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Physical Properties of Fruit and Seeds Ingested by Primate Seed Predators with Emphasis on Sakis and Bearded Sakis

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ABSTRACT

Several primate radiations exhibit dental adaptations that enable them to gain access to seeds embedded in well-protected fruit. To a database drawn from published sources in which hardness of fruit and seeds were tested in the field, we added an additional 100+ species of plants used as resources by pitheciin primates (specifically, South American white-faced sakis (*Pithecia pithecia*) and bearded sakis (*Chiropotes* spp.). This sample allowed us to compare hardness of fruit and seeds and deduce the relative incisive and masticatory capability of several primate taxa (New World monkeys, Old World monkeys, prosimians and chimpanzees). Pitheciins have very well developed and highly modified anterior dentition that they use in gaining access to mechanically-protected fruit. In addition, their molars bear thin, but decussated enamel that protects the tooth enamel from crack proliferation. The ability of sakis (*Chiropotes* spp. and *Pithecia pithecia*) to open fruit orally was comparable to larger-bodied Old World seed predators—*Lophocebus* and *Cercocebus*. But, baboons and chimpanzees masticate seeds that are two to three orders of magnitude harder than sakis or mangabeys. In spite of their puncture abilities, ~40% of foods ingested by pitheciins were in the range of a ripe fruit eater (*Ateles paniscus*). This raises the possibility that pitheciins exemplify Liem's paradox, that is, "that phenotypic specialization [is] not accompanied by ecological specialization" (Robinson and Wilson, 1998:224). Last, we examined the possibility that seeds may serve as fallback resources for primate seed predators. While pericarp hardness may vary seasonally for some seed predators (e.g., mangabeys), our data on bearded sakis and white-faced sakis suggest that seeds are their primary resources year round and pericarp hardness is unrelated to seasonal variation in rainfall. Pitheciins evolved specialized dentition that affords them access to relatively abundant and high-quality resources, a feeding strategy that results in minimal variation in resource availability seasonally. Anat Rec, 294:2092–2111, 2011. © 2011 Wiley Periodicals, Inc.

Key words: platyrrhines; food hardness; Liem's paradox; feeding morphology

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"Seeds contain baby plants and so there can hardly be any more important interaction between mammals and plants than this [fact]" (Lucas et al., 2008:382). The strongly frugivorous diets of most anthropoid primates and larger-bodied prosimians in combination with their high biomass in tropical forests (e.g., Hanya et al., in press), their ability to move among isolated food patches, and their gentle treatment of seeds resulting in high germination rates after seed passage (e.g., Stevenson et al., 2002) exemplify the largely commensal relationship between primates and plants. Primates are not only important seed dispersers in the tropics (e.g., Link and Di Fiore, 2006; Chapman and Russo, 2007; Dew, 2008; Lambert, 2011), they also use many plant parts as food resources including bark, gum, pith, leaves, and fruit.

The comment by Lucas et al. above refers to the myriad adaptations developed by plants to minimize the loss of seeds to early removal and predation. Compared to the extraordinary biomass of herbivorous insects in the tropics, the loss of seeds to seed-eating mammals is probably miniscule (Fraenkel, 1959; Janzen, 1971). Nevertheless, estimates of crop loss to primates are not well studied (see Peres, 1991) and some primates are known to include seeds as a substantial and consistent part of their diets. Sifakas and aye-ayes of Madagascar, langurs and leaf monkeys of Asia and Africa, mangabeys of Africa, and capuchins, sakis and uakaris of South America all ingest and masticate seeds from a wide array of plant families and exhibit dental adaptations related to seed eating (e.g., Peres, 1991; Kinzey and Norconk, 1993; Maisels et al., 1994; Yamashita, 1996; Fleagle and McGraw, 2002; Sterling and McCreless, 2006; Kirkpatrick, 2007). We focus on mechanical properties of fruit pericarp and seeds as one of the barriers that primates encounter when selecting foods. Less is known about chemical feeding deterrents beyond the apparent ubiquity of secondary compounds in wild foods (but see Milton, 1979; Rosenthal and Berenbaum, 1992; Lambert, 1998). Tannins, phenolics, alkaloids, and many other compounds affect the digestibility of plant products (e.g., trypsin inhibitors in legume seeds, Altmann, 2009) and while there is some information on proteins in human and nonhuman primate saliva that bind with secondary compounds and reverse their effects (Milton, 1999; Mau et al., 2009), there are few studies of wild primates that have studied this topic (e.g., cyanide tolerance by *Hapalemur*: Glander et al., 1989). Altmann (2009) refers to the mixed nutrient/digestion inhibitor or toxic constituents of primate foods as the "package problem."

The Pitheciini (sakis and uacaris) Gray, 1849 is a monophyletic group of South American monkeys consisting of three extant genera (*Pithecia*, *Chiropotes*, and *Cacajao*) and as many as 11 extinct taxa (Rosenberger, 2002) (Fig. 1). This radiation of Neotropical primate seed predators dates from the early Miocene of Argentina (Kay et al., 1998; Fleagle and Tejedor, 2002) and all share what Rosenberger (2002:156) refers to as "self polarizing" dental morphology and diets that include seeds embedded in tough or thick husks. The presence of several unusual dental traits in the earliest members of the tribe (e.g., procumbent incisors and molars with low cusp relief) is further derived in the modern genera. *Pithecia*, *Chiropotes*, and *Cacajao* share laterally splayed, robust upper and lower canines with a sharp lingual crest, little sexual dimorphism dentally, and nearly featureless molars with crenulated enamel (Kinzey, 1992). Functionally, canines positioned "outside the contour of the dental arcade" allow sakis and uakaris to open fruit that exceed their gape width and enhance their ability to puncture objects "with considerable force" (Kinzey, 1992: 502).

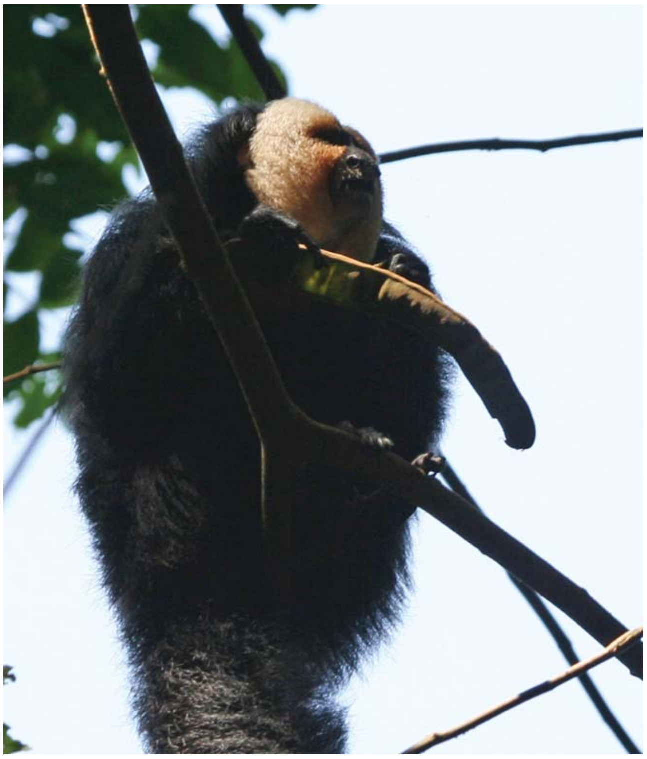

Fig. 1. Male *Pithecia pithecia* feeding on *Inga rubinginosa* at Brownsberg Nature Park, Suriname. [Photo by M. Norconk].

Sakis and uakaris use procumbent incisors to scrape or strip soft mesocarp from the interior of fruit or, in the case of *Pithecia*, to plane the pericarp (outer covering) of fruit that are too large or hard to puncture with the canines (e.g., *Gustavia augusta* and *Lecythis idatimon*, Lecythidaceae) (Norconk, personal observations) (Figs. 2 and 3).

The last premolars in the upper and lower jaw are enlarged and molariform increasing the surface area for mastication. Crenulated enamel on the occlusal surface of molars may aid in holding seeds during mastication, especially if they are smooth-surfaced or slippery with mesocarp (Rosenberger and Kinzey, 1976; Rosenberger, 1992).

With the exception of *Cebus* spp., platyrrhines have thinner enamel than Old World monkeys (Martin et al., 2003). The microstructure of pitheciin enamel contains abundant Hunter-Schreger bands or rods of enamel that extend almost to the surface of the tooth (Martin et al., 2003). The rods are crossed or decussated at the enamel-dentine junction and retard crack proliferation through the enamel and into the dentine even though the layer of enamel on the tooth surface is thin (Lucas et al., 2008). Thus, both the morphology of the teeth and substructure of enamel is specialized for opening well-protected fruit and masticating seeds that have a wide range of hardness values. Interestingly, Lucas et al.

Fig. 2. *Lecythis idatimon* (Lecythidaceae) fruit. Instead of accessing the seeds directly through very fibrous pyxidia, white-faced sakis scrape the base of the fruit to remove the seeds. [Photo by M. Norconk].

(2008) noted that both seeds and enamel are designed to resist fracture—the orientation of fibers in fruit pericarp (outer covering) and seed endocarp (or seed coat) is similar to enamel microstructure in mammalian teeth.

The apparent morphological adaptation of pitheciin teeth to the function of opening well-protected fruit pericarp and the diverse diets of sakis and uakaris raises the possibility that they exemplify Liem's paradox in primates. Using durophagous fish, Liem (1980) observed that the well-developed feeding morphology of cichlid fish (*Petrotilapia tridentiger*) did not limit the range of resources they ingested and molluscs represented a relatively small proportion of their diet (Robinson and Wilson, 1998; Binning et al., 2009). The apparent mismatch between the presence of specialized morphology and diet composition (Liem's paradox) is similar to views of critical function of specialized morphologies or behaviors as seasonally significant to survival (Kinzey, 1974; Rosenberger, 1992; Lambert et al., 2004). Recent work on how these critical resources or fallback foods are discovered and implemented during periods of seasonal shortages is of widespread interest currently (Lambert et al., 2004; Marshall and Wrangham, 2007; Lambert, 2009; Marshall et al., 2009).

Fallback foods or fallback behavioral strategies focus attention on how animals bridge periods of scarcity. Altmann (1998:209) identified the two major axes of interest in fallback feeding strategies, abundance and food quality, in his definition of a fallback food as "a resource baboons resort to primarily during those times of the year when more nutritious or less labor-intensive foods are not available." Marshall and colleagues (Marshall and Wrangham, 2007; Marshall et al., 2009) divided fallback foods into two groups based on their frequency of use in periods of seasonal food scarcity. Staple fallback foods are those that are sufficiently abundant to permit animals to rely on those foods exclusively; filler fallback foods fill the gaps when preferred foods are unavailable. This dichotomy in the relative availability and frequency of use of fallback foods reflects on resource quality, search time, and contestability (lower for staple fallback foods) and food processing (lower for filler foods). Herein lies the perspective of Lambert's (2007) paradigm that pivots on anatomical specializations for processing low quality foods and behavioral adaptations related to harvesting high quality fallback foods. Does the concept of fallback foods or critical resources have utility in seed predators like the pitheciins that use seeds year round? Norconk et al. (1998) suggested that sakis may be immune to the vagaries of fruit abundance seasonally by being able to use seeds at both early and late stages of fruit development and also at various stages of fruit or seed hardness.

