

Variation on Frugivory: The Diet of Venezuelan White-Faced Sakis

Marilyn A. Norconk^{1,3} and Nancy Lou Conklin-Brittain²

Received January 8, 2003; accepted February 24, 2003

White-faced sakis (Pithecia pithecia) are Neotropical seed predators that ingest a mixed diet of fruit, leaves, and insects. We report timed feeding data for a 12-mo period on a group of 8 white-faced sakis occupying an island—a portion of their original home range—in Lago Guri, Venezuela. We collected fruit and leaf samples, dried them in the field, and analyzed them to measure nutrient content—free simple sugars (FSS), crude protein (CP), lipids, and total nonstructural carbohydrates (TNC)—and the presence of antifeedants: total tannins, condensed tannins and dietary fiber. We weighted nutrients and antifeedants by timed feeding samples to estimate actual intake. Then we compared intake among months and seasons. Compared with other frugivores, the average monthly intake of lipids was extremely high (16.1% by dry matter estimate (DM)), attributed to ingestion of young seeds and other plant parts that were relatively high in lipids, e.g., seed arils. Intake of FSS and CP were relatively low: 3.4% DM and 6.5% DM, respectively. The average intake of total cell wall or neutral detergent fiber (NDF = 38.4% DM) was only slightly lower than the range reported for colobines. Average intake of tannins was within the range reported for cercopithecines: condensed tannins of 3.3% Quebracho units standard (QU). We suggest that white-faced sakis accept a trade-off for food items that are fibrous or astringent if they are also rich in lipids.

¹Department of Anthropology & School of Biomedical Sciences, 228 Lowry Hall, Kent State University, Kent, Ohio 44242.

²Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts 02138.

³To whom correspondence should be addressed; e-mail: mnorconk@kent.edu.

White-faced sakis expand the typical definition of primate fruit-eater in their high lipid-relatively high NDF-low FSS diet.

KEY WORDS: Neotropics; diet; seed predator; granivory; lipids; tannins; dietary fiber; antifedants; crude protein.

INTRODUCTION

Physical characteristics of fruit provide visual, tactile, and olfactory cues to primates. Characteristics such as fruit type, size, color, toughness, and hardness have been used separately or in combination—syndromes—to show how mammals select fruit for ingestion (Bremer and Eriksson, 1992; Gautier-Hion *et al.*, 1985; Janson, 1983; Jordano, 1992; Kinzey and Norconk, 1990; Lucas *et al.*, 2000; Willson and Whelan, 1990). Study of non-human primate diets began in the 1970s and combined field data collection with chemical analysis of food items (Altmann, 1998; Altmann *et al.*, 1987; Baranga, 1983; Calvert, 1985; Oates *et al.*, 1980). These studies have served not only to increase specific information about primate diets but also to eliminate generalized assumptions about primate nutrition. We analyzed diet from the perspective of intake in addition to examining properties of individual food items (Altmann, 1998).

Jordano (1992:122) described 3 types of avian frugivores: legitimate dispersers swallow fruit and defecate or regurgitate seeds intact; pulp predators ingest only pulp leaving the fruit partially on the tree and dropping or leaving seeds *in situ*; and seed predators, that may discard pulp in order to ingest the seed. While the differences between these categories would be clear from a plant's perspective—seed disperser vs. seed destroyer—the morphological differences of the consumers lies on a continuum that is more difficult to discern (Jordano, 1992). Primate frugivores fit comfortably into the first and last categories, and small primates eating large fruit may act as pulp predators for some fruit, e.g., *Saguinus fuscicollis* feeding on *Parkia* pods. Nevertheless, most primates are closer to the legitimate disperser end of the continuum and we know less about the strategies of seed predators, about the nature of their food rewards, and their effect on plant reproductive success. While the nature of food rewards of seed-eating is the topic of this paper, we have argued elsewhere that neotropical seed predators, including white-faced sakis, can also be effective seed dispersers of particularly small-seeded fruit species (Norconk *et al.*, 1998). Unfortunately, no one has estimated the real cost to the parents of large-seeded fruits.

Most primates ingest some fruit, and the category of fruit-eating is highly diverse (Jolly, 1985; Strier, 2003). Langer and Chivers (1994) attempted to standardize the classification of foods eaten by nonprimate mammals,

primates, and marsupials. Fruit, nuts and cereals, including seeds, became one of 16 categories, called diasporas, which show that this feeding category is large and diverse. Food categories could be substituted for nutrient categories. Milton (1993) categorized foods into 4 useful categories, 1) readily accessible calories, 2) protein, 3) fiber, and 4) chemical defenses. Fruits are high in calories, low in protein, moderate in fiber and low in chemical defenses (Milton, 1993: 91). Sakis still stretch the definition fruit-eaters by ingesting foods that are, on average, low in water soluble carbohydrates, highly variable in protein, and high in fat, dietary fiber, and tannins (Kinzey and Norconk, 1993).

The saki-uacaris (tribe Pitheciini) belong to an ancient Neotropical clade of seed predators (Middle Miocene: Fleagle, 1998). They are distinguishable early in the fossil record by their dental anatomy. Field studies have shown that this morphology allows them to open hard or protected fruit dentally in order to gain access to seeds of ripening fruit (Anapol and Lee, 1994; Kinzey and Norconk, 1990; van Roosmalen *et al.*, 1988). Seeds represent $\geq 60\%$ of their monthly diets (Norconk, 1996). As seed predators or granivores, they may be expected to ingest foods that are relatively rich in both nutrients and protective compounds (Bell, 1978; McKey, 1974). In order to determine what (primate) seed-eating signifies nutritionally, we report on a year-long study of wild white-faced sakis in Lago Guri, Venezuela.

METHODS

Subjects

Pithecia spp. are the smallest-bodied of the pitheciines, and the white-faced sakis, *P. pithecia*, are the smallest species of *Pithecia* (1.4–2.0 kg) (Glander and Norconk, unpubl; Hershkovitz, 1987, Vie *et al.*, 2001). Hershkovitz (1987) recognized two groups of *Pithecia*, the *P. pithecia* group (northeast of the Rio Negro and the Amazon River in Brazil, and particularly throughout the Guianas) and the *P. monachus* group (west of the Rio Negro and south of the Amazon River, including western Brazil and eastern Peru, Colombia, and Ecuador). Sexual dichromatism is striking in the *P. pithecia* group (white- or buffy-faced males contrast with agouti-colored females), but female coloration is similar among species of both groups (Hershkovitz, 1987). Our population sample is from the most westerly *P. pithecia*, with the apparent species boundary being the right bank of the Rio Caroní in eastern Venezuela.

Observations of the study group began in 1990 and habituation was completed before we collected feeding data. The group of 8 sakis consisted

of 2 adult females, 1 subadult female, 4 adult males and 1 subadult male. Despite its relatively large size, the group was cohesive during the study. We analyzed feeding data from samples collected from November, 1991 to October, 1992, a total of 34,674 min.

Study Site

The study site is a forested island in the northern region of Lago Guri, the catchment basin for the Rio Caroní (Alvarez *et al.*, 1986; Norconk and Grafton, 2002; Terborgh *et al.*, 1997). Huber (1986) characterized the vegetation in this portion of the lake as principally deciduous to semideciduous with a strong, prolonged dry season. Annual rainfall ranged from 89.8 to 134.8 mm over a 5-yr period (1992–1996) with an average of 17.4 mm of rainfall in the driest month (March) and 264.6 mm rainfall in the wettest month (July) (EDELCA – Guri, Hidrología annual reports). Tropical wet forests prevail in the southern portion of the lake. The islands range from 0.25 ha to >350 ha. Maximum lake depth was reached in 1986. Our research in Lago Guri began in 1987. We have no evidence that white-faced sakis have traveled between islands since their isolation. There are 2 saki species in the Caroní basin, white-faced sakis (*Pithecia pithecia*) in the northern part of the lake (region of Las Carolinas on Fig. 1) and bearded sakis (*Chiropotes satanas*) in the south (area D on Fig. 1). Before flooding, the Caroní River was apparently the western boundary for white-faced saki distribution in Venezuela and the eastern boundary for bearded sakis. Red howlers (*Alouatta seniculus*) and wedge-capped capuchins (*Cebus olivaceus*) also live on many islands in the lake.

The white-faced saki study group occupied the 12.8-ha Isla Redonda (7° 46'N, 62° 53'W). There is a paucity of studies on white-faced sakis in free-ranging habitats. Buchanan *et al.* (1981) reported home range sizes of 4–10 ha in Suriname, and a recent survey in the Brownsberg Nature Park, Suriname, suggests that this range is appropriate (Norconk, unpublished data). Island vegetation was described by Aymard *et al.* (1997), Parolin (1992), and Norconk and Grafton (2002). Parolin measured a total of 2,213 trees with a diameter at breast height (DBH) of ≤ 5.0 cm in 16-25-m² plots. She tabulated 57 species in 45 genera and 30 families. Three species of Leguminosae represented 52.6% of total stem area (*Peltogyne floribunda* and *P. paniculata* in the Caesalpinoideae subfamily (after Gentry, 1993) and *Acosmium stirtoutii* (Aymard & Gouzález, 2003) in the Papilionoideae subfamily). The highest ranked white-faced saki feeding tree, *Connarus venezuelanus* (Connaraceae), represented 7.5% of total stem area and was ranked fourth in species abundance (Parolin, 1992).

