruit production ($R_s = +0.25, p = 0.52, n = 9$), as measured by the availability of nonpalm fruit resources constituting $>0.5\%$ of the overall diet ($n = 18$), although degree of dietary dominance approaches a significant relationship with fruit availability ($R_s = +0.66, p = 0.053, n = 9$).

Table I. Monthly variation in percentage dietary composition at Lago Caiman

Species	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Mean
Ripe fleshy fruit	76.7	36.5	75.9	83.9	91.4	98.0	97.8	72.6	86.2	71.6	71.4	78.4
Ripe non-fleshy fruit								22.4	6.9		0.4	2.7
Unripe fleshy fruit	0.6	5.2	6.7	6.4	0.6		0.8			3.3		2.1
Unripe non-fleshy fruit		21.6	4.2	1.1	0.6						0.4	2.5
Flowers/flower buds								1.0		16.0	15.5	2.9
Leaf material	22.7	36.6	13.2	7.9	4.1	2.0	1.0	4.0	5.7	8.6	12.3	10.7
Other				0.7	3.3		0.3		1.2	0.6		0.6
# Plant species in diet	11	20	22	21	20	7	9	12	4	16	21	14.8
# Fleshy fruit species in diet	5	8	13	13	13	4	5	8	1	7	9	7.8

Folivorous material usually was <10% of the monthly spider monkey diet (Table I). Towards the middle of the dry season (June–August) leaves constituted a large proportion of the diet ($\leq 36.6\%$), and the monthly degree of folivory in the diet is negatively related to that of ripe fleshy fruit ($R^2 = 0.75, p < 0.001, n = 11$). There is a significant relationship ($R_s = -0.74, p < 0.05, n = 9$) between the degree of folivory and the availability of nonpalm fruit resources constituting >0.5% of the overall diet ($n = 18$). Similarly, there is a significant positive relationship between this resource availability measure and the amount of ripe fruit in the spider monkey diet ($R_s = +0.70, p < 0.05, n = 9$).

Monthly degree of folivory in the diet is not correlated with time spent feeding ($R_s = +0.07, p = 0.83, n = 11$), but shows strong trends with time spent resting ($R_s = +0.57, p = 0.07, n = 11$) and is significantly related to time spent moving ($R_s = -0.64, p < 0.05, n = 11$).

Dominant Dietary Constituents and Keystone Resources

Fruit species that constituted >0.5% of the overall spider monkey diet ($n = 20$) are in Table II, along with details regarding their density and patchiness within the focal community home range. These 20 species account for >80% of the overall spider monkey diet, and 9 of them constitute >2% of spider monkey feeding records. In 10 of 11 sample months the top 3 fruit species accounted for >60% of the spider monkey diet, though the dominance of the top species varied considerably from 20.8% in July to 95.9% in December (Fig. 5).

The important resources were patchily distributed, most extremely so, and densities varied from relatively high for species such as *Euterpe precatoria*, *Brosimum acutifolium*, and both species of *Pseudolmedia*, to extremely low, such as *Byrsonima* sp., *Mussatia hyacinthina*, and both species of *Ficus* (Table II). Electivity indices for the majority of the top 20 fruit resource species are also in Table II. Values are missing for species that are not represented by at least one fruiting individual in the phenology plots.

In June, the dominant dietary fruit type was the very rare and hence patchily distributed *Byrsonima* sp., which was supplemented with other rare and patchy species, i.e., *Ficus americana* and *Bellucia* sp. In July the spider monkeys switched to a more varied diet, becoming more folivorous and preying upon the seeds of *Huberodendron swietenoides*, but also feeding on fruiting individuals of *Brosimum acutifolium* which remained an important resource until October. Fruiting *Ficus americana* also provided significant proportions of the diet along with *Bellucia* sp., *Clarisia racemosa* and *Inga*

Table II. Fruit resource species constituting $\geq 0.5\%$ of overall spider monkey diet at Lago Caïman