Fig. 3. Larger-bodied, more powerful bearded sakis (*Chiropotes sagulatus*) gain access to seeds of *Lecythis idatimon* directly through the pyxidium. [Photo by M. Norconk].

Kinzey and Norconk (1990) referred to sakis and uakaris as sclerocarpic foragers in order to distinguish them from other platyrrhine frugivores. Recently, Norconk et al. (accepted) divided primate seed predators into four groups on the basis of dental and manual adaptations used to extract seeds from fruit pericarps. (1) Sakis and uakaris as sclerocarpic foragers extract seeds from fruits that are held by the hands and pried open by the canines (and premolars). Seeds are extracted by the teeth, moved to the rear of the mouth and masticated. (2) Sakis and uakaris are extractive foragers *sensu lato* in that seeds are embedded resources, but *Daubentonia madagascariensis* (Cartmill, 1974; Kitko et al., 1996; Sterling and McCreless, 2006), *Cebus apella* and close relatives (Kinzey, 1974; Dumont, 1995; Shellis et al., 1998; Fragaszy et al., 2004; Visalberghi et al., 2009), as well as *Theropithecus gelada* and *Papio* spp. (Daegling, 1992) represent a taxonomically diverse group of extractive foragers *sensu stricto* (Gibson, 1986). They rely on manual strength, dexterity and tools (in the case of *Cebus* spp.) to extract resources. (3) Durophagy, the mastication of mechanically resistant foods using enlarged posterior teeth and powerful jaws, characterize two genera of Old World monkeys: *Cercocebus* spp. and *Mandrillus sphinx*. These primates feed on a variety of fruit, but they can also masticate hard, dried, well-protected, post-dispersed fruit and seeds from the forest floor (Chalmers, 1968; Fleagle and McGraw, 1999; 2002; Poulsen et al., 2001; Daegling and McGraw, 2007). We included the arboreal mangabey (*Lophocebus* spp.) in this group (Norconk et al., accepted). *Lophocebus* and *Cercocebus* are no longer regarded as sister taxa (Fleagle and McGraw, 1999), but seeds represent a significant portion of their diets. (4) Finally, there are a number of colobine primates that ingest seeds. Seeds range from 22% to 65% of their annual diets and may exceed 80% of seasonal diets (Fashing, 2007; Kirkpatrick, 2007). Leaf-eating or folivory is their primary adaptation, but the evolution of bilophodont molars also facilitates seed predation (Lucas and Teaford, 1994). Among lemurs, *Propithecus* spp. use pseudo-bilophodont molars to fracture seeds (Maier, 1977; Kay and Hylander, 1978; Yamashita, 1996; Cuozzo and Yamashita, 2006).

Warren Kinzey developed a field method to test the hardness of fresh pericarp and seed samples (Kinzey and Norconk, 1990, 1993). A puncture device mimicked the use of canines to puncture fruit pericarp and a crushing device estimated the force necessary to crack or deform a seed by posterior dentition (see Methods). First used to test the puncture and crushing resistances of fruit ingested by spider monkeys and bearded sakis, the method has now been used to test fruit eaten by several primate seed predators. We collected and analyzed published and unpublished data on puncture and crushing resistance (Table 1) from studies using comparable equipment and sampling strategies to compare hardness values related to puncture resistance and seed crushing and to ask two questions related to seed predation by pitheciins: (a) Are hard foods also fallback resources for primate seed predators? (b) Do pitheciins exemplify Liem's paradox in primates?

MATERIAL AND METHODS

Data

Field studies. Published and unpublished data on feeding ecology and mechanical properties of fruit and seeds eaten by white-faced sakis (*Pithecia pithecia*) and bearded sakis (*Chiropotes* spp.) are presented from three studies conducted at field sites in northern South America dating from 1988 to 2007 and using identical sampling strategies (Kinzey and Norconk, 1990, 1993; Norconk, 1996).

The first study (Sur 1) (Fig. 4) compared diet and mechanical properties of foods eaten by a ripe fruit eater (*Ateles paniscus*) and a seed predator, bearded sakis (*Chiroptes sagulatus*[1]), at the Raleighvallen-Voltzberg Nature Reserve in central Suriname (c. 4° 0′ N, 56° 30′ W) from September 1986 to February 1987 (Kinzey and Norconk, 1990). The sample period included the end of the long dry season, short wet season, and the short dry season (after De Dijn et al., 2007). The field station is now subsumed within the Central Suriname Nature Reserve that was expanded in 1998 to 1.6 million ha of pristine lowland moist tropical rainforest (Boinski et al., 2005).

The second study (Ven) compared the diets of *P. pithecia* and *Ch. satanas* whose populations were isolated by the Caroni River in Estado Bolívar, eastern Venezuela. Construction of the Raul Leoni dam (c. 7° 45′ N, 62° 52′ W) in 1986 and flooding of the Caroni River Basin created hundreds of islands of various sizes (e.g., Alvarez et al., 1986; Terborgh et al., 1997) resulting in both intergroup/population and interspecific isolation. Annual rainfall increases along a north (islands inhabited by *P. pithecia*) to south (islands inhabited by *C. satanas*) gradient. High plant endemism has resulted in very little overlap in plant species on the two study islands separated by only 40 km (Aymard et al., 1997). Data reported here are taken from a 17-month study in 1991–1992. Both study sites in Venezuela have a single dry season between October and April and a single wet season between May and September.

The third study (Sur 2) took place at the Brownsberg Nature Park (c. 4°58′N, 55°07′W) in eastern Suriname from Jan to April, 2007. This study focused on sympatric pitheciins, *Pithecia pithecia* and *Chiropotes sagulatus*. At an elevation of 570 m, the Brownsberg is covered in montane tropical moist forest with habitats ranging from cloud forest at the top of the plateau to lowland wet forest at the base. The study was conducted during the short dry season and early long wet season.

Data on puncture and crushing resistance of fruit and seeds were also collected from published studies in which the same equipment and testing strategy were used (*Cercopithecus ascanius* and *Lophocebus albigena*: Lambert et al., 2004; *Cercocebus galeritus*: Wieczkowski, 2009; *Papio* spp. and *Pan troglodytes*: Peters, 1993). Data for baboons and *Pan* were collected as part of a vegetation survey by Peters (1993), not a primate-specific study—thus the data are not a representation of diet as other studies were. Nevertheless, Peters provides a lot of plant information and since samples were tested fresh as in other studies his data were included in the analysis. Peters' data are listed under "crushing" in Table 2 since that was the only test that he performed. Text in the methods suggests that food preparation was not done exclusively by molars and premolars; seed husks could have been scored with the anterior dentition.

Sampling methods: feeding behavior. Habituated groups of monkeys were followed from sleeping tree to sleeping tree for at least five days/month. Sampling data focused on feeding activities and continuous sampling ensued when a group entered a feeding tree. Trees were identified to species with the assistance of Gerardo Aymard, BioCentro, UNELLEZ, Edo. Portuguesa, Venezuela, and botanists at the National Herbarium of Suriname, Anton de Kom University, Paramaribo, Suriname. Voucher specimens were deposited in herbaria of each institution.

While feeding, data were collected on how the food was processed before ingestion and which portion of fruit

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[1] The taxonomy of bearded sakis is currently undergoing revision (Silva Jr and Figueiredo, 2002). As a result, "northern" bearded sakis have been divided into two groups: *Chiropotes sagulatus* occupying the Guianas and northern Brazil; and *C. satanas* occupying Venezuela. The two species are isolated by the Essequibo River in central Guiana.

TABLE 1. Puncture and crushing values for fruit and seeds ingested by *Ateles paniscus* and two pitheciins: *Pithecia pithecia* and *Chiropotes satanas* (*sagulatus*) sorted by plant family

Plant family	Plant species	N	Min	Mean puncture resistance (kg/mm^2)	Max	N	Min	Mean crushing resistance (kg)	Max	Ingested by	Part eaten
Anacardiaceae	*Spondias mombin*	9	0.36	0.57	1.13					*Chiropotes – Ven*^{a}	m
Annonaceae	*Duguetia lucida*	16	0.60	1.11	1.81					*Chiropotes - Ven*	MS
	Guatteria schomburgkiana	5	2.32	2.59	3.20					*Chiropotes - Ven*	MW
	Xylopia nitida					3	3.60	4.40	5.00	*Chiropotes - Sur 1*^{b}	MS
Apocynaceae	*Apocynaceae sp.*	1	0.77	0.91	1.04					*Chiropotes-Sur 1*	YS
	Aspidosperma excelsum	1	0.79		0.79					*Ateles - Sur 1*^{c}	m
Bignononiaceae^{g}	*Amphilophium sp.*	3	1.11	1.19	1.08					*Chiropotes - Ven*	YS
	Anomoctenium granulosum	1	10.20		10.20					*Chiropotes-Sur 1*	YS
	Arrabidaea charichanensis	2	1.68	1.79	1.89					*Chiropotes - Ven*	YS
	Arrabidaea sp.	9	0.57	0.91	1.38					*Pithecia – Ven*^{d}	YS
	Arrabidaea sp.	5	1.05	1.13	1.18					*Chiropotes - Ven*	YS
	Callichlamys sp.	4	1.68	2.70	3.10					*Chiropotes - Ven*	YS
	Distictella sp.	5	1.89	2.06	2.23					*Chiropotes - Ven*	YS
	Macfaydena unguis-cati	14	2.14	5.15	9.76					*Chiropotes - Ven*	YS
	Mansoa verrucifera	13	1.38	3.07	5.66					*Chiropotes - Ven*	YS
	Matelea sp.	3	0.61	1.50	1.50					*Chiropotes - Ven*	YS
	Mussatia hyacinthina	10	1.52	3.11	7.50					*Chiropotes - Ven*	YS
	Mussatia sp.	17	1.69	3.00	5.74					*Chiropotes - Ven*	YS
	Pleonotoma sp.	4	0.95	1.51	2.04					*Pithecia - Ven*	YS
	Pleonotoma sp.	3	1.73	1.92	2.26					*Chiropotes - Ven*	YS
	Potamogenos microcalyx	3	2.99	4.03	5.37					*Chiropotes - Sur 1*	YS
	Tabebuia serratifolia	10	0.71	0.97	1.52					*Chiropotes - Ven*	YS
	Tanaecium nocturnum	3	1.34	1.51	1.63					*Chiropotes - Sur 1*	YS
	Xylophragma seemannianum	14	0.51	5.05	10.71					*Chiropotes - Ven*	YS
Bombacaceae	*Catostemma fragrans*	5	0.46	0.58	0.88					*Ateles - Sur 1*	m
Boraginaceae	*Cordia sericicalyx*	3	0.13	0.14	0.14					*Ateles - Sur 1*	Mw
	Cordia tetandra	10	0.05	0.07	0.10					*Chiropotes - Ven*	m
Burseraceae	*Protium polybotryum*	4	0.13	0.30	0.49					*Ateles - Sur 1*	m
	Protium tenuifolium	5	0.51	0.65	0.83					*Chiropotes - Ven*	m
	Tetragastris altissima	3	0.18	0.38	0.58	3	9.55	11.65	13.64	*Ateles - Sur 1*	m
	Tetragastris panamensis	3	0.53	0.83	1.21					*Chiropotes - Sur 1*	m
Capparidaceae	*Capparis frondosa*	3	0.10	0.21	0.30					*Chiropotes - Ven*	YS
	Capparis muco	23	0.81	2.80	5.59	4	4.50	7.83	12.70	*Pithecia - Ven*	YS & m
Celestraceae	*Amphyzoma glabra*	1	1.15		1.15	4	22.00	35.67	60.00	*Pithecia Sur 2*	M & MS
	Maytenus sieberiana	2	0.69		0.69					*Pithecia - Ven*	YS
	Peritassa sp.	6	1.15	1.50	1.68	2	12.00	29.00	46.00	*Pithecia Sur 2*^{e}	YS & m
	Tontelea coriaceae	5	0.54	1.13	1.68	1	80.00		80.00	*Pithecia Sur 2*	YS
Chrysobalanaceae	*Chrysobalanus icaco*	7	0.69	2.89	7.35					*Pithecia Sur 2*	YS
	Hirtella racemosa					24	3.64	8.94	12.27	*Pithecia - Ven*	MS
	Licania apetala	10	2.98	3.83	4.80					*Chiropotes – Sur 2*	YS
	Licania densiflora	4	1.15	2.30	3.44					*Chiropotes – Sur 2*	YS
	Licania discolor	102	0.56	2.47	6.77	22	2.00	5.14	10.00	*Pithecia - Ven*	MS
	Licania hypoleuca	7	0.61	1.41	3.64					*Chiropotes - Ven*	YS
	Licania majuscula	1	0.03		0.03					*Ateles - Sur 1*	m
	Licania majuscula	18	1.47	18.07	37.80	1	15.45		15.45	*Chiropotes - Sur 1*	YS
	Parinari excelsa	8	0.13	0.25	0.52					*Ateles - Sur 1*	m

