

Digesta Passage and Fiber Digestibility in Captive White-Faced Sakis (*Pithecia pithecia*)

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Wild white-faced sakis (*Pithecia pithecia*) ingest primarily seeds that provide a diet that is lipid-rich and moderately high in dietary fiber. Although little anatomical information is available on sakis, evidence from other vertebrate seed predators suggests that such a diet is correlated with adaptations in gut morphology or physiology. Milton [1984] reported a 20 hr transit time (TT = transit time or time of first appearance in feces) of a particulate marker for a single monk saki (*Pithecia monachus*). This suggests that TT for *Pithecia* sakis may be four to five times longer than what has been reported for soft-fruit-eating platyrrhines, such as *Ateles* and *Cebus*. During a captive study, we calculated an average TT of 14.7 ± 0.4 hr ($n = 5$ trials started in the evening) for a chromic oxide (Cr_2O_3) marker that follows liquid digesta and TTs of 14.5 hr (trial started the previous evening) and 23.0 hr (trial started the previous morning) for two trials using particulate markers. Mean retention time (MRT) for the liquid marker ranged from 15.3 hr to 37.7 hr in four trials that lasted longer than 90 hr. Marker recovery was incomplete for the particulate markers in these trials, and thus MRT could only be determined for the liquid phase marker. Three 5-day trials on a low-fiber, blended diet revealed high fiber fraction digestibilities (neutral detergent fiber (NDF) = 77.4% and acid detergent fiber (ADF) = 74.4%). Data collected for this study and nutritional data from wild sakis suggest that pitheciin seed predators may have a potential for fiber digestibility that is intermediate between ripe-pulp frugivores and folivores. Am. J. Primatol. 58:23–34, 2002. © 2002 Wiley-Liss, Inc.

Key words: transit time (TT); mean retention time (MRT); seed predator; neutral detergent fiber; acid detergent fiber; chromic oxide (Cr_2O_3); particulate marker; *Chiropotes*; *Cacajao*

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INTRODUCTION

Seed predators face a variety of challenges. Many seeds are protected by hard outer coatings that require removal by teeth or hands prior to seed ingestion [Bodmer, 1991; Davies, 1991; Kinzey and Norconk, 1993; Hemmingway, 1996]. Seeds may be further protected by high levels of cell wall constituents and plant secondary compounds (seed toxins) that deter or impair ingestion or digestion. Nevertheless, the high concentrations of lipids, proteins, and/or other nutrients (such as phosphorous) invested by some plants in their seeds may make seeds a particularly valuable resource for primates [e.g., Whiten et al., 1991; Kinzey & Norconk, 1993; Dierenfeld & McCann, 1999; Flaschka, 2001].

The dental morphology of pitheciins is well adapted to extraction and mastication of seeds [Kinzey, 1992; Rosenberger, 1992; Lucas & Teaford, 1994], and the few existing studies of gut anatomy of pitheciins suggest some enlargement of the hindgut [Hill, 1960; Fooden, 1964; Chivers & Hladik, 1980] (compare with Ferrari and Lopes [1994]). Seeds eaten by pitheciins are relatively high in dietary fiber fractions [Kinzey & Norconk, 1993] (Table I), with the consequence that the average fiber concentrations of the natural diet of white-faced sakis is apparently higher than that of many cercopithecines, although lower than that of colobines and *Alouatta*.

High-fiber diets typically require fermentation and prolonged retention of digesta to be effectively utilized [van Soest, 1994]. Using plastic markers, Milton [1984] reported a 20 hr TT for *Pithecia monachus*, but a TT of only 5 hr for closely related pitheciins, *Cacajao calvus* and *Chiropotes albinasus*. According to Milton [1984:265], “(i)f future work confirms that long retention time is characteristic of the genus, *Pithecia* would appear to have a digestive strategy considerably different than those of the other members of the Pitheciinae or the *Cebus*

TABLE I. Weighted Average Fiber Concentrations of Neutral Detergent Fiber (NDF) and Acid Detergent Fiber (ADF) in Some Wild Primate Diets, Ranked by ADF Values*

Primate species	Diet	NDF	ADF	Reference
<i>Chiropotes satanas</i>	Mixed ^a	26.4 ± 7.2	11.6 ± 4.9 ^c	Norconk and Conklin-Brittain, unpublished
<i>Cercopithecus ascanius</i>	Mixed	31.3 ± 4.0	19.7 ± 3.3	Conklin-Brittain et al. [1998]
<i>Lophocebus albigena</i>	Mixed	32.0 ± 3.3	19.8 ± 2.0	Conklin-Brittain et al. [1998]
<i>Cercopithecus mitis</i>	Mixed	32.3 ± 2.9	20.2 ± 2.2	Conklin-Brittain et al. [1998]
<i>Pan troglodytes</i>	Mixed	33.6 ± 4.5	19.6 ± 5.8	Conklin-Brittain et al. [1998]
<i>Pithecia pithecia</i>	Mixed	38.4 ± 10.5	22.4 ± 6.9	Norconk and Conklin-Brittain, unpublished
<i>Colobus guereza</i>	Leaves ^b	NA	25.2 ^d	Oates [1977]
<i>Trachypithecus johnii</i>	Leaves	NA	30.3 ^d	Oates et al. [1980]
<i>Procolobus badius</i>	Leaves	NA	32.7 ^d	Struhsaker [1975]
<i>Alouatta seniculus</i>	Mixed	56.0	37.6	Crissey et al. [1991]

*Values are expressed as a percentage of the total dry matter. The two saki species are in bold-faced type.