Species	Plant Parts	No. Sample Months in Diet	% Overall Diet	Mean Fruit Mass (g)	Overall Density	Overall Patchiness	Electivity Index
<i>Ampelocera ruizii</i>	RFF	2	16.40	0.81	1.6	P	0.9
<i>Spondias mombin</i>	RFF	3	12.68	7.4	5	P (45.5)	0.75
<i>Ficus americana</i>	RFF	6	9.34	0.25	0.2	P	
<i>Brosimum acutifolium</i>	RFF (UFF&FB)	6	7.11	0.39	7.8	P (30.3)	0.42
<i>Brosimum lactescens</i>	RFF (UFF)	4	5.97	5.8	4.6	P (47.6)	0.37
<i>Euterpe precatoria</i>	RFF	4	5.16	0.9	22.4	P (39.3)	-0.55
<i>Byrsonima</i>	RFF	1	4.54	1.28	0.2	P	
<i>Huberodendron swietenoides</i>	UNF & FL	3	4.02		1.2	P	
<i>Bellucia</i>	RFF (UFF)	5	2.39	12.8	1.2	P	0.34
<i>Sapium laurifolium/marmieri</i>	RNF	1	1.83	2.07	1.8	P	-0.61
<i>Inga 1</i>	RFF	1	1.60	2.2	0.2	P	
<i>Pseudolmedia laevis</i>	RFF	1	1.50	13.9	2.2	P (1.8)	0.47
<i>Ficus guianensis</i>	RFF	1	1.49	1.2	9	P (34.8)	0.07
<i>Didymopanax morototoni</i>	RFF (UFF)	2	1.39	1.4	0.2	P	
<i>Pseudolmedia sp. 3</i>	RFF	3	1.33	2.06	1.6	P	-0.56
<i>Clarisia racemosa</i>	RFF	1	1.22	1.2	20.4	P (37.1)	-0.16
<i>Mussatia hyacinthine</i>	RFF	4	1.10	2.6	4.4	P (23.5)	-0.88
<i>Guazuma aff. ulmifolia</i>	RNF	3	0.88		0.1	P	
<i>Helicostylis tomentosa</i>	RFF	2	0.64	5.75	1.2	P	-0.45
		1	0.52	16.76	5.2	P (41.7)	

Note. Mean Fruit Mass: as derived from Painter (1998). Overall Density: Adjusted density of individuals > 10 cm dbh per ha occurring in focal community home range. Overall Patchiness: For species with ≥ 10 individuals in vegetation plots this is the Moristats Index value using all plots and thus a measure of patchiness within the focal community home range. Species with ≤ 10 individuals were considered patchy (P) given that their density was < 5 individuals per ha (Barrett, 1995). Electivity Index: Calculated for species for which a measure of production was available, i.e., a fruiting individual within the phenology sample.