TABLE 1. Puncture and crushing values for fruit and seeds ingested by *Ateles paniscus* and two pitheciins: *Pithecia pithecia* and *Chiropotes satanas* (*sagulatus*) sorted by plant family (continued)

Plant family	Plant species	N	Min	Mean puncture resistance (kg/mm^2)	Max	N	Min	Mean crushing resistance (kg)	Max	Ingested by	Part eaten
Clusiaceae	*Clusia grandifolia*					4	1.36	1.80	2.73	*Chiropotes - Sur 1*	MS
Connaraceae	*Connarus venezuelanus*	59	0.35	0.77	2.25	19	10.00	15.37	36.00	*Pithecia - Ven*	MS
	Rourea frutescens	1	1.38		1.38	1	5.00		5.00	*Pithecia Sur 2*	MS
Erythroxylaceae	*Erythroxylum schomburgkii*					17	1.36	3.07	7.27	*Pithecia - Ven*	MS & m
Euphobiaceae	*Actinostemon schomburgkii*					5	4.10	4.62	5.40	*Pithecia - Ven*	YS
	Conceiveiba guianensis	5	1.38	1.91	2.30	3	6.00	10.33	13.00	*Pithecia Sur 2*	YS
	Drypetes variabilis	1	0.76		0.76					*Ateles - Sur 1*	m
	Mabea piriri	1	8.72		8.72	3	8.00	11.33	15.00	*Pithecia Sur 2*	YS
	Pausandra martinii	1	2.30		2.30	1	10.00		10.00	*Pithecia Sur 2*	YS
	Sapium aubletianum					3	3.60	4.80	6.40	*Chiropotes-Ven*	MS
Fabacaceae	*Fabaceae sp. 1*	1	1.16		1.16					*Chiropotes - Ven*	YS
Fabaceae:	*Brownea coccinea*	4	1.69	1.97	2.27					*Chiropotes - Ven*	YS
Caesalpinoidea	*Copaifera officinalis*	8	0.29	0.35	0.49					*Chiropotes - Ven*	YS
	Copaifera officinalis					1	25.00		25.00	*Pithecia - Ven*	MS
	Eperua falcata	1	6.06		6.06					*Chiropotes - Sur 1*	MS
	Hymenaea courbaril	13	1.61	3.79	6.66	3	3.60	11.80	22.70	*Chiropotes - Ven*	MS
	Peltogyne floribunda	33	0.10	0.90	1.52	1	1.80		1.80	*Pithecia - Ven*	YS
Fabaceae:	*Calliandra laxa*	5	1.43	1.56	1.65					*Chiropotes - Ven*	YS
Mimosoideae	*Entada polystacha*	5	0.64	0.65	0.66					*Chiropotes - Ven*	YS
	Inga acrocephala	2	0.89	0.99	1.08					*Chiropotes - Sur 1*	m
	Inga acrocephala	2	2.23	2.26	2.30					*Pithecia Sur 2*	m
	Inga alba	4	0.39	0.58	0.97					*Ateles - Sur 1*	m & Mw
	Inga alba	1	4.36		4.36					*Pithecia Sur 2*	m
	Inga borgoni	1	1.20		1.20					*Chiropotes - Sur 1*	m
	Inga cinnamonea	4	2.44	3.13	4.97					*Chiropotes - Sur 1*	m
	Inga rubiginosa	4	1.84	2.94	4.28					*Pithecia Sur 2*	m
	Inga sp.	1	1.28		1.28					*Chiropotes - Ven*	m
	Inga sp. 1	3	0.92	1.07	1.26					*Pithecia Sur 2*	m
	Inga sp. 2	1	2.53		2.53					*Pithecia Sur 2*	m
	Inga sp. 3	1	3.29		3.29					*Chiropotes Sur2*[f]	m
	Inga sp. 4	1	1.38		1.38					*Pithecia Sur 2*	m
	Piptadenia leucoxylon	16	0.28	0.57	1.82	7	4.10	8.63	20.40	*Pithecia - Ven*	MS
	Pithecellobium sp.	1	0.37		0.37					*Chiropotes - Ven*	MS
Fabaceae:	*Clathrotropis brachypetala?*	1	4.94		4.94					*Pithecia Sur 2*	YS
Papilionoidea	*Dioclea guianensis*	6	0.70	0.91	1.16	1	4.54		4.54	*Pithecia - Ven*	YS
	Lecointea amazonica	5	0.27	0.27	0.27					*Chiropotes - Ven*	YS & m
	Lonchocarpus dipteronervus	5	0.63	0.71	0.78					*Chiropotes - Ven*	YS
	Pterocarpus acapulcensis	14	2.30	3.49	5.05					*Chiropotes - Ven*	YS; MS
	Swartzia benthamiana	2	0.83	0.97	1.09					*Ateles - Sur 1*	YS & m
	Swartzia benthamiana	3	1.20	1.22	1.23	1	6.80		6.80	*Chiropotes - Sur 1*	YS
	Swartzia laevicarpa	2	1.53	1.61	1.68	1	36.00		36.00	*Chiropotes Sur 2*	YS
	Swartzia reticulata?	2	1.15	1.61	2.07					*Chiropotes Sur 2*	YS
	Swartzia schomburgkii	6	1.14	1.25	1.40					*Ateles - Sur 1*	YS
	Swartzia schomburgkii	2	1.36	1.98	2.60					*Chiropotes - Sur 1*	YS
Flacourtiaceae	*Casearia arborescens*					16	0.91	2.15	3.64	*Pithecia - Ven*	MW
	Casearia spinescens	2	0.52	0.59	0.66					*Chiropotes - Ven*	MW
Guttifferae	*Rheedia macrophylla*	4	0.67	0.68	0.72	1	47.73		47.73	*Ateles - Sur 1*	MS

TABLE 1. Puncture and crushing values for fruit and seeds ingested by *Ateles paniscus* and two pitheciins: *Pithecia pithecia* and *Chiropotes satanas* (*sagulatus*) sorted by plant family (continued)

Plant family	Plant species	N	Min	Mean puncture resistance (kg/mm^2)	Max	N	Min	Mean crushing resistance (kg)	Max	Ingested by	Part eaten
Humiriaceae	*Sacoglottis cydonioides*	1	0.63		0.63	1	35.45		35.45	*Ateles - Sur 1*	m & MS
Lecythidaceae	*Couratari stellata*	1	0.79		0.79					*Ateles - Sur 1*	YS
	Couratari stellata	15	1.00	3.00	7.33					*Chiropotes - Sur 1*	YS
	Couratari stellata	7	2.30	2.95	3.90					*Chiropotes Sur 2*	YS
	Eschweilera chartaceae					1	2.30		2.30	*Chiropotes -Sur 1*	YS
	Eschweilera coriaceae	7	1.84	3.24	4.97	3	7.00	12.28	18.00	*Pithecia - Sur 2*	YS
	Eschweilera coriaceae					3	8.33	12.28	18.00	*Chiropotes – Sur 2*	YS
	Eschweilera corrugata					6	1.40	3.90	12.30	*Chiropotes - Sur 1*	YS
	Gustavia augusta	13	2.30	3.22	4.59	9	10.33	28.88	55.00	*Pithecia Sur 2*	a
	Lecythis chartaceae	5	0.65	0.90	1.11	1	2.27		2.27	*Chiropotes - Sur 1*	YS
	Lecythis corrugata	8	0.58	0.70	0.95					*Ateles - Sur 1*	a
	Lecythis corrugata	20	0.44	1.06	2.19	6	1.36	3.90	12.27	*Chiropotes - Sur 1*	YS
	Lecythis corrugata	4	2.41	1.37	2.98	1	12.00		12.00	*Pithecia Sur 2*	YS
	Lecythis idatimon	1	2.30		2.30	3	10.00	12.83	18.00	*Chiropotes Sur 2*	YS
	Lecythis idatimon	25	2.75	5.41	9.18	6	11.00	21.75	41.00	*Pithecia Sur 2*	YS
Loganiaceae	*Strychnos fendleri*	13	0.01	0.98	1.99					*Pithecia - Ven*	m
	Strychnos mitcherlichii	3	0.38	0.95	1.39					*Pithecia - Ven*	m
	Strychnos mitcherlichii	2	1.98	2.02	2.05					*Pithecia - Ven*	m
	Strychnos mitcherlichii	12	0.56	0.90	1.21					*Chiropotes - Ven*	m
	Strychnos tomentosa	8	0.47	0.73	0.92					*Ateles - Sur 1*	m
	Strychnos tomentosa	1	4.02		4.02					*Chiropotes Sur 2*	m
Loranthaceae	*Oryctanthus alveolatus*					5	0.09	1.10	1.40	*Chiropotes-Ven*	MW
Meliaceae	*Carapa procera*	9	0.72	0.89	0.15	10	0.45	1.30	1.82	*Chiropotes - Sur 1*	MS
	Cedrela odorata	3	2.07	2.65	3.13					*Chiropotes - Sur 1*	YS
	Guarea grandifolia	1	1.79		1.79					*Chiropotes - Sur 1*	MS & a
	Guarea grandifolia	9	0.69	1.26	2.07					*Pithecia Sur 2*	MS & a
	Trichilia lepidota	8	1.39	1.68	2.27	9	0.91	1.06	1.36	*Pithecia - Ven*	YS
	Trichilia sp #4	1	0.89		0.89					*Chiropotes - Ven*	YS
Moraceae	*Bagassa guianensis*	4	0.03	0.15	0.27					*Ateles - Sur 1*	m
	Brosimum alicastrum	63	0.24	0.78	1.43	6	1.80	9.80	13.60	*Chiropotes - Ven*	YS
	Brosimum alicastrum	12	0.30	0.56	0.81	8	6.40	11.00	23.20	*Chiropotes - Ven*	MS
	Brosimum lactescens	20	0.03	0.30	0.88					*Ateles - Sur 1*	m
	Brosimum lactescens	5	0.17	0.21	0.24	6	3.70	10.20	16.36	*Chiropotes - Sur 1*	MS & m
	Brosimum parinarioides	3	0.37	0.47	0.62					*Chiropotes - Sur 1*	MS & m
	Brosimum sp. 2	1	0.30		0.30					*Chiropotes - Ven*	YS
	Clarisia racemosa	1	0.03		0.03					*Ateles - Sur 1*	m
	Clarisia racemosa	1	0.03		0.03	7	4.55	6.90	11.36	*Chiropotes - Sur 1*	YS
	Ficus amazonica	9	0.24	0.78	1.43					*Chiropotes - Ven*	MW
	Ficus sp?	1	0.99		0.99					*Pithecia Sur 2*	MW
	Heliocostylis tomentosa					3	2.27	2.88	3.64	*Chiropotes - Sur 1*	MS
	Maclura tinctoria	1	0.05		0.05	9	1.40	2.50	4.60	*Chiropotes - Ven*	MS
	Moraceae sp. 1	4	1.03	1.12	1.20					*Chiropotes - Ven*	
	Naucleopsis guianensis	3	0.03	0.09	0.15					*Ateles - Sur 1*	m
	Naucleopsis guianensis	5	0.57	1.45	1.84	4	3.64	5.00	6.36	*Chiropotes - Sur 1*	MS
	Pourouma guianensis	3	0.47	0.60	0.74					*Ateles - Sur 1*	m
	Pourouma guianensis					2	10.50	14.80	19.10	*Chiropotes - Sur 1*	MS - ne
	Pseudolmedia laevis									*Ateles - Sur 1*	m

