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Seed Dispersal by Neotropical Seed Predators

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From a plant's perspective, the difference between a seed predator and a seed disperser should be straightforward: attract animals that will disperse seeds and defend seeds from potential predators. Unlike pulp-eating frugivores, seed predators regularly encounter diverse plant protective mechanisms. The purpose of this paper is to examine feeding constraints, morphological adaptations, and the mechanical process of seed predation. While there is evidence that some seed predators cause severe losses to seed crops, there is also evidence that seed predators enhance seed dispersal and germination. We also examine four methods by which neotropical seed predators may contribute to dispersal. 1) Seed predators examined here ingested fruit when seeds were full-sized, but not yet mature (i.e., seeds of mature fruit may be avoided by seed predators and available for dispersal by other frugivores). 2) Sympatric seed predators may ingest seeds from different plants thus reducing overall predator load on any individual plant. 3) Seed predators that manipulate seeds (e.g., remove pericarp and seed coat) may enhance germination if the prepared seeds are dropped, discarded, or buried and not ingested. 4) Small seeds may miss mastication and swallowed intact with a food bolus. The last mechanism is the most likely to contribute to seed dispersal by the widest array of vertebrate seed predators, but primate seed predators may facilitate seed dispersal using all four mechanisms. Therefore, the traditional dichotomy of seed predator vs. seed disperser oversimplifies the interactions between seed predators and plants. Am. J. Primatol. 45:103–126, 1998.

Key words: seeds; predispersal and postdispersal seed predation; seed protection; nutrition; Pitheciinae; Colobinae

INTRODUCTION

Morphological and behavioral adaptations associated with leaf eating are well known and have been investigated from numerous perspectives [gut morphology: e.g. Bauchop & Martucci, 1968; Chivers & Hladik, 1980; Lucas & Teaford, 1994; food passage rates: Milton, 1984; food selection and gut physiology: Oates et al., 1980; McKey et al., 1981; Dasilva, 1994; Maisels et al., 1994]. Investigations into the feeding strategies of fruit eaters have focused less on structural adaptations and more on behavioral mechanisms that aid in food search [e.g., Chapman, 1988;

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Milton, 1988; Garber, 1989; Janson, 1996]. However, frugivores specializing in eating seeds regularly encounter the same plant defenses that protect seeds from invertebrate predators. For these animals, adaptations in the dentition and gut, as well as behavioral mechanisms that enable them to avoid plant toxins, should be expected.

Seed predators are defined as animals that ingest seeds year-round or as a seasonally important component of their diet. Primate seed predators are found in each of the major evolutionary radiations and appear to exhibit morphological and behavioral adaptations that allow them both to gain access to seeds and to digest them [strepsirhines: *Daubentonia madagascariensis:* Sterling, 1994; Kitko et al., 1996; *Propithecus* spp.: Meyers & Wright, 1993; Yamashita, 1994; Hemmingway, 1996; Strait & Overdorff, 1996; catarrhines: colobines (see Table I), baboons: Whiten et al., 1992; Peters, 1993; *Cercopithecus aethiops:* Wrangham & Waterman, 1981; Peters, 1993; *Cercocebus* spp.: Waser, 1977; Horn, 1987; *Pongo pygmaeus*: Leighton 1993; Ungar, 1995; *Pan troglodytes*: Boesch & Boesch, 1983; and platyrrhines: pitheciines and *Cebus apella* (see Table II)]. In order to more fully understand the relationship between seed predators and their effects on plants, we intend to discuss relevant theoretical issues, explore the range of adaptations exhibited by seed predators, place platyrrhines (particularly pitheciins) within the neotropical seed predator guild of mammals and birds, and to suggest four ways that members of this guild might favorably tilt the balance of seed predation from the cost of seed loss to the benefit of seed dispersal.

SEED PREDATION AS A FEEDING STRATEGY

Seed predators are often divided into two groups: “predispersal” and “postdispersal” predators [Janzen, 1971]. Predispersal seed predators include arboreal, scansorial, and volant species that remove immature and mature fruit from the tree crown and ingest the seeds. Postdispersal seed predators are partly or entirely terrestrial and ingest mature seeds that have dropped to the ground. Seed predators can also be characterized by their degree of resource specialization, (e.g., primarily invertebrates that depend on a few plant species and primarily vertebrates that ingest seeds from a diverse array of species) [Crawley, 1992]. All the seed predators discussed below are generalists that extract seeds from a variety of tree species and therefore confront a diversity of seed protections.

The presence of defenses in seeds or seed coats provides the best indirect evidence that predators have had an evolutionary influence on strategies of seed survival and dispersal. Defenses against ingestion or digestion include alkaloids (Solanaceae and legumes), sticky latex (Sapotaceae), toxic oils (Anacardiaceae, Euphorbiaceae) and condensed tannins that bind proteins and reduce or eliminate their nutritional value (Leguminosae, Hippocrataceae) [Janzen, 1969; Bell, 1978; Waterman, 1984; Ganzhorn, 1988; Davies , 1991]. Defenses that hinder harvesting and mastication include the development of hard husks or brittle seed testa (Chrysobalanaceae, Lecythidaceae, Sapotaceae), seeds enclosed in a stone (Lauraceae, Eleaocarpaceae), very large seeds (Anacardiaceae), poisonous hairs (Mimosaceae), and spines (Palmae and Papilionaceae) [Janzen, 1969; Fischer & Chapman, 1993]. The mechanisms that animal consumers have developed to deal with this diverse array of possible plant defenses range from precise coevolutionary interactions between plants and animals [e.g., ant–*Acacia*, ant–*Cecropia*, wasp–*Ficus*: Janzen, 1979; Howe & Westley, 1988] to flexible, diffuse interrelationships. Most plant–vertebrate interactions are loosely structured with plants

TABLE I. Seed Predation by African and Asian Colobines: % Seeds in Diet, Stage of Development When Seeds Are Ingested, Seasonal Variation, and the Most Frequently Used Plant Families

Taxon	% seeds eaten[a]	Maturation	Seasonal variation in consumption	Most frequently used plant families for seeds
Colobus angolensis [Maisels et al., 1994]	49.9	Primarily unripe	50% (April), 40% (May) to 70–88% (July–Sept. period of high abundance)	Leguminosae, Annonaceae, Olacaceae
C. badius [Maisels et al., 1994]	30.8	Primarily unripe	<20% (Dec.–July) to 65–75% (Aug.–Nov. period of high abundance)	Leguminosae, Olacaceae, Loganiaceae
C. polykomos [Dasilva, 1994]	34.6[b]	Primarily unripe	0–75% (maximum in dry and dry–wet transitional months)	Leguminosae
C. satanas [McKey et al., 1981]	53.2[c]		27–90% (period of high abundance)	Euphorbiaceae, Ochnaceae, Caesalpiniaceae
C. satanas [Harrison, 1986]	60.0		32–82% (annual range)	
Nasalis larvatus [Bennet & Sebastian, 1988]	15.0			Leguminosae, Myristicaceae
N. larvatus (Yeager, 1989]	37.0	Primarily unripe	Jan.–May (primarily frugivorous); June–Dec. (primarily folivorous)	Celastraceae, Myrtaceae, Euphorbiaceae
Presbytis johnii [Oates et al., 1980]	25.1[b]			Icacnaceae, Myristicaceae, Vitaceae
P. rubicunda [Davis, 1991]	19.2[c]		1–87% (Aug.–period of high abundance)	Meliaceae, Leguminosae, Sapindaceae
Procolobus verus [Oates, 1988]	14.0	Unripe and ripe	25% (unripe, early dry) to 26% (ripe, late dry)	Caesalpiniaceae, Myrtaceae, Apocynaceae
Trachpithecus auratus [Kool, 1993]	22.4[b] (7.1)[d] 30.9[b] (19.0)[d]	Primarily unripe		Moraceae

[a] Percent of feeding records unless otherwise noted.
[b] Reported as fruit and seeds.
[c] Monthly average.
[d] Seeds only.

TABLE II. Seed Predation by Platyrrhines: % Seeds in Diet, Stage of Development When Seeds Are Ingested, Seasonal Variation, and the Most Frequently Used Plant Families

Taxon	% seeds eaten[a]	Maturation	Seasonal variation	Most frequently used plant families for seeds
Cacajao calvus [Ayres, 1989]	67.0	Unripe	20-30% (Mar.–Apr.) to 97% (Sept.–Jan.)	Lecythidaceae Sapotaceae Moraceae
Callicebus personatus [Müller, 1996]	12.3[b] (21.9)[c]			Myrtaceae Sapotaceae Rubiaceae
Cebus apella [Terborgh, 1983]	25.0	Ripe	0%(wet) to 25%(dry)	Palmae
Chiropotes albinasus [Ayres, 1989]	36.0	Unripe	12% (wet) to 82% (dry)	Lecythidaceae Sapotaceae Moraceae
C. satanas [van Roosmalen et al., 1988]	66.2	Unripe	Lecythidaceae	
C. satanas [Norconk, 1996]	49.4[b–d]	Unripe	33.3% (late wet) to 61.4% (late dry)	Sapotaceae Moraceae Euphorbiaceae
Lagothrix l. cana [Peres, 1994]	7.0	Unripe	21-38% (Oct.- Nov. -early wet)	Moraceae Leguminosae Lecythidaceae
Pithecia albicans [Johns, 1986]	18.5	Unripe		Leguminosae Moraceae Loganaceae
P. albicans [Peres, 1993]	44.3	Unripe		Sapotaceae Leguminosae Lecythidaceae
P. pithecia pithecia [Buchanan et al., 1981]	55.0	Unripe		Lecythidaceae Sapotaceae Simaroubaceae
P. pithecia pithecia [Norconk, 1996]	55.8[b,d]	Unripe	21.9% (late wet) to 76.1% (early wet)	Connaraceae Chrysobalanaceae Loganaceae
P. pithecia chrysocephala [Setz, 1994]			26-31%	

[a] Percent of feeding records unless otherwise noted.
[b] Only the seeds of drupes and berries.
[c] Seeds only.
[d] Annual average.

attracting a wide range of dispersers and animals ingesting a wide range of plant resources [e.g., Janzen, 1980b; Herrera, 1985].

