SEASONAL VARIATION IN THE DIETS OF WHITE-FACED AND BEARDED SAKIS *(Pithecia pithecia* AND *Chiropotes satanas*) IN GURI LAKE, VENEZUELA

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INTRODUCTION

Variation in rainfall provides the most readily quantifiable method to interpret seasonal influences on plant production and animal response to environmental change. But the effects of rainfall on an animal's behavior are complex, indirect, and less predictable, than the simple measurement of rainfall might convey. From the perspective of the primate consumer (or the human observer), periods of perceived stress or food shortage often correspond to periods of lower than average rainfall, but successful "response" depends on variables that may only be indirectly related to rainfall. Knowledge of an animal's diet, morphological or physiological adaptations of the digestive tract, variability in local plant production, duration of food shortage, body weight at the onset of the season, and reproductive or general health status all might help predict the degree of stress individuals might experience during seasonal changes in the resource base. Indeed, some examples of responses to seasonality by primates are well known, including apparent detrimental direct effects (e.g. weight loss presumably due to reduced food intake: Goldizen et al, 1988; Morland 1992) as well as indirect effects (e.g. timing of weaning: Pereira, 1992; Wright and Meyers, 1992). But there are also reports of an insignificant or lack of effect of seasonality on other population and environmental variables: infant mortality (Crockett & Rudran 1987), diet and range use (Chapman 1988), diversity of resource used in the diet (Garber 1993). Even when seasonality does appear to affect feeding behavior, the expectation of the *dry* season as the most stressful season is not always borne out (Cords, 1993).

The purpose of this paper is to examine seasonal effects on seed production and seed use by two pitheciins, white-faced sakis (*Pithecia pithecia*) and bearded sakis (*Chiropotes satanas*).

We combined traditional measures estimating seasonal variation in food availability and diet breadth with new methods that characterized the changing physical and chemical composition of the fruit ingested over an annual cycle. We previously identified two critical features of saki diets that might limit access to specific foods (seed hardness and toxic properties of seed coats: Norconk & Kinzey 1994). These limitations are also examined within the context of seasonal variation.

The saki response to seasonal variation in rainfall is complex, but appears to be closely tied to fruiting phenophases of a few important resources. Sakis are seed predators of young seeds, primarily, and these seeds are most abundant during the dry season. The dry season may be a period of low fruit abundance or be characterized by a shift from fruit to leaves or insects for ripe fruit frugivores, but it is difficult to recognize this season as a period of scarcity or food stress for sakis. Both saki species are adapted to ingesting seeds (Kinzey and Norconk, 1993) and their ability to utilize fruit during more than one stage of maturity appears to dampen seasonal effects of food scarcity.

METHODS

Study Sites

Data were collected on two islands about 40 km apart in Guri Lake, eastern Bolívar State, Venezuela. Guri Lake is the catchment area for the Raúl Leoni dam and hydroelectric plant. It reached it's present size of 4,240 km^2 in 1986 exposing more than 100 islands of varying size (Alvarez et al, 1986; Kinzey et al, 1988). *Chiropotes satanas* occupy only southern islands and *Pithecia pithecia* only northern islands in the lake. Groups of *Cebus olivaceus* and *Alouatta seniculus* occupy islands throughout the lake.

We studied sakes on three islands in the lake, one island in the south and two islands in the north. Chiropotes Island is approximately 365 ha in size (7°21'N, 62°52'W) and had one group of *Chiropotes* and several groups each of *Cebus olivaceus* and *Alouatta seniculus*. Pithecia Island (also known as "Pithecia II" in Walker, this volume (Fig. 2) & Parolin, 1993) (7°45'N, 62°52'W) is about 15 ha in area and had one group of *Pithecia pithecia* and one group of *Alouatta seniculus*. Home range size in terra firme is not known exactly for either saki species, but the two study islands were chosen to roughly approximate the maximum area used by these species under free-ranging conditions. (Ayres (1981) estimated a home range for *Chiropotes albinasus* at 300 ha.) Base camp was located in the village of Guri at the site of the hydroelectric plant.

The study islands differed in vegetational composition as well as primate fauna. Pithecia Island was small, oval and completely forested. Trees rarely exceeded 18 m in height, averaged 11 cm in dbh, and undergrowth was composed primarily of saplings (see Parolin 1993). Although there was evidence of mixed flora from as far as the Caribbean areas in the north to the Gran Sabana in south, Aymard et al. (in press) found several examples of floristic endemism on northern islands (e.g. *Ouratea guianensis*, Ochnaceae; *Sloanea boliviensis*, Elaecarpaceae).

The southern islands in the vicinity of Chiropotes Island were about half the distance to the junction of Caroni and Paragua Rivers (the southern boundary of the lake) and tended to support taller, wetter forests on clay soil (e.g. *Ceiba pentandra*, Bombacaceae with dbh exceeding 200 cm and 28 m in height were not rare). Chiropotes Island was irregularly shaped, consisted of 4 peninsulas (up to 2 km long) running north-south away from a central strip of land that was as narrow as 200m in some places. The logistics of

working on two islands each month resulted in a loss of one or two days at the beginning or end of the month. Thus, rainfall is presented as monthly averages in Fig. 1.

Vegetation Sampling

A total of 2,275 trees > 10 cm dbh were identified to species, measured (dbh, height, and canopy breadth) and mapped on Chiropotes Island. This sample represents both feeding trees of *Chiropotes* and strip samples collected by A. Peetz, I. Homburg, and S. Walker. In like manner, 3,570 trees were identified, measured and mapped on Pithecia Island. The Pithecia Island sample included smaller trees (> 5 cm dbh) measured in 16 ¼-ha quadrats (Parolin 1992) and feeding trees and lianas of *Pithecia*. Shrubs used by *Pithecia* were not measured, but they were identified.

Phenology trees were selected to focus on saki monkey feeding trees and were well-dispersed throughout the two islands. They were sampled monthly for leafing, flowering, and fruiting status by A. Peetz, I. Homburg, C. Wertis, and C. Butler. Leafing, flowering, and fruiting were given 0 to 4 scores on more than 300 trees monthly, where zero indicated lack of leaves, flowers, fruit and "4" indicated peak stage of leafing, flowering or fruiting. Data reported below are confined to fruiting activity from a subset of the sample, 11 of the top 25 species used by *Pithecia* and 12 of the top 25 species used by *Chiropotes*.

One hundred fruit traps constructed of nylon mesh draped over wire hoops (1 m in circumference) were suspended between saplings or stakes about 1.5 m off the ground and approximately 3 m on either side of main trails on both islands. Care was taken to position bags to avoid overhanging branches so that fruit fall was from the canopy. Contents of traps, collected once a month, were usually air-dried in the mesh bags unless rainfall was very recent. Fruit were divided into four categories: legumes, drupes/berries, nuts, and samaras, identified to species when possible, counted, and weighed. After Terborgh (1983:17), we estimated the volume of each trap to be 0.08 m^2 and the total weight the fruit in 100 traps was divided by 0.8 to provide a total weight measure (kg/ha) per month. Traps on Chiropotes Island were placed the entire length of a north-south peninsula (c. 2 km) and sampled both low-lying evergreen and deciduous slope or higher elevation habitats. Approximately 2/3 of the traps on Pithecia Island followed the perimeter of the island and the remainder were placed along a trail that crossed the crest of the island from north to south.

The *Pithecia* study group consisted of eight independently locomoting individuals 2 adult females, 3 adult males, 2 subadults (one male, one female) and 1 juvenile male. A female infant was born during the study. *Pithecia* were individually recognizable using distinctive facial patterns, and feeding activities (species of feeding tree & part of plant ingested) were recorded for all individuals that were visible at each 5 minute interval for a total of 44,776 feeding minutes. This rigorous sampling regime was possible because *Pithecia* have shorter total active days and visibility was better for *Pithecia* who move and feed in lower levels of the canopy than *Chiropotes*. The two sampling methods (group scores of *Chiropotes* vs. individual scores of *Pithecia*) confounded direct comparison of results (albeit both measured feeding duration) so monthly and seasonal averages were weighted by the total feeding time for each plant species.