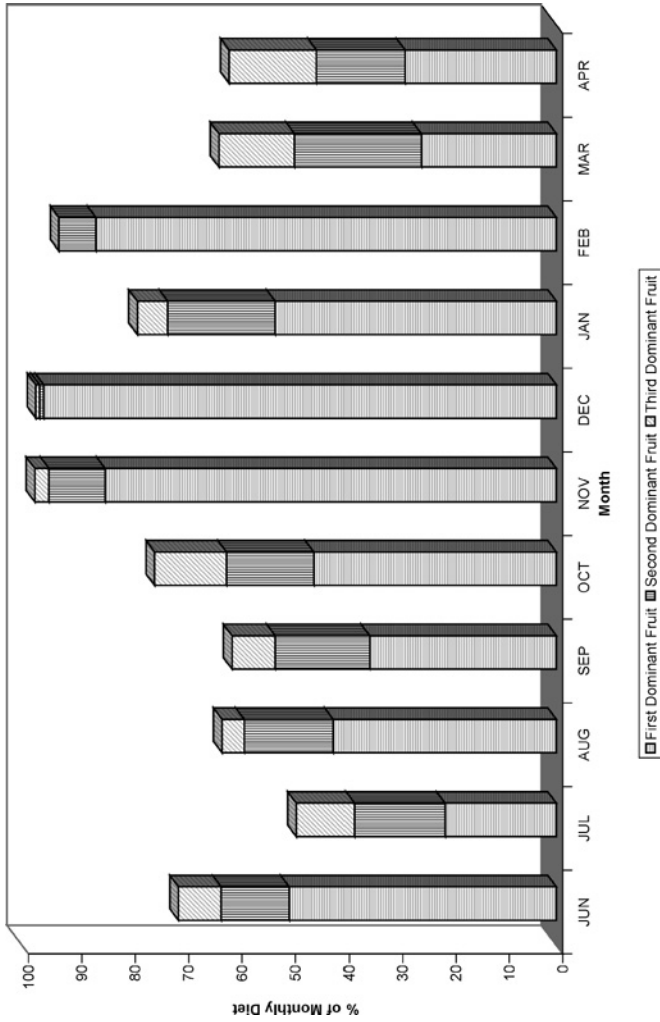


Fig. 5. Seasonal variations in degree of dietary dominance for black spider monkeys (*Ateles chamek*) at Lago Caïman.

sp. In October, *Brosimum lactescens* replaced its congener as the dominant dietary constituent and 3 species of the relatively common *Pseudolmedia* also became important.

The spider monkey diet in the early wet season (November and December) was almost totally dominated by *Ampelocera ruizii*, with other fruit species such as *Pouteria* sp. and *Ficus guianensis* individually contributing small proportions. This pattern of dominance repeats in January and February, with *Spondias mombin*, the critical resource species, and non-fleshy fruit species such as *Sapium* sp. and *Mussatia hyacinthina* also contributing. In the late wet season and early dry season (March and April) *Ficus americana* and *F. guianensis* again became important, as well as 2 species of palms, the relatively common *Euterpe precatoria* and the rarer *Maximiliana maripa*.

DISCUSSION

Seasonal Activity Patterns

Previous researchers also demonstrated seasonal variations in spider monkey activity budgets (Castellanos, 1995; Klein and Klein, 1977; McFarland Symington, 1988b; Nunes, 1995). The negative relationship between moving and resting supports the broad observation from several primate studies that resting time acts as a reserve from which necessary additional time in other behaviors can be drawn (Dunbar, 1988).

The trend between moving and feeding time may appear counterintuitive, given that energetically the cost of an increase in time moving might be expected to lead to a corresponding increase in feeding time in order to fuel this behavior. However, spider monkeys are highly frugivorous relying on a patchy and energetically variable resource distribution (Chapman *et al.*, 1995; McFarland Symington, 1988a), and therefore may spend more time moving between resources that are patchy but of a relatively high quality. Spider monkeys spent more time feeding as mean monthly dominant fruit consumed size decreased, presumably because manipulation times increased with decreasing fruit size. Goodall (1986) also reported that temporal variations in fruit mass influenced feeding rates and hence time spent feeding for highly frugivorous chimpanzees.

Overall Dietary Composition

Lago Caiman spider monkeys are clearly ripe fleshy fruit specialists. Nevertheless, as in previous studies, spider monkeys fed on a diverse array

of food types (Castellanos, 1995; van Roosmalen, 1985; van Roosmalen and Klein, 1988). Both in terms of the number of species consumed and total percentage of diet, Moraceae was by far the most important family, providing fruit resources from ≥ 20 species. Other families such as Ulmaceae, Anacardiaceae, Palmae, Malpighiaceae, Araliaceae, Bombacaceae, Euphorbiaceae and Melastomataceae provided relatively large proportions of the overall diet in the form of a few species each.