NA, data not available.

^aA mixed diet included fruit, leaves, and seeds.

^bLeaves of all ages.

^cNorconk and Conklin-Brittain, unpublished and Conklin-Brittain et al. [1998] are weighted averages (percentage of feeding time) of 12 mo samples.

^dThe colobine samples were compiled by Waterman and Kool [1994:272] as “weighted intake levels” using feeding records as the weighting function.

species.” We sought to evaluate this hypothesis by measuring digesta passage in white-faced sakis (*P. pithecia*) using liquid and particulate markers. We also conducted digestion trials to obtain preliminary information on fiber utilization in this species.

METHODS

Digesta Passage Trials

Six trials were conducted on four captive white-faced sakis (*Pithecia pithecia*) at Roger Williams Park Zoo, Providence, RI, to monitor digesta passage (Table II). Since Milton [1984] found that no particulate markers were excreted in the first 8 hr post-morning ingestion by *Pithecia monachus*, we started all but one trial in the evening. Three males and one female were off-exhibit. One male was housed alone; the other sakis were housed in social groups. The sakis were fed a mixed diet of vegetables, nuts, commercial primate diets, and vitamin supplements twice a day, at approximately 0830 and 1330 hr (diet sample #1 [Frampton, 2000]). Water was available ad libitum. All individuals eliminated well-formed fecal pellets typical of wild sakis (Norconk, personal observation) before and during the trials. There was no evidence of illness that would have adversely affected digestive function. The sakis had been trained by zoo personnel to stand voluntarily on an electronic bench scale placed in their home cages. They did so readily in exchange for small quantities of food. Weights obtained before and after the study indicated that body mass did not change during the study.

Digesta passage was evaluated by two markers: 2-mm polyethylene beads and chromic oxide (Cr_2O_3). A pulse dose of Cr_2O_3 was given in each trial and was calculated as approximately 2% of the estimated dry weight of the substrate in which it was mixed (either Zupreem® canned primate diet and/or yogurt). Our

TABLE II. Transit Time and Mean Retention Time of the Liquid Phase Marker (Chromic Oxide, Cr_2O_3) and the Particulate Marker (Beads)*

Subject and trial no.	Age (y) and body mass (kg)	Time of marker administration/ duration of collection (hr) and marker dose	TT Cr_2O_3 (hr)	TT beads (hr)	MRT Cr_2O_3 (hr)
Male 1, trial 1	4.6 y 1.83 kg	08:45/128 h 0.6 g Cr_2O_3 +100 beads	5.0	23.0	26.2
Male 1, trial 2	—	17:30/166 h 1.7 g Cr_2O_3	15.0	NA	15.3
Male 2, trial 3	8.0 y 1.86 kg	17:00/111 h 0.3 g Cr_2O_3	15.0	NA	37.7
Male 2, trial 4	—	17:20/92 h 0.3 g Cr_2O_3	14.0	NA	23.3
Male 3, trial 5	1.2 y 1.52 kg	17:20/41 h 0.3 g Cr_2O_3 +50 beads	14.5	14.5	NA
Female 1, trial 6	8.0 y 1.64 kg	17:00/65 h 0.3 g Cr_2O_3	15.0	NA	NA

*A pulse dose of chromic oxide (approximately 2% of the estimated dry weight of the substrate, either yogurt or Zupreem) was given in each trial with the exception of trial 2 in which the dose was 2% of the wet weight of the substrate. Trials of female 1 and male 3 (socially housed individuals) were discontinued once visual detection of the marker became unreliable.

intent was that the beads would indicate passage of large particles, while the Cr_2O_3 would indicate fluid passage. Polyethylene beads and Cr_2O_3 were given as a pulse dose in two trials (trials 1 and 5; see Table II). Unfortunately, the sakis destroyed some beads by mastication, and spat out other beads, such that the number of beads consumed could not be determined with accuracy. Therefore, the beads were only used to estimate transit time (TT or time to first appearance in feces), whereas Cr_2O_3 was used both for TT and estimates of mean retention time (MRT). In the four remaining trials that included only the liquid marker, a pulse dose of Cr_2O_3 (see above) was given to each individual in yogurt.