Fruit and Seed Hardness Measurements and Biochemical Analysis

Methods used to estimate the dental force or resistance to puncturing pericarp and crushing seeds have been reported elsewhere (Kinzey & Norconk, 1990). All samples of whole or partial fruit and seeds were collected at the time the samples were dropped by the monkeys and measured on the same day.

Specimens of fruit and leaves were either collected while the monkeys were feeding, or we returned to the tree after feeding was completed and collected fruit and leaf samples that appeared to be representative of the stage of maturity at which feeding occurred. Samples were transported to base camp in Guri within 24 hours of sample collection and prepared for drying: seeds were separated from mesocarp, seed coat, pericarp and weighed ("wet weight"). Samples were dried at a uniform temperature (50°C) in an electric laboratory oven for up to two weeks until repeated weights ceased to change. Dried samples were transported to the U.S. and analyzed by Dr. N. Conklin-Brittain. Methods are described in Kinzey & Norconk (1993) and Norconk & Conklin (in prep). Only seasonal weighted averages for macronutrients (water soluble carbohydrates, crude protein, lipids), acid detergent fiber, and condensed tannins are presented below.

Analysis

Statistical comparisons between islands were made using nonparametric tests, Kendall's τ and Spearman rank correlation coefficient to measure association and Mann-Whitney test to examine differences in medians, with acceptance of significance level $\leq .05$.

RESULTS

Seasonal Variation in Rainfall and Fruit Availability

Guri Lake, at between 7° and 8° north latitude, has a single wet season and a single dry season, each lasting about 6 months annually. Annual rainfall averaged 1,258.6 mm (N = 4 years) on Chiropotes Island and 1,030.2 mm/yr (N = 3 years) on Pithecia Island. Wet and dry seasons were further subdivided into early and late periods so that each "season" represented three months. Annual rains began to fall in May and peaked in July or August. Average monthly rainfall was strongly correlated between the two islands (Spearman rank correlation coefficient, r_s = .791, P < .01, N = 12), but Chiropotes Island was
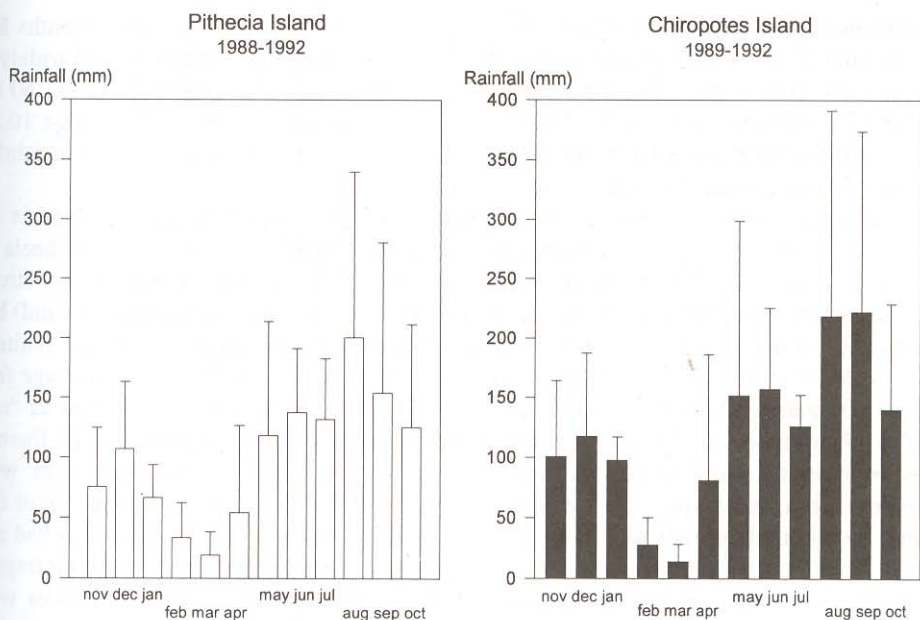
Figure 1. Rainfall data collected on Pithecia Island and Chiropotes Island (average & standard deviation) over a period of three to four years.
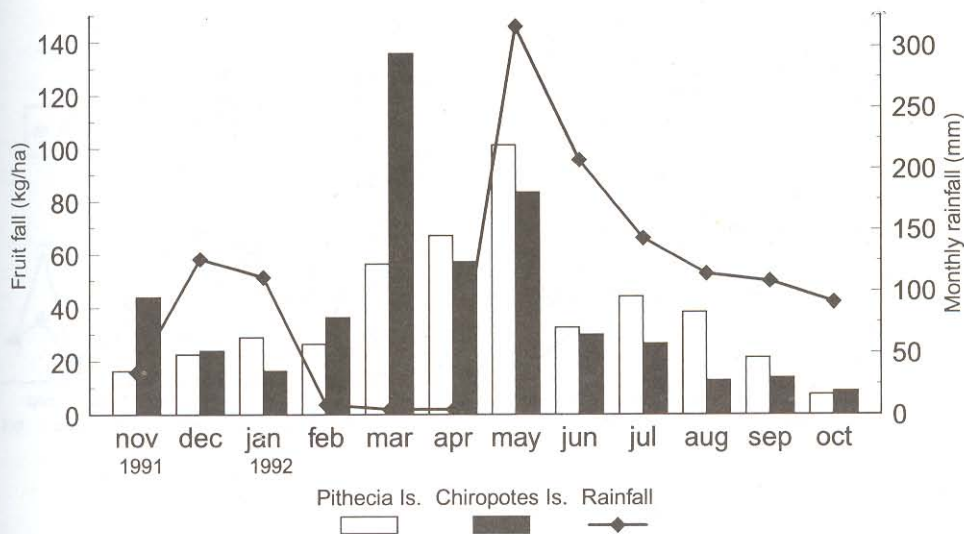

Figure 2. Monthly volume of fruit fall (kg/ha) collected from 100 fruit traps each on Pithecia and Chiropotes Islands compared with rainfall during the same period. Since the seasonal patterns of rainfall are the same between islands, rainfall from only Chiropotes Island was plotted.

significantly wetter (Mann Whitney test, $Z = 2.59$, $P < .01$) (Fig 1). Some months had similar rainfall totals between the years of the samples, but other months varied widely in rainfall from year to year. The mean annual deviation in monthly rainfall ($\sum |x - \bar{x}|/N$) averaged 39.6 mm (range 8.3 - 83.7 mm) for Pithecia Island and 58.6 mm (range 10.2 - 125.5 mm) for Chiropotes Island (Fig 1). Dry season months had less variation in rainfall than wet season months for both islands.

Fruit fall (kg/ha) was negatively correlated with rainfall on Chiropotes Island ($\tau = -.424$, $P < .05$, $N = 12$ months), but rainfall was not correlated with fruit fall on Pithecia Island: $\tau = -.061$, ns) (Fig 2). Nevertheless, fruiting cycles showed a moderately strong correlation between islands ($\tau = .424$, $P < .05$). The wetter island, (Chiropotes Island) had significantly more fruit species in the monthly traps than Pithecia Island (Mann Whitney U: $Z = 2.94$, $P = .003$, $N = 12$ months), although there was no difference in average fruit weight between islands (Z: .51, ns) (Fig. 3). Because of the nature of fruit traps as "random" collections of canopy fruits, a few large, heavy fruits could cause marked fluctuations in monthly fruit weight estimates. Fruit from a range of fruiting stages were recovered from fruit traps: fruit that was very young and either aborted by the tree or dislodged by arboreal animals to legume pods that fell into traps long after the seeds had dispersed. Thus, it is difficult to obtain a monkey's view of fruit abundance from fruit traps.