SEEDS AS FOOD

Seeds are valuable resources compared to ripe fruit pulp both in terms of their nutrient composition, and their relative abundance in space and time. They are small packages of resources essential for the survival of a germinating seedling, often found to be rich in lipids, sugars, and protein and relatively low in tannins [Harper et al., 1970; Janzen, 1981a; Waterman, 1984]. They are also potentially plentiful at a single location, and the temporal availability of unripe fruit (and immature seeds) on tropical plants has been found to be three to four times longer than that of ripe fruit [Leighton & Leighton, 1982; Milton, 1988; Norconk, 1996]. Thus, seed predators not only ingest relatively high quality resources but may also avoid seasonal bottlenecks in food availability that confront ripe fruit frugivores [Norconk, 1996; but see Glanz et al., 1982; Smythe et al., 1982]. Data from seeds ingested by bearded (*Chiropotes satanas*) and white-faced (*Pithecia pithecia*) sakis in Venezuela highlight the variation in nutrient value and seasonal predictability of seed availability (Figs. 1, 2). These data suggest that seed eating carries no promise of consistently high nutritional value, nor do seed predators always behave as might be predicted based solely on nutrition. On a dry matter basis, seeds ranged from <5% to >45% Kjeldahl crude protein (CP), <2% to >35% lipids, and <5% to >30% water-soluble carbohydrates (WSC) (Fig. 1) [for an explanation of field methods and analysis see Kinzey & Norconk, 1993]. Intraspecific differences in the macronutrient composition of seeds were not as marked as interspecific differences, but still showed interannual and

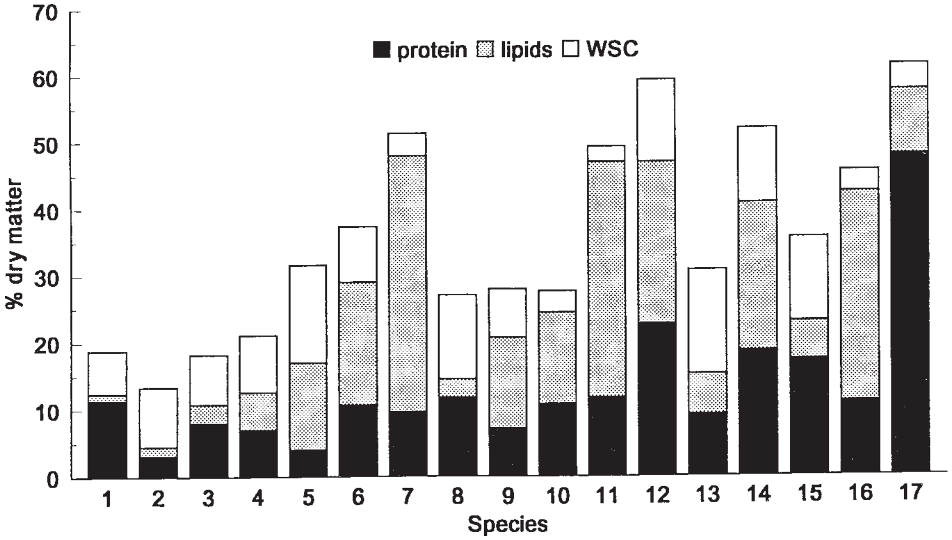

Fig. 1. Variation in nutrient value (water-soluble carbohydrates, crude protein, lipids) of seeds ingested by bearded sakis (*Chiropotes satanas*) and white-faced sakis (*Pithecia pithecia*) in Venezuela. Key to plant species: 1, B*rosimum alicastrum*; 2, *Brownea coccinea*; 3, *Chrysophyllum lucentifolium*; 4, *Strychnos fendleri*; 5, *Pradosia caracasana*; 6, *Solanum paludosum*; 7, *Oryctanthus alveolatus*; 8, *Morinda tenuiflora*; 9, *Amaioua corymbosa*; 11, *Sapium glanulosum*; 12, *Actinostemon schomburgkii*; 13, *Erythroxylum steyermarkii*; 14, *Capparis muco*; 15, *Licania discolor*; 16, *Lepidocordia punctata*; 17, *Connarus venezuelanus*.

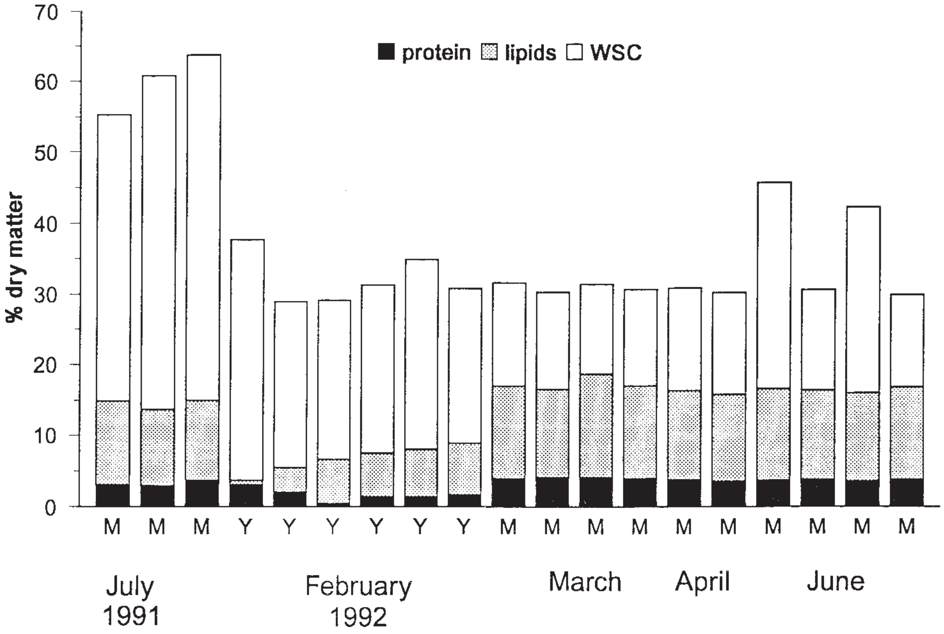

Fig. 2. Interannual (1991–1992) and seasonal variation in the nutrient content of *Pradosia caracasana*. M, mature seeds; Y, young seeds. Dry season months are October through April; wet season months are May through September.

interseasonal variation. Nineteen samples of seeds taken from the top-ranked resource used by bearded sakis (*Pradosia caracasana*: Sapotaceae) exhibited both seasonal and inter-annual variation in nutrient composition but considerable within-season uniformity (Fig 2). Mature seeds had significantly higher percentages of lipids and protein than young seeds (two-tailed, Mann Whitney U test $n_1 = 6$, $n_2 = 10$, $Z = 115$ and 131, respectively, $P < 0.025$) with no significant difference in WSC values. The samples from the 1991 wet season were significantly higher in all nutrients than the samples from the wet season of 1992 ($n_1 = 3$, $n_2 = 10$, $P < 0.025$). In contrast, the sample of mature seeds from the late dry and early wet season of 1992 (right half of Fig. 2) was quite uniform.

Curiously, the season when the *Pradosia* seeds were found to be most valuable nutritionally (the wet season months of June and July) was not also the peak season of seed ingestion. We identified two variables that may explain why nutrition alone did not predict intake. First, tannin levels increased as seeds aged, and, second, handling time related to gaining access to seeds also increased as seed coats hardened with maturity. Using condensed tannins (CT) as a measure of chemical protection and in this analysis using quebracho tannin as the standard, we report results here as % quebracho (QE) equivalents on a dry matter basis. CT values of the seeds ranged from 6.8% (fruit from 1 tree; 0.2 g dry weight) in February when the seed embryos were very young and embedded in gelatinous endosperm through a period of intensive use of full-sized but young seeds in April (average CT = 7.9%, seeds from five trees; 8.02 g dry weight), and finally to a period of decreased ingestion of mature seeds in June (average CT= 11.1%, seeds from one tree; 18.35 g dry weight). In June, seed eating shifted to ingestion of mesocarp only (i.e. seeds were dropped).

The handling time of extracting mature seeds also increased with fruit age.

Sakis usually remove seed coats before ingesting seeds even though seed coats appear to be highly variable in deterrent qualities (Table III). High NDF and ADF levels in combination with the smooth, slippery surface of the seed coats of mature *Pradosia caracasana* may have influenced decisions by bearded sakis to remove the exocarp and lick the mesocarp off the surface of the seed coat, then drop many fruit with the seed compartment intact. The time spent removing mature seeds from the seed compartment ($\bar{x}$ = 102.83 seconds; N = 16) was markedly longer than ingesting mesocarp and dropping the seeds ($\bar{x}$ = 17.33 seconds; N = 44).

SEED PREDATORS AND THEIR MORPHOLOGICAL ADAPTATIONS

Seed predators destroy seeds and seed dispersers swallow or transport seeds, but, just as seed dispersers often fail to deposit viable seeds in favorable habitats for germination [e.g., Herrera, 1985; Chapman, 1989], seed predators may not rob a tree of an entire seed crop. With the exception of the specialist pre- and postdispersal seed predators (invertebrates) that are often host-specific [Janzen, 1980a; Crawley, 1992], mammals and birds which act as seed predators for some plant species may disperse seeds of other plant species.