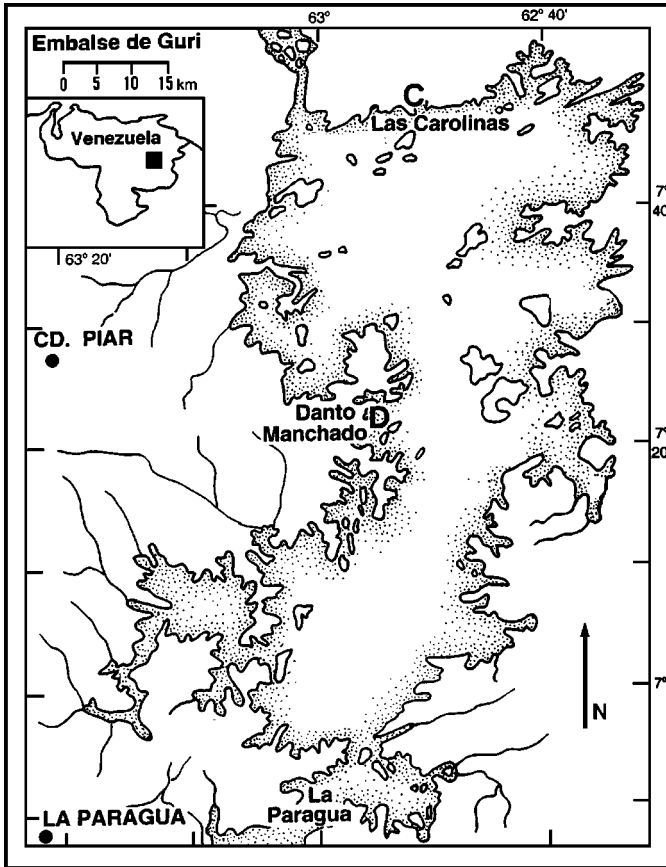


Fig. 1. Embalse de Guri (Guri Lake – stippled area, and surrounding mainland) and the approximate location of the study island in the region of Las Carolinas –C. The dam and hydroelectric plant are located ca. 12 km due west of Isla Redonda. Adapted from Aymard *et al.*, 1997, with permission from the author.

Sampling Techniques

We collected feeding data 5 days per mo for a 17-mo period in 1991–1992. We report on the last 12 mo of the sample: November 1991 to October 1992. We used all-occurrence, all-individual sampling while the subjects fed. We documented the time of entry (to the nearest min) of each individual into a feeding tree (start feeding), identification of plant species, and the exit time (stop feeding) to the nearest min. For each feeding bout, we calculated

the total feeding time of each individual. Individual sampling was facilitated by the excellent habituation and cohesive nature of the group. If individuals became involved in activities that interrupted feeding activities, e.g., mobbing a predator or chasing a conspecific, we considered the feeding sample incomplete and stopped sampling. Data taken while in a feeding tree included the part of the fruit ingested—seed only, pulp only, exocarp only, or whole fruit which included seed and exocarp—and if any part of the fruit was dropped: seed, pulp, seed coat, or exocarp. Plant species were identified by G. Aymard, Herbarium, UNELLEZ, Estado Portuguesa, Venezuela (see Aymard *et al.*, 1997).

We collected fruit and leaf samples of food items from representative samples of the same plant species at the same stage of maturity that they were eaten and often at the time of feeding. We separated seeds from pulp, seed coats, and exocarp while wearing plastic gloves. We weighed plant parts and dried them separately. We analyzed samples nutritionally within a year, but macronutrients and tannins are slow to deteriorate. We obtained a wet weight and dried the samples at 50°C to a constant weight in an electric laboratory oven at the base camp in Guri. Once dried, we stored samples in sterile, whirl-pak[®] plastic bags. We also collected plant parts and occasionally plant species that were not eaten, but we were very specific about the items collected for this category. For example, if the seed was eaten and, during the process of ingesting it, the exocarp was dropped, the exocarp would be considered not eaten. Sakis often discard the exocarp and seed coat before ingesting seeds. Food species selected for nutritional analysis included both portions of fruit eaten and portions not eaten.

Two further points must be clarified about our sampling methods. First, we do not present data on insect-eating, since only a small portion of the insect prey has been sampled nutritionally and many of the objects (presumed invertebrates) were never identified. In 1991–1992, *Pithecia* spent <3% of their time averaged among 4 seasons ingesting insects (Norconk, 1996). Our concentration on collecting adequate samples of plant species ingested yielded a minimum of 82% of the plant diet sampled each month. Thus, we feel that we recorded a reasonably accurate picture of white-faced saki nutrition even in the absence of the insect data. Second, we used time-based estimates of intake instead of weight-based estimates (g dry weight). We used this method so that the data collected on white-faced sakis would be comparable to those collected for bearded sakis over the same annual cycle (Norconk and Conklin-Brittain, in prep). Unlike the white-faced sakis, for which we could collect both time-based and weight-based samples, we were not able to distinguish between individual bearded sakis and were limited to collecting group timed-based data. Furthermore, in a recent analysis, we tested the assumption that time-based samples and weight-based samples are

significantly different and found no statistical difference in the comparison of nutrients ingested via the 2 methods for *Pithecia* (Norconk and Conklin-Brittain, 2000; Knott, 1999). Therefore, we report time-based estimates of intake.

Nutritional Analysis

We conducted nutritional analysis in the nutritional chemistry laboratory in the Anthropology Department at Harvard University. We determined crude protein (CP) via the Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Pierce and Haenisch, 1947). We used the detergent system of fiber analysis (Goering and van Soest, 1970) as modified by Robertson and van Soest (1980) to determine the neutral-detergent, or total cell wall fraction (NDF) which includes hemicellulose (HC), cellulose (Cs), sulfuric acid lignin (Ls) and cutin. We measured lipid content via petroleum ether extraction for 4 days at room temperature, a modification of the method of the Association of Official Analytical Chemists (AOAC, 1984).

We estimated free simple sugars (FSS) (formerly referred to as water soluble carbohydrates (WSC): Conklin-Brittain *et al.*, 1998) via a phenol/sulfuric acid calorimetric assay of Dubois *et al.* (1956) as modified by Strickland and Parsons (1972). Sucrose was the standard. We calculated total nonstructural carbohydrates (TNC) as follows: $TNC = 100 - \%NDF - \%lipids - \%CP - \%ash$ (Conklin-Brittain *et al.*, 1998). We represent results of these analyses as a percentage of dry matter.

We measured condensed tannin (CT) content via the proanthocyanidine test of Bate-Smith (1975) and modified by Porter *et al.* (1986). We measured total bioactive tannins (both condensed and hydrolyzable tannins) by the radial diffusion method (Hagerman, 1987). Quebracho (QU) was the standard for both tannin assays. We report the tannin results as a percentage of quebracho units, and not as a percentage of dry matter.

Statistical Analysis

We computed monthly, seasonal, and annual weighted averages (“intake”) by multiplying the chemical fraction of each plant part or species by the time spent feeding on that plant part or species each mo: $intake = \Sigma(F_i \times X_i) / \Sigma F_i$, where in F_i is the daily time budget invested in feeding per day (in min) and X_i is the value of each chemical parameter for the i th item [Davies *et al.*, 1988]. We divided the annual cycle into 4 seasons: early wet (May through July), late wet (August to October), early dry (November

through January) and late dry (February through April) based on rainfall data (Norconk, 1996). We multiplied monthly intake times the (3) respective months to obtain values for seasonal intake.

We entered results of the chemical assays into SPSS[®] 9.0 for Windows[™]. Some of the data were not distributed normally, so we used nonparametric tests to measure intermonthly and interseasonal variation in intake and to determine correlations between nutrients and antifeedants. For multiple regressions, we log transformed the dependent variable, i.e., percent time feeding, but not the independent variables. All tests are two-tailed with the level of significance set at ≤ 0.05 unless otherwise noted.

RESULTS

Dietary Composition

The majority of dietary items ingested ($88.3\% \pm 6.9\%$, $n = 12$ mo) were fruit, followed by $5.7\% \pm 4.8\%$ young leaves, $3.0\% \pm 3.2\%$ insects, $1.8\% \pm 1.7\%$ flowers, $0.0 \pm 0.1\%$ pith (Fig. 2). Less than 1.5% of the timed samples are from unidentified sources. We further divided fruit into seeds of nuts and drupes, winged seeds (family Bignoniaceae), legume seeds, whole drupes, of Loranthaceae whole fruit, and mesocarp (pulp). The ingested seeds were primarily from nuts and drupes, though as much as 33.8% of the early dry season samples were legumes and 2.1% of the early dry season sample was winged (Bignoniaceae) seeds. The average monthly seed consumption of all types, excluding seeds eaten with the pulp, is $63.2\% \pm 32.7\%$ (ranging from a 3-mo average of 94.2% in the early dry season to 30.8% in the late wet season).

Leaves were the most important resource after fruit. They made $\leq 14.3\%$ of the late dry season diet (April), but were also $>8\%$ of the monthly diet in the wet season months of June and July and the dry season month of December (Fig. 2). We collected phenological data concurrently with the feeding data by Homburg (1997) and Peetz. They collected monthly data on 270 stems in 39 species representing 68.4% of the species tabulated by Parolin in her vegetation sample of the island (1992). Homburg (1997) showed that young leaf production peaked in the early wet season (May and June) when approximately 50% of stems in the phenological sample had young leaves. However, we found no correlation between the phenological patterns in young leaf production and saki feeding (Spearman $\rho = 0.23$, ns, $n = 12$ mo).

Flowers averaged approximately 3% of the monthly white-faced saki diet in the dry season (November to April, range 0.6% to 4.3%) and then declined in the wet season ($\bar{X} = 0.9\%$, range = 0 – 2.7%). This is opposite the pattern in the phenological samples (Spearman $\rho = -0.61$, $p < 0.05$).