About one-half of the top 25 plant species used by *Pithecia* and *Chiropotes* were sampled monthly for fruiting status. A phenological score (monthly score assessed on a scale of 0 to 4 divided by the number of sample trees for each species) provided information on the relative abundance of unripe and ripe fruit over a 12 month period (Tables 1 and 2). The most striking aspect of these results are the relatively low phenology scores. Although individual trees might produce abundant fruit crops, scores rarely exceeded 2.5 when averaged across all of the sample trees. Unripe fruit was available for a longer period than ripe fruit on both islands, although the difference was greater on the drier island. Pithecia Island fruit production averaged 6.6 months of unripe fruit and 4.7 months of ripe

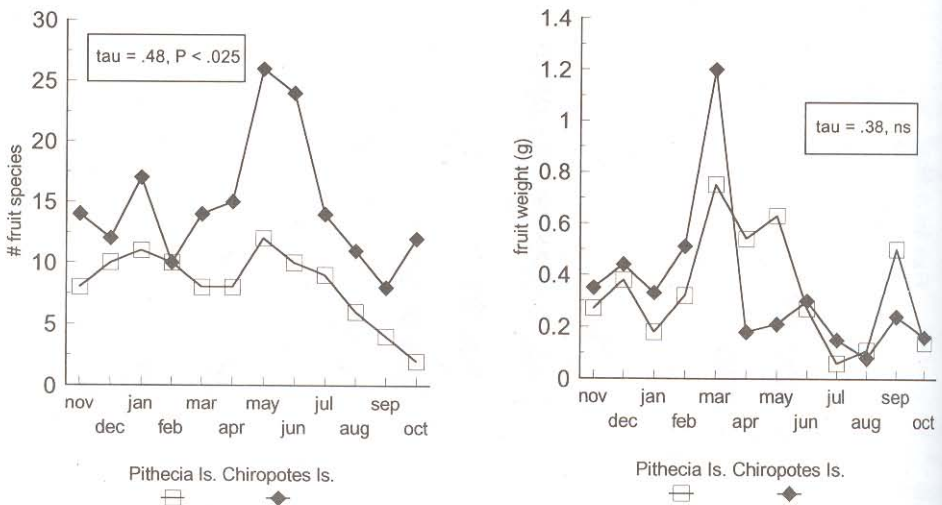

Figure 3. Two results from fruit trap data are compared from both study islands. There was a significant correlation between the two islands for diversity of fruit species found in the traps, but not for average weight of fruit. Note that fruit weight did not peak in the wet season with production of fleshy drupes. Samples were collected on both islands from November 1991 to October 1992.

Table 1. Phenology scores for 11 feeding tree species used by *Pithecia pithecia* on Pithecia Island (Guri Lake). Scores are averages and were calculated for unripe fruit/ripe fruit by dividing the sum of the total monthly score by the number of sample trees[1]. Trees were scored on a 0 to 4 scale for unripe and ripe fruit such that a score of 4.0/0 would indicate that all sample phenology trees were in full production of unripe fruit, but no trees had ripe fruit. Phenology sample was collected from November 1991 to October 1992

Plant species (N)[1]	Rank[2]	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Connarus venezuelanus (10)	1	.9/0	.7/0	.7/.2	.4/.5	.3/.5	.3/.5	.4/.5	.1/.5	.1/.4	.2/.2	0/.1	0/0
Licania discolor (10)	2	.3/.9	.2/.9	.7/.2	.6/.2	.3/.6	.2/.4	0/.2	.4/.2	.2/.2	0/0	.6/0	.5/.7
Strychnos fendleri (10)	3	.1/0	0/0	0/0	0/0	0/0	0/0	1.2/0	2.8/0	2.8/0	.9/1.1	.4/1.0	0/0
Peltogyne floribunda (11)	4	.8/.5	.1/1.4	0/.9	0/.7	0/.4	0/.1	0/0	0/0	1.1/0	.5/.1	.5/.3	0/.1
Erythroxylum steyermarkii (14)	5	.1/0	.1/0	0/0	0/0	0/0	0/0	2.4/0	2.4/0	1.7/1.7	.5/.1	.1/.1	0/0
Strychnos mitscherlichii (7)	8	2.3/0	2.0/0	1.6/0	1.1/1.1	1.0/1.0	.7/1.0	.1/.1	0/0	0/0	0/0	0/0	0/0
Xylopia sericea (5)	9	1.6/.6	.3/.1	.8/.6	0/.1	0/0	0/0	1.6/0	1.4/0	1.4/0	.6/.6	.8/.8	0/0
Piptadenia leucoxylon (10)	10	1.8/0	1.8/0	1.7/0	.9/.6	0/.8	0/.5	0/0	0/0	1.8/0	0/0	0/0	0/0
Coccoloba striata (7)	12	0/0	0/0	0/0	0/0	0/0	0/0	1.7/0	1.3/0	.6/0	0/0	0/0	0/0
Alibertia latifolia (5)	17	0/0	0/0	0/0	0/0	0/0	2.8/0	2.0/0	1.8/.4	.4/0	0/0	0/0	0/0
Copaifera pubiflora (10)	25	1.3/0	1.4/0	1.4/0	1.2/.3	0/.7	0/.1	0/0	0/0	0/0	0/0	0/0	0/0

[1] N = number of trees sampled monthly for phenological status
[2] Rank = feeding tree rank assessed after 18 months of feeding samples

Table 2. Summary of phenology scores for a sample of trees in the top 25 species of feeding trees used by *Chiropotes satanas* on Chiropotes Island. (Guri Lake). See Table 1 for note on how scores were calculated. The phenology sample was collected from November 1991 to October 1992, with the exception that the August sample is from 1991

Plant species (N)[1]	Rank[2]	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug[4]	Sep	Oct
Pradosia caracasana (13)	1	3.4/0	2.7/0	2.2/0	1.8/0	1.8/0	.8/.3	0/.9	0/.6	0/.6	0/.1	.6/0	.3/0
Brosimum alicastrum (12)	3	1.9/0	2.3/0	1.8/0	1.3/0	1.3/0	1.3/0	1.5/0	1.2/.8	.1/.8	.4/.1	.1/.2	.2/0
Chrysophyllum lucentifolium (9)	4	2.9/0	2.6/0	2.6/0	2.1/0	2.1/0	2.1/0	.4/.2	.2/.2	.2/0	.1/0	0/0	0/0
Melicoccus bijugatus (8)	5	0/0	0/0	0/0	0/0	0/0	.5/0	.7/0	.8/0	0/.2	0/.2	0/.1	0/0
Sapium aubletianum (6)	7	0/0	0/0	0/0	0/0	0/0	0/0	.2/0	0/0	2.5/0	0/0	.8/1.0	0/0
Lepidocordia punctata (6)	9	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2.0/0	0/0	0/0
Cecropia peltata (11)	13	0/.8	0/.3	0/.6	0/.5	0/.8	0/1.3	0/1.6	0/1.8	1.3/1.6	0/1.6	.3/.7	0/.1
Spondias mombin (12)	14	.3/.1	.3/.3	0/0	0/0	0/0	.3/0	1.8/0	2.0/0	1.8/.2	3.0/.1	.1/0	0/0
Hymenaea courbaril (4)	16	3.6/1.5	.8/3.5	0/2.8	0/1.8	0/1.5	0/.3	.3/.3	2.3/0	1.8/0	3.5/0	.1/0	0/0
Maclura tinctoria (7)[3]	19	0/1.7	0/0	0/0	0/0	0/0	0/0	0/0	0/0	.4/0		0/0	0/0
Tabebuia serratifolia (8)	22	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0		0/0	0/0	0/.1
Luehea speciosa (8)	26	0/0	0/0	1.0/0	1.5/0	1.3/0	.1/.6	0/.1	.2/0	.2/0	0/.6	0/.1	0/.1

[1] N = total number of trees of each species scored monthly for phenology.

[2] Rank = feeding tree rank based on group feeding durations over a period of 18 months.