Feces were collected hourly for 40 hr post-ingestion (depending on whether the subject defecated during that hour, and excluding the sleep period during which the monkeys did not defecate) and approximately every 4 hr thereafter (depending on positive identification of the subject and feces). Collection periods lasted a maximum of 166 hr. For example, in trial 1, a pulse dose of dye and beads was given at 0845 hr on 4 July 95. Feces were collected until 1715 hr on 8 July 95, 123 hr after administration of the marker and more than 24 hr after the disappearance of color. The liquid marker for trial 2 was given at 1730 hr on 8 July 95, and feces were collected until 12 July 95 at 1140 hr (90 hr). A final sample was collected on 15 July 95 (166 hr) to detect any residual chromium by atomic absorption. Likewise, in trial 3 (male 2) a pulse dose of chromium was given at 1700 hr on 5 July 95, and feces were collected until 0800 hr on 10 July 95. Trial 4 began at 1720 hr on 17 July 95 and ended at 1430 hr on 21 July 95. The green color of feces, attributable to Cr_2O_3 , was undetectable an average of 40.5 hr post-marker ingestion ($n = 4$ trials started at the same time of day). The dye was still visible at 46 hr in trial 6. For subjects that were housed in social units, difficulty identifying the source of feces dictated that feces could only be collected when the act of defecation was observed. The floors of the enclosures were cleaned of all feces before lights were turned off, and no feces were found in the enclosures when lights were turned on the next morning. All feces were frozen following their collection.

At the National Zoo's nutrition laboratory, fecal samples were dried to a constant weight at 100°C . Dried samples were ground in a Thomas-Wiley intermediate mill (Thomas Scientific, Swedesboro, NJ) fitted with a #20 (0.86 mm) screen. Fecal subsamples ranging from 0.05 to 0.1 g were digested using nitric and perchloric acids. They were then assayed for chromium at 357.9 nm in a Smith-Hieftje 12 atomic absorption spectrophotometer (Thermo Jerrell Ash, Franklin, MA) (AAS) using a nitrous oxide-acetylene flame. Standard solutions were used to recalibrate the AAS every three to five sample readings. The average of three sequential readings was used to calculate the % Cr in the feces. T_{max} is the time of peak marker elimination.

According to the method of van Soest [1994], TT was taken to be the time to first appearance of the marker. MRT (the point at which one-half of the marker was eliminated) was calculated as $t_{(\text{avg})} = \sum_{i=1}^n m_i t_i / \sum_{i=1}^n m_i$ where t = time post-dosing, and m_i is the amount of marker eliminated at the i th defecation after dosing [Warner, 1981].

Fiber Digestion Trials

Three individuals (male 1 and female 1 (Table II), and an additional male: 1.25 yr old, 1.21 kg) were fed twice a day on a homogeneous blended diet composed of Zupreem® (440 gm), monkey biscuits (8 gm), bulgur wheat (230 gm), walnuts (8 gm), bananas (400 gm), and PolyViSol multivitamins (0.5 ml). The diet was readily accepted after the first day it was offered. Fresh batches were made daily

and any unused diet was discarded at the end of the day. After a 2-day acclimation period, a 5-day trial was started. The sakis were allowed to feed ad libitum for 1 hr after the food was delivered. All food offered was weighed, and uneaten food was collected and dried. Food intake was estimated as the difference between the dry matter (DM) (g) in the offered diet and the DM of the refusals. All feces eliminated by the subjects were collected and frozen. The female was dosed with Cr_2O_3 (2% of the wet weight of food offered) every 48 hr during the digestion trial to permit visual discrimination between her feces and those of her cage-mate.

Samples of each batch of diet were dried and analyzed. We followed van Soest [1994] in determining neutral detergent (NDF) and acid detergent fiber (ADF) fractions of food and feces. NDF and ADF were measured on separate samples. Lipid content of the supplemental diet was estimated by the Soxhlet method [Association of Official Analytical Chemists, 1990] and protein content was estimated by the Kjeldahl method for total organic nitrogen. Nitrogen values were multiplied by 6.25 to calculate percent crude protein [Association of Official Analytical Chemists, 1990]. On a DM basis, the diet was found to be $15.04\% \pm 0.36\%$ crude protein ($n=5$), $7.07\% \pm 0.53\%$ lipids ($n=4$), $15.07\% \pm 2.4\%$ NDF ($n=4$), and $5.82\% \pm 2.05\%$ ADF ($n=9$).

DM digestibility was calculated as the difference between DM intake and fecal DM output expressed as a percentage of DM intake. Digestibility coefficients were calculated for NDF and ADF as follows. Apparent digestibility (% AD) = $(1 - (C_F * \text{DM}_F) / (C_D * \text{DM}_D)) * 100$, where C_F = concentration in feces (DM basis), C_D = concentration in diet (DM basis), DM_F = DM output in feces (g), and DM_D = DM intake in diet (g). Data were entered into SPSS v. 7.0. Differences among individuals in the digestion trials were tested using the Kruskal-Wallis test, using two-sided probabilities, with α set to 0.05.

RESULTS

Fecal Output

Fecal output data (collected in both marker passage and fiber digestion trials) peaked early in the day (Fig. 1). Samples collected between 0830 hr and 1000 hr represented between 65% and 92% of the total daily fecal output by dry weight. The sakis did not defecate during rest/sleep hours (1700–0600 hr).