TABLE 1. Puncture and crushing values for fruit and seeds ingested by *Ateles paniscus* and two pitheciins: *Pithecia pithecia* and *Chiropotes satanas* (*sagulatus*) sorted by plant family (continued)

Plant family	Plant species	N	Min	Mean puncture resistance (kg/mm^2)	Max	N	Min	Mean crushing resistance (kg)	Max	Ingested by	Part eaten
Myristicaceae	*Iryanthera sagotiana*	4	1.38	1.75	2.30	2	20.00	42.50	65.00	*Pithecia Sur 2*	a & MS
	Virola melinonii	1	2.18		2.18					*Pithecia Sur 2*	a
	Virola melinonii	15	0.75	0.88	1.11					*Ateles - Sur 1*	a
	Virola melinonii					6	20.45	21.10	22.27	*Chiropotes - Sur 1*	MS
	Virola surinamensis	6	0.53	0.70	0.84					*Ateles - Sur 1*	a
Myrtaceae	*Myrcia guianensis*					3	1.00	1.33	2.00	*Pithecia - Sur 2*	MS
	Psidium sartorianum	2	0.10	0.14	0.19	19	9.50	14.26	17.20	*Pithecia - Ven*	MS
Opiliaceae	*Agonandra brasiliensis*	1	0.81		0.81					*Pithecia - Ven*	YS
Passifloraceae	*Passiflora glandulosa*	3	0.46	0.59	0.69					*Pithecia Sur 2*	m & MS
	Passiflora sp.	1	2.53		2.53					*Pithecia Sur 2*	m & MS
Polygalaceae	*Moutabea guianensis*	12	0.32	0.88	1.62	8	6.36	13.00	18.18	*Chiropotes - Sur 1*	MS
Polygonaceae	*Coccoloba latifolia*	1	1.14		1.14	8	28.00	32.00	37.00	*Pithecia - Ven*	MS
	Coccoloba latifolia					5	29.00	32.00	36.00	*Pithecia - Ven*	YS
	Coccoloba striata					19	3.18	4.11	5.00	*Pithecia - Ven*	YS
	Coccoloba striata					4	5.00	5.11	6.36	*Pithecia - Ven*	MS
Quiinaceae	*Lacunaria crenata*					1	3.67		3.67	*Pithecia - Sur 2*	YS
Rubiaceae	*Alibertia latifolia*	6	0.56	0.68	0.81	3	3.64	23.94	52.27	*Pithecia - Ven*	YS
	Amaioua corymbosa	1	0.68		0.68	2	8.20	8.65	9.10	*Pithecia - Ven*	MS
	Amaioua corymbosa					1	3.60		3.60	*Pithecia - Ven*	YS
	Chiococca alba	1	0.01		0.01	3	2.00	2.00	2.00	*Pithecia - Ven*	MW
	Guettarda acreana	1	0.69		0.69					*Ateles - Sur 1*	Mw
	Guettarda malacophylla					19	2.70	4.92	7.30	*Pithecia - Ven*	MS
Rutaceae	*Angostura trifoliata*	5	0.61	0.92	1.11	5	0.45	0.82	1.36	*Pithecia - Ven*	YS
	Zanthoxylum martiniscensis					10	0.10	3.60	5.00	*Chiropotes - Ven*	MS
Sapindaceae	*Allophylus occidentalis*					6	4.50	4.90	5.40	*Chiropotes - Ven*	MS
	Cupania scrobiculata	6	0.51	0.60	0.76	2	1.36	2.27	3.18	*Pithecia - Ven*	YS
	Matayba arborescens	10	0.25	0.39	0.67					*Chiropotes - Ven*	a
	Melicoccus bijugatus	25	0.25	0.70	1.12	5	1.80	3.30	5.00	*Chiropotes - Ven*	YS
	Melicoccus bijugatus	3	0.49	0.56	0.67					*Chiropotes - Ven*	MF
	Paullinia leiocarpa	4	1.24	1.32	1.52	6	0.90	1.50	2.30	*Chiropotes - Ven*	YS
	Paullinia leiocarpa	3	0.25	0.39	0.67	3	2.7	4.4	6.8	*Chiropotes - Ven*	MS
	Paullinia spicata	6	0.66	0.72	0.80					*Chiropotes - Sur 1*	YS
	Talisia hexaphylla	19	0.46	0.99	1.84					*Chiropotes - Ven*	m
Sapotaceae	*Achrouteria pomifera*	26	1.43	2.29	3.30	3	1.36	1.50	1.82	*Chiropotes - Ven*	MS
	Chrysophyllum argenteum	9	0.46	0.88	1.15	5	29.00	37.40	45.00	*Chiropotes Sur 2*	YS
	Chrysophyllum argenteum	3	0.81	0.27	1.90	5	29.00	37.40	45.00	*Pithecia - Ven*	YS
	Chrysophyllum argenteum	15	0.25	0.36	0.61					*Chiropotes - Ven*	M
	Chrysophyllum eximium	1	0.92		0.92					*Chiropotes – Sur 2*	MS
	Chrysophyllum cuneifolium	1	1.84		1.84	1	42.00		42.00	*Pithecia Sur 2*	YS
	Chrysophyllum lucentifolium	15	0.88	2.24	5.73	11	5.40	23.75	36.60	*Pithecia - Ven*	YS
	Chrysophyllum lucentifolium	66	1.01	1.52	2.29	16	3.20	9.70	20.50	*Chiropotes - Ven*	YS
	Chrysophyllum lucentifolium	13	0.15	0.58	1.52					*Chiropotes - Ven*	m
	Chysophyllum eximium	11	0.69	1.05	1.84					*Chiropotes Sur 2*	YS
	Ecclinusa guianensis	21	0.03	0.31	0.62	10	1.60	2.70	5.91	*Chiropotes - Sur 1*	MS & m
	Eremoluma sagotiana	3	0.10	0.21	0.29					*Ateles - Sur 1*	MW
	Eremoluma sagotiana	22	0.37	0.59	0.81					*Chiropotes - Sur 1*	YS & m
	Pouteria guianensis	4	1.36	1.67	2.27					*Ateles - Sur 1*	m

TABLE 1. Puncture and crushing values for fruit and seeds ingested by *Ateles paniscus* and two pitheciins: *Pithecia pithecia* and *Chiropotes satanas* (*sagulatus*) sorted by plant family (continued)

Plant family	Plant species	N	Min	Mean puncture resistance (kg/mm^2)	Max	N	Min	Mean crushing resistance (kg)	Max	Ingested by	Part eaten
	Pradosia caracasana	4	10.33	17.99	33.84	47	2.30	6.90	15.50	*Chiropotes - Ven*	MS
	Pradosia caracasana	50	0.88	1.74	3.44	11	0.90	4.30	6.80	*Chiropotes - Ven*	MS & m
	Pradosia caracasana	153	0.54	1.36	2.56					*Chiropotes - Ven*	YS
	Pradosia caracasana	55	1.14	1.96	2.48					*Chiropotes - Ven*	MS
	Pradosia caracasana	79	1.11	1.52	2.15					*Chiropotes - Ven*	MS
	Pradosia ptychandra	2	2.18	2.47	2.75					*Chiropotes Sur 2*	YS
	Prieurella sp.	16	0.45	0.81	1.18					*Ateles - Sur 1*	m
	Prieurella sp.	4	1.37	1.43	1.50					*Chiropotes - Sur 1*	YS
	Sapotaceae sp. 1	3	0.92	1.07	1.15					*Chiropotes Sur 2*	YS
Simaroubaceae	*Quassia simarouba*	8	0.40	0.92	1.11	4	4.55	6.10	7.27	*Chiropotes - Sur 1*	MS
Solanaceae	*Solanum paludosum*	13	0.34	0.45	0.91					*Pithecia - Ven*	YS
Steculiaceae	*Byttneria catalpifolia*	7	2.07	5.05	6.43	12	1.80	3.00	5.50	*Chiropotes - Ven*	MS
	Sterculia excelsa					2	12.27	15.90	19.55	*Chiropotes - Sur 1*	MS
Tiliaceae	*Apeiba schomburgkii*	1	1.04		1.04					*Chiropotes - Ven*	MS & m
	Luehea speciosa	3	3.18	3.56	3.84					*Chiropotes - Ven*	MS
Ulmacaceae	*Celtis iganea*	7	0.40	0.78	1.26					*Chiropotes - Ven*	MS
Urticaceae	*Cecropia peltata*					2	2.70	4.30	5.90	*Chiropotes - Ven*	MS
Verbenaceae	*Vitex capitata*	6	0.03	0.09	0.10					*Pithecia - Ven*	
	Vitex compressa	4	0.35	14.08	32.80					*Chiropotes - Ven*	
Vochisiaceae	*Qualea dinizii*	2	2.45	2.57	2.68					*Chiropotes - Sur 1*	YS
	Qualea rosea	3	1.72	2.22	2.64					*Chiropotes Sur 2*	YS
	Vochysia guianensis	2	1.15	1.49	1.84					*Pithecia Sur 2*	YS
Unknown	Liana No. 2	2	0.32	0.43	0.54	1	3.64		3.64	*Chiropotes - Sur 1*	YS
	Drupe No. 1	1	1.68		1.68	1	33.00		33.00	*Pithecia - Sur 2*	MS

N = number of samples for each plant taxon. Parts of fruit eaten: m, mesocarp of ripe fruit; MS, mature seed masticated; MW, mature fruit ingested whole, seed masticated; Mw, mature fruit ingested whole, seed swallowed; YS, young seed masticated; a, aril scraped off the seed.