METHODS OF MANIPULATING SEEDS

A few primates use masticatory and manipulative hand strength or tool use alone to gain access to mechanically protected seeds, (e.g., *Cebus apella*, baboons, mangabeys, and chimpanzees) [Kinzey, 1974; Boesch & Boesch, 1983; Terborgh, 1983; Horn, 1987; Peters, 1993]. However, most primates that ingest seeds in preference to fruit pulp exhibit adaptations in the dentition and the gut that appear to improve the ability to manipulate and digest seeds. While primate seed dispersers, like spider monkeys, ingest fruit after only minimal preparation and can rely on intestinal action to remove adherent pulp [van Roosmalen, 1985], seed eating more closely resembles leaf eating in difficulty of digestion. Seeds require mastication prior to swallowing and enlargement of either the foregut or hindgut to be digested.

Colobine primates may be adapted to eating both seeds and leaves. Lucas and Teaford [1994] described the functional duality of colobine bilophodont molars, both as wedges that break down relatively soft seeds and blades that sever leaf laminae. The elaborate colobine foregut and system of fermentation that has been adapted to digesting fibrous and chemically protected leaves may also be adapted to breaking down complex starches of seeds [McKey et al., 1981; Kay & Davies, 1994]. Chivers [1994] further characterized some colobines by identifying differences in the digestive tracts of species where the natural diet was composed mostly of leaves compared with those that ingested at least 20% seeds. Stomach volume was found to be larger in the more folivorous colobines (*Colobus polykomos* and *C. guereza*, *Trachypithecus* spp.), but stomach weight was heavier and colons more voluminous in the seed-eating colobines (*Presbytis melalophos, Procolobus badius, Semnopithecus entellus, Nasalis larvatus*). Both Chivers [1994] and Oates et al. [1994] noted a difference in body size between the “leaf eaters” and “seed eaters”: larger-bodied colobines tended to eat more leaves, and smaller-bodied colobines ate more seeds.

Dental adaptations are also clearly present in the seed-eating strepsirhines. *Propithecus diadema* is among the largest (at 6.5 kg) of the diurnal lemurs at Ranomafana National Park. Lucas and Teaford [1994] found similarities in the

TABLE III. Biochemistry of Seed Coats Discarded by Sakis Before the Seed is Ingested*

Plant Species	CP	WSC	Lipids	NDF	ADF	Cellulose	Hemi-cellulose	CT	Lignin
Connarus venezuelanus[a]	10.6	4.3	64.2	33.6	3.0	6.5	10.5	0.4	1.2
Ouratea roraima[a]	7.0	10.1	0.3	31.9	22.8	13.1	9.2	46.8	9.6
Chrysophyllum lucentifolium[a]	2.8	3.2	0.6	81.3	50.7	31.9	30.6	0.7	18.8
Peltogyne floribunda[a]	7.9	6.2	0.6	54.2	47.6	22.1	6.6	8.0	25.5
Pradosia caracasana[b]	2.4	4.4	0.3	80.7	61.0	33.1	19.6	8.3	27.9

*CP, Crude Protein; WSC, Water Soluble Carbohydrates; NDF, Neutral Detergent Fiber; ADF, Acid Detergent Fiber; CT, Condensed Tannin. See Kinzey and Norconk [1993] for Methods used in the Analysis. Plant species are ranked by increasing lignin values and values are expressed as percentages.

[a] N = 1 sample per species.

[b] N = average of three samples per species.

bilophodont dentition of the sifakas and the colobines, but the nonmolar dental specializations and seed extraction capability of *Daubentonia madagascariensis* are even more remarkable. Sterling [1994] and Kitko et al. [1996] described the uses of the enlarged, ever-growing lower incisors of aye-ayes and the specialized third finger in opening the highly protected endocarp of *Canarium* spp. (Burseraceae) seeds. Body size may also be a relevant issue in the evolution of seed predation in prosimians since both *Propithecus* and *Daubentonia* are among the largest members of the modern strepsirhine radiation. *Daubentonia* is the largest (3 kg) of the nocturnal lemurs [Mittermeier et al., 1994]

Seed-eating pitheciins (*Pithecia*, *Cacajao*, and *Chiropotes*) probably have both dental and gastrointestinal adaptations, but there is more direct evidence for dental adaptation than gut modification. The procumbant incisors and robust, laterally splayed canines are particularly distinctive and facilitate both seed extraction and scraping of seeds from their compartments [Kinzey, 1992]. In comparison to the high-crested bilophodont molars of the colobines, pitheciin molars are simple and low-crowned, functioning more like mashing or grinding platforms than dicers [Kinzey, 1992]. Crenulated enamel on pitheciin molars may facilitate stabilization of seeds during crushing [Rosenberger, personal communication].

Although there have been few published studies of gut anatomy that include pitheciins [e.g. Hill, 1960], saki-uakaris may have enlarged ceca and relatively slow food bolus passage rates. Chivers [1994] reported that the pitheciin cecum was voluminous relative to the size of the stomach and similar to the hindgut enlargement seen in *Alouatta*. Thus, fermentation and slowed transit of food through the gut may be as necessary to the digestion of seeds as it is to leaves and unripe fruit.

Comparative data on the nutritional value of seeds ingested by primate seed predators are still limited, but it appears that colobines ingest seeds that are higher in protein and dietary fiber (ADF) than seeds ingested by pitheciins (Table IV). Weighted by intake, protein values were higher and condensed tannins lower for seeds eaten, than seeds not eaten, by the colobines. Protein values of seeds ingested by the pitheciins were relatively low and did not apparently play a role in seed selection. The mechanism used by animals to determine protein content is not clear. Human detection of purified amino acids is poor to nil [Birch and Kemp, 1989], and it is likely that any flavor associated with amino acids would be swamped when mixed with the stronger flavors of lipids and tannins. ADF values (i.e., cell wall components that are primarily lignin and cellulose) did not appear to play a role in seed selection for colobines, but it did for pitheciins; the pitheciins did not ingest seeds that were as high in ADF as the colobines. ADF would act as indigestible gut ballast for the sakis, but volatile fatty acids generated by fermentation of structural carbohydrates provide colobines with an important source of energy [Bauchop & Martucci, 1968; Stevens, 1988].

Nonprimate Seed Predators in the Neotropics

Neotropical seed predators are found in several diverse taxonomic groups of mammals and birds. Psittacids are the volant, generalist seed predators with the highest biomass [Terborgh, 1986; Terborgh et al., 1990]. Squirrels combine locomotor skills and dental modifications to use both pre-dispersed and post-dispersed seeds. Ungulates and rodents are generalist post-dispersal seed predators. The range of taxonomic diversity is evident in the body size differences among these taxa (Fig. 3) with the ungulates (brocket deer, white-lipped and collared peccary, and tapir) being the largest and the seed-caching mice the smallest.

TABLE IV. Biochemical Properties of Seeds Eaten and Seeds Not Eaten by Colobines [from Waterman & Kool, 1994] and Pitheciins [Norconk & Conklin-Brittain, unpublished]

Primate species	N (eaten)	Protein	ADF	CT	N (not eaten)	Protein	ADF	CT
Colobus polykomos	8	29.9	31.9	0.2	6	13.6	28.8	12.3
Colobus satanas	5	13.7	—	1.4	12	7.0		3.9
Presbytis melalophos	4	9.6	29.7	0.9	6	6.5	39.8	3.4
Presbytis rubicunda	16	9.0	22.3	11.1	6	8.3	25.0	3.8
Pithecia pithecia	20	6.7	10.5	4.7	4	10.4	20.0	9.2
Chiropotes satanas	10	6.0	8.2	3.7	4	6.7	26.6	3.8

*Values are Weighted by Intake "($T = \sum(m_s \times p_s)/\sum p_s$) where T is the Final Weighted Value, m is the Biochemical Measure, p is the Percentage of Relevant Feeding Records, and s is the Species" [Waterman and Kool, 1994:271].

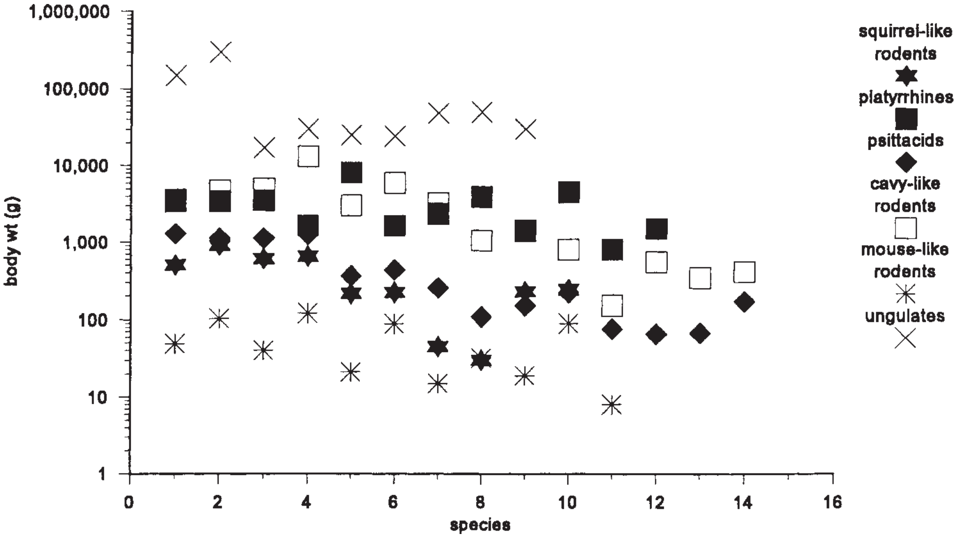

Fig. 3. Body weights reported for six groups of neotropical seed predators. Filled symbols are arboreal, predispersal seed predators; lined or outlined symbols are terrestrial seed predators. Data are from Mittermeier [1977], Ayres [1986], Karr et al. [1990], Terborgh et al. [1990], Emmons [1990], and Janson and Emmons [1990].