Marker Passage

In the trial started in the morning, neither liquid phase (Cr_2O_3) nor particulate (beads) markers were visible in the feces in the first 8 hr, but a small amount (0.04% of total) of Cr_2O_3 was detected by atomic absorption at 5.0 hr post-ingestion, representing TT (see Table II). In this trial, the first appearance of beads occurred with the first defecation the following morning (at 23.0 hr post-ingestion). In the five trials started in the evening, Cr_2O_3 was both visible (green coloration) and measurable by atomic absorption in the first feces produced the next morning (TT = 14.7 ± 0.4 hr post-ingestion). Beads were also present in this first morning sample in the one trial in which beads were given in the evening (TT = 14.5 hr).

Figure 2 shows elimination of Cr_2O_3 in four trials in which feces were collected for 4 days or longer; in the other two trials, it was not possible to distinguish feces of the trial animal once the green coloration of Cr_2O_3 vanished. In these four trials, MRT ranged from 15.3 hr to 37.7 hr (see Table II). Elimination peaks (T_{max}) ranged from 16.0 hr to 24.0 hr after ingestion of

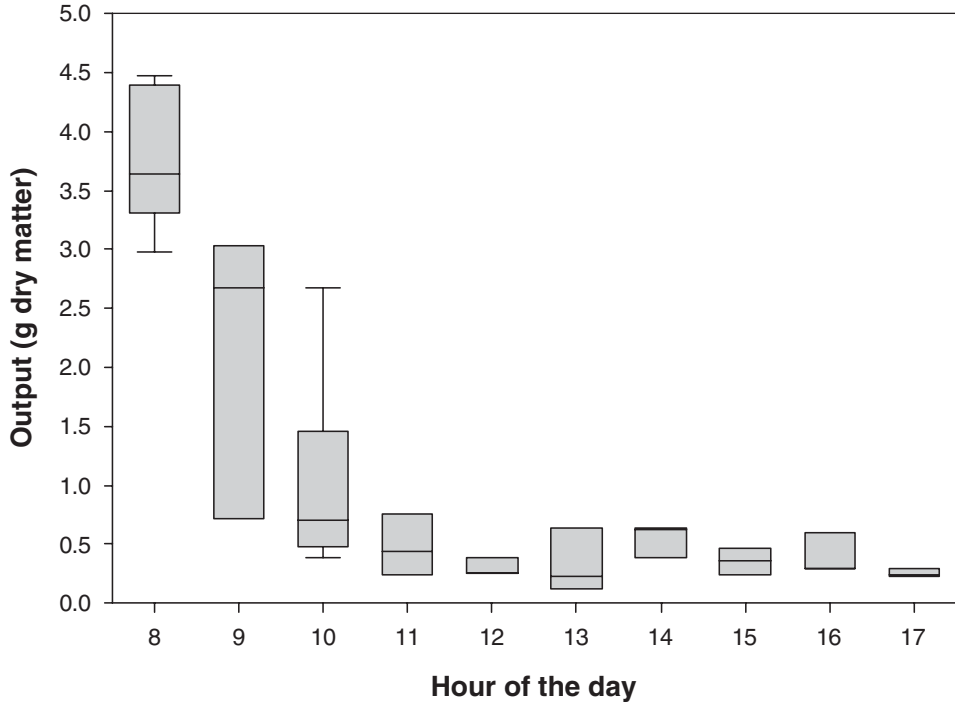


Fig. 1. Average fecal output (g dry weight) of four sakis in relation to time of day. Data represent five collection days. Feces were collected hourly, but there were some hours in which feces were not passed. For the samples collected at 0800 and 1000 hr, box plots show median (line), 25–75th percentile (hatched box), and range (whiskers).

marker (see Fig. 2). Although the sakis may have continued to excrete small amounts of Cr_2O_3 after our fecal collection period, the effect on calculated MRT would have been negligible as most of the marker was excreted prior to 90 hr post-dose (Fig. 3).

Fiber Digestion

DM intake averaged 58.7 g/day, representing 2.8% of body mass. We found no significant differences in the daily DM intake (Kruskal-Wallis $H = 1.26$, $df = 2$, $P = 0.53$) or in daily fecal fiber output of the three animals (NDF output: $H = 1.06$, $df = 2$, $P = 0.59$; ADF output: $H = 1.34$, $df = 2$, $P = 0.51$). DM digestibilities expressed as a percent of DM intake averaged $89.5\% \pm 1.4\%$ (range = 88.0–90.6%, $n = 3$). Apparent digestion coefficients averaged $77.6\% \pm 2.6\%$ NDF (range = 74.7–79.5%, $n = 3$ trials) and $74.4\% \pm 5.8\%$ ADF (range = 68.7–80.2%, $n = 3$).