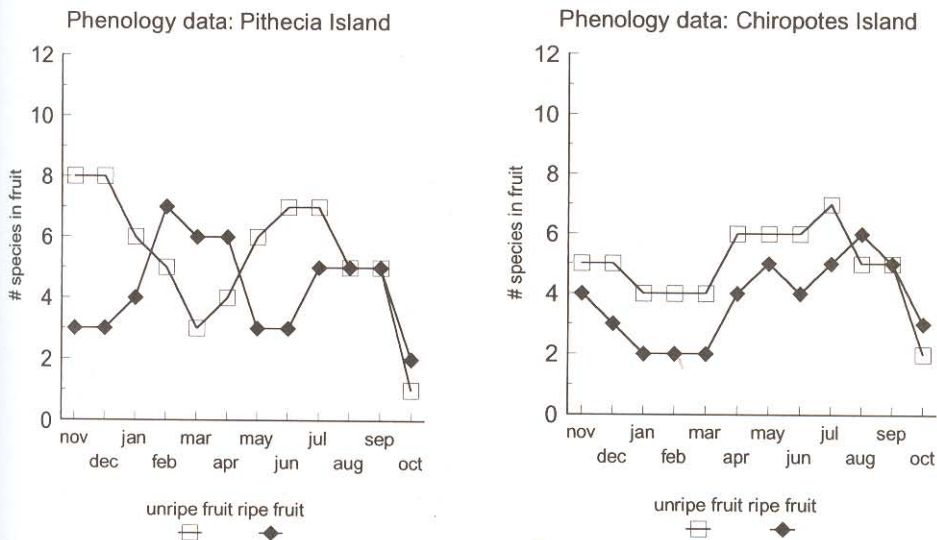[3] Phenology samples for *Maclura* began in September 1991.

Figure 4. Relative proportion of feeding trees producing unripe and ripe fruit, documenting the number of plant species in fruit (not fruit abundance per species). Samples were obtained from phenology trees and the figures were derived from column totals of Tables 1 & 2. Chiropotes Island had a lower proportion of phenology species in fruit during the dry season and had more species producing unripe fruit than ripe fruit for all but two months in the wet season.

fruit compared with Chiropotes Island that averaged 4.9 months of unripe fruit and 3.75 months of ripe fruit.

The number of months that phenology tree species bore ripe and unripe fruit were compared between islands (Fig. 4). There were more trees species producing fruit (ripe or unripe) on Pithecia Island than Chiropotes Island, except during the late wet season when availability of fruit from high ranking species dropped precipitously. Unripe fruit was more abundant on high ranking food species throughout the dry season on Chiropotes Island, but trees on Pithecia Island showed a bimodal peak of unripe fruit production in early dry and early wet seasons. *Transitions* between seasons, particularly wet to dry, may be more difficult for the sakis than the dry season itself.

Fruiting periodicity detected by phenological methods and fruit traps is compared to the number of months the sakis ingested fruit of the same species in Tables 3 and 4. Fruiting cycles that characterized *high-ranking plant species* took two forms: 1) trees that fruited synchronously with very extended fruiting cycles (e.g. *Pradosia caracasana*, *Chrysophyllum lucentifolium* var. *pachycarpum*, and *Strychnos fendleri*) and 2) individual trees that fruited asynchronously so that at least some trees produced fruit in nearly every month of the year (e.g. *Connarus venezuelanus*, *Licania discolor*, and *Brosimum alicastrum* var. *bolivarense*). High ranking tree species achieved this rank because the sakis ingested fruit from the entire fruiting cycle. *Lower ranking feeding trees* were characterized by short, synchronous fruiting cycles where fruit matured quickly and monkeys ingested fruit as it became available (e.g. *Alibertia latifolia*, *Sapium aubletianum*, *Lepidocordia punctata*, *Erythroxylum steyermarkii*) or were tree species that had long cycles, but fruit were eaten only during one stage of maturity (e.g. *Peltogyne floribunda*, *Piptadenia leucoxylon* and *Spondias mombin*).

Table 3. Characteristics of fruiting cycles for 12 plant species in the diet of *Pithecia pithecia* and two methods for assessing fruiting cycles compared with number of months the fruit species was included in the diet. Phenology and fruit trap samples are reported for the same 15 month period from September 1991 to November 1992. Rank of feeding trees and "characteristics of fruiting cycle" were determined over a 19 month period. (Phenology data from Homburg, in prep.)

Plant species (N)[1]	Rank	Periodicity of fruiting[2]	Synchronicity of fruiting	Duration of fruiting[3]	Fruiting peak	Months in traps	Months in phenology sample	Months in feeding sample
Comarus venezuelanus (10)[4]	1	sub-annual	asynchronous	long	late dry-early wet	13	12	15[9]
Licania discolor (10)[4]	2	annual	asynchronous	short	early dry	3	13	13
Strychnos fendleri (10)[5]	3	annual	synchronous	long	early wet	8	10	9
Peltogyne floribunda (11)[6]	4	super-annual	asynchronous	long	early dry	13	13	6
Erythroxylum steyermarkii (14)[7]	5	annual	synchronous	short	late wet	5	7	5
Ouratea roraimae (1)[4]	7	-	-	-	-	3	2	3
Strychnos mitscherlichii (7)[5]	8	annual	synchronous	long	early dry	2	12	6
Xylopia sericea (5)[4]	9	annual	synchronous	long	late wet-early dry	0	13	6
Piptadenia leucoxylon (10)[8]	10	annual	synchronous	long	late wet-early dry	5	10	4
Coccoloba striata (7)[7]	12	annual[10]	asynchronous	short	early wet	4	3	4
Alibertia latifolia (5)[4]	17		synchronous	short	early wet	2	4	2
Copaifera pubiflora (10)[7]	25	super-annual	synchronous	short	early dry	6	7	4

[1] N = total number of trees (or lianas) of each species scored monthly for phenology (14 months).
[2] Periodicity: sub-annual = interval between fruiting is less than a year; super-annual = fruiting interval is greater than a year.
[3] Duration: short = fruiting less than 6 months; long = fruiting 6 months or more.
[4] Predate mature-sized seeds; color change of exocarp may not be complete.
[5] Ingest mesocarp; drop seeds below tree canopy.
[6] Predate young seeds; (usually) drop mature seeds.
[7] Predate mature seeds with mesocarp; do not ingest young fruit.
[8] Predate young seeds; mature seeds dispersed by wind (anemochorous).
[9] Months feeding on Comarus exceeded months in fruit trap and phenology samples because the monkeys went to the ground to ingest seeds from old, aborted fruit.
[10] Phenology sample collected for 12 months only.

Table 4. Characteristics of fruiting cycles for 12 plant species in the diet of *Chiropotes satanas* and two methods for assessing fruiting cycles compared with number of months the fruit species was included in the diet. Phenology and fruit trap samples are reported for the same 15 month period from September 1991 to November 1992. Rank of feeding trees and "characteristics of fruiting cycles" were determined over an 18 month period. (Phenology data from Peetz, in prep)

Plant species (N)[1]	Rank	Periodicity of fruiting[2]	Synchronicity of fruiting	Duration of fruiting[3]	Fruiting peak	Months in traps	Months in phenology sample	Months in feeding sample
Pradosia caracasana (13)[4]	1	annual	synchronous	long	early wet	2	14	15
Brosimum alicastrum (12)[4]	3	annual	asynchronous	long	early dry	4	13	12
Chrysophyllum lucentifolium (9)[4]	4	annual	synchronous	long	early dry	2	11	10
Melicoccus bijugatus (8)[4]	5	super-annual	asynchronous	short	early wet	0	5	11
Sapium aubletianum (6)[5]	6	annual	synchronous	short	early wet	4	4	3
Lepidocordia punctata (6)[6]	9	annual	synchronous	long	late wet	2	3	4
Cecropia peltata (11)[6]	13	annual	asynchronous	long	late wet	4	12	9
Spondias mombin (12)[7]	14	annual	synchronous	long	early wet	3	10	6
Hymenaea courbaril (4)[4]	16	annual	synchronous	long	late wet	1	6	7
Maclura tinctoria (7)[8]	19	super-annual	asynchronous?	short	early wet	0	2	2
Tabebuia serratifolia (8)[5]	22	super-annual	synchronous	short	early wet	1	2	2
Luehea speciosa (8)[5]	26	sub-annual	synchronous	short	late dry	1	12	6

[1] N = total number of trees of each species scored monthly for phenology (15 months)
[2] Periodicity: sub-annual = interval between fruiting is less than a year; super-annual: fruiting interval is greater than a year
[3] Duration: short = fruiting less than 6 months; long = fruiting six months or longer
[4] Predate young seeds; usually drop mature seeds and ingest mesocarp.
[5] Predate young seeds; mature seeds dispersed by wind (anemochorous).
[6] Predation of seeds with some dispersal (zoochorous) - (i.e. seeds found in feces).
[7] Ingests mesocarp of ripe fruit, drops seeds.
[8] Ingests whole fruit, including seed.