Like primates, other vertebrate seed predators exhibit a range of anatomical specializations associated with seed predation. Seed-eating birds have capacious crops, muscular gizzards and long small intestines compared to pulp-eating birds [Moermond and Denslow, 1985; Stevens, 1988]. Nevertheless, precise systematic action of the beak is important to open seeds. Janzen [1981b] estimated that all 2,695 seeds found in the crop of an orange-chinned parakeet were cracked and most were thoroughly crushed. Ungulates and caviomorph rodents are strictly terrestrial and take mature, postdispersed seeds from the ground. Although chemical protection of seeds may be relaxed by the plant during maturation to facilitate dispersal, hardness of the exocarp and seed testa appear to peak in many mature seeds. The larger ungulates deal with mechanical and chemical protections using the same two general adaptations described for the primates. The sacculated forestomach of peccaries may assist in detoxifying seed toxins, but their masticatory system and well-protected skulls are adapted to breaking down hard, mechanically protected seeds [Kiltie, 1989; Bodmer, 1991]. Other ungulates (deer and tapir) swallow fruit whole, but nearly all the seeds ingested by deer were destroyed in the abomasum [Bodmer, 1991]. Deer depend on ruminant digestion (microbial action and changes in pH) to breakdown seeds in the gut. The stomachs of tapirs are enlarged relative to other perissodactyls and the large intestines are voluminous and complex [Stevens, 1988]. Indeed, Janzen [1981a] described the transit time of tapirs to be sufficiently long to permit seed germination in the gut.

ACTIVITIES OF SEED PREDATORS THAT MAY INFLUENCE SEED PREDATION AND SEED DISPERSAL IN THE NEOTROPICS

While conducting studies on feeding ecology of bearded and white-faced sakis and red and green macaws [see site descriptions and methods in Kinzey &

TABLE V. Mechanisms by Which Vertebrate Seed Predators Contribute to Seed Dispersal.

Mechanism	Class of seed predator most likely to be involved	Potential benefit to plant
Seed predators ingest either young or mature seeds but do not ingest seeds throughout the entire period of seed production	Predispersal (primates & psittacids)	If seed loss is limited to only one stage of seed maturation, at least some seeds may survive predation
Sympatric seed predators ingest seeds from different plant species	Pre- or postdispersal	Predation is reduced on any given plant species if sympatric seed predators diversify seed selection
Seed handling increases the possibility of seed germination if the seed compartment is altered before the seed is discarded or ingested	Pre- or postdispersal	Removal of seed coat may facilitate successful germination if seed is dropped unharmed and if the seed is transported away from the seed shadow of the parent tree
Seed size influences probability of dispersal by seed predators	Pre- or postdispersal (larger seed predators: primates and ungulates; some birds)	Seeds ingested by a seed predator may bypass mastication and digestion if they are very small

Norconk, 1990, 1993; Norconk et al., 1997], we realized that some seeds ingested by these seed predators escaped destruction by mastication and digestion. Four observations made during the course of these field studies may explain how animals that are traditionally thought of as seed predators may actually assist in seed dispersal (Table V). Published studies of primate and nonprimate neotropical seed predators are reviewed below in the context of these observations. The germination success rate after seed dispersal by seed predators is still largely uninvestigated, except in the case of scatter-hoarding rodents (see below).

Seed Predators Ingest Either Young or Mature Seeds But Do Not Ingest Seeds Throughout the Entire Period of Seed Production

This observation is most relevant to arboreal or volant seed predators that have access to both young and mature seeds. If only a partial seed crop is removed and seeds survive predation while young, are these same seed predators likely to ingest mature fruit? The primates included in the analysis were all pitheciines for which there are data on the proportion of unripe and ripe seeds in the diet and woolly monkeys, *Lagothrix lagothricha* (Fig. 4). Woolly monkeys were included in this analysis because the taxonomic diversity of seeds ingested by woolly monkeys seasonally was as high as or higher than some of the pitheciines. A subset of Desenne's [1994] study of 15 sympatric species of psittacids in Venezuela made up the comparative sample (Fig. 5). We found three differences between the psittacids and the primates. First, the proportion of diet invested in seeds is higher in the macaws and parrots than the monkeys. Second, the plant diversity of seeds ingested is lower in the psittacids than the primates. Third, some psittacids ingested nearly equal proportions of seeds from ripe and unripe sources.

Both macaws and sakis ingested some mature seeds, and rarely, mature and

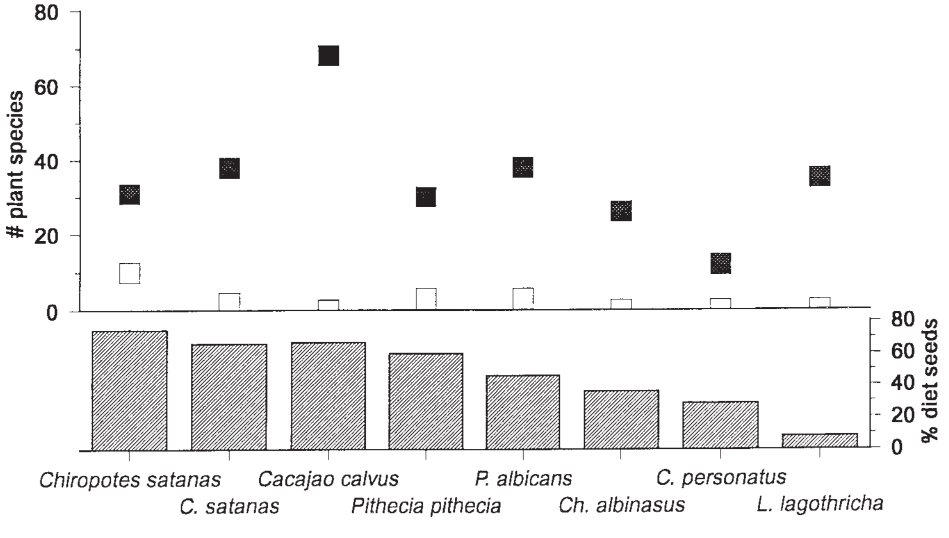

Fig. 4. Comparison of the proportion of unripe seeds (filled squares) and ripe seeds (open squares) in the diet of seven platyrrhine primates. The histograms document the percentage of seeds in the annual diet. From left to right, dietary data are from van Roosmalen et al. [1988], Norconk [1996], Ayres [1986], Peres [1993], Ayres [1989], Müller [1996], and Peres [1994].

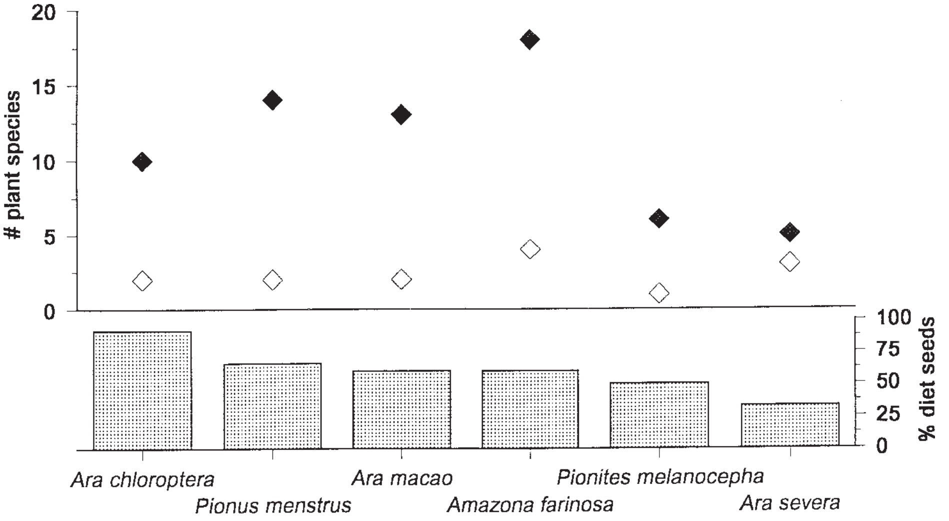

Fig. 5. Comparison of the proportion of unripe seeds (filled diamonds) and ripe seeds (open diamonds) in the diet of five psittacid species. The histograms document the percentage of seeds in the annual diet. Data are from Desenne [1994].

immature fruits were ingested from trees of the same plant species or even the same tree. Of the 23 seed sources used by the three sympatric macaws in southern Venezuela, four plant species were used very intensively. Young seeds, mature seeds, and ripe fruit pulp were ingested from *Euterpe precatoria* (Palmae), *Inga laterifolia* (Mimosaceae), *Sterculia excelsa* (Sterculiaceae), and *Micropholis melinoneana* (Sapotaceae) [Desenne, 1994]. In the case of bearded sakis and uakaris, seeds of young fruit and mesocarp of mature fruit were ingested primarily from the Sapotaceae family [Ayres, 1986; Norconk and Kinzey, 1994]. In order to examine the effect of bearded sakis on the dispersal of their top-ranked resource, we observed 20 *Pradosia caracasana* (Sapotaceae) trees through their peak fruiting period. We estimated that an average of 23.5% of the seeds that were dropped intact, but with the pericarp removed by the sakis, were secondarily moved away from the feeding tree [Norconk et al., 1995]. Thus, saki-uakaris are seed predators of young seeds but they also appear to facilitate seed dispersal of some mature seeds.