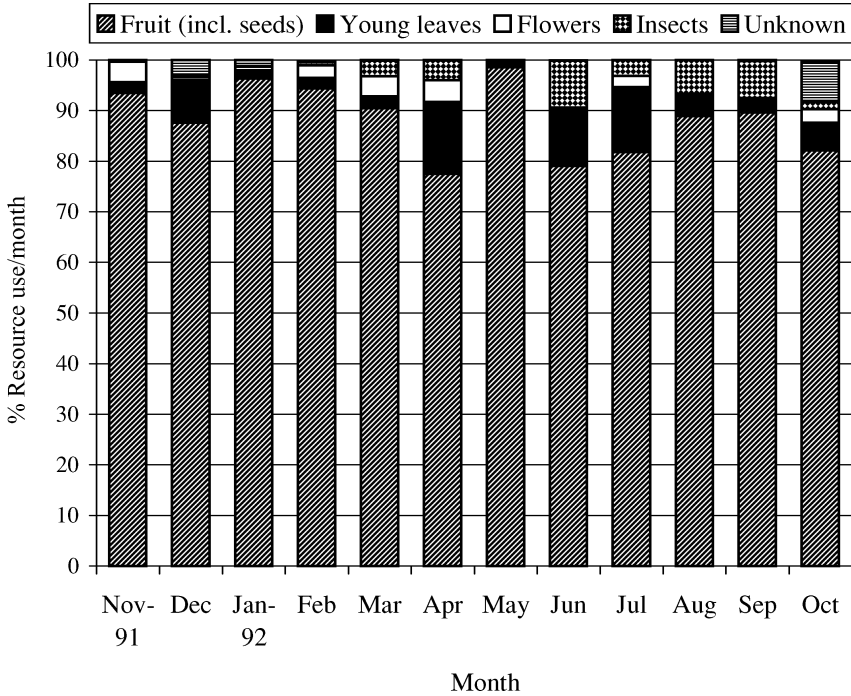


Fig. 2. White-faced saki diet from November 1991 to October 1992 as represented by percentages of all-occurrence timed samples during which fruit, including seeds, leaves, flowers, and insects were ingested.

Phenology revealed that flower production was relatively constant over the course of the year. Stems in flower represented 5–15% of each monthly sample ($\bar{X} = 8.7\% \pm 3.4\%$ per month year-round) (Homburg, 1997: Figure 3.6). Availability of the broad range of resources in the phenological samples was not a particularly good predictor of flower availability since the samples included few lianas that were important in the flower portion of the saki diet, e.g., from Bignoniaceae, Polygalaceae, and Passifloraceae. Insects were more commonly eaten in the wet season, particularly during June, August, and September (see Fig. 2); we have no information about availability of this resource.

Nutrient Analysis of Plant Items

We sampled an average of 92.6% (n = 12 mo, range = 82–100%) of the plant species ingested by white-faced sakis during 1991–1992 for nutrients and antifeedants. We divided plant items into 10 categories: arils, seeds

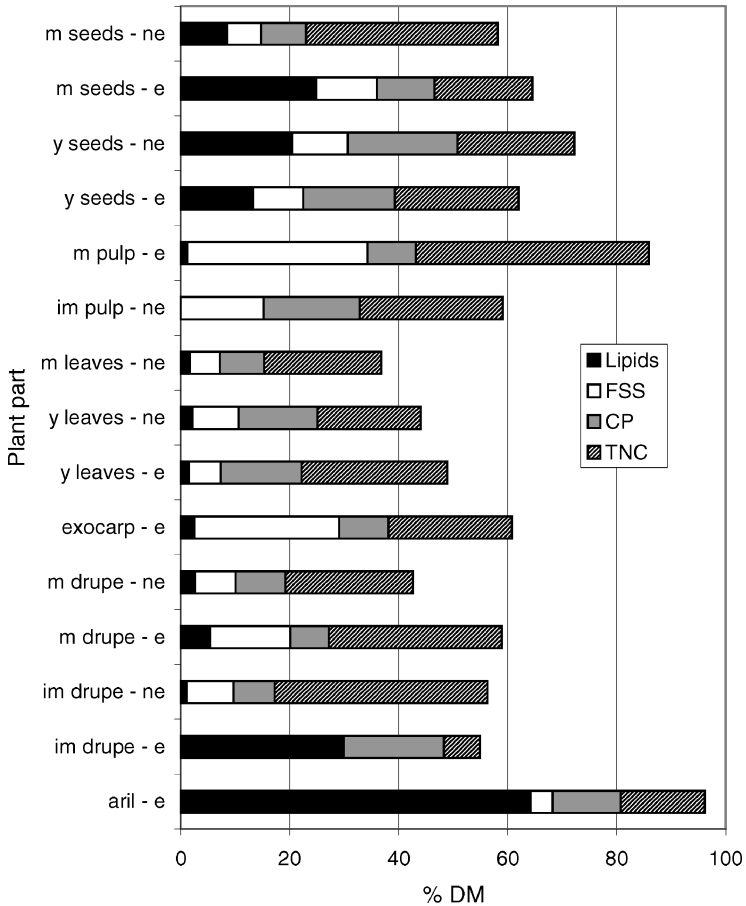


Fig. 3. Proportion of macronutrients in plant parts that were eaten (e) and not eaten (ne). The macronutrients are: Lipids, FSS – free simple sugars; CP = crude protein; and, TNC = total nonstructural carbohydrates. All items are compared as a % of DM (dry matter). With regard to plant parts, the following abbreviations indicate relative maturity: m = mature, y = young; im = immature.

(young and mature), pulp or mesocarp, whole drupes (young and mature, included seeds), flowers, exocarp and leaves (young and mature) (Table II). We also collected both eaten and not eaten plant parts from 13 species for nutritional analysis (Table II and Fig. 3).

The most lipid-rich resources were arils of *Connarus venezuelanus* that were >60% lipids by dry matter (DM) (Table I). Both young and mature seeds were also relatively high in lipids. Fruit pulp, young and mature leaves,

Table 1. Nutritional analysis of plant parts eaten (E) and not eaten (NE) by white-faced sakis in Lago Guri, alphabetized by genus. In the case of seeds, the designations immature and mature refer to fruit maturity and dispersal capability, not necessarily to seed size. Seeds of immature fruit were usually full-sized when eaten, but the fruit had not yet dehisced, or color of fruit indicated that it was not fully ripe. Values expressed in % DM (dry matter), except tannins (expressed in % QU: quebracho units). (FSS = free simple sugars; TNC = total nonstructural carbohydrates; NDF = neutral detergent fiber; ADF = acid detergent fiber; CT = condensed tannins; RD = radial diffusion of hydrolyzable tannins.) Maturity: I = immature; M = mature. Plant species used in the multiple regression analysis are indicated (*)

Plant species	Plant family	Eaten/ not eaten	Plant part and maturity		Lipids	FSS	CP	TNC	NDF	ADF	Lignin	CT	RD
<i>Actinostemon schomburgkii</i> *	Eup*	E	seed (I)	24.2	14.7	22.7	12.3	23.1	12.6	5.2	0.0	18.0	
<i>Alibertia latifolia</i> *	Rub	E	drupe (M)	1.3	28.8	6.1	29.7	31.9	21.0	13.1	0.2	0.0	
<i>Alibertia latifolia</i>	Rub	E	seed (I)	0.7	7.1	22.1	14.3	52.0	21.6	13.4	0.3	0.0	
<i>Amatoua corymbosa</i> *	Rub	E	drupe (M)	13.6	6.5	7.1	11.9	58.6	39.7	15.7	3.9	2.8	
<i>Amatoua corymbosa</i>	Rub	NE	drupe (M)	2.6	7.5	9.1	23.4	53.5	39.0	21.5	3.8	3.9	
<i>Amphilophium paniculatum</i>	Big	E	seed (I)	18.6	—	21.5	—	—	—	—	0.0	—	
<i>Angostura trifoliata</i> *	Rut	E	seed (I)	—	2.1	24.2	—	50.2	40.1	35.0	17.7	13.9	
<i>Bignoniaceae</i> pod #187*	Big	E	seed (I)	2.0	—	14.7	10.9	66.2	52.3	15.5	0.0	—	
<i>Brosimum guianense</i>	Mor	E	drupe (M)	2.3	—	7.6	—	—	—	—	—	—	
<i>Capparis flexuosa</i> *	Cap	E	leaves (Y)	2.1	9.4	14.3	20.6	51.8	37.2	16.6	0.3	—	
<i>Capparis muco</i>	Cap	NE	leaves (Y)	1.6	3.6	16.2	7.3	62.1	40.0	14.5	0.0	—	
<i>Capparis muco</i> *	Cap	E	pulp (M)	3.1	21.4	18.7	39.4	11.9	8.3	1.1	0.7	0.0	
<i>Capparis muco</i>	Cap	NE	pulp (I)	0.0	15.2	17.7	26.2	37.3	11.6	1.0	0.0	—	
<i>Capparis muco</i>	Cap	E	seed (M)	18.6	10.1	22.2	12.4	33.0	22.7	8.4	0.1	0.0	
<i>Capparis muco</i>	Cap	NE	seed (I)	8.2	14.7	37.0	0.0	39.7	27.5	6.7	0.2	—	
<i>Casearia spinescens</i>	Fia	E	seed (I)	—	1.8	23.3	—	41.8	31.5	13.0	13.4	9.0	
<i>Casearia sylvestris</i> *	Fia	E	drupe (I)	29.9	—	18.4	6.6	41.7	30.4	13.2	—	2.1	
<i>Chiococca alba</i> var. <i>purpure</i> *	Rub	E	drupe (M)	7.8	—	6.7	49.0	31.7	20.0	5.5	0.3	0.7	
<i>Chrysophyllum lucentifolium</i> *	Sapo	E	seed (I)	9.0	26.4	15.7	22.4	24.0	2.5	0.1	0.0	0.5	
<i>Coccoloba fallax</i> *	Polygo	E	leaves (Y)	0.8	2.3	15.4	33.0	42.8	36.6	20.4	10.7	26.4	
<i>Coccoloba fallax</i>	Polygo	NE	leaves (M)	1.4	2.2	7.9	21.6	63.1	54.0	22.9	6.2	27.7	
<i>Coccoloba striata</i>	Polygo	NE	drupe (I)	1.1	8.6	7.5	39.1	43.7	28.7	16.5	2.9	16.3	
<i>Coccoloba striata</i> *	Polygo	E	drupe (M)	0.9	15.9	6.1	40.1	34.9	21.0	11.4	2.2	13.9	
<i>Connarus venezuelanus</i> *	Con	E	aril (M)	64.2	4.0	12.6	15.4	3.8	2.5	1.0	0.4	0.0	
<i>Connarus venezuelanus</i> *	Con	E	seed (I)	48.7	2.3	11.3	15.1	20.2	14.3	7.4	2.1	5.6	
<i>Copaifera pubiflora</i>	Cae	NE	seed (I)	5.9	14.8	9.8	51.7	15.2	7.9	2.8	1.5	5.5	
<i>Copaifera pubiflora</i> *	Cae	E	seed (M)	4.8	21.4	7.4	41.9	22.2	14.4	7.0	4.1	4.5	
<i>Dendrothorea ottonis</i>	Lor	E	seed (I)	18.3	—	8.2	18.8	54.6	23.7	17.6	2.6	11.1	