The total number of months in fruit (both immature and mature fruit) and number of months in which ingestion occurred were not significantly different for *Chiropotes* (Mann Whitney test: $Z = -.783$, ns), but time in the phenological sample was significantly longer than ingestion periods for *Pithecia* ($Z = -2.1$, $P = .036$). An exact overlap between fruiting phenophase and ingestion indicated that the sakis ingested parts of both ripe and unripe fruit, but masked an important detail of dietary selection mentioned above. Ingestion during the entire fruiting phase often meant that seeds were ingested from young fruit and mesocarp was ingested from mature fruit (e.g. *Pradosia caracasana*, *Brosimum alicastrum*, *Melicoccus bijugatus*, Table 4). Both sakis preferred young seeds over mature seeds, but only *Chiropotes* were found to use some plant species throughout fruit maturation.

The traps provided a better estimate of the period of fruit ingestion for *Pithecia* than *Chiropotes* (Tables 3 and 4). At 4% the size of Chiropotes Island, it is not surprising that 100 traps on Pithecia Island provided a closer fit to fruit availability than for the larger Chiropotes Island. However, some resources important to *Pithecia* were undersampled by traps because they were shrubs at the same height or lower than the traps (e.g. *Xylopia sericea*, *Morinda tenuiflora*, *Hirtella racemosa* var. *racemosa*).

Seasonal Variation in the Components of Saki Diets

Sakis are predominantly young seed predators and ingested seeds from a diversity of sources (Table 5). Seeds of nuts, capsules and drupes made up the dominant resources for both saki species and only became relatively rare in early and late wet seasons for *Chiropotes* and in the late wet season for *Pithecia*. In the *early wet season*, *Chiropotes* shifted from seeds to ingesting primarily ripe mesocarp of *Pradosia caracasana*, *Melicoccus bijugatus* and *Brosimum alicastrum* (Table 5). Seeds from these sources were mature and were usually dropped intact below the tree canopy. The *late wet season* was marked by a reduction in the ingestion of seeds by both sakis; *Pithecia* ingested mesocarp primarily and *Chiropotes* shifted to the soft, small drupes of the parasite *Oryctanthus alveolatus* (Loranthaceae).

Table 5. Seasonal differences in dietary composition of seeds and mesocarp ingested by *Pithecia* and *Chiropotes*. Sample is taken from the top 50 species ingested during an annual cycle (November 1991 to October 1992) and values are expressed as percent of fruit ingestion. The top two resoucess during each season are in bold-faced type

Plant Item	Early dry		Late dry		Early wet		Late wet	
	Pithecia	*Chiropotes*	*Pithecia*	*Chiropotes*	*Pithecia*	*Chiropotes*	*Pithecia*	*Chiropotes*
Seeds of nuts and drupes[1]	**62.47**	**58.25**	**62.78**	**61.41**	**76.09**	44.47	21.94	33.33
Winged seeds[2]	2.09	4.09	1.13	11.54	0.20	0.66	0	2.11
Legume seeds[3]	33.76	2.65	9.99	7.72	0.54	1.68	8.30	2.66
Parasite[4]	0.24	**30.31**	0.09	**16.97**	0	11.44	0.05	**42.71**
Whole fruit[5]	2.14	1.81	5.39	0.39	**21.54**	0.79	19.37	11.63
Mesocarp only[6]	0.29	2.90	**20.62**	1.96	1.64	**40.97**	**50.34**	8.55

Plant families represented in feeding samples include:

[1] Sapotaceae, Chrysobalanaceae, Connaraceae, Moraceae, Sapindaceae, Anacardiaceae, Rubiaceae.
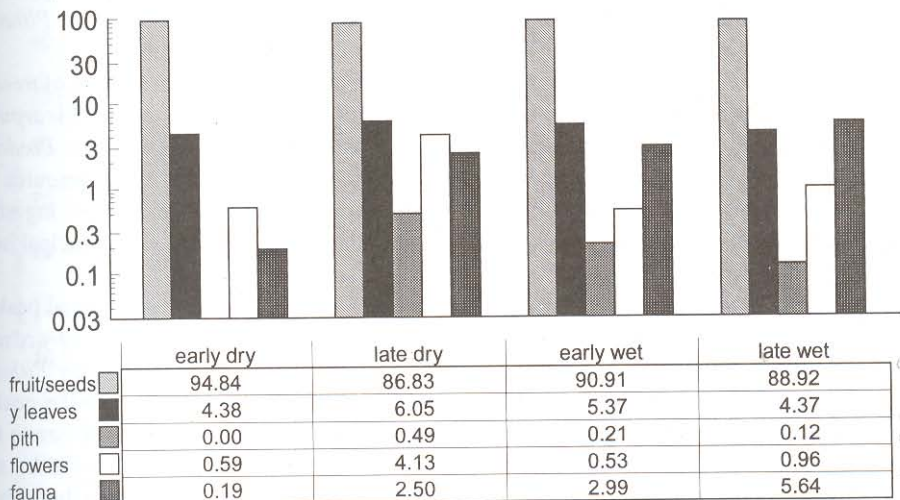
[2] Bignoniaceae, Polygalaceae, Combretaceae, Tiliaceae.

[3] Caesalpiniaceae, Papilionaceae, Mimosaceae.

[4] Loranthaceae.

[5] Rubiaceae, Erythroxylaceae, Boraginaceae, Moraceae: monkeys ingested pericarp and seed.

[6] Primarily from Meliaceae, Loganiaceae, Sapotaceae.

% components of items ingested

	early dry	late dry	early wet	late wet
fruit/seeds	94.84	86.83	90.91	88.92
y leaves	4.38	6.05	5.37	4.37
pith	0.00	0.49	0.21	0.12
flowers	0.59	4.13	0.53	0.96
fauna	0.19	2.50	2.99	5.64

Figure 5. Seasonal variation in fruit and non-fruit (young leaves, pith, flowers, and fauna, primarily insects) in the diet of *Pithecia pithecia*. Percentage of the components are expressed as log values.

Many of the samaras ingested by the sakis were seeds from Bignoniaceae lianas that flowered in the late wet season and contributed to the "peak" of flower ingestion for *Chiropotes* (Figures 5 and 6). Winged seeds represented a larger proportion of the diet of *Chiropotes* than of *Pithecia*. Pod maturity and subsequent dehiscence occurred during windy weather conditions in the winter dry season and the ingestion of these seeds was reduced in the wet season diet. *Peltogyne floribunda* (Caesalpiniaceae) is the dominant tree species on Pithecia
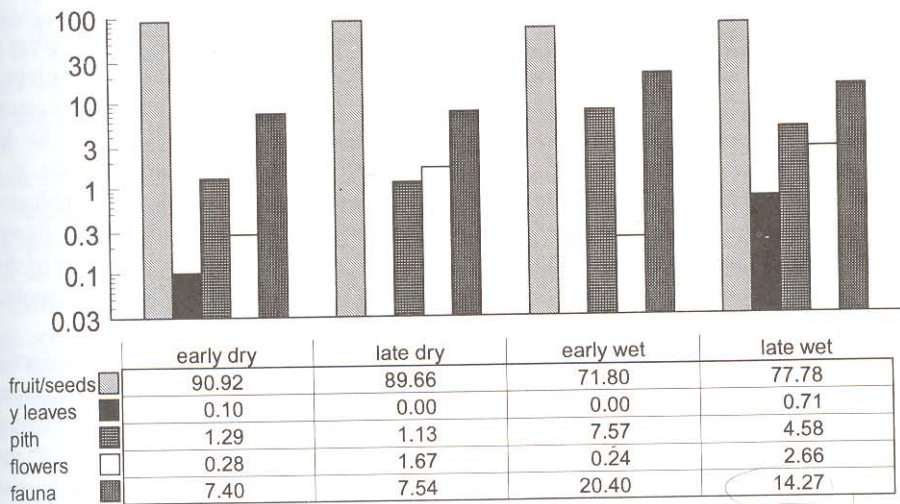
% components of items ingested

	early dry	late dry	early wet	late wet
fruit/seeds	90.92	89.66	71.80	77.78
y leaves	0.10	0.00	0.00	0.71
pith	1.29	1.13	7.57	4.58
flowers	0.28	1.67	0.24	2.66
fauna	7.40	7.54	20.40	14.27

Figure 6. Seasonal variation in fruit and non-fruit (young leaves, pith, flowers, and fauna, primarily insects) in the diet of *Chiropotes satanas*. Percentage of the components are expressed as log values.

