

SHORT COMMUNICATION

Seed Predation by Monkeys and Macaws in Eastern Venezuela:
Preliminary Findings

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ABSTRACT. Feeding data collected concurrently on bearded sakis (*Chiropotes satanas*) and red and green macaws (*Ara chloroptera*) on a large island in Guri, Venezuela provides preliminary evidence that these two seed predators have similar diets. Individuals of both species were equally capable of opening very hard, protected fruits. Of the seven fruit species used by macaws during the study period, four species were also ingested by sakis at the same stage of ripeness, two species were ingested at different stages of ripeness (macaws earlier than sakis), and one species was never observed to have been eaten by sakis. The second finding, that macaws ingest young seeds of the Anacardiaceae and Burseraceae families and the bearded sakis ingest only the ripe mesocarp of these species suggests that the most distinguishable difference in their diets might be a tolerance of toxins by the macaws that act as feeding deterrents for the monkeys. Although we did not document the location of local clay licks in eastern Venezuela, the use of clay licks by macaws in Peru (MUNN, 1992) suggests that this activity (that is not practiced by the sakis) may be helpful in detoxifying or ameliorating the effects of ingesting chemically protected fruit.

Key Words: Neotropics; Bearded saki monkey (*Chiropotes satanas*); Red and green macaw (*Ara chloroptera*); Puncture resistance; Mechanical seed protection; Dietary toxins.

INTRODUCTION

Many plants invest in some mechanism to protect seeds from ingestion by seed predators. FISCHER and CHAPMAN (1993) recently documented characteristics of fruit sampled from five localities worldwide. More than 75% of the genera sampled demonstrated mechanical protection (e.g. hardness, spines, stinging hairs) (FISCHER & CHAPMAN, 1993, p. 476). Although most likely an adaptation by the parent plant to protect fruit from boring insects and scatter hoarding rodents (FORGET, 1993; JANZEN, 1978; SMITH, 1975), primates that ingest seeds encounter those same seed protections. Seeds are worth the efforts expended by seed predators because the nutritional rewards for successfully opening and digesting seeds can be very high. Seeds, protected and unprotected, are often found to be balanced nutritionally since the plant sequesters starches, lipids, and amino acids in the seed compartment to provide for the development of seed embryos during germination (ESAU, 1977; JANZEN, 1978).

Seeds that are masticated and digested make up a substantial portion of the diets of two subfamilies of primates, the colobines (Catarrhini) (DASILVA, 1994; KOOL, 1993; MAISELS et al., 1994) and the pitheciines (Platyrrhini) (AYRES, 1986, 1989; KINZEY & NORCONK, 1990, 1993; VAN ROOSMALEN et al., 1988). Evidence for seed predation outside of these

groups has been documented for a number of primates: *Cebus apella* (PERES, 1991; TERBORGH, 1983), *Lagothrix lagotricha* (PERES, 1994), *Cercocebus* spp. (WASER, 1984), *Mandrillus sphinx* (LAHM, 1986), *Pongo pygmaeus* (UNGAR, 1995), and *Propithecus diadema* (WRIGHT et al., 1994; YAMASHITA, 1994, 1996), with evidence for seasonal dependence on specific seed resources by *Cebus*, *Lagothrix*, and *Propithecus*.

In addition to primate seed predators, other mammals (particularly sciurids: EMMONS, 1980, 1982; GALETTI et al., 1992; GLANZ et al., 1982; GLANZ, 1984) and birds (psittacids: COATES-ESTRADA et al., 1993; DESENNE, 1994; GALETTI & RODRIGUES, 1992; KARR et al., 1990; MUNN, 1992) remove seeds from the tree crown at an early (predispersal) stage of seed maturation. AYRES (1986) and PERES (1991) suggested that macaws and primates might share similar skills in their abilities to open hard fruit, but such capabilities have not been quantified. We conducted a brief study of seed predation by red and green macaws (*Ara chloroptera*) during a long-term study of bearded sakis (*Chiropotes satanas chiropotes*) in eastern Venezuela. The results of the study provide preliminary information on the characteristics of fruit ingested by macaws and bearded sakis, the relative age of the seeds at the time of ingestion, and fruit and seed coat hardness of successfully opened fruit.