Table I. Continued

Plant species	Plant family	Eaten/ not eaten	Plant part and maturity	Lipids	FSS	CP	TNC	NDF	ADF	Lignin	CT	RD
<i>Dendrophthora ottonis</i>	Lor	E	seed (M)	47.7	—	9.0	8.3	35.0	25.0	20.3	—	—
<i>Dioecia guianensis</i>	Pap	E	flowers	—	—	—	—	37.1	14.9	—	—	—
<i>Erythroxylum steyermarkii</i> *	Ery	E	drupe (M)	11.7	—	3.5	50.3	34.5	20.6	2.7	2.2	2.8
<i>Eugenia monticola</i>	Myr	E	drupe (M)	1.2	—	5.1	52.9	37.5	19.0	10.8	1.6	5.5
<i>Hirtella racemosa</i> *	Chr	E	drupe (M)	2.3	—	7.1	0.9	72.6	67.3	41.0	12.1	9.7
<i>Licania discolor</i>	Chr	NE	leaves (M)	1.5	6.7	6.7	18.3	67.4	54.7	28.9	11.6	12.1
<i>Licania discolor</i> *	Chr	E	exocarp (M)	2.5	26.6	9.0	22.7	39.2	29.9	16.4	8.8	9.0
<i>Licania discolor</i> *	Chr	E	seed (M)	49.7	1.9	6.6	0.4	39.9	36.6	31.1	9.9	6.3
<i>Maprounea guianensis</i>	Eup	NE	seed (M)	41.7	3.3	16.4	10.5	28.1	23.1	14.2	1.1	0.0
<i>Maprounea guianensis</i>	Eup	NE	seed (l)	47.3	1.0	13.6	12.6	25.5	21.0	11.9	1.0	2.4
<i>Maytenus guianensis</i>	Cel	NE	leaves (M)	3.2	7.7	8.3	22.8	52.3	41.7	15.3	8.6	—
<i>Maytenus guianensis</i> *	Cel	E	leaves (Y)	2.6	13.4	12.8	30.6	35.2	25.9	13.7	15.9	—
<i>Morinda tenuiflora</i> *	Rub	E	drupe (M)	7.4	7.6	14.2	19.2	46.6	30.4	11.2	1.4	0.0
<i>Oryctanthus abveolatus</i> *	Lor	E	drupe (M)	38.3	3.4	9.6	28.8	19.9	10.5	6.5	2.4	4.9
<i>Ouratea guildingii</i>	Och	E	seed (l)	0.0	7.4	12.3	40.0	37.3	11.3	5.7	25.7	22.2
<i>Ouratea guildingii</i>	Och	NE	seed (M)	0.3	10.0	9.7	46.5	31.9	22.6	9.6	44.8	52.0
<i>Ouratea rotundifolia</i> *	Och	E	seed (M)	3.2	—	4.3	26.3	63.0	16.1	11.3	—	—
<i>Ouratea schomburgkii</i>	Och	NE	leaves (M)	0.3	—	9.9	23.2	62.7	58.3	38.0	9.5	15.3
<i>Peltogyne floribunda</i>	Cae	NE	seed (M)	0.6	5.9	7.9	29.8	54.2	47.6	25.5	8.0	25.3
<i>Peltogyne floribunda</i> *	Cae	E	seed (l)	2.7	11.1	6.6	52.8	24.2	9.9	5.8	6.8	10.1
<i>Piptadenia leucoxylon</i> *	Mim	E	seed (l)	3.2	—	25.6	36.0	31.5	22.0	8.0	3.9	5.5
<i>Pyrostegia dichotoma</i>	Big	E	flower	1.4	—	16.1	58.5	21.5	15.1	4.0	—	—
<i>Securidaca scandens</i> *	Polyga	E	seed (M)	47.6	—	13.8	16.5	20.6	15.4	—	0.0	0.0
<i>Solanum paludosum</i> *	Sol	E	seed (l)	18.3	10.1	10.7	4.5	53.6	38.2	20.5	0.3	0.0
<i>Strychnos fendleri</i>	Log	NE	seed (M)	5.6	5.8	7.0	17.3	62.3	24.8	4.2	0.0	0.0
<i>Strychnos mitscherlichii</i>	Log	NE	seed (M)	0.8	—	3.2	58.8	36.0	14.5	6.5	0.0	0.0
<i>Strychnos mitscherlichii</i> *	Log	E	mesocarp (M)	0.2	44.7	1.1	38.2	14.8	9.5	2.8	0.0	0.0
<i>Tabebuia serratifolia</i> *	Big	E	YL	1.6	—	24.5	20.9	48.6	22.3	6.1	—	—
<i>Talisia retusa</i>	Sapin	NE	seed (M)	1.8	—	5.5	48.1	43.1	3.8	1.0	1.3	44.4
<i>Talisia retusa</i> *	Sapin	E	mesocarp (M)	0.4	—	6.9	50.6	39.1	30.1	21.3	11.9	31.9
<i>Xylopia aromatica</i> *	Ann	E	seed (M)	2.2	—	10.8	20.0	65.0	53.3	27.6	14.0	13.2

* Ann = Annonaceae; Big = Bignoniaceae; Bor = Boraginaceae; Bur = Burseraceae; Cae = Caesalpinioideae (Leguminosae); Cap = Cappariaceae; Cel = Celastraceae; Chr = Chrysobalanaceae; Con = Connaraceae; Ery = Erythroxylaceae; Eup = Euphorbiaceae; Fla = Flacourtiaceae; Log = Loganiaceae; Lor = Loranthaceae; Mim = Mimosoideae (Leguminosae); Mor = Moraceae; Myr = Myrtaceae; Och = Ochmeaceae; Pas = Passifloraceae; Pap = Papilionoideae (Leguminosae); Polyga = Polygalaceae; Polygo = Polygonaceae; Rub = Rubiaceae; Rut = Rutaceae; Sapot = Sapotaceae; Sapin = Sapindaceae; Sol = Solanaceae.

flowers, and immature and mature drupes were uniformly low in lipids (<5% lipids DM).

Free simple sugars were 3 times higher in the only sample of fruit pulp (*Capparis muco*: 26.6% DM) than in young seeds ($\bar{X} = 13.2\% \pm 14.7\%$, $n = 13$). Pulp and seeds were ingested together in small drupes that were masticated whole. The FSS of these samples ($\bar{X} = 14.7\% \pm 10.3\%$, $n = 9$) is lower than pulp only, but higher than the average for young seeds only ($9.2 \pm 14.7\%$ DM, $n = 13$) (Table II).

Average crude protein (CP) values are >8% DM in all items ingested by the white-faced sakis. The highest crude protein values are for young seeds, young drupes and young leaves. CP is uniformly lower in mature seeds, drupes, and leaves.

Total nonstructural carbohydrates (TNC) are lowest (<16% DM) in immature drupes that were eaten and aril of *Connarus venezuelanus* and highest in the only sample of flowers with a sufficient sample (58.5% DM, $n = 1$) and mature drupes ($31.8\% \pm 19.5\%$, $n = 9$).

Neutral detergent fiber (total cell wall fiber = NDF) is lowest in flowers, aril and fruit pulp, and $\geq 40\%$ DM for all other items: seeds, drupes with seeds, and leaves. Acid detergent fiber (NDF minus hemicellulose) followed the same pattern. The ADF of seeds, drupes with seeds, and leaves are $\geq 23\%$ DM.

A few items tested had little or no evidence of CTs: aril of *Connarus venezuelanus*; immature pulp of *Capparis muco*. The highest CT values are in mature seeds (average $>11.0\% \pm 19.1\%$ QU, $n = 6$) and mature leaves (average $9.0\% \pm 2.2\%$ QU, $n = 4$). Total bioactive tannins are also highest in some mature seeds and leaves ($>18\%$ QU).

Comparison of Eaten and Not Eaten Plant Parts

White-faced sakis ingest many seeds from immature fruit. We have designated them immature, but they are usually full-sized seeds embedded in an immature fruit (Norconk *et al.*, 1998). If the sakis ingested pulp or aril, it was usually from mature fruit since these structures are undeveloped in immature fruit. If they ingested leaves, they were uniformly young ones. Thus, we had available a variety of combinations of eaten and not eaten plant parts from the same plant species—the not eaten specimens were often collected at the opposite stage of maturity or a different plant part than that ingested.