DISCUSSION

We found that TT for liquid and particulate markers for *Pithecia pithecia* are similar to what Milton [1984] reported for a particulate marker fed to a single *P. monachus*. These findings, combined with relatively long MRTs for the liquid marker, are consistent with the suggestion by Chivers [1994] and Lambert [1998] that seed predation is a feeding strategy intermediate between frugivory and

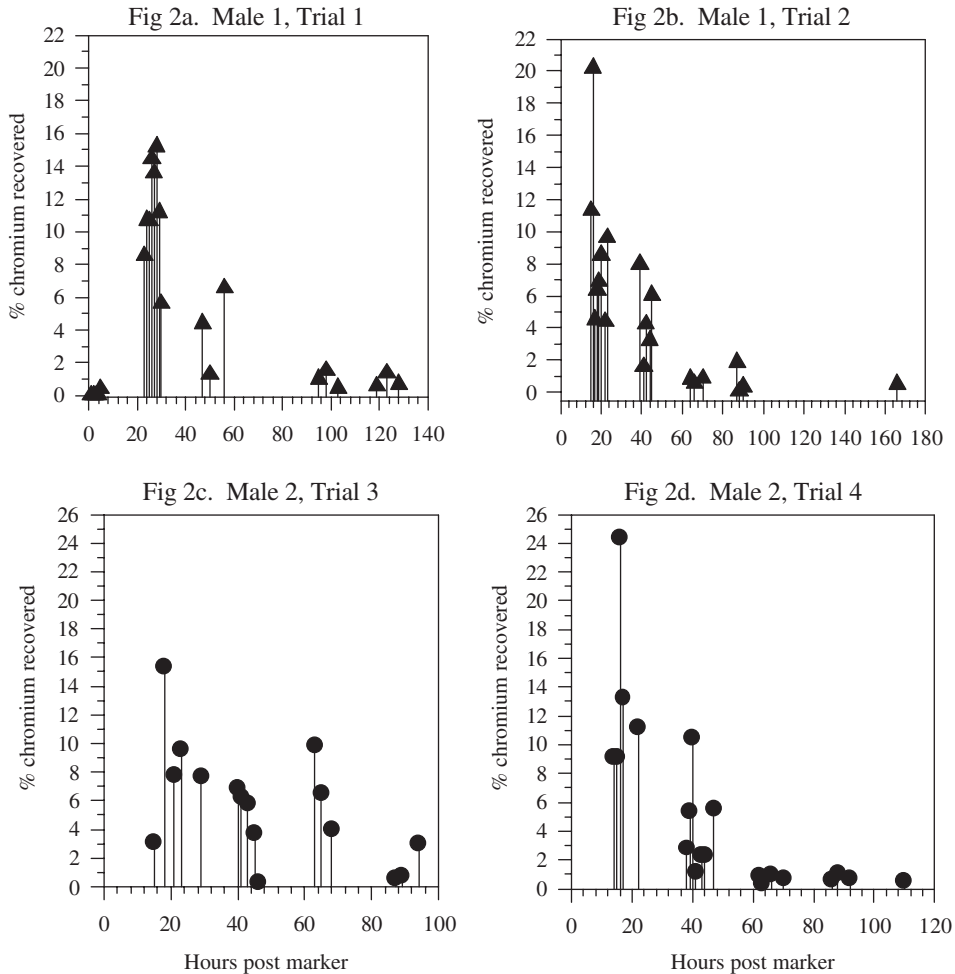


Fig. 2. Elimination of a digesta fluid marker (chromic oxide) by sakis following marker ingestion at time 0. Each point represents the percentage of total recovered marker in hourly collection periods. **a-d:** The four trials that extended >100 hr (see text).

folivory, in which relatively long retention (compared with frugivores) provides an opportunity for fermentation.

The marker recovery curve for white-faced sakis is characteristic of nonruminants with a limited capacity for hind-gut retention, with the caveat that the method used to assess digesta retention was designed for ungulate continuous-flow models of digestion [van Soest, 1994]. Sakis retain digesta during sleeping hours and defecate most of the daily excreta within 4 hr of waking. Thus, measurements of TT are biased by the time of day the marker is administered [Milton, 1998], and the bias is unavoidable if the TT is longer than the waking period.

The minimum TT for white-faced sakis ingesting a particulate marker (14.5 hr) is intermediate between *Alouatta*, which can digest moderately fibrous foods (TT=21 hr [Crissey et al., 1991] and 20.4 hr [Milton, 1981]), and platyrrhine fruit-eaters of both smaller body mass (e.g., *Cebus* spp. c. 3.25 kg,