Primate seed predators appear to specialize in eating either young or mature seeds of a given species, but it is difficult to evaluate dispersal effectiveness without evidence of fruit production rates and fruit loss to predation. There are a few estimates of extremely severe crop damage that can be attributed to predispersal seed predators. Dasilva [1994:671] reported “virtual elimination” of *Pentaclethra macrophylla* (Mimosaceae) seeds by *Colobus polykomos*. Peres [1991] calculated that more than 90% of the fruit crop of ten *Cariniana micrantha* (Lecythidaceae) trees was destroyed by *Cebus apella* and 77% of a fig fruit crop was removed by psittacids [Jordano, 1983]. Thus a preference for young fruit does not preclude the possibility that entire seed crops can be destroyed by seed predators.

Sympatric Seed Predators Ingest Seeds From Different Plant Species

The intensity of seeds lost to predation may also vary according to the diversity of food species used by seed predators. Predation success could be interpreted on the basis of demographic profiles of seed predator populations, knowledge of the intensity of competition among competitors for the same resources, feeding rates and the ability of predators to move between food sources, and the size and synchronicity of fruit crops. We know of no study in which all of these variables have been identified. However, if we start simply with a comparison of food lists, there does appear to be tentative support for this observation from rodents and primates. Smythe et al. [1982] found the food species overlap to be relatively high for agoutis and pacas on Barro Colorado Island, but the highest-ranking items in their diets were different. Agoutis preferred nuts of *Dipteryx panamensis* and *Astrocaryum standleyanum*, and pacas preferred softer fruit of *Ficus* spp. Of the ten highest-ranking food sources used by *Presbytis melalophos* and *P. rubicunda* at Kuala Lompat, they shared only one species used for seeds [Davies et al., 1988]. Buchanan et al. [1981] and Mittermeier [1977] calculated that only approximately 6% of seed species were shared by sympatric *Pithecia pithecia* and *Chiropotes satanas* (Fig. 6). A comparison of more distantly related primate seed predators in Amazonia was only marginally different: woolly monkeys (*Lagothrix lagotricha*) shared 11% of the same seed species ingested by buffy sakis (*Pithecia albicans*) [Peres, 1993, 1994].

Sympatric macaws shared a higher proportion of plant species (15–42%) [Desenne, 1994] than the sympatric primates. Macaws may be able to tolerate a more extensive dietary overlap since their population densities are lower than primates (approximately two individuals/km^2 [Terborgh et al., 1990]). Macaws also travel farther per day than most arboreal primates. Munn [1992] estimated that macaws flew a maximum distance of 9 km daily between clay licks. This estimate is three times the distance traveled by bearded sakis and nine times the distance covered by the smaller pitheciines (*Pithecia* and *Callicebus* spp.) [Robinson et al., 1987; Norconk & Kinzey, 1994; Müller, 1995].

Species overlap in food items ingested by red brocket deer (*Mazama americana*), collared peccary (*Tayassu tajacu*), white-lipped peccary (*Tayassu pecari*), and tapir (*Tapirus terrestris*) was calculated from data published by Bodmer [1990a,b, 1991]. Like primates and psittacids, the degree of food species overlap ranged widely, from a low of 12% between deer and collared peccary to a

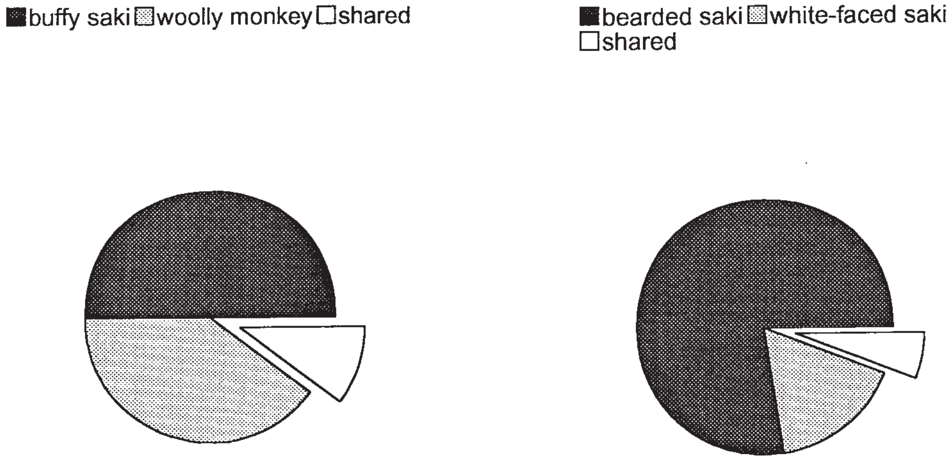

Fig. 6. Proportion of the seed species shared in the diets of four platyrrhines. Data from food lists compiled by Peres [1993, 1994] for buffy sakis and woolly monkeys (11% overlap), and Buchanan et al. [1981] for bearded sakis and white-faced sakis (6% overlap).

high of 50% between collared and white-lipped peccaries. Unfortunately, plant species identification (except for palms) was not as precise for the ungulates. "Shared resources" were denoted at the level of plant family [Bodmer, 1991].

Seed Handling Increases the Possibility of Seed Germination If the Seed Compartment Is Altered Before the Seed Is Discarded or Ingested

Seed handling includes scratching, scarifying or removing parts of the fruit by hands or teeth, reducing seed size with the teeth, swallowing seeds whole and depending on long retention time to break down and digest seeds, transporting seeds in cheek pouches where digestion may begin, and burying seeds and recovering them at a later time (Table VI). The most dextrous of the seed predators (primates, psittacids, and rodents) often undertake intensive fruit manipulation before the seed is ingested. Does this manipulation contribute to seed survival if the seed is dropped or dispersed instead of eaten?

The literature on scatter-hoarding rodents [squirrels, agoutis, acouchis, murid rodents: Smythe, 1978; Glanz et al., 1982; Dubost, 1988; Vander Wall, 1990; Forget, 1993] provides the strongest support for seed dispersal by post dispersal predators through seed manipulation. But, Galetti and Rodrigues [1992], studying blue headed parrots in Brazil, also demonstrated that predispersal seed predators contributed to seed dispersal. They calculated that half the *Inga* sp. (Mimosaceae) seeds removed from the tree were dropped to the ground and available for secondary dispersal by agoutis. Primate seed predators also drop seeds during preparation. At face value, it is difficult to assess whether seed dropping is intentional (e.g. if fruit contains evidence of insect destruction or if it is discarded because it has not reached or has surpassed a particular maturational state) or is unintentional (i.e. dropped during preparation for ingestion). The success of secondary dispersal by vertebrates also depends on species-specific modes of dispersal. Dropping partially opened fruits containing seeds that are adapted for wind dispersal does not contribute to dispersal once the fruit is on the ground. For example, more than 30% of the *Cariniana micrantha* (Lecythidaceae) seed crop was lost due to the action of *Cebus apella*, not eating, but dropping the capsule unopened [Peres, 1991].

Seed Size Influences the Probability of Dispersal

Pitheciin primates and neotropical ungulates often select fruit with one or few large seeds (Figs. 7, 8). Seeds >1 cm in maximum dimension represented 80% or more of the diet of pitheciins (Fig. 7) and 80% of the diet of *Presbytis rubicunda* [Davies, 1991]. Fruit with fewer than six seeds made up the highest proportion of pitheciin diets (Fig. 8). Nevertheless, the sakis do ingest fruit with multiple, small seeds. For example, we have found only seeds <2 mm in length (*Lepidocordia punctata*: Burseraceae; *Cecropia peltata*: Moraceae; *Alibertia latifolia*, Rubiaceae; *Actinostemon schomburgkii*, Euphorbiaceae) in the feces of white-faced and bearded sakis. Bodmer [1991] also noted that small seeds remained intact as they moved through the guts of Amazonian ungulates, and Corlett and Lucas [1990] found that only small seeds (3–4 mm wide) were swallowed by long-tailed macaques. Larger seeds were spat out. Since small seeds are often ingested along with adherent fruit pulp, it is possible that seed predators are attracted to the fruit pulp or aril and that the seed is swallowed as part of the package.

Smaller seeds have a higher chance of dispersal than larger seeds for several

TABLE VI. Seed Manipulation Reported for a Variety of Seed Predators That May Have a Positive Effect on Seed Dispersal

Seed predators involved	Activity	Possible contribution to seed dispersal
Pitheciins and psittacids [this study; Desenne, 1994]	Remove seed coat and pericarp during seed preparation	Unknown effect on seedling germination or survival
Tapir [Janzen, 1981]	Scarify seed coats of legumes	Seeds do not germinate without damage to seed coat
Heteromyid rodents [Vander Wall, 1990]	Seed-decomposing (mycorrhizal) fungi in cheek pouches	Reported to enhance seedling survival
Agoutis [Forget, 1992]	Scatter-hoarding rodents transport and bury seeds away from parent plant	Positive influence on seedling establishment
Tapir and peccary [Bodmer, 1991]	Spitting palm seeds	Transport seeds away from seed shadow
Blackbirds [Barnea et al., 1990]	Abrasion of seed coat	Increased germination rate of ingested seeds relative to non-ingested controls

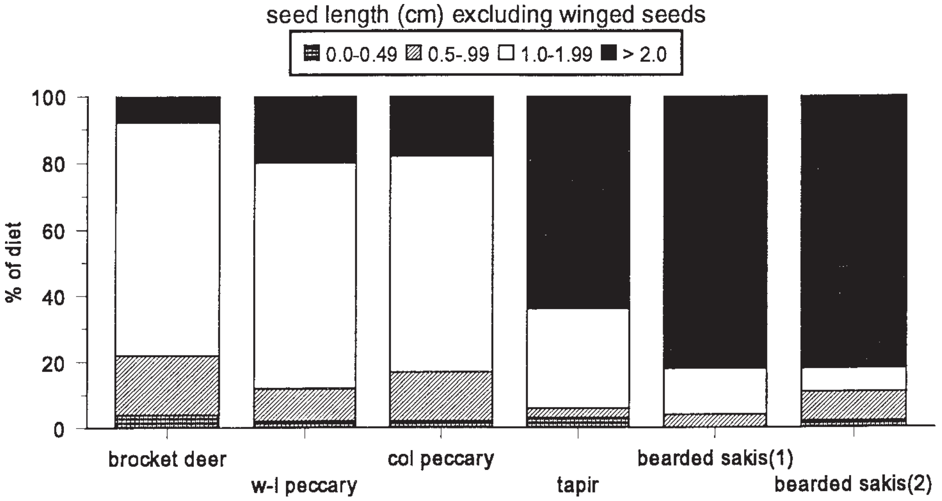

Fig. 7. Size of seeds (seed length in centimeters) ingested by some neotropical seed predators. From Bodmer [1991], except (1) Norconk [unpublished] and (2), from van Roosmalen et al. [1988].

reasons. Gape width limits the size of seeds that can be ingested by birds and bats [Moermond & Denslow, 1985]. The smaller the seeds, the more likely they will be dispersed by a wider variety of volant frugivores. Small seeds are more likely to miss destruction through mastication and pass through the gut intact in mammalian frugivores. Small seeds can also be ingested in larger quantities, and Levey [1986] found that small seeds passed through the gut at a slower and more variable rate than did large seeds. All of these variables improve the possibility that the small seeds will both survive the transit through the gut and be dispersed away from the parent tree.