A comparison of all seeds, both from young ($n = 16$ spp) and mature ($n = 13$ spp) fruit and whether eaten or not eaten (Figs. 3 and 4), showed a significant difference only in %DM of crude protein. Young seeds were

Table II. Mean (\pm sd) chemical values of plant parts ingested by white-faced sakis. Values are expressed in %DM except for CT and RD that are expressed in % quebracho units (QU). Chemical abbreviations are the same as in Table I.¹ n = number of species sampled; ²eaten (y) or not eaten (n); ³im = immature; ⁴m = mature; ⁵y = young

Plant part	Eaten? ²	n ¹	Lipids	FSS	CP	TNC	NDF	ADF	CT	RD
aril	Y	1	64.2	4.0	12.6	15.4	3.8	2.5	0.4	0.0
im ³ drupe	Y	1	29.9	—	18.4	6.6	41.7	30.4	—	2.1
im drupe	N	1	1.1	8.6	7.5	39.1	43.7	28.7	2.9	16.3
m ⁴ drupe	Y	9	5.4 \pm 4.9	14.7 \pm 10.3	7.1 \pm 3.0	31.8 \pm 19.5	43.5 \pm 14.9	29.9 \pm 16.7	3.0 \pm 3.9	4.4 \pm 5.0
m drupe	N	1	2.6	7.5	9.1	23.4	53.5	39.0	3.8	3.9
m exocarp	Y	1	2.5	26.6	9.0	22.7	39.2	29.9	8.8	9.0
flowers	Y	1	1.4	—	16.1	58.5	21.5	15.1	—	—
y ⁵ leaves	Y	2	1.5	5.9	14.9	26.8	47.3	36.9	5.5	—
y leaves	N	2	2.1	8.5	14.5	19.0	48.7	33.0	8.0	—
m leaves	N	4	1.6 \pm 1.2	5.5 \pm 2.9	8.2 \pm 1.3	21.5 \pm 2.2	61.4 \pm 6.4	52.2 \pm 7.2	9.0 \pm 2.2	18.4 \pm 8.2
im pulp	N	1	0.0	15.2	17.7	26.2	37.3	11.6	0.0	—
m pulp	Y	3	1.2 \pm 1.6	33.1 \pm 16.5	8.9 \pm 9.0	42.7 \pm 6.8	21.9 \pm 14.9	16.0 \pm 12.3	4.2 \pm 6.7	10.6 \pm 18.4
y seeds	Y	13	13.2 \pm 14.7	9.2 \pm 7.8	16.8 \pm 6.7	22.7 \pm 15.3	39.9 \pm 15.4	23.3 \pm 14.7	5.6 \pm 8.3	8.7 \pm 7.4
m seeds	N	3	20.5 \pm 23.3	10.2 \pm 7.9	20.1 \pm 14.7	21.4 \pm 27.0	26.8 \pm 12.3	18.8 \pm 10.0	0.9 \pm 0.7	4.0 \pm 2.2
m seeds	Y	7	24.8 \pm 22.7	11.1 \pm 9.8	10.6 \pm 6.0	18.0 \pm 13.4	39.8 \pm 17.9	26.2 \pm 14.2	5.6 \pm 6.2	4.8 \pm 5.5
m seeds	N	6	8.5 \pm 16.4	6.3 \pm 2.8	8.3 \pm 4.5	35.2 \pm 19.0	42.6 \pm 13.4	22.7 \pm 14.5	11.0 \pm 19.1	20.3 \pm 23.9

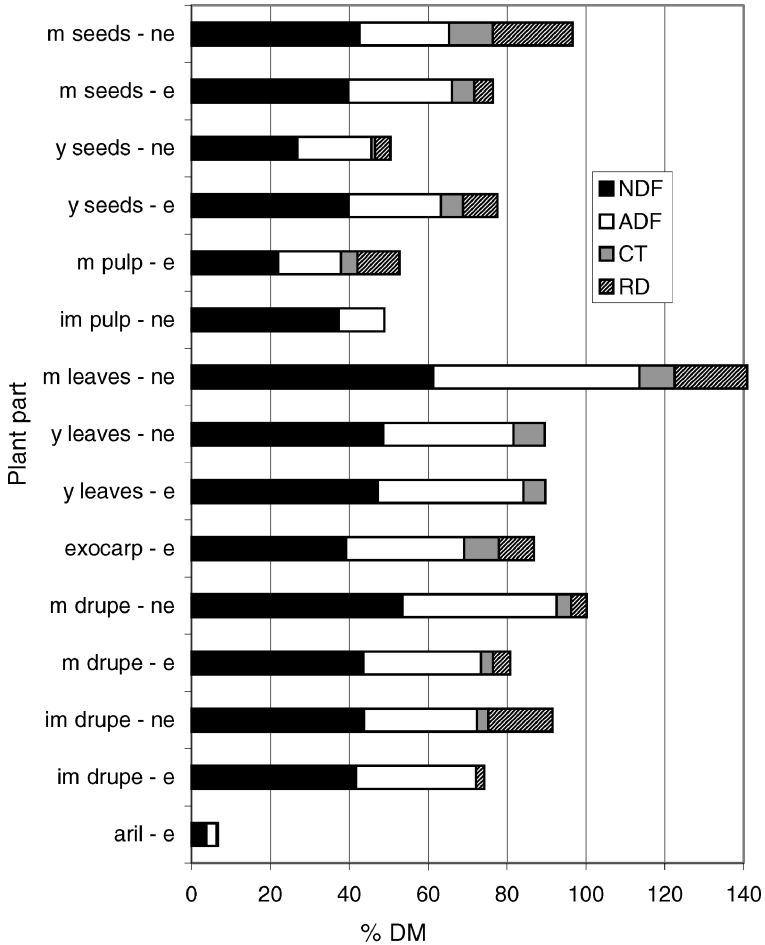


Fig. 4. Proportion of fiber and tannins in plant parts that were eaten (e) and not eaten (ne). The abbreviations used to describe the relative maturity of the plant parts are the same as in Fig. 3. NDF = neutral detergent fiber, ADF = acid detergent fiber, CT = condensed tannins, RD = radial diffusion (total tannins). CT & RD expressed as % QU.

higher in CP than mature seeds (Mann Whitney Test, $Z = 38.5$, $p < 0.01$). We found no difference in nutrient or deterrent properties of young seeds that were eaten and those that were not eaten. Mature seeds that were eaten ($n = 7$ spp) are higher in lipids than mature seeds that were not eaten ($n = 6$ spp) ($Z = 7.0$, $p = 0.05$) (Fig. 3). Thus, young seeds that were eaten by sakis could not be distinguished from young seeds that were not eaten by higher nutritional content or lower levels of NDF, ADF, or tannins, but the sakis

appeared to be more selective of the mature seeds they ingested. Although the sample sizes are small, mature seeds that are ingested are higher in lipids (24.8% vs. 8.5%) ($p < 0.05$) and FSS (11.1% vs. 6.3%) (ns), and lower in CT (5.6% vs. 11.0%) (ns) and RD (4.8% vs. 20.3%) (ns).

We found no significant difference in the average levels of tannin (CT and RD) values for plant parts eaten and not eaten (CT: Mann Whitney Test, $Z = -0.06$, ns, $n_1 = 7$ categories of uneaten parts; $n_2 = 7$ categories of eaten parts; RD: $Z = -1.22$, ns., $n_1 = 7$ categories of uneaten parts; $n_2 = 5$ categories of eaten parts: Table II). Some seeds that were eaten were $>10\%$ QU (e.g. *Angostura trifoliata*: Rutaceae; *Hirtella racemosa*: Chrysobalanaceae; and *Xylopia aromatica*: Annonaceae) (Table I).

Analysis of plant parts that are commonly included in the diets of many frugivores, i.e., fruit pulp and arils, showed that mature pulp is higher in FSS and TNC than immature pulp. Arils of *Connarus venezuelanus* are $>60\%$ lipids (Figs. 3 and 4).

Sakis ingested young leaves only ($n = 2$ spp analyzed), and they are higher in CP, and lower in NDF, ADF and CT than mature leaves are. However, many plant parts ingested by white-faced sakis are $>40\%$ NDF. They include immature and mature drupes and seeds from young and mature fruit (Fig. 4). There is no difference between young leaves that were eaten and young leaves that were not eaten, but the sample size is small (Figs. 3 and 4).

In summary, of the 3 major food sources used by white-faced sakis—seeds from young fruit, seeds from mature fruit, and mature drupes—young seeds are highest in crude protein, mature seeds are highest in tannins and lipids, and mature drupes are highest in FSS, TNC, and dietary fiber. The only significant difference is in CP levels in young seeds compared to mature seeds and mature drupes (Kruskal-Wallis $H = 12.9$, $df = 2$, $p < 0.01$). Since CT values ranged $>10\%$ QU and NDF values were often $>40\%$ DM for many plant parts ingested, the sakis did not avoid food items that are relatively high in tannins or total fiber.

Monthly and Seasonal Intake

We weighted the nutrient content of each resource by the time spent feeding during each month of the study. Then we added nutritional values of each resource together to estimate intake monthly (Fig. 3) and seasonally (Table III). The sample period for each month consists of 5 complete and contiguous days of sampling. Intake of lipids and TNC showed significant differences among months, but FSS and CP did not (Table IV). Among the antifeedants, we found a significant difference among months for NDF,

Table III. Seasonal and annual weighted averages for *Pithecia*. Seasons are 3-mo long each: early dry (Nov-Jan), late dry (Feb-Apr), early wet (May-Jul), and late wet (Aug-Oct). The nutrient fractions are weighted by total feeding time each month and grouped together to provide seasonal estimates of intake. DM = dry matter, QU = quebracho units (see Methods)

Season	CP*	FSS	Lipids	NDF	HC	Ls	Cs	TNC	Cutin	CT	RD
	% DM								% QU		
Early dry	7.75	4.00	21.65	40.76	16.81	16.83	11.26	23.52	8.50	5.66	5.49
Late dry	10.69	11.36	27.46	25.35	6.69	9.03	6.21	22.12	2.90	2.47	3.70
Early wet	12.64	7.77	21.65	29.97	10.61	8.91	10.14	24.26	1.70	2.21	7.62
Late wet	3.98	21.31	11.43	31.46	9.97	8.15	7.41	32.51	3.80	5.50	2.78

*CP = crude protein, FSS = free simple sugars, NDF = neutral detergent fiber, HC = hemicellulose; Ls = lignin, Cs = cellulose, TNC = soluble carbohydrates, CT = condensed tannins, RD = radial diffusion method of detecting bioactive tannins.