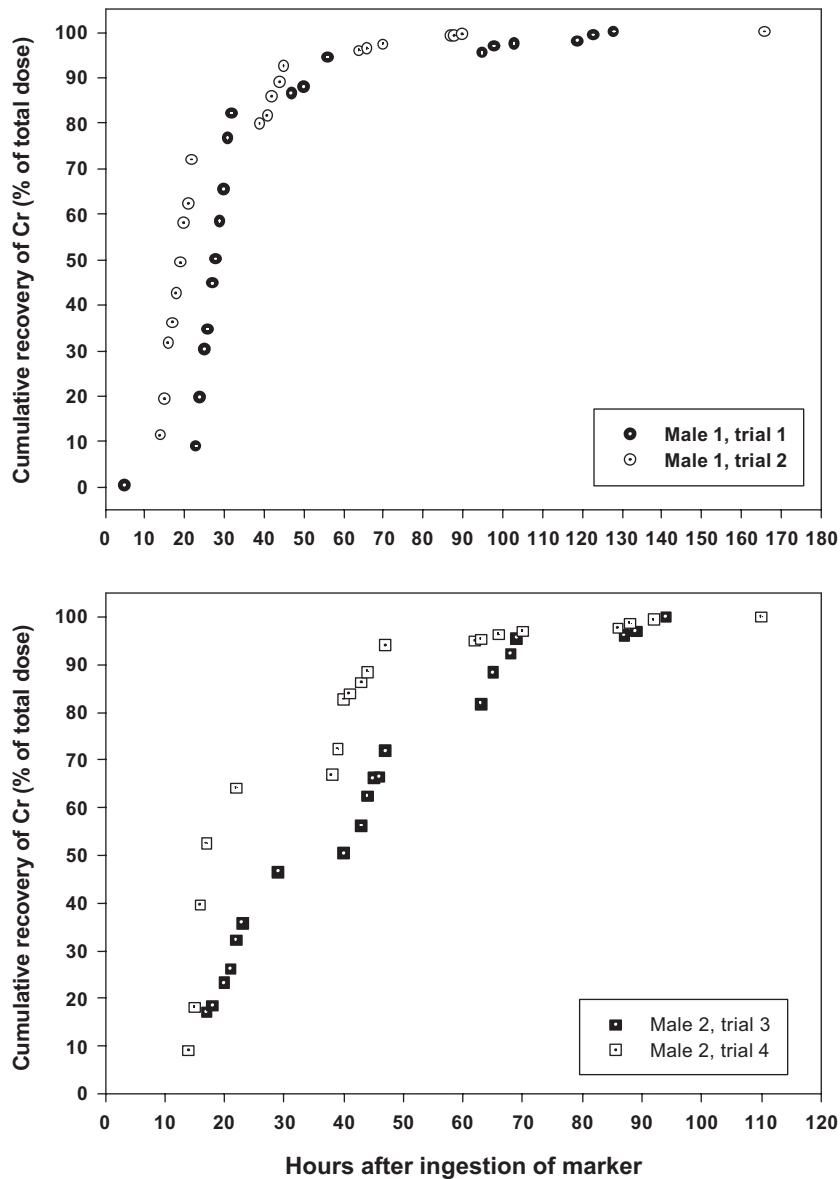


Fig. 3. Cumulative recovery of a fluid marker (chromic oxide) from sakis in relation to time after marker ingestion. Each point represents the percentage of total marker recovered in hourly collection periods. **a:** Marker recovery from male 1. **b:** Marker recovery from male 2. (See details in text.)

$\bar{x} = 3.5$ hr) and larger body mass (e.g., *Ateles geoffroyi* $\bar{x} = 7.6$ kg, $\bar{x} = 4.4$ hr) [Milton, 1984]. Edwards and Ullrey [1999] reported an average TT of 15.6 hr for a liquid marker administered to three species of *Alouatta* on low-fiber diets (15% ADF). TT for particulate markers was longer (32.3 hr).

We were unable to feed particulate markers to the sakis with sufficient marker recovery to calculate MRT, and thus can only report the MRT for the

liquid marker. Studies that calculate MRT for liquid digesta markers are relatively rare in primates, but Edwards and Ullrey [1999] calculated MRT (liquid) for hindgut fermenters (howlers) to be 30.1 hr on a low-fiber diet (15% ADF), and MRT (liquid) for foregut fermenters (colobines) to be 30.7 hr. Campbell et al. [1999] calculated MRT (liquid) for two species of *Propithecus* (hindgut fermenters and seed predators) [Hemmingway, 1996; Yamashita, 1996; Overdorff & Strait, 1998] to be between 30 and 36 hr. Although we did not determine the effect of altering dietary fiber or the other dietary constituents that might influence digesta passage in white-faced sakis, three of four MRTs were longer than 20 hr, which may be sufficiently long to permit some fermentation of soluble and perhaps small particulate matter.

Apparent digestibility of fiber exceeded 70% for both NDF and ADF, and is comparable to the values computed for macaques and colobines fed a low-fiber diet [Sakaguchi et al., 1991; Edwards & Ullrey, 1999]. Compared with colobines, howlers had lower NDF and ADF digestibilities (45% and 42%, respectively) on the same diet [Edwards & Ullrey, 1999]. The high digestibility of ADF in our study may be associated in part with the inclusion of pectin in the acid detergent portion of the diet, because samples for ADF analysis had not been previously extracted with neutral detergent [van Soest, 1994]. However, Milton and Demment [1988] found that fiber digestion in chimpanzees was positively related to retention time and inversely proportional to the amount of fiber in the diet. The lower the fiber content of the diet, the greater was the amount digested, particularly if retention was relatively long.