Island (Parolin, 1993) and young seeds from undehisced fruit of this species and *Piptadenia leucoxylon* (Mimosaceae) were both ranked in the top 10 plant species used by *Pithecia*. Fruiting and ingestion peaked in the early dry season on Pithecia Island (Table 5).

Three species of Loranthaceae have invaded the crowns of several species of trees in Guri Lake (e.g. *Protium tenuifolium* and *Chrysophyllum lucentifolium* var. *pachycarpum*), but are particularly notable on the highest ranked feeding tree of *Chiropotes*, *Pradosia caracasana*. Of the Loranthaceae species, *Oryctanthus alveolatus* is a major resource for *Chiropotes* and was ranked second in three of the four seasons (Table 5). Low ingestion rates on the northern island may be due to low abundance (and absence of principal host, *Pradosia caracasana*).

Mesocarp ingestion peaked during the wet season for both sakis. The annual peak of mesocarp ingestion by *Chiropotes* corresponded to the ripening of *Pradosia caracasana* and *Melicoccus bijugatus* in June, July, and August. Ingestion of mesocarp by *Pithecia* was tied closely to the fruiting phenophase of two species of *Strychnos*. *S. fendleri* peaked in availability in the early wet season; ingestion peaked once fruit reached full size in late wet season. Likewise, the fruiting peak for *S. mitscherlichii* occurred in the early dry season and fruit was ingested in the late dry season. The "whole fruit" category included both fleshy berries and arillate seeds like *Lepidocordia punctata* (Boraginaceae). Whole fruit appeared to be a more important resource for *Pithecia* than *Chiropotes*, representing close to 20% of *Pithecia* diet in the early and late wet seasons.

Non-fruit items were secondary resources for both sakis during all seasons (Figs 5 and 6) with one exception. Caterpillars were extremely abundant on *Pradosia caracasana* trees in the 1992 early wet season and represented 20% of the diet. Young leaves were relatively important to *Pithecia* and showed little annual variation by season. Pith was relatively important to *Chiropotes* and ingestion peaked in the early wet season. Flowers of six species were ingested by *Pithecia* in the late dry month of April and represented the flower ingestion increase in the late dry season. The only non-plant item of food intake was the "fauna" category. This included the odd egg and wasp nest taken by *Pithecia*, but was dominated by caterpillars in the wet season by *Chiropotes* and aseasonal ants, spiders, and caterpillars by *Pithecia*. Larger-bodied *Chiropotes* invested more time during all seasons in insect search and ingestion than did *Pithecia*.

Both saki species maintained a relatively diverse diet (plant species and plant parts used) year-round (Figure 7). The twelve plant species for which we have phenology data represented about half of the top 25 feeding species. In turn, these high ranking resources represented at most 40% of the monthly diet of *Pithecia* and at most 50% of the diet of *Chiropotes*. *Pithecia* were very uniform in the total number of plant species in each monthly diet. In contrast, *Chiropotes* appeared to increase diet breadth with a reduction in rainfall in the late dry season (Fig 7), although months of low rainfall did not always result in a more diverse diet (r_s = -.477, ns, N = 12 months). The sharp reduction of dietary diversity from April to May was due to the ripening of *Pradosia caracasana* (Sapotaceae) mesocarp on Chiropotes Island which was available for only about 8 weeks.

Using these data it is clear that the two saki species differed in their selection of food items by their degree of seed maturation. *P. pithecia* were more selective, ingesting fruit or seeds at specific stages (but not necessarily the same stage) of fruit development. For example, *Connarus venezuelanus* var. *orinocensis* seeds were ingested from mature (with reddish colored pericarp) fruit. *Peltogyne floribunda* and *Piptadenia leucoxylon* seeds were ingested only when they were immature. The mesocarp of *Strychnos* spp. was ingested more often at the mature than at the immature stage; seeds and exocarp were spat out. Berries of *Erythroxylum steyermarkii* and *Coccoloba striata* were ingested whole
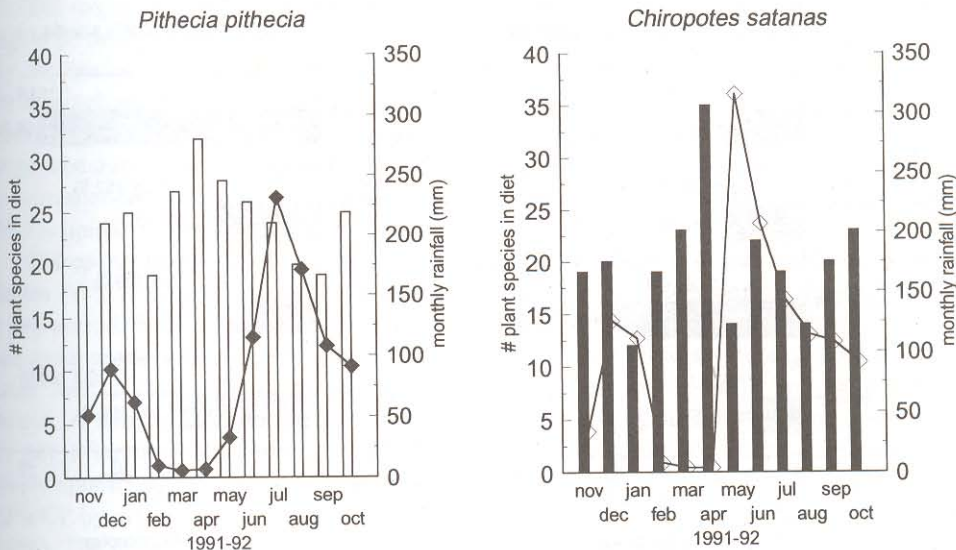
Figure 7. Comparison of the number of plant species (histograms) in the monthly diets of *Pithecia pithecia* and *Chiropotes satanas* from November 1991 to October 1992 compared to rainfall (line) during the same months.

only when ripe, but seeds of *Alibertia latifolia* were ingested throughout its relatively short fruiting cycle (see Table 3).

Seasonal Variation in the Mechanical and Chemical Composition of Fruit

There was little variation by season in the average hardness of fruit and seeds ingested by the sakis (Fig 8). Food items opened in the dry season were not harder than during the wet season, although there was some evidence of within season variability. Food items opened in the early wet season by *Chiropotes* were significantly harder than items in the late wet season (Wilcoxon $Z = 3.36$, $P < .01$). The high average and maximum puncture values for *Chiropotes* during the early wet season were due to the ingestion of both woody *Vitex compressa* (Verbenaceae) fruit and some mature *Pradosia caracasana* (Sapotaceae) seeds that were well-protected by hard, brittle seed testa.

Seasonal variation in *seed hardness* values was more marked than in *pericarp hardness* values (Fig. 8). *Pithecia* ingested (and masticated) harder seeds than *Chiropotes* during all seasons except the early dry season, when average values were comparable. Seeds were hardest in the late wet and early dry seasons for both *Pithecia* and *Chiropotes*. Although seed hardness and pericarp hardness cannot be compared directly since the methods of obtaining data and the measurements themselves are different, there was a weak inverse relationship between seed hardness and pericarp hardness particularly in the late wet season. Fruits of many species were mature at this time of year with a soft pericarp and mature seeds encased in a hard testa.