Painter (1998) classified all fruit collected at the Lago Caiman research site in terms of size, mass, shape, color, texture, degree of protection, and seed number, size and mass. Fruits consumed by spider monkeys ranged in size from the tiny fruit of *Ficus mathewsi* (0.05 g) to seeds of unripe nonfleshy fruits of *Chorisia* sp. and *Huberodendron swietenoides* of the Bombacaceae (>250 g). Fruits also varied in shape, color, texture and degree of protection; however, the majority of those consumed ripe possessed the morphological traits associated with species consumed by arboreal frugivores (Gautier-Hion *et al.*, 1985). In terms of texture, most ripe fruits were fleshy (85%, $n = 61$) or fibrous (8%), with little or no protection of the fruit pulp (96%). Most ripe fruit in the spider monkey diet were brightly colored (84%); yellow, orange, red or magenta.

Spider monkeys ingested at least some of the seeds of the majority of the fruit species that they consumed (≥ 60 of 75 species), and feces suggested that the majority of them are passed intact. I only observed seed predation for 10 species. It was most frequent in the dry season and tended to be concentrated on the unripe nonfleshy fruit of 4 species of the Bombacaceae: *Ceiba pentandra*, *Chorisia* sp., *Eriotheca globosa*, *Huberodendron swietenoides*. Nevertheless, 29 species of plant contributed some unripe fruit to the diet, and consumption at this developmental stage equates with seed predation. Unripe fruit may be an important source of protein for spider monkeys, given that seeds from unripe fruit are not fully developed, are more vulnerable to digestion, and are rich in proteins (Esau, 1977). This theory is supported by the observation that spider monkeys spend very little time feeding on more obvious sources of protein such as invertebrates (Chapman, 1987; van Roosmalen and Klein, 1988). The general dietary breakdown is typical of previously studied *Ateles* (Castellanos, 1995; Chapman, 1987; McFarland Symington, 1988a; Nunes, 1998; van Roosmalen and Klein, 1988: Table III).

Seasonal Variations in Overall Diet

In general, as availability of preferred fruit resources increases so does the degree to which spider monkeys are able to concentrate feeding on a few highly selected species. Nevertheless, even at times of resource

Table III. Dietary constituent percentage breakdown for 6 study sites of *Ateles*

Study Site	Species	Ripe Fruit	Unripe Fruit	Flowers	Leaves	Other	Source
Bolivia ¹	<i>A. chamek</i>	81.1	4.7	2.9	10.7	0.6	This study
Peru ²	<i>A. chamek</i>	75	No Data	No Data	No Data	No Data	McFarland Symington (1988a)
Colombia ³	<i>A. belzebeth</i>	(83)	—	0.1	7	10	Klein and Klein (1977)
Surinam ⁴	<i>A. pariscus</i>	(82.9)	—	6.4	7.9	2.7	van Roosmalen (1985)
Brazil ⁵	<i>A. belzebeth</i>	88.5	Included in Other	Included in Other	8.3	3.2	Nunes (1998)
Costa Rica ⁶	<i>A. geoffroyi</i>	(77.7)	—	9.8	11.1	1.3	Chapman (1987)

Note. Values in parentheses indicate sum of ripe and unripe categories. In all cases ripe fruit dominated this value.

abundance they appear to select for some diversity in the diet, perhaps in order to vary nutrients in the diet. That dietary diversity is particularly high in the late afternoon (Wallace, 1998), when spider monkeys travel to sleeping sites. Thus they may be trying to keep their stomach full on suboptimal resources en route to sleeping sites.

In the month of least resource abundance—July—an uncharacteristically high 21.6% of the diet was composed of unripe nonfleshy fruits that were essentially seed predation events. Maisels *et al.* (1994) found that on poor soils in Central Africa two species of colobine monkeys, *Colobus angolensis* and *C. badius*, spent a large proportion of time feeding on seeds. This atypical dietary quirk was largely attributed to the poor nutritional quality of mature foliage in the forests, which is in turn attributable to relatively poor soil. The Lago Caiman region is also characterized by poor soils (Peres, 1997; PLUS-CORDECRUZ, 1994), which is reflected by extremely low densities of arboreal folivores within nonriverine forests of the region (Wallace *et al.*, 1998; 2000). Thus, spider monkeys may also be selecting seed predation over extensive folivory during periods of fleshy fruit scarcity.