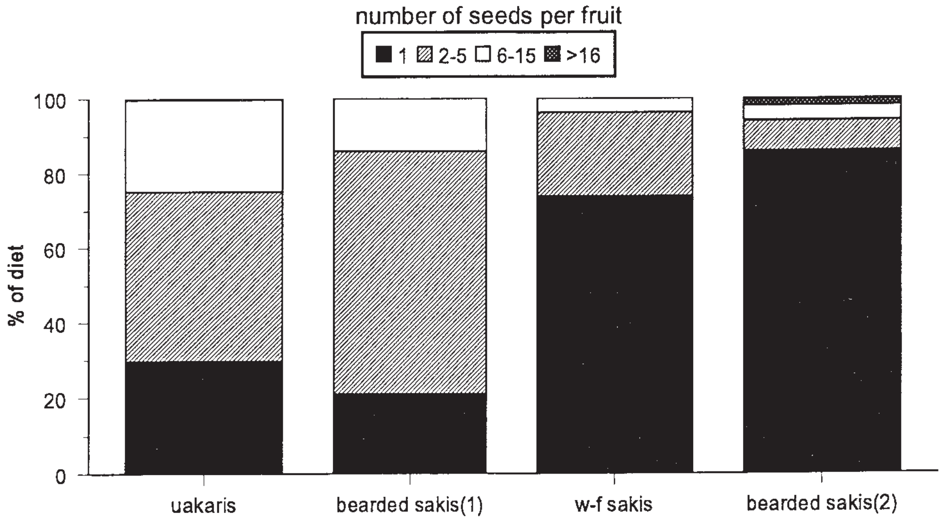

Fig. 8. Seed number in fruit ingested by pitheciin primates. From Ayres [1986] and (1) van Roosmalen et al. [1988]. White-faced (w-f) sakis & bearded sakis (2) from Norconk (unpublished).

Nevertheless, small seeds that are masticated and digested appear to be important resources for seed predators. Seeds of some Euphorbiaceae (*Sapium glandulosum* and *Actinostemon schomburgkii*) are high-ranking resources in the diets of bearded sakis, white-faced sakis, and red and green macaws [Norconk, 1996; Norconk et al., 1997]. These Euphorbiaceae species produce very small fruit (<6 mm in diameter) with three cocci, each containing a tiny seed. The reward for time spent extracting the seed is a food item that is very high in lipids (see Fig. 1). The effectiveness of seed predators destroying small seeds was reported above in Janzen's [1981b] study of orange-chinned parakeets. More investigations on the interrelationship between seed size, seed number, nutrient value, and handling methods would help us more fully appreciate the seed-dispersal vs. seed-destruction capabilities of predators.

DISCUSSION

Primate seed predators (particularly the pitheciins and colobines) exhibit specializations in the digestive tract and dental anatomy to suggest a long evolutionary history of ingesting seeds. Pitheciins have been dental seed predators from the early Miocene [Rosenberger, 1992], and Lucas and Teaford [1994] suggested that the earliest colobines may have masticated seeds. Many extant primates also appear to ingest seeds seasonally, but it is clear that seed predators do not always destroy the seeds they handle or ingest.

Platyrrhine primates and psittacid macaws/parrots are most likely to contribute to seed dispersal in two ways: 1) they express a preference for ingesting seeds at only one stage of maturation (usually mature-sized young seeds), and 2) they disperse small seeds that miss destruction by the teeth and survive the passage through the gut. Preparation of fruit by macaws and primates prior to ingestion may also have a positive effect on seed dispersal but only if the seeds are sufficiently mature to be capable of germination. While scratching the surface of the seed may accelerate germination, removal of the seed coat may make the seed vulnerable to an early death from exposure to terrestrial microbes and invertebrate postdispersal seed predators.

The feeding activities of arboreal monkeys and psittacids are very different from terrestrial seed predators. Limited in food choice to seeds that have fallen to the ground, terrestrial seed predators are confronted with an array of plant defenses in mature fruit, both biochemical and mechanical. All members of this group exhibit specializations in the gut to manipulate or crush seeds. These seed predators ingest primarily large seeds [Bodmer, 1991]. However, to be a small seed in a large, many-seeded fruit (like figs) that attracts the attention of large-bodied seed predators may also increase the likelihood of dispersal after swallowing and defecation [Janzen, 1979].

Sciurids possess the locomotor skills to compete with the crown-feeding primates and psittacids, but they are more dependent on mechanically protected nuts than either the pitheciines or macaws. Unlike many soft seeds or seeds of fleshy fruit, nuts can survive manipulation and burial. The seed caching habit of squirrels and other hoarding tropical rodents has provided an ability to calculate seedling survival rates [e.g., Becker & Wong, 1985; Forget 1990, 1992]. Their strategies of burying mature seeds, ingesting cotyledons of developing seedlings, and recovering seed resources months after the plants have fruited are very different from the monkeys and macaws. Incomplete recovery of seeds and protection from other seed predators through burial provides the best support to date for the dispersal capabilities of vertebrate seed predators.

CONCLUSIONS

1. Seeds provide consumers with relatively high quality resources but at some cost; they are often either protected mechanically or chemically.

2. Primates and other vertebrates that ingest seeds as a regular and consistent component of their diet exhibit modifications of the gut that enhance seed handling and digestion.

3. Seed predators can potentially deprive plants of their reproductive investment, and the cost to plants should be measured as well as estimating the benefit to consumers.

4. Observations of platyrrhines and reports on psittacids, rodents, and ungulates suggest that these seed predators may contribute to seed dispersal under some circumstances. Despite a preference for large-seeded fruit, seed predators also ingest small seeds. The evolution of small seed size seems to be correlated with improved dispersal rates by a wide range of vertebrates, including primates. Preference for seeds at a particular stage of maturation and diversity of selection of seeds from a range of plant species in a community may also reduce deleterious effects of seed predation on individual plants.

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REFERENCES

Ayres, J.M. UAKARIS AND AMAZONIAN FLOODED FOREST. Ph.D. dissertation, Cambridge University, 1986.

Ayres, J.M. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. JOURNAL OF HUMAN EVOLUTION 18:697–716, 1989.

Barnea, A., Yom-Tov, Y., Friedman, J. Differential germination of two closely related species of *Solanum* in response to bird ingestion. OIKOS 57:222–228, 1990.

Bauchop T.; Martucci, R.W. Ruminant-like digestion of the langur monkey. SCIENCE 161:698–700, 1968.

Becker, P.; Wong, M. Seed dispersal, seed predation, and juvenile mortality of *Aglaia* sp. (Meliaceae) in lowland dipterocarp rainforest. BIOTROPICA 17:230–237, 1985.

Bell, E.A. Toxins in seeds. Pp. 143-161 in BIOCHEMICAL ASPECTS OF PLANT AND ANIMAL COEVOLUTION. J.B. Harborne, ed. London, Academic Press, 1978.

Bennett, E.L., Sebastian, A.C. Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. INTERNATIONAL JOURNAL OF PRIMATOLOGY 9:233–255, 1988.

Birch, G.G.; Kemp, S.E. Apparent specific volumes and tastes of amino acids. CHEMICAL SENSES 14:249–258, 1989.

Bodmer, R.E. Fruit patch size and frugivory in the lowland tapir. JOURNAL OF ZOOLOGY, LONDON 222:121–128, 1990a.

Bodmer, R.E. Responses of ungulates to seasonal inundations in the Amazon floodplain. JOURNAL OF TROPICAL ECOLOGY 6:191–201, 1990b.

Bodmer, R.E. Strategies of seed dispersal and seed predation in Amazonian ungulates. BIOTROPICA 23:255–261, 1991.

Boesch, C.; Boesch, H. Optimisation of nutcracking with natural hammers by wild chimpanzees. BEHAVIOUR 83:265–286, 1983.

Buchanan, D.B.; Mittermeier, R.A.; van Roosmalen, M.G.M. The saki monkeys, genus *Pithecia*. Pp. 391–417 in ECOLOGY AND BEHAVIOR OF NEOTROPICAL PRIMATES. A.F. Coimbra-Filho, R.A. Mittermeier, eds. Rio de Janeiro, Academia Brasileira de Ciencias, 1981.

Chapman, C.A. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. BEHAVIOUR 105:99–116, 1988.

Chapman, C.A. Primate seed dispersal: The fate of dispersed seeds. BIOTROPICA 21:148–154, 1989.