ADF, and hemicellulose, as well as both CT and RD, but not for lignin and cellulose.

Intake by season shows that the ingestion of lipid-rich resources, i.e., average lipid values >20% DM, peaked in the late dry and early wet seasons with the ingestion of young seeds from *Connarus venezuelanus* and *Actinostemon schomburgkii*. Lipid intake was low (11.4%) in the late wet season when FSS intake peaked with an increase in the ingestion of mesocarp or fruit pulp, e.g., *Capparis muco*, *Chiococca alba*, and *Morinda tenuiflora*. Intake of total fiber (NDF) was highest in the early dry season (36.4% to 44.2% DM). Leaf-eating increased in December (Fig. 1), an early dry season month, but the annual peak of leaf-eating was in April, late dry season, when intake of NDF was relatively low (29.3% DM). Therefore, high levels of NDF were not associated with leaf-eating. Instead, they corresponded to

Table IV. Monthly intake: average, standard deviation (Std). Wilcoxon signed rank Z scores are presented for each nutrient/antifeedant. The data were compared among months, n = 12. Two-tailed P values are reported for significant differences (≤ 0.05), otherwise the significance level is ns (not significant)

Nutrient/antifeedant	Mean	Std	Z score	Significance
Lipids	16.05	8.60	2.35	0.019
FSS	3.40	3.59	1.49	ns
TNC	20.54	17.83	2.59	0.010
CP	6.45	4.45	0.31	ns
NDF	38.40	10.53	3.06	0.002
ADF	22.38	6.86	3.06	0.002
Hemicellulose	11.02	4.48	2.59	0.010
Lignin	11.16	6.03	1.80	ns
Cellulose	7.96	4.06	1.33	ns
CT	3.29	2.92	2.67	0.008
RD	3.74	2.25	2.04	0.040

high intake of seeds from *Licania discolor* (22.3% of intake) and *Ouratea roraimae* (12.6% intake) (Table I: NDF values). Cutin levels also peaked in the early dry season, which was not unexpected given the marked seasonality of the forest.

Multiple Regression of Feeding Time and Nutrients

In order to examine feeding selectivity, we calculated percent feeding time of 31 resources ingested in 1991-2 and chose 6 relatively correlation-free chemicals that could be examined relative to feeding time. The 31 resources represented 81% of the annual saki diet, and were chosen for the relative completeness of their nutritional data (Table I). The 6 chemicals analyzed are lipids, CP and FSS, hemicellulose, lignin, and condensed tannins. Using data from the intake sample, lipids \times FSS, and lipids \times CP are not correlated ($\rho = 0.52$, ns, & 0.48 , ns, respectively). The CP \times FSS are significantly correlated ($\rho = 0.69$, $p < 0.05$). Since the fiber fractions are all strongly correlated with each other, both in terms of extraction method and biology, we chose one fiber fraction, hemicellulose, that may be partially digestible by sakis and lignin because it is completely indigestible. We chose condensed tannins (CT) because in high levels it is likely to be a deterrent. It is not correlated with any of the other 5 variables.

We log transformed percent feeding time and used it as the dependent variable with the 6 chemicals as independent variables in the multiple regression equation using the backward elimination method (Norušis, 1993). There were some missing values that were based on the size of dried sample. Missing values (3 for lipids, 2 for CP, 14 for FSS, 0 for hemicellulose, 2 for lignin, and 9 for CT) were treated via the pairwise missing-value approach in the multiple regression equation. The probability of F-to-remove the variable was 0.10. The variable with the smallest partial correlation coefficient to feeding time was removed first: FSS. This was followed sequentially by CP, then lignin, then CT, and then hemicellulose (Table V). The lipid variable was the last one to be removed and the most strongly correlated with feeding time ($F = 11.5$, $p = 0.007$). The 6 variables combined explained $>80\%$ of the variance in feeding time ($R^2 = .824$). Lipids alone explained *ca.* 50% of the variance ($R^2 = .535$).

In the process of examining the multiple regressions, we found several correlations among the independent variables in the sample. The FSS and lipids are negatively correlated (Pearson $R = -0.51$, $p = 0.046$, one-tailed probability, $n = 12$), as are FSS and CT ($R = -0.594$, $p = 0.21$, one-tailed probability, $n = 12$). Lignin is positively correlated with CT ($R = 0.691$, $p = 0.006$, $n = 12$) and weakly correlated with lipids ($R = 0.473$, $p = 0.06$, one-tailed probability, $n = 12$).

Table V. Multiple regressions: % feeding time on each plant species (log transformed dependent variable) on 6 nutrients/deterrents, the independent variables: lipids, crude protein (CP), free simple sugars (FSS), hemicellulose (Hc), condensed tannins (CT), and lignin (Ls). The independent variables were eliminated in a backward elimination so that the variable least correlated with feeding time was eliminated first

Regression model	Sum of squares	df	Mean square	F	Sig.
CT, CP, Hc, Lipids, FSS, Ls	7.043	6	1.174	3.902	0.078
CT, CP, Hc, Lipids, Ls	6.991	5	1.398	5.393	0.032
CT, Hc, Lipids, Ls	6.786	4	1.696	6.744	0.015
CT, Hc, Lipids	6.084	3	2.028	6.589	0.015
Hc, Lipids	5.179	2	2.589	6.919	0.015
Lipids	4.574	1	4.574	11.513	0.007

DISCUSSION

Milton (1993) characterized the diets of primate frugivores as being low in protein (compared those to insectivores and folivores), highest in accessible calories (FSS and total non-structural carbohydrates), moderate in dietary fiber and low in chemical defenses. Kay (in Tattersall *et al.*, 1988) projected a similar nutritional profile for frugivores with the addition that lipid intake depended on seed ingestion. White-faced sakis ingested a wide variety of fruit resources: seeds of mature and immature fruit; whole drupes; pulp and aril, young leaves and insects, but most of the plant items in their diet each month could be classified as fruit. Despite the relative homogeneity that might be expected in a diet that is mostly fruit, it was nutritionally quite variable. While there is little variation in crude protein, free simple sugars, and the two tannin measurements (CT and RD) in the month-to-month intake (Table IV and Fig. 5), more variation occurs in lipids, TNCs and total fiber. Plant parts that are high in lipids are mostly seeds, though arils of *Connarus venezuelanus* surpassed all seed lipid values (Table I).

Nevertheless, Milton (1993) and Kay (in Tattersall *et al.*, 1988) were mostly correct in their broad-stroke attempt to characterize frugivore nutrition. Crude protein values for the white-faced saki diets are $\frac{1}{2}$ – $\frac{1}{4}$ that reported for a sample of colobines, but ADF intake for the sakis is close to the lower level reported for them (*Colobus guereza*, 25.2% DM: Waterman and Kool, 1994:272; they did not report NDF values). The CT intake by the sakis is within the range of variation reported for colobines (0.1% QU to 9.4% QU) (Waterman and Kool, 1994). Thus ADF and CT intake is relatively high for sakis that weigh only 1.5 to 2.0 kg compared to larger-bodied colobines (minimum biomass = 5 kg: Oates *et al.*, 1994).

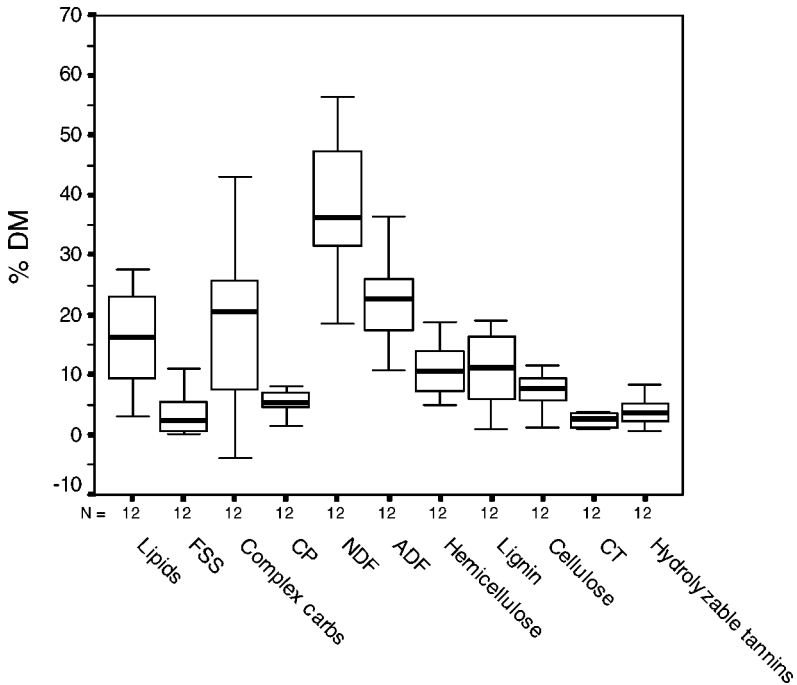


Fig. 5. Intermonthly comparison of food intake weighted by time spent feeding. Each box plot exhibits the median and 25th to 75th interquartile range. The range is indicated by vertical lines. FSS = free simple sugars, Complex carbs = total non-structural carbohydrates, CP = crude protein, NDF = neutral detergent fiber; ADF = acid detergent fiber, CT = condensed tannins (% QU).