Lago Caiman spider monkeys were also able to switch to a more folivorous diet when fruit resources were scarce. Similar dietary flexibility was also noted in *Ateles* by Castellanos (1995), Chapman (1987), McFarland Symington (1988a), Nunes (1995), and van Roosmalen (1985), and in other primate species by Chapman (1987), and Oates (1987). Nevertheless, several lines of evidence suggest that there is a limit to their flexibility. Firstly, the monthly degree of folivory in the diet does not correlate with time spent feeding, showed strong trends with time spent resting, and is significantly related to time spent moving, which suggests that spider monkeys do not compensate for a lack of energetically rich resources with an increase in absolute time feeding.

The digestive system of *Ateles* is designed essentially for a frugivorous diet (Chivers and Hladik, 1980), therefore, they are presumably physiologically constrained in how much folivorous material they are able to digest (Rosenberger and Strier, 1989). As the degree of folivory in the diet increases they are forced to spend more time resting and less time moving, thereby conserving energy. Resting also aids digestion in more folivorous species, for e.g., *Alouatta* spp. (Neville *et al.*, 1988). Indeed, the end of prolonged resting bouts were often characterized by several individuals defecating, acting as an early warning to observers that the subgroup was about to leave the resting location.

Secondly, spider monkey body condition dropped dramatically during the period of a more folivorous diet. Most adults became noticeably thin with the rib cage outline evident, and several individuals suffered from patches of dermatitis of undetermined etiology (Karesh *et al.*, 1998). The

community did not begin to recuperate until the late dry season/early wet season, when ripe fleshy fruit again became the superdominant constituent type within the diet. Thus, whilst spider monkeys may well be flexible enough to survive short-term reductions in the availability of preferred dietary constituents it is likely that prolonged periods of scarcity would result in population declines.

Dominant Dietary Constituents

Lago Caiman spider monkeys are not merely responding to overall ripe fruit availability. Some fruit species are more highly selected than others. The majority of dominant fruit species were relatively rare, and taken as a whole, the top 20 fruit resource species made up only 16.7% of the overall stem density within the home range. This percentage is considerably reduced when we consider that only a percentage of individuals of each species actually produced fruit, because they were dioecious and/or because of reproductively immature individuals. Fruiting individuals of *Ficus amerciana* always became a focal point for spider monkeys and most other frugivores, and similarly the top 5 dietary fruit species were all highly selected (Table II).

In contrast, the 3 most abundant species—*Euterpe precatoria* and both species of *Pseudolmedia*—were not highly selected by the focal community. The 2 species of *Pseudolmedia* fruited at the same time as another classic Moraceae, *Brosimum lactescens*, which was both considerably larger and occurred in larger patches (Table II). Therefore, as with all of the resources, the relative importance of *Pseudolmedia* may vary on annual basis. *Euterpe* provided much fruit during March and April when very few other resources were available; however, despite making up a large proportion of the diet spider monkeys did not seem to select it.

In the absence of nutritional analyses we are left to speculate that highly selected species produce fruits that are energetically particularly valuable. Observational data suggest that spider monkeys may be able to distinguish between the relative energetic qualities of individual plants and fruits (Wallace pers. obsv.). Castellanos (1995) demonstrated that *Ateles belzebuth* feed preferentially on species bearing relatively energy-rich fruits. Van Roosmalen (1985) suggested that *Ateles paniscus* feed in individuals of a tree species that produce subjectively sweeter fruits than others. Observers standing beneath feeding patches are often hit by falling fruit, much of which is being rejected by foraging individuals thereby implying selectivity (van Roosmalen, 1985; pers. obsv.). Recent captive experiments revealed that *Ateles* has an extremely sensitive sweet-taste capacity (Laska

et al., 1996), and support the hypothesis that spider monkeys use sweetness as a criterion for food selection.