[a] *Chiropotes satanas* Ven = Danto Manchado, Lago Guri, Venezuela.

[b] *Chiropotes sagulatus* Sur 1 = Raleighvallen-Voltzberg, Central Reserve, Suriname.

[c] *Ateles paniscus* Sur 1 = Raleighvallen-Voltzberg, Central Reserve, Suriname.

[d] *Pithecia pithecia* Ven = Round Island, Las Carolinas, Lago Guri, Venezuela.

[e] *Pithecia pithecia* Sur 2 = Brownsberg Nature Park, Suriname.

[f] *Chiropotes sagulatus* Sur 2 = Brownsberg Nature Park, Suriname.

[g] Generally, seeds were tested if ingested and masticated. However, seeds of Bignoniaceae fruit are flat winged seeds and could not be tested for crushing resistance.

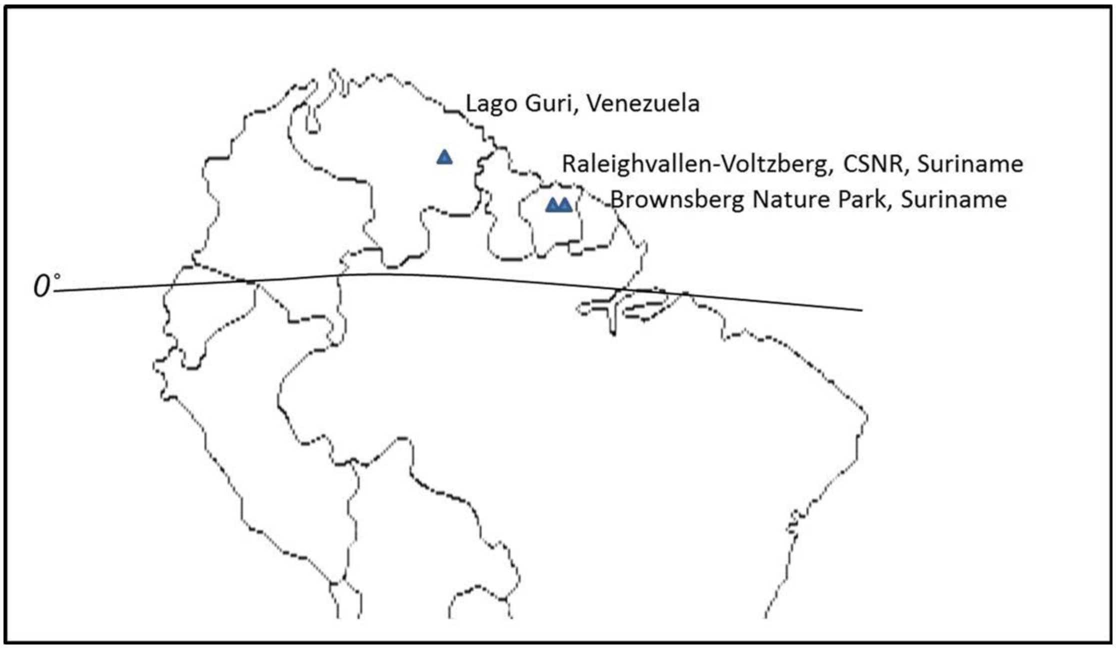

Fig. 4. Location of South American field sites used in the study. CSNR, Central Suriname Nature Reserve.

was ingested, that is, seeds only, mesocarp only, arils only, fruit pulp only, whole fruit including seeds. Notations were also made about fruit and seed ripeness. Seeds embedded in ripe fruit were assumed to be fully mature and likewise, seeds from immature fruit were assumed to be young (immature).

Sampling methods: laboratory analysis. Monkeys are selective about what they eat and they often drop partially eaten fruit and fruit husks while feeding (e.g., Dew, 2003). Samples of fruit (that were visually equivalent to what was ingested) were collected during feeding bouts and labeled with fruit species and tree number. Puncture resistance of fruit pericarp was tested on the same day as collected using a mechanical force gage (models FDK 10 and 30, capacities of 5 and 10 kg, respectively: Wagner Instruments, P.O. Box 1217, Greenwich CT 06836). Crushing resistance of seeds was estimated using a Rimac Spring Tester (capacity to 160 kg). Since many fruit are harder than 10 kg, Kinzey adapted a 1.6 mm diameter pin (a replica of the mechanical force gage pin dimension) to the spring tester for measurements of harder fruit (see Kinzey and Norconk, 1990: 1993) (Fig. 5). The average of three puncture measurements was taken of each sample (unless the sample was very small) and the average value was divided by the area of the pin recorded as kg/mm^2. A single crushing measurement was taken of seeds and/or whole fruit that were masticated whole including seeds. Minimum, average and maximum values were recorded for each species (Table 1), but only maximum values were used in the analysis since our goal was to estimate the upper range of pericarp protection and seed hardness at the stage of ripeness in which the food item was eaten. Some data were collected on uneaten items, for example, puncture and crushing values were taken of fruit at a wider range of maturity than the stage the item was ingested (e.g., Kinzey and Norconk, 1993). Since the goal of this study is to compare puncture and crushing resistance values of foods ingested, we will not attempt to address the issue of why some food items were dropped or not eaten.

Field tests of mechanical properties of food have also been analyzed using the Darvell tester (see Lucas et al., 2000; Lucas et al., 2003; Lucas 2004 for a review of food and tooth physical properties). Puncture resistance (measured in this study as the force required to initiate a crack in fruit pericarp or seed coats) is similar to the "indentation test" using the Darvell tester, but the simple puncture test does not follow crack propagation through the material (elastic modulus). Observations of sakis suggest that they rely heavily on anterior dentition, particularly canines, to open fruits to extract seeds. Likewise, our crushing resistance estimates measure structural strength of a food and are intended to mimic masticatory force of the posterior dentition.

Analysis

Descriptive statistics (mean ± sd, minimum, maximum) were taken on raw data, but given the wide range of values among species, puncture and crushing resistance maximum values and body mass values were logged (base$_{10}$) before statistical analysis. Data on body mass for correlation with puncture and crushing values were taken from Smith and Jungers (1997). Since the feeding data are not reported as sex-specific in published sources, body mass was averaged for sexually dimorphic species.

Parametric procedures on logged data were used to test for differences between species or between sites using Student's independent sample T tests and Pearson R correlations. Samples from multiple species or more than two study sites were analyzed using one-way ANOVAs (SPSS 16.0). Bonferroni post hoc tests were employed in cases where ANOVAs uncovered significant

TABLE 2. Puncture and crushing resistance values reported in the literature for lemurs, cercopithecoids, and chimpanzees; (N = number of plant species tested)

Superfamily	Taxon	Puncture values (kg/mm^2)				Crushing values (kg)			
		N	Min	Mean ± sd	Max	N	Min	Mean ± sd	Max
Lemuroidea	*Lemur catta*[a]	9	0.13	0.61 ± 0.52	1.49				
	Eulemur fulvus rufus[a]	19	0.15	0.63 ± 0.37	1.24				
	Eulemur rubiventer[a]	20	0.21	0.69 ± 0.41	1.38				
	Propithecus diadema[a]	22	0.13	0.70 ± 0.36	1.45				
	Propithecus v. verreauxi[1]	6	0.15	0.61 ± 0.45	1.20				
Ceboidea	*Ateles paniscus* Sur 1	26	0.03	0.69 ± 0.36	1.40				
	Chiropotes sagulatus Sur 1	32	0.03	3.36 ± 6.71	37.80	19	1.82	9.23 ± 6.55	22.27
	Chiropotes sagulatus- Sur 2	12	0.92	2.32 ± 1.06	4.02	4	17.50	29.12 ± 13.64	45.00
	Chiropotes satanas – Ven	60	0.05	3.30 ± 6.06	33.84	14	1.82	9.91 ± 7.63	23.20
	Pithecia pithecia – Ven	25	0.01	1.80 ± 1.73	6.77	26	1.36	15.48 ± 15.40	52.27
	Pithecia pithecia - Sur 2	28	0.69	3.05 ± 2.25	9.18	16	2.00	31.29 ± 24.82	80.00
Cercopithecoideae	*Cercopithecus ascanius*[b]	25	0.01	1.19 ± 1.18	4.00				
	Cercopithecus aethiops[c]					1	49.30		49.30
	Erythrocebus patas[c]					1	4.80		4.80
	Cercocebus galeritus[d]	19	0.10	2.81 ± 3.59	5.20	13	0.10	23.3 ± 17.11	54.10
	Lophocebus albigena[be]	34	0.01	2.53 ± 3.59	17.00	14	1.00	8.34 ± 5.90	19.25
	Papio spp.[c]					9	5.00	75.33 ± 105.07	338.06
Hominoidea	*Pan troglodytes*[c]					4	13.00	86.43 ± 84.57	224.85

Ceboid samples summarized from database in Table 1 for *Chiropotes* spp. (bearded sakis), *Pithecia pithecia* (white-faced sakis), and *Ateles paniscus* (spider monkeys). See notes at the end of Table 1 and Methods for location of field sites.

[a] Yamashita (1996).

[b] Lambert et al. 2004.

[c] Peters, 1992.

[d] Wieczkowski, 2009; crushing values for *Lophocebus* included 10 spp of bark.

Fig. 5. Rimac spring tester fitted with a 1.6 mm diameter pin to test puncture resistance of fruit >10 kg/mm^2. *Tontelea coriaceae* (Celastraceae) partially eaten by *Pithecia pithecia* is pictured. [Photo by M. Norconk].

differences. All tests were nondirectional and the level of significance was set at $P = 0.05$.