A number of ecological similarities exist between bearded saki monkeys and red and green macaws that suggest that there might be considerable overlap in their food resources and similarities in their adaptations for removing seeds from fruit still attached to tree crowns (young or predispersed seeds). Both macaws and sakis depend on seeds for a large portion of their diets. Red and green macaws ingested >90% of their total diet as seeds in southern Venezuela (DESENNE, 1994); bearded sakis ingested fruit items as >90% diet with at least 65% of fruit ingested as seeds (KINZEY & NORCONK, 1990; VAN ROOSMALEN et al., 1988). Bearded sakis and macaws exceed 1 kg of body weight (red and green macaws range from 1.05 to 1.25 kg; KARR et al., 1990; bearded sakis average 3.0 kg; FLEAGLE & MITTERMEIER, 1980). Both species are diurnal and are very mobile. Bearded sakis travel an average of 3.2 km a day (NORCONK & KINZEY, 1994) and MUNN (1992) estimated a maximum travel distance of 9 km for *Ara chloroptera* in Peru.

METHODS

The study took place on a 365-ha island in Guri Lake, Venezuela (7°22'N, 62°55'W). The island has been isolated from mainland forest since 1983 after completion of the Raúl Leoni hydroelectric plant and the third stage of flooding of the Caroní and Paragua Rivers by EDELCA (Electrificación del Caroní) in 1986. The island is entirely forested with a mixed tropical dry/transitional wet forest (see ALVAREZ et al., 1986; AYMARD et al., in press; KINZEY & NORCONK, 1993, for site description). The monkeys and macaws used the entire island during foraging and feeding activities, an area that represents a portion of their original, pre-flooded ranges.

Feeding data of macaws and bearded sakis were collected concurrently by two teams of observers during the peak wet season (May to August) of 1991. The bearded saki study group of 18 individuals was well-habituated and cohesive during the study period and shared the island with at least six social groups of howler monkeys (*Alouatta seniculus*) and three groups of capuchins (*Cebus olivaceus*). Observers followed the sakis from sleeping tree to sleeping tree for five consecutive days each month. As the monkeys arrived at a feeding tree, we noted the identity of the tree, time of arrival, and exit from the tree, and collected fruit that was partially eaten or dropped unopened.

Ara chloroptera was the only macaw species observed in this region of eastern Venezuela, approximately 150 km south of the Orinoco River in Bolívar State. The macaws rarely roosted on the island, rather they began to arrive shortly after dawn and departed shortly before dusk. We monitored approximately 23 adult macaws in three ways: 1) sightings from a high point on the island using a Nikon (20×) sighting scope; 2) discovering macaw feeding trees via communication by hand-held radio between monkey observers and macaw observers; and 3) "stake-outs" at known macaw feeding trees. Samples of fruit were obtained during encounters with macaws at feeding trees (using methods 2 & 3), however our observations were limited by the macaws ability to cover long distances over short periods of time and their poor tolerance of human observers. Thus, the food list for the macaws is probably incomplete.

The field techniques used to measure the hardness or puncture resistance of pericarp have been described in detail (KINZEY & NORCONK, 1990). Briefly, we collected fruit opened and dropped by the macaws and monkeys at every feeding tree and tested puncture resistance the same day using a Force Dial with compression plunger (1mm in diameter) (Wagner Instruments Models FDK 5 that measures puncture resistance to 2.5 kg/mm² and FDK 10 to 5.0 kg/mm²). To test very hard fruit, we attached a 1-mm (diameter) pin to the upper force plate of a Rimac soil crusher that allowed us to measure puncture resistance accurately to 110 kg/mm² (see KINZEY & NORCONK, 1990). We considered fruit "protected" if puncture resistance exceeded 1.25 kg/mm². This value is just above the hardest fruit opened by *Ateles paniscus*, a seed disperser and ripe fruit specialist ingesting soft, mature fruit (KINZEY & NORCONK, 1990).

RESULTS

CHARACTERISTICS OF FRUIT INGESTED BY MACAWS AND SAKIS

Macaws manipulated unopened fruit with their feet, beak, and tongue. They opened fruit and cracked resistant seed coats with their beak, and reduced the size of seeds with beak and tongue prior to swallowing. Bearded sakis manipulated unopened fruit with their hands and usually opened fruit and resistant seed coats with canines mimicking the action of the macaw beak. Sakis masticated seeds and both the empty pericarps and seed coverings were usually discarded.