Most of the dominant dietary species were extremely synchronous in their fruiting patterns, with a few such as both species of *Brosimum*, *Bellucia* sp., *Clarisia racemosa* and *Euterpe precatoria* showing a more staggered phenological pattern. Only 2 species—*Ficus americana* and *F. guianensis*—could be considered species that truly display an asynchronous phenological strategy. Thus, a few species are extremely important to the spider monkey diet, but most are only consumed for 1 or 2 mo.

As in Surinam (van Roosmalen, 1985), 3 or 4 fruit types tended to dominate the diet each month. In summary, 3 clear generalizations can be made: dominant species tend to shift dramatically from month to month; most dominant species are only important for brief periods, usually for just 1 or 2 months; and most dominant species are rare and highly selected. Here, it is important to recognize that my study documents one sample year and observations made during the preceding habituation year underline the dynamic nature of fruit abundance at Lago Caiman. For example, during the habituation year, *Talisia cerasina*, *Clarisia racemosa*, *Helicostylis tomentosa*, and *Perebea mollis mollis* were all much more important components of the diet than they were during the focal year. Fruiting individuals of these tree species were also far more common during the habituation year, and many species apparently show interannual variations in phenological pattern. This adds to the weight of evidence that suggests that the spider monkey diet responds to the temporal availability of a few dominant ripe fleshy fruit species.

Candidate Keystone Resources

During the focal year at Lago Caiman, the early and mid-dry season (June–July) was a scarce period for ripe fleshy fruit. This finding is similar to previous phenological studies across the tropics that generally indicate that resource bottlenecks occur during the late wet season and early dry season (Peres, 1994; Terborgh, 1983; White, 1994). During June and July, spider monkeys fed on the following fleshy fruit resources: *Ficus americana*, *F. mathewsii*, *Byrsonima* sp., *Brosimum acutifolium*, and *Bellucia* sp. Accordingly, they could be considered keystone resources for spider monkeys.

Further observations from Lago Caiman lead to a broadening of the keystone resource definition; during most of the year, a large percentage of the spider monkey monthly diet consisted of a few dominant species. Indeed, during certain months, resources were abundant because of the contribution of one fruit species, e.g., *Spondias mombin* or *Ampelocera*

ruizii. Phenological data indicate that a lack of these tree species within the community range would have resulted in a time of extreme fruit scarcity (Wallace and Painter, 2002). Thus, even though they are relatively abundant, they might also be considered keystone species for spider monkeys.

My results further underline the need to consider the role of keystone resources in the management of tropical forests. For example, relatively inexpensive techniques such as avoiding potential non-timber keystone resources during the construction of roads and skid trails and directional felling to minimize incidental damage to potential keystone resources, could significantly reduce the logging impact on the critical resource base and hence the frugivore community (Terborgh, 1986b; Wallace and Painter, 1997; White, 1994). In cases where potential keystone resources are also commercially valuable, the most pressing management decision will be to determine the extraction intensity that the frugivore community can tolerate over longterm harvesting. Studies that gauge how frugivore communities react to differing degrees of potential keystone resource loss, and hence provide recommendations regarding extraction intensity, are a conservation priority.

In conclusion, spider monkeys fed on an array of fleshy fruit resource species, but the majority of the diet was made up of a few dominant species that were available at temporally distinct periods across the year. The majority of the species display synchronous fruiting patterns and are found in discrete patches, which vary considerably in size and quality. Thus, most of the important spider monkey fruit resource species are ephemeral, occur at relatively low densities, and are distributed extremely patchily across the focal community home range. Tropical forest managers should recognize the seasonal nature of fruit abundance for forest frugivores and consider potential keystone resources as special elements when producing integrated management plans (Wallace and Painter, 2002).

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