RESULTS

Puncture Resistance of Fruit Pericarp

Maximum puncture resistance values for 104 fruit (93 species) ranged from 0.03 to 37.8 (mean = 3.20) kg/mm^2 for three populations of *Chiropotes* and 0.01–9.18 (mean = 2.46) kg/mm^2 for 53 fruit (48 species) ingested by *Pithecia* (Table 1). Despite the higher maximum values for *Chiropotes*, means were not significantly different ($t = 0.27$, ns; Fig. 6). Significant differences in puncture resistance values were found between the two *Pithecia* geographic populations ($t = 2.92$, $P < 0.01$), but not among the three *Chiropotes* populations (ANOVA, $F = 0.514$, df = 2, ns).

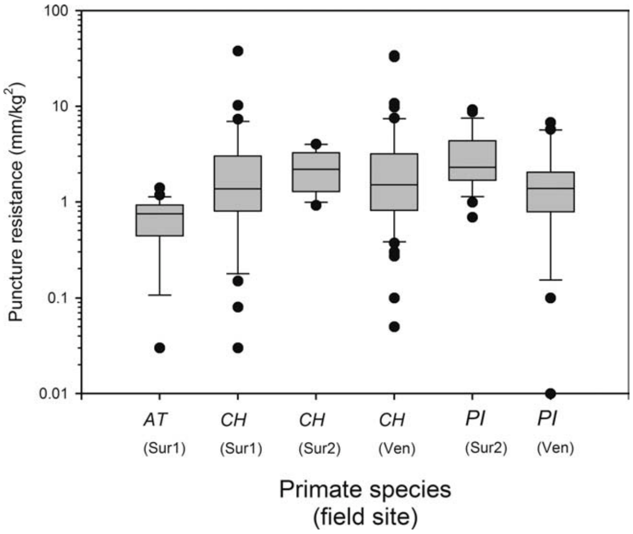

Fig. 6. Box plots represent 25th and 75th percentiles with median as the horizontal line within the box. Whiskers denote 10th and 90th percentiles and outliers are represented by dots. The line inside the box represents the median score for that "population": Ven = Lago Guri, Venezuela; Sur 1 = Raleighvallen-Voltzberg, Suriname; Sur 2 = Brownsberg Nature Park, Suriname. *Ateles* (AT) values were significant lower than either *Chiropotes* (CH) or *Pithecia* (PI) and there were significant differences between the two *Pithecia* samples (see text).

Using 1.4 kg/mm^2 as the maximum puncture resistance value of *Ateles*, a ripe fruit sample, 44.2% (46/104) of fruit species in the *Chiropotes* diet and 37.7% (20/53) in the *Pithecia* diet were below the threshold, i.e., relatively soft. As expected based on previous data (Kinzey and Norconk, 1990), *Ateles* ingested significantly softer fruit than *Chiropotes* and *Pithecia* (ANOVA: $F = 11.24$, df = 2, $P < 0.001$). Bonferroni post hoc tests confirmed that the difference was driven by both *Chiropotes* (mean difference = 0.489, $P < 0.001$) and *Pithecia* (mean difference = 0.512, $P < 0.001$). However, the quantity of fruit species bearing pericarps that are below the *Ateles* puncture threshold suggests that a substantial portion of the diets of both pitheciins is made up of fruits with "soft" pericarps. Lemurs fall within the *Ateles* range, except for *Lemur catta*, whose maximum puncture resistance score was modestly higher at 1.49 kg/mm^2. There were no significant differences among lemurs ($F = 0.441$, df = 4, ns), nor among lemurs and *Ateles* ($F = 0.297$, df = 5, ns).

The maximum puncture resistance value of fruit successfully opened by a medium-sized Old World monkey (red-tailed guenon: *Cercopithecus ascanius*) without specialized adaptations in the masticatory system was 4.0 kg/mm^2 for *Uvariopsis congensis*, Annonaceae (Lambert et al., 2004) (Table 2). More than 15% of fruit samples opened by *Chiropotes* (18/104) and 20.7% (11/53) opened by *Pithecia* were tougher than the highest reported value for the guenon.

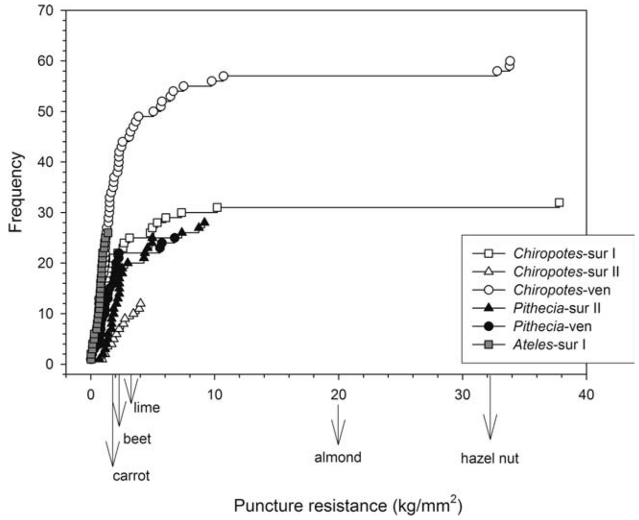

Fig. 7. Puncture resistance of foods ingested by *Ateles paniscus*, *Chiropotes* spp., and *Pithecia pithecia*. Frequency (number of of food species sampled) is plotted by the (maximum) puncture resistance of the pericarp. Each marker represents a food species, except in cases when the same species was used in at multiple stages of maturity (e.g., *Pradosia caracasana*, see Table 1) or by different primate species. Most values are below 10 kg/mm^2 and many fall within the narrow range of values used by *Ateles*. The three field sites are abbreviated as Sur 1 = Raleighvallen-Voltzberg, Suriname, Sur 2 = Brownsberg Nature Park, Suriname, Ven = two islands in Lago Guri, Venezuela (see Methods). For scale, puncture resistance values (kg/mm^2) were conducted on uncooked vegetables and raw nuts in their husks: carrots, 0.89, N = 1; beets, 0.9, N = 2; lime, 1.88, N = 2; almonds, 20.0, N = 4; hazel nuts, 32.51, N = 8).

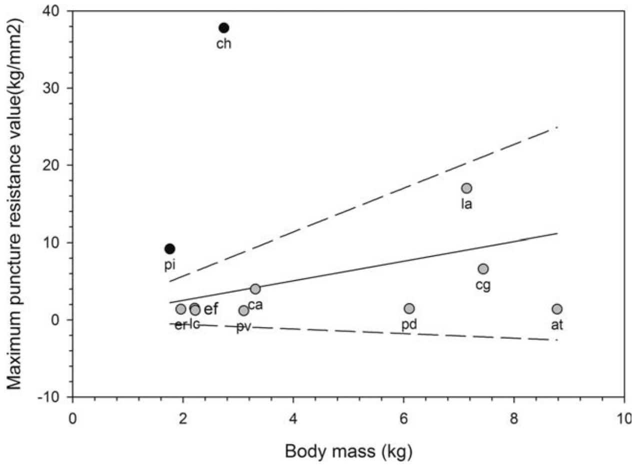

Fig. 8. Body mass (kg) is plotted against the maximum puncture resistance values for three genera of New World monkeys (*Pithecia pithecia* (pi), *Chiropotes* spp. (ch), and ap = *Ateles paniscus*), five species of prosimians (*Eulemur rufus* = er, *E. fulvus* = ef, *Lemur catta* = lc, *Propithecus verrauxi* = pv, *Propithecus diadema* = pd) and three species of Old World monkeys (*Cercopithecus ascanius* = ca, *Lophocebus albigena* = la, and *Cercocebus galeritus* = cg). Body mass data was taken from Smith and Jungers (1997). Male and female body masses were averaged because puncture resistance values were not reported by sex. Key: the two pitheciin genera are in black; other taxa in gray.

The mangabeys, *Cercocebus* and *Lophocebus*, are now recognized as belonging to different Old World monkey clades, but both have powerful jaws and thick enamel and are known to open and masticate hard/tough foods (Fleagle and McGraw, 2002; Lambert et al., 2004; Daegling and McGraw, 2007). Data collected for *Cercocebus galeritus* (Wieczkowski, 2009) had significantly higher average puncture resistance values than *Lophocebus albigena* (Lambert et al., 2004) ($t = 2.08$, $P < 0.05$). Puncture resistance scores for sakis were significantly different from those recorded for mangabeys ($F = 22.61$, df = 3, $P < 0.001$), but Bonferroni post hoc tests suggested that fruit opened by the sakis (*Chiropotes* and *Pithecia*) and *Cercocebus galeritus* was significantly harder than fruit opened by *Lophocebus albigena*.

The maximum puncture resistance values for *Pithecia* was 30.0 kg/mm^2 (Lecythidaceae: *Lecythis idatimon*) and *Chiropotes* was 37.8 kg/mm^2 (see Figs. 2 and 3), almost double the mangabey published maximum. Nevertheless, these mechanically resistant saki resources represented only a few plant species at each site and only 3% of the total sample of foods ingested by the sakis (*Pradosia caracasana* and *Vitex compressa* (Ven), *Licania majuscula* (Sur 1) (Fig. 7). While the maximum value for *Pithecia* was about 10 kg/mm^2 from wild foods, captive *Pithecia pithecia* can open commercial hazel nuts by repeatedly scaring the smooth endocarp until they could puncture it with their canines (Norconk, unpublished). Despite the relatively few very hard foods punctured by sakis, some of them were probably important to their seasonal diets (see below). Finally, body mass was not correlated with puncture resistance values (Pearson R = 0.85, ns, N = 11) ($r^2 = 0.01$), and only *Chiropotes* and *Pithecia* were outside of the 95% confidence limits (Fig. 8).

Summarizing the puncture resistance data above, (1) there were no significant differences among five lemur taxa that included two *Propithecus* spp.; (2) fruit eaten by lemurs fell within the range of puncture resistance values of fruit eaten by *Ateles*, a platyrrhine that ingests a high proportion ripe fruit pulp; (3) between two species of mangabeys, available data suggest that *Cercocebus galeritus* has a more resistant diet overall than *Lophocebus albigena*, even though the latter had a higher recorded maximum puncture resistance score; (4) the puncture resistance of foods opened by both *Pithecia* and *Chiropotes* fell within the range or exceeded the hardness of fruits opened by mangabeys, the Old World monkey seed specialists; (5) the most resistant fruit opened by sakis made up a small proportion of the total number of species used (one-quarter to one-third of foods in the diet fall within the narrow range of fruits opened by *Ateles* and < 3% of fruit exceeded the range of values used by *Lophocebus*); and (6) body mass was not a good predictor of maximum puncture resistance values.