White-faced saki lipid intake was *ca.* 4 times higher, CP was 2–3 times lower, and total fiber was slightly higher compared with the nutritional values for other frugivores, e.g. red-tailed monkeys: *Cercopithecus ascanius* (Conklin-Brittain *et al.*, 1998). Of the fiber fractions, lignin intake by the sakis is higher than any of the catarrhines sampled by Conklin-Brittain *et al.* (1998), and lignin in our study correlates positively with lipids. If sakis select for lipids as our data suggest, then the resources that they had available to them on Isla Redonda are also low in FSS.

Returning to the presumption that frugivores avoid foods that are relatively high in dietary fiber or condensed tannins, the ability to ignore or even utilize food items that are relatively high in fiber can be explained in part by their relatively long transit time (14–15 h) and mean retention time (25.6 h: Norconk *et al.*, 2002). Digesta transit time estimates are comparable to those of several cercopithecines (Maisels, 1993; Lambert, 1998, 2002).

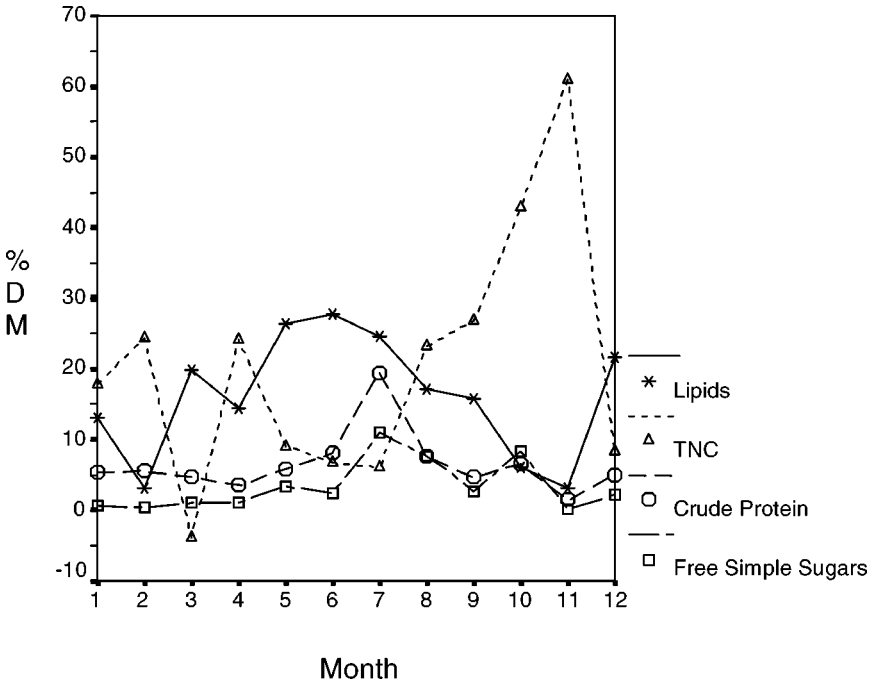


Fig. 6. Variation in the intake of the 4 macronutrients by month: lipids; total non-structural carbohydrates (TNC); crude protein; and, free simple sugars. Months are indicated numerically beginning with January = 1, February = 2, etc.

Relatively long retention time may allow at least partial digestion of cellulose and hemicellulose (classified as Class 2 forage components: variable digestibility depending on degree of binding to lignin which is indigestible, Class 3: van Soest, 1994). In the multiple regressions of feeding time on 6 nutrient/deterrent variables, FSS, CP, and lignin were excluded before CT. Not much of a deterrent and some highly ranked foods are also high in CT values (Table I).

Intake of crude protein is low in sakis relative to that of colobines that ingest significant quantities of leaves, though the CP averages reported by Conklin-Brittain *et al.* (1998) for 3 species of catarrhine monkeys and chimpanzees is more than twice that of white-faced sakis. With the exception of young leaves of *Tabebuia serratifolia*, intake of leaves by the sakis was haphazard, grabbing and ingesting a leaf here and there as they moved through the forest. Leaves made up only 5.7% of the white-faced saki diet in the annual cycle, but we suspect there is wide interannual variation in CP intake due to the variability in insect availability. For example, grasshoppers

(*Tropidacris* sp.: Orthoptera) were not present on the island during the 1991–1992 sample period, but appeared in large numbers in the dry season of 1995. They are very high in CP (58% DM, Norconk and Conklin-Brittain, unpubl), but due to the intermittent availability and perhaps unpredictability it is likely that white-faced sakis depend on resources that are quite low in CP (Fig. 6). Some seeds were >20% CP, e.g. young *Actinostemon schomburgkii* and *Alibertia latifolia* seeds (Table I), and the pulp of one fruit was 18.7% CP (*Capparis muco*), but monthly weighted averages suggest that much of their intake of CP is relatively low. Thus, white-faced saki diets that are predominantly seeds are not necessarily very high in CP, unlike diets of catarrhine seed predators, i.e. black colobus and geladas (Waterman, 1984).

Kinzey and Norconk (1993) suggested that white-faced sakis may accept a trade-off for food items that are high in antifeedants if they are also high in nutrients. Specifically, Kinzey and Norconk (1993) proposed that white-faced sakis might be willing to ingest relatively astringent foods (high CT values) if the foods were also high in fat. Reynolds *et al.* (1998) proposed that a similar trade-off existed for chimpanzees; figs that are high in sugars are also high in tannins. They found no difference between eaten and not eaten foods based on CT values, but they found significant differences in the sugar content (sucrose, fructose, and glucose) of the two kinds of foods. We found that lipids explain >50% of the variance in percent feeding time, suggesting that sakis pay a lot of attention to lipids, even when lipids are negatively correlated with FSS and positively correlated with lignin.

Even though intake of FSS was low for frugivores, white-faced sakis might use FSS to gauge levels of CP and lipids (correlated in the intake sample, but not the total sample) and tannins as a cue to gauge levels of NDF (NDF and CT are positively correlated and NDF and RD show a strong positive trend ($p = 0.06$) in the intake sample, but not the total sample). There may also be a general trend with regard to fruit ripening, e.g. correlations between FSS and fiber levels. In both our study and that of Remis *et al.* (2001: lowland gorillas), there are significant (or nearly significant) negative correlations between FSS and both NDF and ADF in fruit.

We calculated the crude protein values as %N \times 6.25 because we believe that the 4.3 conversion factor is an overly severe correction (Conklin-Brittain *et al.*, 1999). While the 4.3 conversion factor reflects how much true protein is present, it does not measure any of the nonprotein nitrogen (NPN) present. Although the ability of simple-stomached animals to utilize NPN has not been thoroughly studied, humans can incorporate some NPN sources into their body proteins (Rikimaru *et al.*, 1985). We recommend instead, if more exact measures of protein are required, that the acid-detergent insoluble-N be determined and subtracted from the total N present (Conklin-Brittain *et al.*, 1999). However, that requires larger food sample sizes and more money

to perform the additional correction analyses. The adoption of 4.3 as a conversion factor is not urgent, since we still do not know the extent to which NPN can be utilized by our study species.

We are confident that we have described the diet of white-faced sakis living in a tropical dry forest in eastern Venezuela, however this study begs for comparative data. Our subjects are at the far western edge of the distribution of the species and, while a variety of habitats are tolerated by white-faced sakis, many populations in the Guyanas inhabit wetter habitats. It remains to be seen whether we have described species-specific or habitat-specific patterns of food intake. Nevertheless, two general conclusions can be made. What we found nutritionally is not surprising for animals specializing on seeds, regardless of why they are specializing on seeds, and seed-eaters give a very different nutrient profile from those of pulp-eaters.

ACKNOWLEDGMENTS

We are grateful to EDELCA (Electrificación del Caroní) for permission to work in Lago Guri and particularly to Estudios Básicos-Guri and Luis Balbás, Martín Lubín, and Quique Pacheco for their logistical support. The study has been supported by NSF (BNS 90-20614 to W. G. Kinzey and M. A. Norconk and BCS 98-07516 to M. A. Norconk), Wenner Gren Foundation for Anthropological Research, and Research and Graduate Studies at Kent State University. We are grateful to Joanna Lambert and two anonymous reviewers for their constructive comments.

REFERENCES

- Altmann, S. A. (1998). *Foraging for Survival: Yearling Baboons in Africa*, University of Chicago Press, Chicago, IL, 609 pp.
- Altmann, S. A., Post, D. G., and Klein, D. F. (1987). Nutrients and toxins of plants in Amboseli, Kenya. *Afr. J. Ecol.* 25: 279–293.
- Alvarez, E., Balbás, L., Massa, I., and Pacheco, J. (1986). Aspectos ecológicos del Embalse Guri. *Interciencia* 11: 325–333.
- Anapol, F., and Lee, S. (1994). Morphological adaptation to diet in platyrrhine primates. *Am. J. Phys. Anth.* 94: 239–262.
- AOAC (1984). In Whilliams, S. (ed.), *Official Methods of Analysis of the Association of Official Analytical Chemists*. Association of Official Analytical Chemists, Arlington, VA.
- Aymard, G., and Gouzález, V. (2003). A new species of *Acosmium* (Leguminosae: Papilionoideae, Sophovlae). *Harvard Papers in Botany* 7: 399–402.
- Aymard, G., Norconk, M., and Kinzey, W. (1997). Composición florística de comunidades vegetales en islas en el Embalse de Guri, Río Caroní, Estado Bolívar, Venezuela. *BioLlania Edición Especial*. 6: 195–233.
- Baranga, D. (1983). Changes in chemical composition of food parts in the diet of Colobus monkeys. *Ecology* 64: 668–673.
- Bate-Smith, E. (1975). Phytochemistry of proanthocyanidins. *Phytochemistry* 14: 1107–1113.