While the active period for the zoo sakis (9 hr) may seem short for wild primates, it is very close in duration to the activity pattern seen in Venezuelan white-faced saki monkeys. Wild sakis become active between 0555 and 0620 hr; they stop feeding and are relatively inactive by 1500–1530 hr for about an hour before selecting a sleeping tree [Setz, 1999; Brush, 2000]. Emmons [1980] found the same pattern of early retirement for squirrels, seed predators that also ingested seeds high in lipids and fiber. Both of these small-bodied seed-eaters appear to employ relatively long digestion periods compared to ripe-fruit- and pulp-eating frugivores. While it appears that a slowed rate of digesta passage would provide the opportunity to digest dietary fiber, we do not know to what extent this may contribute to fermentation of the higher fiber levels in wild saki foods.

All pitheciins are seed predators, but in the only known comparative study, Milton [1984] found a much shorter TT (5 hr) for a particulate marker in bearded sakis and uacaris, which are about 40% larger than white-faced sakis. Although they are larger in body mass, bearded sakis and uacaris may have lower fiber intakes than white-faced sakis. In addition to the fiber ingested in seeds, leaves represented >5% of the white-faced saki annual diet in Venezuela [Kinzey & Norconk, 1993; Norconk, 1996]. This is compared with negligible amount of leaves in the bearded saki diet in Venezuela [Norconk, 1996] and Suriname [van Roosmalen et al., 1988]. Boubli [1999] and Barnett and Brandon-Jones [1997] documented low levels of leaf-eating by uacaris (*Cacajao melanocephalus*), but recently Barnett and de Castilho [2000] suggested that uacaris may ingest relatively high levels of leaves seasonally. A better understanding of digestive function of pitheciin seed predators will require study of these closely related species, use of markers that closely track fibrous particles in seeds (e.g., by mordanting chromium to fibrous constituents), and examination of responses to change in type and amount of fiber in the diets of captive animals.

TT and MRT of white-faced sakis are intermediate between those of primates that ingest primarily fruit (such as *Cebus* spp and *Ateles* spp) and those of primates that ingest quantities of leaves (such as colobines and *Alouatta* spp). White-faced sakis also appear to be quite efficient at fiber digestion, at least when fed a low-fiber diet. These findings suggest that sakis are capable of a degree of fiber fermentation, and may help explain how sakis can cope with relatively high intakes of NDF and ADF in the wild. We hypothesize that white-faced sakis, the smallest members of the pitheciin clade of neotropical seed predators, use fermentation to digest fibrous seeds and/or leaves in a fashion similar to that seen in the prosimian seed predator, *Propithecus*. Reports of relatively short TT in the larger sakis/uacaris (*Chiropotes* and *Cacajao*) require further study, but suggest that digestive capability within the saki-uacari clade may be quite variable.

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REFERENCES

- Association of Official Analytical Chemists. 1990. Official methods of analysis. 15th ed. Washington, DC: AOAC. 1,200 p.
- Barnett AA, Brandon-Jones D. 1997. The ecology, biogeography and conservation of the uacaris, *Cacajao* (Pitheciinae). *Folia Primatol* 68:223–235.
- Barnett AA, de Castilho CV. 2000. Report on a short study of the dry season feeding ecology and habitat preferences of the golden-backed uacari or bicó, *Cacajao melanocephalus ouakary* (Cebidae: Pitheciinae), on the lower Rio Jaú, Amazonas, Brazil. No. 2 of the Igapó Study Project Report Series, Fundação Vitória Amazônica, Manaus, Brazil.
- Bodmer RE. 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23:255–261.
- Boubli JP. 1999. Feeding ecology of black-headed uacaris (*Cacajao melanocephalus melanocephalus*) in Pico da Neblina National Park, Brazil. *Int J Primatol* 20:719–749.
- Brush JA. 2000. Sleeping ecology of white-faced saki monkeys in Lago Guri, Venezuela. Master's thesis, Kent State University, Kent, OH.
- Campbell JL, Eisemann JH, Glander KE, Crissey SD. 1999. Intake, digestibility, and passage of a commercially designed diet by two *Propithecus* species. *Am J Primatol* 48:237–246.
- Chivers DJ, Hladik CM. 1980. Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *J Morphol* 166:337–386.
- Chivers DJ. 1994. Functional anatomy of the gastrointestinal tract. In: Davies AG, Oates JF, editors. *Colobine monkeys: their ecology behaviour and evolution*. Cambridge: University Press. p 205–228.
- Conklin-Brittain NL, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int J Primatol* 19:971–998.
- Crissey SD, Edwards MS, Oftedal OT, Currier JA, Rudran R. 1991. The role of fiber in natural and manufactured diets fed to red howler monkeys (*Alouatta seniculus*). In: Meehan TP, Thompson SD, Allen ME, editors. *Proceedings of the 8th Dr. Scholl Conference on the Nutrition of Captive Wild Animals*. Chicago, IL: Lincoln Park Zoological Gardens. p 135–147.