Crushing Resistance of Foods

Data on crushing resistance of food items are available for five species of Old World monkeys, the two pitheciins, and chimpanzees (Table 2; Fig. 9). Most of these items are fruit or seeds, but a substantial proportion of samples from *Lophocebus* (10/14) was bark, a fallback resource (Lambert et al., 2004). Baboons and chimpanzees appear to be capable of crushing seeds that are several times harder than seeds ingested by mangabeys or

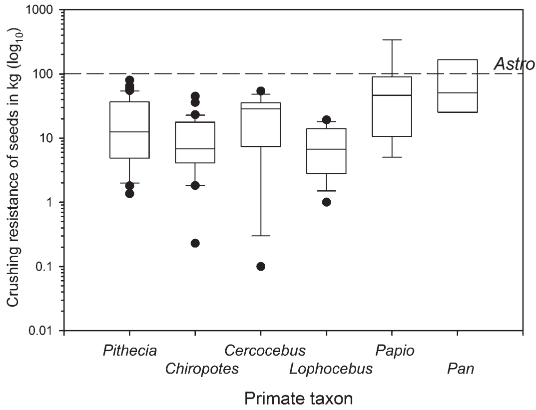

Fig. 9. Box plots of logged base$_{10}$ crushing resistance scores demonstrating the range of variation in hardness of seeds masticated by five primate genera. Box plots represent 25th and 75th percentiles with median as the horizontal line within the box. Whiskers denote 10th and 90th percentiles and outliers are represented by dots. The dashed line (100 kg) is the lowest crushing resistance value of dried nuts and seeds masticated whole by peccaries (Kiltie, 1982). Peccary crushing resistance of palm fruit ranged from 100 kg (*Astrocaryum and Jessenia* spp.) to 390 kg (*Mauritia flexuosa*). Fruit pulp has essentially no resistance = 0.01 kg (Norconk, personal observation).

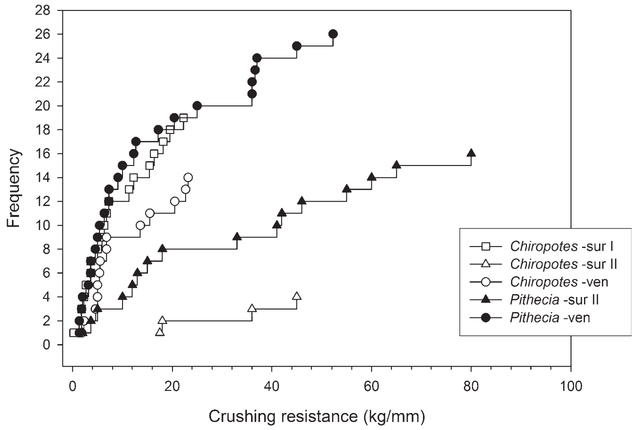

Fig. 10. Crushing resistance of seeds ingested by *Chiropotes* sp. and *P. pithecia* at three field sites in northern South America. Sites are the same as those in Figure 3.

pitheciins. Crushing values of seeds eaten by chimpanzees were not significantly different from baboons (t = 0.67, df = 12, ns), thus we combined these samples for comparison with the mangabey and pitheciin samples. Seeds masticated by chimpanzees and baboons were significantly harder than seeds or bark masticated by mangabeys (F = 7.0, df = 2, $P < 0.01$), but whereas Bonferroni post hoc tests demonstrated a significant difference between *Lophocebus* and the baboon-chimpanzee samples (mean difference = 0.83, $P < 0.01$), the difference between *Cercocebus* and the baboon-chimpanzee samples was marginal (mean difference = 0.566, P = 0.057). The latter reflects the relatively greater hardness values of foods ingested by *Cercocebus* than *Lophocebus*.

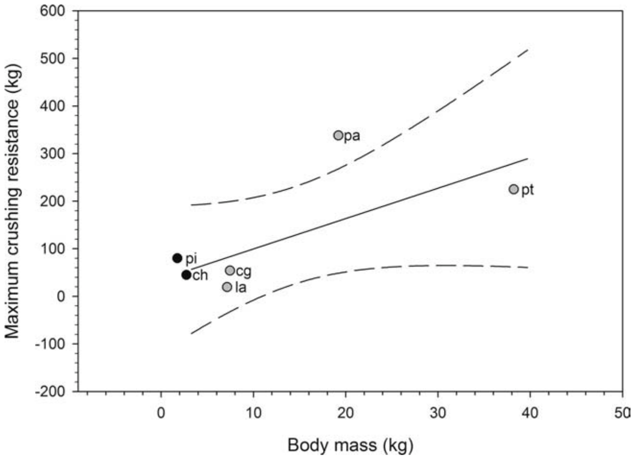

Fig. 11. Body mass is plotted against the maximum crushing resistance values. Dashed lines represent 95% confidence limits. Key: the two pitheciin genera are in black; other taxa in gray. "See Fig. 8 for species' codes. In addition, *Pan troglodytes* = pt and *Papio anubis* = pa."

Seeds masticated by *Pithecia* were significantly harder than those eaten by *Chiropotes* (t = 2.21, $P < 0.03$, *Pithecia* N = 42, *Chiropotes* N = 33) (Table 2; Fig. 10), but there was no difference between sakis and mangabeys (*Lophocebus* and *Cercocebus*) (F = 2.08, df = 3, ns). Baboons and chimpanzees crushed much harder seeds than the two species of sakis (F = 5.72, df = 3, $P < 0.01$). A Bonferroni post hoc test showed that *Pithecia* seeds were significantly softer than those masticated by chimpanzees (mean difference = 0.668, $P < 0.03$), but not baboons. Seeds eaten by *Chiropotes* were significantly softer than both baboons and chimpanzees (F = 17.02, df = 2, $P < 0.001$). Only chimpanzees appear to be able to crush seed coats in the range of 100 kg (Table 2), the average value for *Jessenia* sp. seeds and well below the maximum capability of peccaries (Kiltie, 1982).

Finally, body mass was not correlated with crushing resistance (Pearson R = 0.60, N = 6, ns) (Fig. 11). Even though it was not significant, body mass accounted for about 1/3 of the variance in crushing resistance (r^2 = 0.36, N = 6, ns). Sakis, mangabeys, and chimpanzees were close to the regression line determined by maximum crushing resistance scores and body mass.

In summary, seeds crushed by baboons and chimpanzees are two to three orders of magnitude harder than seeds eaten by mangabeys or sakis and the crushing resistance of seeds masticated by sakis are comparable to those eaten by mangabeys. Nineteen percent of seeds crushed by *Chiropotes* and 38% of seeds crushed by *Pithecia* were tougher than the *Lophocebus* maximum (19.25 kg), but only a few species of seeds in the *Pithecia* diet and none in the *Chiropotes* diet were harder than the *Cercocebus* maximum (54.1 kg). Body mass was not significantly correlated with crushing resistance of seeds, although there is a positive trend relating body mass to crushing resistance.

Seasonality of Puncture Resistance Values

Rainfall was not correlated with pericarp hardness for bearded sakis (rho = –0.347, ns, N = 12 months for

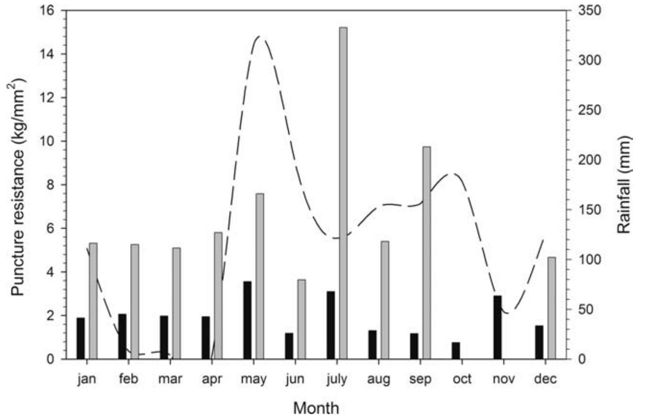

Fig. 12. Seasonality in the puncture resistance scores for bearded sakis (Lago Guri, 1991–1992). Monthly rainfall is indicated by the dashed line. The black bars represent the average of all puncture resistance values for each month; the gray bars are maximum values designated as values >3.3 kg/mm^2, the annual average. If there were multiple values >3.3 kg/mm^2 in a monthly sample, the values were averaged.

average values; rho = –0.122, ns, N = 10 months for maximum values) (Fig. 12) or white-faced sakis (rho = −0.473, ns, N = 11; rho = 0.657, ns, N = 6) (data not shown). However, we did document interannual variation in average and maximum puncture resistance values for the principal food sources of bearded sakis (*Pradosia caracasana* Sapotaceae) in Lago Guri that may have been related to difference in annual rainfall (1992 was an El Niño year). In July 1991, average and maximum puncture resistance values were 1.86 and 3.44 kg/mm^2, respectively (N = 20). In July 1992, the measurements were 24.5 and 33.8, respectively (N = 2) (Norconk, unpublished). Whereas, *P. caracasana* made up 80% of the July 1991 diet, it made up only 44% of the July 1992 diet.

DISCUSSION

This synthesis is an early attempt to relate the use of well-protected resources by an array of primate seed predators. Even though the methods used to measure fruit and seed resistance to being opened or masticated were standardized by using the same equipment, there are some noticeable deficits in the data. For example, comparable data are not always available for both puncturing and crushing measurements. If the pericarp is not removed before mastication, then it is logical to collect only crushing resistance measurements, but that might not be the case for all fruit in the diet. Second, data are missing from some well-known seed predators, for example, mandrills (*Mandrillus sphinx*), orangutans (*Pongo pygmaeus*) (see Lucas et al., 1994; Taylor, 2006), uakaris (*Cacajao* spp.), capuchins (*Cebus* spp., but see Wright, 2005, for assessment of toughness of fruit eaten by capuchins and sakis), and colobines (McKey et al., 1981; Yeager, 1989; Maisels et al., 1994).

Third, studies are not of comparable length or may not have included an entire annual cycle making it difficult to evaluate the timing of the use of mechanically resistant resources relative to food preferences or food availability (see below). Fourth, there is generally a lack of within-species data with which to compare male-female and age-related differences in feeding behavior. While it is rare to find significant sex-specific differences at the level of species composition or items included in the diet, there are many possible areas of subtle variation. For example, Fleagle et al. (2010) noted that much of the interspecific diversity in primate cranial dimensions is due to male morphotypes. Mandibles that are larger, longer, capable of more masticatory force or able to withstand more increased loads may signal subtle dietary differences in food handling and processing that could translate to variation in nutritional intake. Fleagle and McGraw (2002) demonstrated that lower premolars were relatively larger in male *Cercocebus* spp. *Lophocebus* spp. and *Mandrillus sphinx* compared to females. How these differences in dental metrics translate into feeding differences is not yet known, but Chancellor and Isbell (2009) found that female mangabeys (*Lophocebus albigena*) engaged in long bouts of bark stripping using anterior dentition that included higher rates of aggression and displacement among females than in fruit trees. Thus, behavioral data support the findings of Daegling and McGraw (2007): *Lophocebus* females specifically (and *Lophocebus* spp. in general relative to *Cercocebus* spp.) have very narrow mandibular arches and are capable of powerful incision.