We observed macaws feeding from trees of 7 fruit species during the four month sample period and bearded sakis ingested fruit from 16 species during the same sample period (Table 1). Of the seven fruit species used by macaws, only one (*Centrolobium paraense*) was not also used by sakis. Since all day observations of macaws were not possible, the macaw sample is certainly an underestimation of diet breadth during this period of time.

RELATIVE AGE OF SEEDS AT THE TIME OF INGESTION

Macaws ingested both young and mature seeds in approximately equal proportions in our small sample (Table 1). Bearded sakis appeared to express a preference for young over mature seeds, but in two cases (*Pradosia caracasana* and *Chrysophyllum lucentifolium*) they ingested seeds and mesocarp from both young and mature fruit. Seeds of the very small capsules (c. 0.5 × 0.5 × 0.4 cm) of young *Sapium glandulosum* were ingested by both monkeys and macaws during the sample period. Seeds of ripe samaras of *Pterocarpus*

Table 1. Identity and characteristics of fruit and seeds ingested by *Ara chloroptera* and *Chiropotes satanas*.

Fruit species	Family	Mechanical protection	<i>Ara chloroptera</i>		<i>Chiropotes satanas</i>	
			Item ingested	Stage of maturity	Item ingested	Stage of maturity
<i>Arrabidaea carichanensis</i>	Bignoniaceae	Hard pericarp	NE		Seed	Young
<i>Brosimum alicastrum</i>	Moraceae	None	NE		Seed	Young
<i>Calliandra laxa</i>	Mimosaceae	Hard pericarp	NE		Seed	Young
<i>Centrolobium paraense</i>	Papilionaceae	Spines	Seed	Mature	NE	
<i>Chrysophyllum lucentifolium</i>	Sapotaceae	Hard seed coat	Seed	Young	Seed (& mesocarp)	Young (& mature)
<i>Duguetia lucida</i>	Annonaceae	Hard pericarp	NE		Seed & mesocarp	Mature
<i>Licania hypoleuca</i>	Chrysobalanaceae	Hard pericarp	NE		Seed	Young
<i>Luehea speciosa</i>	Tiliaceae	None	NE		Seed	Young
<i>Oryctanthus alveolatus</i>	Loranthaceae	None	NE		Whole fruit	Mature
<i>Melicoccus bijugatus</i>	Sapindaceae	None	NE		Mesocarp	Mature
<i>Phthirusa adunca</i>	Loranthaceae	None	NE		Whole	Mature
<i>Pradosia caracasana</i>	Sapotaceae	Hard pericarp & hard seed coat	Mesocarp	Mature	Seed & mesocarp	Young & mature
<i>Protium tenuifolium</i>	Burseraceae	None	Seed	Young	Mesocarp	Mature
<i>Pterocarpus acapulcensis</i>	Papilionaceae	Hard seed coat	Seed	Mature	Seed	Young & mature
<i>Sapium glandulosum</i>	Euphorbiaceae	None	Seed	Young	Seed	Young
<i>Spondias mombin</i>	Anacardiaceae	Fibrous pericarp	Seed	Young	Mesocarp	Mature
<i>Strychnos dariensis</i>	Loganiaceae	None	NE		Seed	Young

Mechanical protection (i.e. physical characteristics of fruit or seeds) includes hardness of pericarp or seed coat and presence of spines. NE: Items that were not observed to have been eaten. Items ingested included seed only, mesocarp only, or whole fruit to include seed and pericarp.

Table 2. Puncture resistance (kg/mm^2) of fruit ingested by *Ara chloroptera* (macaws) and *Chiropotes satanas* (bearded sakis).