Weighted averages of macronutrients (water soluble carbohydrates (WSC), crude protein (CP), and lipids), fiber (ADF = cellulose + lignin), and condensed tannins are presented in Figure 9. These values represented 65% of the plant species used in 1991–1992 by *Pithecia* and 83% of annual diet of *Chiropotes*.
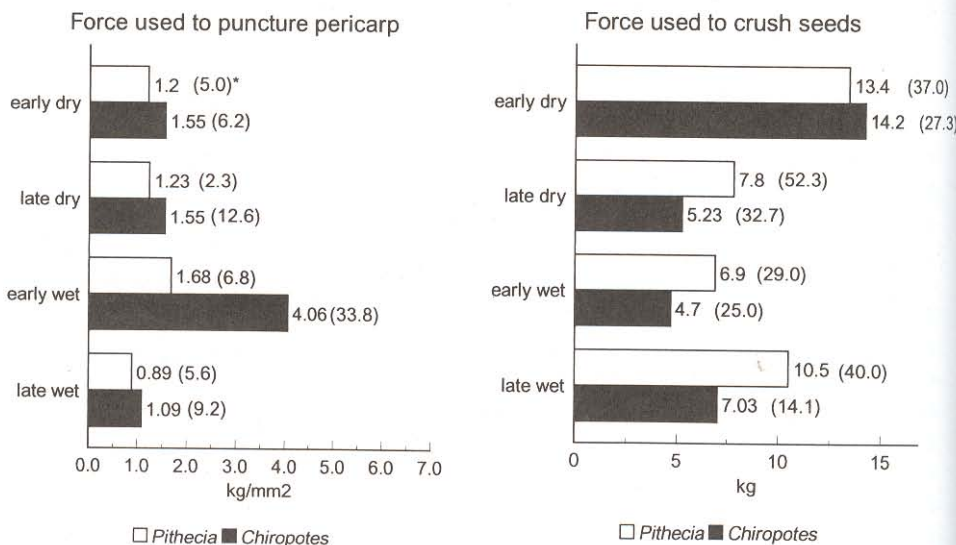
Force used to puncture pericarp

early dry — 1.2 (5.0)* / 1.55 (6.2)
late dry — 1.23 (2.3) / 1.55 (12.6)
early wet — 1.68 (6.8) / 4.06 (33.8)
late wet — 0.89 (5.6) / 1.09 (9.2)

x-axis: 0.0 1.0 2.0 3.0 4.0 5.0 6.0 7.0 kg/mm2

□ Pithecia ■ Chiropotes

Force used to crush seeds

early dry — 13.4 (37.0) / 14.2 (27.3)
late dry — 7.8 (52.3) / 5.23 (32.7)
early wet — 6.9 (29.0) / 4.7 (25.0)
late wet — 10.5 (40.0) / 7.03 (14.1)

x-axis: 0 5 10 15 kg

□ Pithecia ■ Chiropotes

Figure 8. Comparison of average puncture and crushing resistance values and maximum values (in parentheses) of fruit and seeds ingested by *Pithecia* and *Chiropotes* in Guri Lake. Methods used to determine values were reported in Kinzey & Norconk, 1990.

Pithecia pithecia

y-axis: % dry wt (%QE), 0–25
x-axis: early dry, late dry, early wet, late wet — season

■ WSC ▨ crude protein □ lipids ▩ ADF ▦ CT

Chiropotes satanas

y-axis: % dry wt (%QE), 0–25
x-axis: early dry, late dry, early wet, late wet — season

■ WSC ▨ crude protein □ lipid ▩ ADF ▦ CT
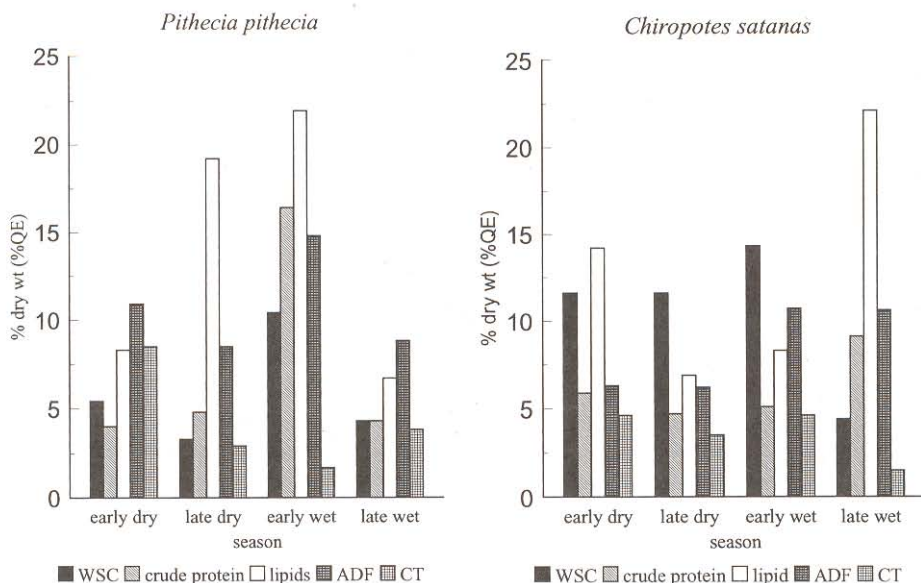
Figure 9. Seasonal variation in the biochemical properties of fruit and leaves ingested by *Pithecia pithecia* (N = 23 samples) and *Chiropotes satanas* (N = 19 samples). Values are averages of water soluble carbohydrates, crude protein, lipids, acid detergent fiber, and condensed tannins weighted by total feeding minutes.

The major resource for *Pithecia*, *Connarus venezuelanus* (Connaraceae) seeds, was found to be nearly 50% lipids/g dry weight and seeds were heavily ingested in late dry and early wet seasons. Lipid intake peaked in the early wet season with the addition of *Actinostemon schomburgkii* (Euphorbiaeae) seeds (24.2% lipids). There was no significant difference in an annual average of lipid intake for either primate species, although lipid intake peaked during opposite seasons, late wet and early dry, for *Chiropotes*. High lipid intake corresponded to peak ingestion of the parasite *Oryctanthus alveolatus* (Loranthaceae) at 38.3% lipids.

Chiropotes ingested food items that were significantly higher in water soluble carbohydrates (WSC) than *Pithecia*. The source of WSC for *Chiropotes* during the early and late dry periods and the early wet period appears to have been their major resource *Pradosia caracasana* whose seeds decreased from 34.0% to 14.6% as the dry season progressed and as the seeds matured. Protein intake peaked in the early wet season for *Pithecia*. A similar annual peak was not apparent for *Chiropotes*, but annual averages were not different (6.8% *Pithecia*; 6.0% *Chiropotes*). The source of the protein peak for *Pithecia* appears to have been *Actinostemon schomburgkii* and *Capparis muco* seeds (both > 22% CP by dry wt), but young leaves (e.g. *Capparis flexuosa*) also had high CP values (13.8%). The higher proportion of time invested in insect search and insect consumption may have off-set lower protein values of seeds and the negligible intake of leaves by *Chiropotes*.

Seasonal and annual ADF values were lower for *Chiropotes* than *Pithecia*. Higher fiber values not only reflected ingestion of more leaves by *Pithecia*, but some seeds ingested by *Pithecia* were also relatively high in lignin or cellulose (e.g. ADF values of seeds: *Licania discolor* 42.0%, *Amaioua corymbosa* 40.6%, *Angostura trifoliata* 40.0% exceeded values of young leaves: *Capparis flexuosa* 37.2% and *Coccoloba fallax* 36.6%). The ADF peak in the early wet season is not due to the ingestion of leaves, but rather to the ingestion of fibrous seeds.

Condensed tannin levels exhibited little seasonal variation and averaged less than 5% QE (quebracho units) annually for both sakis. The diversity of resources ingested may account for the low average since some high ranking resources (seeds) were relatively high in CT values (e.g. *Pradosia caracasana*: range 6.8% to 17.7% QE and *Licania discolor*: range 3.9% to 9.7% QE).