In spite of the considerable shortcomings in our current understanding of the variation and significance of seed eating as a feeding strategy in primates, we offer two tentative conclusions from our analysis:

1. Body mass is not correlated with seed predation *per se*. While the ability to masticate tough seeds or bark showed a positive, albeit nonsignificant trend, there was no relationship between body mass and puncture resistance of fruit and seeds. Sakis and bearded sakis exhibit the most derived and specialized anterior dentition of the seed predators. Among platyrrhines, *Cebus apella* followed by *Chiropotes*, *Cacajao*, and *Pithecia* have the best positioned masticatory muscles for biting at the molars (i.e., mastication) and at the incisors (i.e., incision) in a study that compared all 16 genera of platyrrhines (Norconk et al., 2009; also see Anapol and Lee, 1994; Wright, 2005). Sakis appear to have similar capabilities as mangabeys, but the opportunistic samples collected from baboons and chimpanzees (Peters, 1993) suggest that these genera have much higher crushing abilities.
2. Turning from maximum capabilities to more routine food use, many species of fruit in the diet of seed predators are within the range ingested by nonseed-eating frugivores and are not mechanically challenging. Primate seed predators can extend their range of suitable foods to include very well-protected fruit and seeds, but about 40% of the fruits opened by sakis and bearded sakis are “soft” as defined by the range of *Ateles* hardness values. While some foods ingested by sakis are not commonly found on food lists of other primates (e.g., Bignoniaceae seed pods, species of indehiscent, well-protected, and mesocarp-deficient drupes of Lecythidaceae and Chrysobalanaceae), there are many genera that are used widely among primates (e.g., *Inga, Brosimum, Ficus, Virola, Passiflora, Chrysophylum, Paullinia, Melicoccus, Solanum,* and

Cecropia) (e.g., Estrada and Coates-Estrada, 1984; Stevenson, 2005; Simmen et al., 2007).

Are Hard Foods also Fallback Foods for Primate Seed Predators?

There are multiple definitions of fallback feeding strategies related to how consumers deal with variation in food availability and changes in rank of preferred resources (e.g., recent papers: Lambert et al., 2004; Lambert, 2007; Marshall and Wrangham, 2007; Altmann, 2009). Lambert (2007) recognized two types of fallback foods: foods of lower nutrient density, but relatively high abundance (i.e., leaves, bark, fungus), and foods that are nutrient rich, but are less abundant. Lambert placed seeds in the second category which makes sense in terms of their relatively high nutritional quality, but this placement is complicated by their relative abundance (see below) and the expectation that primates solve the problem of access to resources behaviorally, not morphologically (e.g., *Cebus* spp., some of which use stone tools to crush hard seed coverings (endocarps) of palm seeds: Fragaszy et al., 2004; Vizalberghi et al., 2009). Indeed, tool use by capuchins (Fragazsy et al., 2004; Visalberghi et al., 2009) and chimpanzees (e.g., McGrew, 1992; Matsuzawa, 1994; Yamakoshi, 1998) appears to extend their abilities to open very well-protected fruit or seed coats. For pitheciins, the extraction of seeds is clearly facilitated by dental adaptations (and digestion of seeds may be enhanced by gut adaptations, Milton, 1984; Norconk et al., 2002), but there may also be a premium placed on remembering the location of seed-producing trees. This perspective is well documented by Cunningham and Janson (2007) for white-faced sakis. They found that sakis fed from highly productive (*Licania discolor* and *Capparis muco*) trees preferentially (Table 1), approached feeding trees from a variety of locations, did not use habitual paths when fruiting trees were abundant, and behaved as if they remembered the relative the productivity of fruiting trees. The ability to find and eat seeds regardless of season may also explain why the larger-bodied pitheciins have the largest home ranges of any platyrrhine (Boyle et al., 2009; Norconk, 2011; Gregory, 2011). Thus seeds as potential fallback foods may fall into both categories—providing morphological and cognitive challenges—or neither.

Do pitheciins encounter periods of food scarcity or periods in which preferred resources decline? Do they fall back on nonpreferred resources and what would those be? The lack of correlation between pericarp hardness and rainfall suggests a particular evenness in their diets and this has been noted by others looking at the proportion of fruit in *Chiropotes* annual diets (e.g., Ayres, 1981; Boyle, 2008). The data presented in this study are better for Lago Guri than the free-ranging sites in Suriname, but it appears that high-ranked resources are those species that have a relatively long fruiting cycle and remain preferred resources across a wide range of hardness values. The top two resources for *Pithecia* (Lago Guri site) produced unripe or ripe fruit for 11 months and three of the top four species fed on by *Chiropotes* produced fruit for 10–12 months annually (Norconk, 1996). Veiga (2006) also noted that bearded sakis used high ranked species for long periods of time (six to eight months) and seed ingestion peaked during the dry season (*cf*., Ayres, 1981; Peetz, 2001). Thus the concept of seasonal scarcity of preferred resources is challenged by sakis.

Fig. 13. Large *Strychnos tomentosa* (Loganiaceae) fruit opened by *Chiropotes sagulatus* at Brownsberg Nature Park. The fruit from this high-climbing liana is protected by a nondehiscent, thick, corky pericarp. Sakis ingest the mesocarp adhering to seeds and generally have not been observed to eat *Strychnos* spp. seeds. [Photo by M. Norconk].

Saki diets are not uniform. They contain a high proportion of fruit throughout the year and fruit are derived from variable sources. For example, Boyle (2008), Peetz (2001), and Norconk (1996) have noted the high proportion of seeds extracted from liana fruit. This point is interesting in light of Marshall et al.'s (2009) suggestion that lianas may provide important fallback foods for primates. Once again however, sakis (particularly bearded sakis) provide a twist on the typical view of fallback foods. While sakis do ingest fleshy fruit from lianas (e.g., *Salacia cordata*, Celastraceae and *Strychnos* spp, Loganiaceae) (Fig. 13), they primarily eat winged seeds from a young Bignoniaceae pods (Table 1). Seeds are extracted from these (often) large, woody pods before they dehisce and these pods rank among the hardest fruits opened by the sakis during the dry season. Dental adaptations enable sakis to gain access to mature and young seeds for long durations and minimize fluctuation in resource type.

Even if interseasonal variation is dampened by long fruiting cycles and access to young and mature seeds, there is some evidence that interannual variation in food availability could present different challenges and expose the use of "critical" resources or fallback strategies. Lambert et al. (2004) found that *Lophocebus albigena* in Kibale National Park, Uganda, included more fruit, seeds and bark in their diets than sympatric guenons, but the differences were most apparent in an extremely dry year. Gray-cheeked mangabeys were able to crack hard *Diospyros abyssinica* seeds and also ingested bark at higher frequencies during a dry El Niño year compared with previous years of "normal" rainfall (Lambert et al., 2004). Thick enamel and powerful jaws enabled *Lophocebus* to crush hard post-dispersed seeds and gain access to critical (or fallback) resources during times of fruit scarcity. We found a similar situation while studying bearded sakis. *Pradosia caracasana* (Sapotaceae) is the highest ranked resource in the diet of bearded sakis in Lago Guri and *Pradosia* seeds and/ or mesocarp is available (Norconk, 1996) and ingested every month of the year (Norconk et al., 1998). The crop during the El Niño year largely failed. Hardness values peaked and proportion of *Pradosia* in the diet was halved in July of the El Niño year. Still, it is difficult to imagine that old, dried *Pradosia* fruit is a fallback fruit whereas the seeds of the same species are the dominant resource in most seasons and most years or that processing strategies are different. While studies conducted on islands suggest that hard foods may be the foods of last resort, in a recent study on free-ranging bearded sakis in Suriname, *Licania majuscula* (Lecythidaceae) ranked 4th in percentage of total feeding samples out of 112 species (Gregory, 2011), which would place this species with very hard pericarp among a short list of preferred resources. Morphological and behavioral strategies related to seed predation appear to widen niche breadth (temporally and in terms of plant species diversity) and minimizes periods of resource scarcity that are encountered by other frugivorous primates. As such, seed predators do not fit neatly into current views of fallback feeding strategies.

Fallback feeding strategies predict that animals will resort to eating low-quality or less preferred foods when resource abundance declines. Optimal foraging predicts the opposite: animals should eat preferred foods when they are abundant and broaden their diet breadth when resources are scarce (Robinson and Wilson, 1998). This view appears to fit the saki strategy better than employing fallback strategies. Seeds are relatively abundant year-round and their dental and behavioral specializations enable them to take advantage of these resources. Resource rank seems to bear little resemblance to the mechanical properties of fruit—although the chemical properties of seeds may influence food choice.

We have not addressed feeding habits of the third pitheciin genus, *Cacajao* spp. or uakaris. A study of black uakaris by Boubli and Tokuda (2008) confirm the general pattern outlined above for bearded sakis and white-faced sakis. Black uakaris had a high intake of seeds embedded in well-protected husks, ingested both young and mature seeds from specific species for more than eight months, and primary resources were asynchronous resulting in a relatively even temporal distribution of resources. No "fallback" resources were mentioned by Boubli and Tokuda (2008) although Barnett et al. (2005) studying golden-backed uakaris suggested that leaves may be fallback foods for that species.

Do Pitheciins Provide a Primate Model for Liem's Paradox?

Liem (1980) drew attention to the apparent mismatch between specialized morphologies and yet the "jack-of-all-trades" feeding strategies of some cichlid fish. Sakis have very specific adaptations of both anterior and posterior dentition used in extracting and masticating seeds, yet their diets are much broader than would be expected if their morphology limited their food choice. In a recent study of durophagous cichlid fish, Binning et al. (2009) used feeding data extrapolated from stomach contents and stable isotopes of tissue to test whether hypertrophied jaws were correlated with high frequency of feeding on hard-shelled molluscs. Jaw morphology is developmentally induced by crushing hard prey in these fish. Even so, molluscs represented an average of only about 5% of the diet over the 30-month and provided support for Liem's paradox in fish.

While specialized masticatory morphologies of some fish and primates provide access to a range of resources that are either unavailable or unattractive to sympatric members of the community, their morphologies do not appear to limit their access to soft foods. On the basis of our finding that both white-faced and bearded sakis exhibit highly specialized dental anatomy and they open very hard pericarps rarely, with most fruit opened falling well into the category of fruit eaten by a wide variety of primates, we acknowledge that sakis and bearded sakis may exemplify Liem's paradox in primates. On the other hand, Robinson and Wilson (1998) proposed an alternative view that resolves Liem's paradox—some resources (e.g., ripe fruit in a tropical forest) are easy to use by all consumers. Specialists can "have their cake and eat it too" (Robinson and Wilson, 1998:231) using easily extractable resources when they are available.

With their very divergent dental adaptations, pitheciins represent one type of primate seed predator. The duration of seed availability relative to fruit pulp ingested by most primates has made seeds a valuable and reliable (seasonal or year-round) resource for several lineages. Dental adaptations have extended the ability of primates to open mechanically protected resources and with the implementation of tools in some groups (capuchins, chimpanzees, orangutans, and humans), they have virtually foiled the protective mechanisms of plants. Even though seeds or nuts are not a major resource for many frugivorous primates, the diversity of both behavioral and masticatory adaptations, attest to the valuable nature of seeds as potential resources. The most important advantages of seed predation in primates may be related to dampened fluctuation in seasonal plant productivity and a broadened niche in gaining access to reproductive plant parts.

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