- Davies AG. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of Northern Borneo. *Int J Primatol* 12:119-144.
- Dierenfeld ES, McCann CM. 1999. Nutrient composition of selected plant species consumed by semi free-ranging lion-tailed macaques (*Macaca silenus*) and ring-tailed lemurs (*Lemur catta*) on St. Catherine's Island, Georgia, U.S.A. *Zoo Biol* 18:481-494.
- Edwards MS, Ullrey DE. 1999. Effect of dietary fiber concentration on apparent digestibility and digesta passage in non-human primates. II. Hindgut- and foregut-fermenting folivores. *Zoo Biol* 18:537-549.
- Emmons LH. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecol Monogr* 50: 31-54.
- Ferrari SF, Lopes MA. 1994. Comparison of gut proportion in four small-bodied Amazonian cebids. *Am J Primatol* 35:139-142.
- Flaschka M. 2001. Analysis of dietary mineral and macronutrient levels for white-faced sakis (*Pithecia pithecia*) and red howler monkeys (*Alouatta seniculus*) from Guri, Venezuela. MA thesis, Kent State University, Kent, OH.
- Fooden J. 1964. Stomach contents and gastro-intestinal proportions in wild shot Guianan monkeys. *Am J Phys Anthropol* 22:227-231.
- Frampton T. 2000. White-faced saki (*Pithecia pithecia*) North American regional stud-book. Metro publication #2000.10324.zoo.a. Portland: Metro Regional Services.
- Hemmingway CA. 1996. Morphology and phenology of seeds and whole fruit eaten by Milne-Edwards' sifaka, *Propithecus diademata edwardsi*, in Ranomafana National Park, Madagascar. *Int J Primatol* 17: 637-660.
- Hill WCO. 1960. Primates: comparative anatomy and taxonomy. IV Cebidae, Part A. Edinburgh: University Press.
- Kinzey WG. 1992. Dietary and dental adaptations in the Pitheciinae. *Am J Phys Anthropol* 88:499-514.
- Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int J Primatol* 14:207-227.
- Lambert JE. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evol Anthropol* 7:8-20.
- Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology behaviour and evolution. Cambridge: University Press. p 173-203.
- Milton K. 1981. Food choice and digestive strategies of two sympatric primate species. *Am Nat* 117:496-505.
- Milton K. 1984. The role of food-processing factors in primate food choice. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates. New York: Columbia University Press. p 249-279.
- Milton K, Demment MW. 1988. Digestion and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human data. *J Nutrition* 118: 1082-1088.
- Milton K. 1998. Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. *Int J Primatol* 19:513-548.
- Norconk MA. 1996. Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In: Norconk MA, Rosenberger AL, Garber PA, editors. Adaptive radiations of neotropical primates. New York: Plenum. p 403-423.
- Oates JF. 1977. The guereza and its food. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. London: Academic Press. p 275-321.
- Oates JF, Waterman PG, Choo GM. 1980. Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45:45-56.
- Overdorff DJ, Strait SG. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *Am J Primatol* 45:69-82.
- Rosenberger AL. 1992. Evolution of feeding niches in New World monkeys. *Am J Phys Anthropol* 88:525-562.
- Sakaguchi EI, Suzuki K, Kotera S, Ehara A. 1991. Fiber digestion and digesta retention time in macaque and colobus monkeys. In: Ehara A, Kimura T, Takenaka O, Iwamoto M, editors. Primatology today. Amsterdam: Elsevier Science Publications. p 671-674.
- Setz EZF. 1999. Sleeping habits of golden-faced sakis in a forest fragment in the central Amazon. *Am J Primatol* 49:100.
- Struhsaker TT. 1975. The red colobus monkey. Chicago: University Press. 311 p.
- van Roosmalen MGM, Mittermeier RA, Fleagle JG. 1988. Diet of the northern bearded saki (*Chiropotes satanas chiropotes*): a neotropical seed predator. *Am J Primatol* 14:11-35.
- van Soest PJ. 1994. Nutritional ecology of the ruminant. 2nd ed. Ithaca: Cornell University Press. 476 p.

- Warner ACI. 1981. Rate of passage of digesta through the gut of mammals and birds. Commonwealth Bureau of Nutrition. Nutr Abstr Rev Ser B 51:789–820.
- Waterman PG, Kool KM. 1994. Colobine food selection and plant chemistry. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology behaviour and evolution. Cambridge: University Press. p 251–284.
- Whiten A, Bryne RW, Barton RA, Waterman PG, Henzi SP. 1991. Dietary and foraging strategies of baboons. Phil Trans R Soc Lond B 334:187–197.
- Yamashita N. 1996. Seasonality and site specificity of mechanical dietary patterns in two Malagasy lemur families (Lemuridae and Indriidae). Int J Primatol 17: 355–387.