Chivers, D. Functional anatomy of the gastrointestinal tract. Pp. 205–228 in COLOBINE MONKEYS: THEIR ECOLOGY BEHAVIOUR, AND EVOLUTION. A.G. Davies; J.F. Oates, eds. London, Cambridge University Press, 1994.

Chivers, D.J.; Hladik, C.M. Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. JOURNAL OF MORPHOLOGY 166:337–386, 1980.

Corlett, R.T.; Lucas, P.W. Alternative seed-handling strategies in primates: Seed-spitting by long tailed macaques (*Macaca fascicularis*). OECOLOGIA 82:166–171, 1990.

Crawley, M.J. Seed predators and plant population dynamics. Pp. 157–192 in SEEDS: THE ECOLOGY OF REGENERATION IN PLANT COMMUNITIES. M. Fenner, ed. Oxon, UK, C.A.B. International, 1992.

Dasilva, G.L. Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. INTERNATIONAL OF PRIMATOLOGY 15:655–680, 1994.

Davies, A.G. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. INTERNATIONAL JOURNAL OF PRIMATOLOGY 12:119–144, 1991.

Davies, A.G.; Bennett, E.L.; Waterman, P.G. Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *P. melalophos*) in relation to plant chemistry. BIOLOGICAL JOURNAL OF THE LENIN SOCIETY 34:33–56, 1988.

Desenne, P. Estudio preliminar de la dieta de 15 especies de psitácidos en un bosque siempreverde, Cuenca del Río Tawadu, Reserva Forestal El Caura, Edo. Bolívar. Pp. 25–42 in BIOLOGIA Y CONSERVACION DE LOS PSITACIDOS DE VENEZUELA. G. Morales; I. Novo; Déborah Bigio; A. Luy; Franklin Rojas-Suarez, eds. Caracas, Gráficas Giavimar, 1994.

Dubost, G. The ecology and social life of the red acouchy, *Myoprocta exilis*: Comparison with the orange-rumped agouti, *Dasyprocta leporina*. JOURNAL OF ZOOLOGY, LONDON 214:107–123, 1988.

Emmons, L.H. NEOTROPICAL RAINFOREST MAMMALS. Chicago, The University of Chicago Press, 1990.

Fischer, K.E.; Chapman, C.A. Frugivores and fruit syndromes: Differences in patterns at the genus and species level. OIKOS 66:472–482, 1993.

Forget, P.-M. Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. JOURNAL OF TROPICAL ECOLOGY 6:459–468, 1990.

Forget, P.-M. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). BIOTROPICA 24:408–414, 1992.

Forget, P.-M. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. OECOLOGIA 94:255–261, 1993.

Galetti, M.; Rodrigues, M. Comparative seed predation on pods by parrots in Brazil. BIOTROPICA 24:222–224, 1992.

Ganzhorn, J.U. Food partitioning among Malagasy primates. OECOLOGIA (BERLIN) 75:436–450, 1988.

Garber, P.A. Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. AMERICAN JOURNAL OF PRIMATOLOGY 19:203–216, 1989.

Glanz, W.E.; Thorington, R.W., Jr.; Giacalone-Madden, J.; Heaney, L.R. Seasonal food use and demographic trends in *Sciurus granatensis*. Pp. 239–252 in THE ECOLOGY OF A TROPICAL FOREST. E.G. Leigh, Jr.; A.S. Rand; D.M. Windsor, eds. Washington DC, Smithsonian Institution, 1982.

Harper, J.L., Lovell, P.H., Moore, K.G. The shapes and sizes of seeds. ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS 1:327–356, 1970.

Harrison, M.J.S. Feeding ecology of black colobus, *Colobus satanas*, in central Gabon. Pp. 323–353 in PRIMATE ECOLOGY: STUDIES OF FEEDING AND RANGING BEHAVIOUR IN LEMURS, MONKEYS AND APES. T.H. Clutton-Brock, ed. London, Academic Press, 1986.

Hemmingway, C.A. Morphology and phenology of seeds and whole fruit eaten by Milne-Edwards' sifaka, *Propithecus diadema edwardsi*, in Ranomafana National Park, Madagascar. INTERNATIONAL JOURNAL OF PRIMATOLOGY 17:637–660, 1996.

Herrera, C.M. Determinants of plant-animal coevolution: The case of mutualistic dispersal of seeds by vertebrates. OIKOS 44:132–141, 1985.

Hill, W.C.O. PRIMATES: COMPARATIVE ANATOMY AND TAXONOMY. IV Cebidae, Part A. Edinburgh University Press, Edinburgh, 1960.

Horn, A.D. The socioecology of the black mangabey (*Cercocebus aterrimus*) near Lake Tumba, Zaire. AMERICAN JOURNAL OF PRIMATOLOGY 12:165–180, 1987.

Howe, H.H., Westley, L.C. ECOLOGICAL RELATIONSHIPS OF PLANTS AND ANIMALS. Oxford University Press, New York, 1988.

Janson, C.H. Toward and experimental socioecology of primates: Examples from

Argentine brown capuchin monkeys (*Cebus apella nigritus*). Pp. 309–325 in ADAPTIVE RADIATIONS OF NEOTROPICAL PRIMATES, M.A. Norconk, A.L. Rosenberger, P.A. Garber, eds. New York, Plenum, 1996.

Janson, C.H.; Emmons L.H. Ecological structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. Pp. 237–269 in FOUR NEOTROPICAL FORESTS. A. Gentry, ed. New Haven, Yale University Press, 1990.

Janzen, D.H. Seed-eaters versus seed size, number, toxicity and dispersal. EVOLUTION 23:1–27, 1969.

Janzen, D.H. Seed predation by animals. ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS 2:465–492, 1971.

Janzen, D.H. How to be a fig. ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS 10:31–51, 1979.

Janzen, D.H. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. JOURNAL OF ECOLOGY 68:929–952, 1980a.

Janzen, D.H. When is it coevolution? EVOLUTION 34:611–612, 1980b.

Janzen, D.H. Digestive seed predation by a Costa Rican Baird's tapir. BIOTROPICA 13 (Suppl):59–63, 1981a.

Janzen, D.H. *Ficus ovalis* seed predation by an orange-chinned parakeet (*Brotogeris jugularis*) in Costa Rica. AUK 98:841–844, 1981b.

Johns, A. Notes on the ecology and current status of the buffy saki, *Pithecia albicans*. PRIMATE CONSERVATION 7:26–29, 1986.

Jordano, P. Fig-seed predation and dispersal by birds. BIOTROPICA 15:38–41, 1983.

Karr, J.R.; Robinson, S.K.; Blake, J.G.; Bierregaard, R.O., Jr. Birds of four neotropical forest. Pp. 237–269 in FOUR NEOTROPICAL FORESTS. A. Gentry ed. New Haven, Yale University Press, 1990.

Kay, R.; Davies, G. Digestive physiology. Pp. 229–250 in COLOBINE MONKEYS: THEIR ECOLOGY, BEHAVIOUR, AND EVOLUTION. A.G. Davies; J.F. Oates, eds. London, Cambridge University Press, 1994.

Kiltie, R.A. Peccary jaws and canines: Sizing up shape in fossil and recent species. ADVANCES IN NEOTROPICAL MAMMALOLOGY 1989:317–336, 1989.

Kinzey, W.G. Ceboid models for the evolution of hominoid dentition. JOURNAL OF HUMAN EVOLUTION 3:193–203, 1974.

Kinzey, W.G. Dietary and dental adaptations in the Pitheciinae. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 88:499–514, 1992.

Kinzey, W.G.; Norconk M.A. Hardness as a basis of fruit choice in two sympatric primates. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 81:5–15, 1990.

Kinzey, W.G.; Norconk M.A. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. INTERNATIONAL JOURNAL OF PRIMATOLOGY 14:207–227, 1993.

Kitko, R.E.; Strait; S.G.; Overdorff, D.J. Physical properties of *Canarium* seeds and food processing strategies of the Aye-aye in Ranomafana, Madagascar. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 22(Suppl.):139, 1996.

Kool, K.M. The diet and feeding behavior of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. INTERNATIONAL JOURNAL OF PRIMATOLOGY 14:667–700, 1993.

Leighton, M. Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. INTERNATIONAL JOURNAL OF PRIMATOLOGY 14:257–313, 1993.

Leighton, M.; Leighton, D.G. The relationship of size of feeding aggregate to size of food patch: Howler monkeys (*Allouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. BIOTROPICA 14:81–90, 1982.

Levey, D.J. Methods of seed processing by birds and seed deposition patterns. Pp. 147–158 in FRUGIVORES AND SEED DISPERSAL, A. Estrada; T.H. Fleming, eds. Tasks for Vegetation Science 15. Dordrecht, Dr. W. Junk, 1986.

Lucas, P.W.; Teaford, M.F. Functional morphology of colobine teeth. Pp. 173–204 in COLOBINE MONKEYS: THEIR ECOLOGY, BEHAVIOUR, AND EVOLUTION. A.G. Davies; J.F. Oates, eds. London, Cambridge University Press, 1994.

Maisels, F.; Gautier-Hion, A.; Gautier, J.-P. Diets of two sympatric colobines in Zaire: More evidence on seed-eating in forests on poor soils. INTERNATIONAL JOURNAL OF PRIMATOLOGY 15:655–701, 1994.

McKey, D.B.; Gartlan, J.S.; Waterman, P.G.; Choo, G.M. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. BIOLOGICAL JOURNAL OF THE LINNAEAN SOCIETY 16:115–146, 1981.

Meyers, D.M.; Wright, P.C. Resource tracking: Food availability and Propithecus seasonal reproduction. Pp. 179–192 in LEMUR SOCIAL SYSTEMS AND THEIR ECOLOGICAL BASIS. P.M. Kappeler; J.U. Ganzhorn, eds. New York, Plenum, 1993.