- Bell, E. A. (1978). Toxins in seeds. In Harborne, J. B. (ed.), *Biochemical Aspects of Plant and Animal Coevolution*, Academic Press, London, pp. 143–161.
- Bremer, B., and Eriksson, O. (1992). Evolution of fruit characters and dispersal modes in the tropical family Rubiaceae. *Biol. J. Linn. Soc.* 47: 79–95.
- Buchanan, D. B., Mittermeier, R. A., and van Roosmalen, M. G. M. (1981). The saki monkeys (genus *Pithecia*). In Coimbra-Filho, A. F., and Mittermeier, R. A. (eds.), *Ecology and Behavior of Neotropical Primates*, Vol. 1, Academia Brasileira de Ciências, Rio de Janeiro, pp. 391–417.
- Calvert, J.J. (1985). Food selection by western gorillas (*G.g.gorilla*) in relation to food chemistry. *Oecologia* 65: 236–246.
- Conklin-Brittain, N. L., Wrangham, R. W., and Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int. J. Primatol.* 19: 971–998.
- Conklin-Brittain, N. L., Dierenfeld, E. S., Wrangham, R. W., Norconk, M., and Silver, S. C. (1999). Chemical protein analysis: A comparison of Keldahl crude protein and total ninhydrin protein from wild, tropical vegetation. *J. Chem. Ecol.* 25: 2601–2622.
- Davies, A. G., Bennett, E. L., and Waterman, P. G. (1988). Food selection by two south-east Asian colobine monkeys (*Presbytis rubiunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 34: 33–56.
- Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A., and Smith F. (1956). Colorimetric method for determination of sugar and related substances. *Anal. Chem.* 28: 350–356.
- Fleagle, J. G. (1998). *Primate Adaptation and Evolution*, 2nd edn, Academic Press, New York, 596 pp.
- Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketweiler, P., Mougazi, A., Roussillon, C., Thiollay, J.-M. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* (Berlin) 65: 324–337.
- Gentry, A. H. (1993). *A field guide to the families and genera of woody plants of Northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa*, The University of Chicago Press, 895 pp.
- Goering, H. K., and van Soest, P. J. (1970). Forage fiber analysis. *Agricultural Handbook No. 379*, Agricultural Research Service, U.S. Dept. of Agriculture.
- Hagerman, A. E. (1987). Radial diffusion method of determining tannin in plant extracts. *J. Chem. Ecol.* 13: 437–449.
- HersHKovitz, P. (1987). The taxonomy of South American sakis, genus *Pithecia* (Cebidae, Platyrrhini): A preliminary report and critical review with the description of a new species and a new subspecies. *Am. J. Primatol.* 12: 387–468.
- Homburg, I. (1997). Ökologie und sozialverhalten einer gruppe von weissgesicht-sakis (*Pithecia pithecia pithecia* Linnaeus 1766) im Estado Bolívar, Venezuela, Unpublished Dissertation, Universität Bielefeld, Germany.
- Huber, O. (1986). La vegetación de la cuenca del Rio Caroní. *Interiencia* 11: 301–310.
- Janson, C. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219: 187–189.
- Jolly, A. (1985). *The Evolution of Primate Behavior*, 2nd edn, Macmillan Publishing Company, New York, 526 pp.
- Jordano, P. (1992). Fruits and frugivory. In Fenner, M. (ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. C.A.B. International, pp. 105–155.
- Kay, R. F. (1988). Diet. In Tattersall, I., Delson, I., and Van Couvering, J., *Encyclopedia of Human Evolution and Prehistory*. Garland Publishing, New York, pp. 155–179.
- Kinzey, W. G., and Norconk, M. A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *Am. J. Phys. Anthropol.* 81: 5–15.
- Kinzey, W. G., and Norconk, M. A. (1993). Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int. J. Primatol.* 14: 207–227.

- Knott, C. D. (1999). *Reproductive, Physiological and Behavioral Responses of Orangutans in Borneo to Fluctuations in Food Availability*. PhD Thesis, Harvard University, Cambridge, MA.
- Lambert, J. E. (1998). Primate digestion: Interactions among anatomy, physiology, and feeding ecology. *Evol. Anthropol.* 7: 8–20.
- Lambert, J. E. (2002). Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). *Int. J. Primatol.* 23: 1169–1185.
- Langer, P., and Chivers, D. J. (1994). Classification of foods for comparative analysis of the gastro-intestinal tract. In Chivers, D. J., and Langer, P. (eds), *The Digestive System in Mammals*, Cambridge University Press, pp. 74–86.
- Lucas, P. W., Turner, I. M., Dominy, N. J., Yamashita, N. (2000). Mechanical defences to herbivory. *Ann. Bot.* 86: 913–920.
- Maisels, F. (1993). Gut passage rate in guenons and mangabeys: another indicator of a flexible dietary niche? *Folia Primatol.* 61: 35–37.
- McKey, D. (1974). Adaptive patterns in alkaloid physiology. *Amer. Nat.* 108: 305–320.
- Milton, K. (1993). Diet and primate evolution. *Sci. Amer.* August, 1993: 86–93.
- National Research Council (2003). Carbohydrates and fiber. In Committee on Animal Nutrition (eds.), *Nutrient Requirements of Nonhuman Primates*, 2nd rev. edn, National Academies Press, Washington D.C, Chap. 3, pp. 58–74.
- Norconk, M. A. (1996). Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In Norconk, M. A., Rosenberger, A. L., and Garber, P.A. (eds.), *Adaptive Radiations of Neotropical Primates*, Plenum Press, New York, pp. 403–423.
- Norconk, M. A., Conklin-Brittain, N. L. (2000). Methods for assessing nutrient intake in wild primates: temporal- vs. weight-based estimates. *Am. J. Phys. Anthropol.* Suppl. 32: 113–114.
- Norconk, M. A., and Grafton, B. W. (2002). Changes in forest composition and potential feeding tree availability on a small land-bridge island in Lago Guri, Venezuela. In Marsh, L. M. (ed.), *Primates in Fragments*, Kluwer Academic/Plenum Publishers, New York.
- Norconk, M. A., Grafton, B. W., and Conklin-Brittain, N. L. (1998). Seed dispersal by neotropical seed predators. *Am. J. Primatol.* 45: 103–126.
- Norconk, M. A., Oftedal, O., Power, M., Jakubasz, M., and Savage, A. (2002). Digesta passage and fiber digestibility in captive white-faced sakis, *Pithecia pithecia*. *Am. J. Primatol.* 58: 23–34.
- Norusis, M. J. (1993). *SPSS® for Windows™ Base System User's Guide*, Release 6.0. SPSS, Inc. Chicago, 828 pp.
- Oates, J. F., Waterman, P. G., and Choo, G. M. (1980). Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45: 45–56.
- Parolin, P. (1992). *Characterization and Classification of the Vegetation in an Island of Lake Guri, Venezuelale*. Unpublished MA Thesis, University of Bielefeld, Germany, March, 1992.
- Pierce, W., and Haenisch, E. L. (1948). *Quantitative Analysis*, 3rd edn, John Wiley & Sons, New York.
- Porter, L., Hrstich, L. M., and Chan, B. G. (1986). The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. *Phytochemistry* 25: 223–230.
- Remis, M. J., Dierenfeld, E. S., Mowry, C. B., and Carroll, R. W. (2001). Nutritional aspects of western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic. *Int. J. Primatol.* 22: 807–836.
- Reynolds, V., Plumtre, A. J., Greenham, J., and Harborne, J. (1998). Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Oecologia* 115: 331–336.
- Rikimaru, T., Fujita, Y., Okuda, T., Kajiwara, N., Date, C., Heywood, P. F., Alpers, M. P., and Koishi, H. (1985). Utilization of urea nitrogen in Papua New Guinea highlanders. *J. Nutr. Sci. Vitam.* 31: 393–402.
- Robertson, J., and Van Soest, P. J. (1980). The detergent system of analysis and its application to human foods. In James, W.P.T., Theander, O. (eds.), *The Analysis of Dietary Fiber in Food*, Marcel Dekker, New York, Chap. 8, pp. 123–158.

- Strickland, J., Parsons, T. R. (1972). *A Practical Handbook of Seawater Analysis, Bulletin 167*, 2nd edn, Fisheries Research Board of Canada, Ottawa.
- Strier, K. B. (2003). *Primate Behavioral Ecology*. 2nd edn, Allyn and Bacon, Boston, 422 pp.
- Tattersall, I., Delson, E., and Van Couvering, J. (1988). *Encyclopedia of Human Evolution and Prehistory*. Garland Publishing, New York.
- Terborgh, J., Lopez, L., Tello J., Yu, D., and Bruni A. R. (1997). Transitory states in relaxing ecosystems of land bridge islands. In Laurance, W. F., and Bierregaard, R. O. (eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, Chicago University Press, Chicago, pp. 256–274.
- van Roosmalen, M. G. M., Mittermeier, R. A., Fleagle, J. G. (1988). Diet of the northern bearded saki (*Chiropotes satanas chiropotes*): a neotropical seed predator. *Am. J. Primatol.* 14(1): 11–35.
- Van Soest, P. (1994). *Nutritional Ecology of the Ruminant*, 2nd edn, Comstock Publishing Associates, Cornell University Press, Ithaca, NY.
- Vié, J.-C., Richard-Hansen, C., Fournier-Chambrillon, C. (2001). Abundance, use of space, and activity patterns of white-faced sakis (*Pithecia pithecia*) in French Guiana. *Am. J. Primatol.* 55: 203–221.
- Waterman, P. (1984). Food acquisition and processing as a function of plant chemistry. In Chivers, D. J., Wood, B. A., and Bilsborough, A. (eds.), *Food Acquisition and Processing in Primates*, Plenum, New York, pp. 177–211.
- Waterman, P. G., and Kool, K. M. (1994). Colobine food selection and plant chemistry. In Davies, A. G., and Oates, J. F. (eds.), *Colobine Monkeys: Their Ecology, Behaviour, and Evolution*, Clarendon Press, Oxford, pp. 251–284.
- Willson, M. F., and Whelan, C. J. (1990). The evolution of fruit color in fleshy-fruited plants. *Am. Nat.* 136: 790–809.