DISCUSSION

A diet that is largely seeds instead of fruit pulp may remove sakis from the seasonal effects of low rainfall. Sakis appear to monitor phenophases of individual plant species using two cues, change in seed or seed testa hardness and fluctuation in nutritional value. At the very least, the "dry season" cannot be considered to be a period of scarcity for sakis. They ingested many dry season resources in Guri Lake (winged seeds, legumes, nuts and immature drupes). Seed ingestion declined in the wet season with the ripening of fleshy fruits. The shift was more notable for bearded sakis with the ripening of their #1 resource (that was also ingested by capuchins, howlers, and macaws at this time). White-faced sakes did not have such an abundant resource available, although they too shifted to ripe berries and small drupes.

Resources that provided the sakis with food for long periods of time also tended to be high ranking resources by our measures. These were plant species that either produced relatively synchronous crops of fruit with prolonged periods of fruit development or were

species that fruited asynchonously so that resources were effectively renewable, but on different trees.

The saki species, that are now separated by some 40 km in Guri Lake, were apparently allopatric and found on opposite banks of the Caroní River before flooding. While we found considerable complementarity in the categories of seeds ingested, some plant species are highly endemic in the north and there was little overlap in plant species used for food by the two saki species. Nevertheless, two findings emerged in this study to suggest differences in feeding adaptations: 1) *Chiropotes* appeared to maximize the use of some resources by ingesting seeds at the young stage of maturity and mesocarp at the mature stage of fruit maturity. A similar pattern is found in *Pithecia albicans*, intermediate in size between *Pithecia pithecia* and *Chiropotes* spp. (Peres, 1993). On the other hand, *P. pithecia* appeared to be more selective and ingested fruit only at one stage of maturity, early or late, seeds or mesocarp. 2) *P. pithecia* appeared to adjust to changes in fruit availability and seasonality by maintaining a nearly constant diversity of fruit species in their diet. *Chiropotes satanas* tended to increase diet breadth in the dry season and contract diet breadth in the wet season with maturation of their #1 ranked resource. Although seasonal variation was evident in the relative proportion of seeds, mesocarp, and whole fruit in their diets, it is difficult to find evidence of seasonal shortages.

The fact that *Pithecia* and *Chiropotes* are isolated on different islands contributes to differences in the plant species included in their diets, but patterns of use appear reflect true, albeit subtle, interspecific differences. Ayres (1981) found that terra firme, white-nosed bearded sakis (*Chiropotes albinasus*) ingested seeds and mesocarp from Sapotaceae and Moraceae and while these two categories made up most of their feeding activities, the sources of ripe fruit pulp were different than the sources of young seeds (Ayres 1981). The use of different resources to obtain different parts of fruit was more characteristic of *Pithecia* in our study and island-bound *Chiropotes satanas* in Guri appeared to have intensified their use of some resources (particularly *Pradosia caracasana* and *Brosimum alicastrum)*. The seasonal shift to mesocarp was not only evident in Ayres's study of *Chiropotes albinasus* (1981) but also characterized closely related uakaris *Cacajao calvus* (Ayres 1986). This "sweet tooth" preference by the larger sakis of fruit high in water soluble carbohydrates was not evident in our *Pithecia* feeding samples. Indeed, relative proportion of WSC was one of the very few interspecific differences in the biochemical weighted averages between the Guri sakis.

Pitheciins Compared with Other Seed Predators

Ingestion and mastication of seeds as the major component of the diet is not limited to the pitheciins of the Neotropics, but is also found among some of the colobines (see Kool, 1993; Dasilva, 1994; and Maisels et al, 1994 for surveys of seed predation in colobines and Chivers, 1994 for a review of colobine gut anatomy), and some prosimians (*Propithecus diadema*: Wright, 1994; Yamashita, 1994). Both sakis and colobines prefer young seeds that provide high concentrations of valuable nutrients. Not only have some young seeds been found to have been comparable to young leaves in protein content (as did Dasilva, 1994 in her study of *Colobus polykomos*), but young seeds were also up to 20 times richer in lipids than were young leaves (Norconk, Kinzey & Conklin-Brittain, unpub; Maisels et al, 1994).

Lastly, the adaptation to seed predation appears to involve some mechanism to either penetrate hard seed coverings and thus guarantee access to mechanically protected young seeds or the ability to detoxify chemically protected seed coats or seed embryos

(see Bell, 1978). Saki adaptations appear to be dental primarily, but preliminary work on saki digestion suggests that they may also have an enlarged cecum and a relatively slow transit time (Milton, 1984). Slowing the passage of food through the hindgut, for example, may increase their ability to extract nutrients from highly fibrous seeds. The presence of moderate to high levels of condensed tannins also provide a general indicator of food choice. Average CT values of seeds ingested by colobines were only slightly higher than those ingested by sakis. Sakis do ingest some seeds that are as high as 9% CT (Kinzey and Norconk, 1993), but seasonal averages were low suggesting that they might adjust the volume of intake or increase species diversity to minimize intake of high concentrations of tannins. For example, white-faced sakis were found to balance seed species diversity across all seasons. Colobines also appear to moderate tannin intake and shift back and forth between young leaves and seeds to optimize protein and lipid intake (Dasilva, 1994).

Seasonal variation in the diets of pitheciins is more accurately measured in plant species diversity, seed and pericarp hardness, and nutritional value, rather than abundance and rarity. Seeds are a reliable resource, available in Guri for extensive periods through the dry season (when fleshy fruits become rare) and into part of the wet season. Nutritionally, they are a valuable resource, often higher in lipids and protein than ripe fruit or young leaves.

SUMMARY

Seasonal variation in fruit availability and dietary diversity was compared between *Chiropotes satanas* and *Pithecia pithecia* studied over a period of 17 months in 1991 and 1992 in Guri Lake, eastern Venezuela. The study group of *Pithecia* inhabited a 15 ha island (dry tropical forest) in the northern part of the lake and the study group of *Chiropotes* occupied a 365 ha island (transitional wet forest) 40 km to the south in the southern area of the lake. We collected feeding data for five days each month on each saki group using modified focal animal samples that measured feeding durations on plant species. Fruit abundance and seasonal distribution was measured by fruit traps and phenology.

This region of eastern Venezuela is characterized by a wet season and dry season that are of nearly equal duration. Each season was sub-divided into early and late, wet and dry seasons. There was no difference in the monthly pattern of rainfall between islands, but the southern island was significantly wetter than the northern island.

Both primate species ingested seeds year-round and month to month overlap of plant species and part ingested was high (average of c. 45%). Ingestion of seeds was higher than 60% of the plant portion of the diet in the dry season and first half of the wet season for *Pithecia* and in the dry season for *Chiropotes*. Both sakis shifted to ingesting mesocarp as it became available (and as seeds matured) in the wet season. Non-fruit items were secondary resources during all seasons with the exception of early wet season ingestion of caterpillars by *Chiropotes*.

Three differences were found between the saki species: a) the tendency for *Chiropotes* to use fruit of the same plant species from young to mature seed and mesocarp; *Pithecia* ingested seeds, mesocarp and whole fruit from different species; b) *Pithecia* did not alter plant species diversity or diet breadth on a seasonal basis, but *Chiropotes* increased diet breadth in the dry season and reduced it in the wet season; c) *Chiropotes* ingested items high in water soluble carbohydrates, whereas lipid values were often higher in food items ingested by *Pithecia*.

Sakis are more likely to track phenological differences in resource availability than rainfall per se. Variation in fruit ingested on the same month in consecutive years ranged

from a low of 9% (high predictability) to more 66%. But rainfall probably does provide some predictability. For example, a one month lag was seen in some species that was most likely related to a slight shift in rainfall synchronicity.

Pitheciins and colobines are the only two anthropoid subfamilies that maintain high levels of seeds predation. Seed predation may be related to anatomical specializations in both subfamilies: dental adaptations and perhaps hindgut enlargement in the Pitheciines and foregut adaptations in the digestive tract of Colobines.

ACKNOWLEDGMENTS

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