Milton, K. The role of food-processing factors in primate food choice. Pp. 249–279 in ADAPTATIONS FOR FORAGING IN NONHUMAN PRIMATES. P.S. Rodman;

J.G.H. Cant, eds. New York, Columbia University Press, 1984.

Milton, K. Foraging behaviour and the evolution of primate intelligence. Pp. 285–305 in MACHIAVELLIAN INTELLIGENCE. R.W. Bryrne; A.Whiten, eds. Oxford, Clarendon Press, 1988.

Mittermeier, R.A. DISTRIBUTION, SYNECOLOGY AND CONSERVATION OF SURINAME MONKEYS. Ph.D. dissertation, Harvard University, 1977.

Mittermeier, R.A.; Konstant, W.R.; Meyers, D.M.; Mast, R.B. LEMURS OF MADAGASCAR. Washington DC, Conservation International, 1994.

Moermond, T.C., Denslow, J.S. Neotropical avian frugivores: Patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Pp. 865–897 in NEOTROPICAL ORNITHOLOGY, ORNITHOLOGICAL MONOGRAPHS 36. Washington, D.C., American Ornithologists Union, 1985.

Müller, K.-H. Ranging in masked titi monkeys (*Callicebus personatus*) in Brazil. FOLIA PRIMATOLOGICA 65:224–228, 1995.

Müller, K.-H. Feeding ecology of masked titis, *Callicebus personatus*. Pp. 383–401 in ADAPTIVE RADIATIONS OF NEOTROPICAL PRIMATES. M.A. Norconk; A.L. Rosenberger; P.A. Garber, eds. NewYork, Plenum, 1996.

Munn, C.A. Macaw biology and ecotourism, or "When a bird in the bush is worth two in the hand." Pp. 47–72 in NEW WORLD PARROTS IN CRISIS: SOLUTIONS FROM CONSERVATION BIOLOGY S.R. Geissinger; N.F.R. Snyder, eds: Washington DC, Smithsonian Institution Press 1992.

Norconk, M.A. Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. Pp. 403–423 in ADAPTIVE RADIATIONS OF NEOTROPICAL PRIMATES. M.A. Norconk; A.L. Rosenberger; P.A. Garber, eds. NewYork, Plenum, 1996.

Norconk, M.A.; Kinzey, W.G. Challenge of neotropical frugivory: Travel patterns of spider monkeys and bearded sakis. AMERICAN JOURNAL OF PRIMATOLOGY 34:171–183, 1994.

Norconk, M.A.; Grafton, B.W.; Gleason, T.M. Ecology of an important resource used by wild bearded sakis. AMERICAN JOURNAL OF PRIMATOLOGY 36:146, 1995.

Norconk M.A.; Wertis, C.A.; Kinzey, W.G. Seed predation by monkeys and macaws in eastern Venezuela: Preliminary findings. PRIMATES 38:177–184, 1997.

Oates, J.F. The diet of the olive colobus monkey, *Procolobus verus*, in Sierra Leone. INTERNATIONAL JOURNAL OF PRIMATOLOGY 9:457–478, 1988.

Oates, J.F.; Waterman, P.G.; Choo, G.M. Food selection by the South Indian leafmonkey, *Presbytis johnii*, in relation to leaf chemistry. OECOLOGIA 45:45–56, 1980.

Oates, J.F.; Davies, A.G.; Delson, E. The diversity of living colobines. Pp. 45–74 in COLOBINE MONKEYS: THEIR ECOLOGY, BEHAVIOUR, AND EVOLUTION. A.G. Davies; J.F. Oates, eds. London, Cambridge University Press, 1994.

Peres, C.A. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in Central Amazonia. BIOTROPICA 23:262–270, 1991.

Peres, C.A. Notes on the ecology and diet of buffy sakis (*Pithecia albicans* Gray 1860): A canopy seed predator. AMERICAN JOURNAL OF PRIMATOLOGY 31:129–140, 1993.

Peres, C.A. Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagothricha cana*) in central Amazonia: Comparisons with other atelines. INTERNATIONAL JOURNAL OF PRIMATOLOGY 15:333–372, 1994.

Peters, C.R. Shell strength and primate seed predation of nontoxic species in eastern and southern Africa. INTERNATIONAL JOURNAL OF PRIMATOLOGY 14:315–344, 1993.

Robinson, J.G.; Wright, P.C.; Kinzey, W.G. Monogamous cebids and their relatives: Intergroup calls and spacing. Pp. 44–53 in PRIMATE SOCIETIES. B.B. Smuts; D.L. Cheney; R.M. Seyfarth; R.W. Wrangham; T.T. Struhsaker, eds. Chicago, The University of Chicago Press, 1987.

Rosenberger, A.L. Evolution of feeding niches in New World monkeys. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 88:525–562, 1992.

Setz, E.Z.F. Ecologia alimentar de um grupo de parauacus (*Pithecia pithecia chrysocephala*) em um fragmento florestal na Amazonia Central. BOLETIM DA SOCIEDADE BRASILEIRA DE MASTOZOOLOGIA 28:5, 1994.

Smythe, N. THE NATURAL HISTORY OF THE CENTRAL AMERICAN AGOUTI (*Dasyprocta punctata*). SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY 257. Washington, D.C., 1978.

Smythe, N.; Glanz, W.E.; Leigh, R.G., Jr. Population regulation in some terrestrial frugivores. Pp. 227–238 in THE ECOLOGY OF A TROPICAL FOREST. E.G. Leigh, Jr.; A.S. Rand; D.M. Windsor, eds. Washington, DC, Smithsonian Institution, 1982.

Stebbins, G.L. Adaptive radiation of reproductive characteristics in angiosperms, II: Seeds and seedlings. ANNUAL REVIEW OF ECOLOGY AND EVOLUTION 2:237–260, 1971.

Sterling, E.J. Aye-ayes: Specialists on structurally defended resources. FOLIA PRIMATOLOGICA 62:142–154, 1994.

Stevens, C.E. COMPARATIVE PHYSIOLOGY OF THE VERTEBRATE DIGESTIVE SYSTEM. Cambridge, University Press, 1988.

Strait, S.G.; Overdorff, D.J. Physical properties of fruits eaten by Malagasy primates. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 22(Suppl.):224, 1996.

Terborgh, J. FIVE NEW WORLD PRIMATES. Princeton, NJ, Princeton University Press, 1983.

Terborgh, J. Community aspects of frugivory in tropical forests. Pp. 371–384 in FRUGIVORES AND SEED DISPERSAL, A. Estrada; T.H. Fleming, eds. Tasks for Vegetation Science 15. Dordrecht, Dr. W. Junk, 1986.

Terborgh, J.; Robinson, S.K.; Parker, T.A., III; Munn, C.A.; Pierpont, N. Structure and organization of an Amazonian forest bird community. ECOLOGICAL MONOGRAPHS 60:213–238, 1990.

Tiffney, B.H. Evolution of seed dispersal syndromes according to the fossil record. Pp. 274–305 in SEED DISPERSAL. D.R. Murray, ed. Sydney, Australia, Academic Press, 1986.

Ungar, P.S. Fruit preferences of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. INTERNATIONAL JOURNAL OF PRIMATOLOGY 16:221–245, 1995.

Vander Wall, S.B. FOOD HOARDING IN ANIMALS. Chicago, University of Chicago, 1990.

van Roosmalen, M.G.M. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey [*Ateles paniscus paniscus*, Linnaeus 1758] in Surinam. ACTA AMAZONICA 15(Suppl):1–238, 1985.

van Roosmalen, M.G.M.; Mittermeier, R.A.; Fleagle, J.G. Diet of the northern bearded saki (*Chiropotes satanas chiropotes*): A neotropical seed predator. AMERICAN JOURNAL OF PRIMATOLOGY 14:11–35, 1988.

Waser, P. Feeding, ranging and group size in the mangabey *Cercocebus albigena*. Pp. 183–222 in PRIMATE ECOLOGY—STUDIES OF FEEDING AND RANGING BEHAVIOR IN LEMURS, MONKEYS AND APES. T.H. Clutton-Brock, ed. London, Academic Press, 1977.

Waterman, P.G. Food acquisition and processing as a function of plant chemistry. Pp. 177–211 in FOOD ACQUISITION AND PROCESSING IN PRIMATES. D.J. Chivers; B.A. Wood; A. Bilsborough, eds. New York, Plenum, 1984.

Waterman, P.G.; Kool, K.M. Colobine food selection and plant chemistry. Pp. 251–284 in COLOBINE MONKEYS: THEIR ECOLOGY, BEHAVIOUR, AND EVOLUTION. A.G. Davies; J.F. Oates, eds. London, Cambridge University Press, 1994.

Whiten, A.; Byrne R.W.; Barton, R.A.; Waterman, P.G.; Henzi, S.P. Dietary and foraging strategies of baboons. Pp. 27–37 in FORAGING STRATEGIES AND NATURAL DIET OF MONKEYS, APES, AND HUMANS. A. Whiten; E.M. Widdowson, eds. Oxford, Clarendon Press, 1992.

Wrangham, R.W.; Waterman, P.G. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophlea*: With special reference to preproductive strategies and tannin production. JOURNAL OF ANIMAL ECOLOGY 50:715–731, 1981.

Yamashita, N. Seed eating among three sympatric lemur species in Madagascar. Pp. 365 in HANDBOOK AND ABSTRACTS OF THE XVTH CONGRESS OF THE INTERNATIONAL PRIMATOLOGICAL SOCIETY, Kuta, Bali, Indonesia, 1994.

Yeager, C.Y. Feeding ecology of the proboscis monkey (*Nasalis larvatus*). INTERNATIONAL JOURNAL OF PRIMATOLOGY 10:497–530, 1989.