Fruit species (portion tested)	Macaws				Sakis			
	N	avg	\pm std	max	N	avg	\pm std	max
<i>Arrabidaea carichanensis</i> (pericarp)	NE				5	1.37	0.28	1.87
<i>Brosimum alicastrum</i> (pericarp)	NE				12	0.56	0.17	1.11
<i>Calliandra laxa</i> (pericarp)	NE				5	1.56	0.09	1.65
<i>Centrolobium paraense</i> (seed coat)	4	8.79	1.57	12.60	NE			
<i>Chrysophyllum lucentifolium</i> (pericarp)	NM				66	1.52	0.31	2.29
<i>Duguetia lucida</i> (pericarp)	NE				3	1.36	0.29	1.77
<i>Pradosia caracasana</i> (pericarp-dropped opened)	62	1.49	0.28	2.11	79	1.52	0.21	2.15
<i>Pradosia caracasana</i> (pericarp-dropped unopened)	10	1.64	0.14	1.92	16	2.38	2.14	8.03
<i>Pradosia caracasana</i> (seed coat)	5	6.45	1.01	7.27	24	6.71	3.28	16.06
<i>Pterocarpus acapulcensis</i> (pericarp)	NM				14	3.49	1.02	5.05
<i>Protium tenuifolium</i> (pericarp)	11	1.60	0.38	2.08	NM			
<i>Spondias mombin</i> (pericarp)	70	10.43	4.80	23.4	15	0.57	0.18	1.13

N: Sample size; avg: average values; std: standard deviation of the means; max: maximum values; NE: not observed to have been eaten; NM: no measurements taken, although the fruit was ingested.

acapulcensis were also eaten by both macaws and bearded sakis, although the sakis also ingested these seeds as young seeds. The most significant difference between macaws and sakis emerged with the finding that macaws ingested some young seeds that were never seen to have been ingested by sakis: *Protium tenuiflora* and *Spondias mombin*. Instead, bearded sakis ingested the sweet mesocarp of these fruits at the mature stage (Table 1).

HARDNESS OF THE FRUIT AND SEED COAT

Both macaws and sakis open very hard, protected fruit (Table 2). The hardest fruit opened by macaws in Guri Lake were the young, fibrous *Spondias mombin* fruit (maximum puncture resistance of 23.4 kg/mm²). The pericarp of this fruit is more resistant to puncture than fruit ingested by bearded sakis in Guri, Venezuela (Table 2), but fruit with even higher maximum puncture resistance were opened by bearded sakis at Raleighvallen-Voltzberg, Suriname (37.8 kg/mm²: *Licania majuscula*) (KINZEY & NORCONK, 1990). As a matter of scale, these puncture resistance values are within the range of commercial hazel nuts opened by captive white-faced sakis ($\bar{x} = 41 \pm 20.4$ kg/mm², $N = 5$) (NORCONK, unpubl.).

DISCUSSION

Despite the short-term nature of the observations on the macaws, a more comprehensive study by DESENNE (1994) in southern Venezuela suggests that our observations are broadly representative of red and green macaw diets. Red and green macaws from both sites in Venezuela ingested seeds from the families Anacardiaceae, Burseraceae, Euphorbiaceae, Papilionaceae, and Sapotaceae. Some resources, such as palms and fruit of Moraceae and Lecythidaceae, were missing from the dry forest of Guri, but were used by macaws in the wet forest on the Caura River.

Bearded sakis and red and green macaws have solved successfully the problem of opening mechanically protected fruit. Opening protected fruit involved both the ability to puncture protected fruit or seed coats and manipulative skill (required to remove pericarp and often seed coats before ingestion). The major difference between the two seed predators involved the ingestion of young seeds of *Spondias mombin* (Anacardiaceae) and *Protium tenuifolium* (Burseraceae), the seeds of which were never observed to have been ingested by bearded sakis. Tolerance of these seeds by macaws may be related to an ability to circumvent the plant's chemical protection. These species are in closely related plant families, both of which are known to produce toxic oils and resins (CRONQUIST, 1981), properties that may result in chemical protection to seeds. Sakis do ingest the sweet mesocarp on the seed surface of both species (Table 1) and Anacardiaceae gums are high ranking resources for callitrichine platyrrhines (EGLER, 1993; GARBER, 1984; RYLANDS & DE FARIA, 1993). Gums of *Spondias mombin* and *Anacardium excelsum* are high in minerals, protein, and complex carbohydrates (GARBER, 1984; LEON DE PINTO et al., 1995), but the nutrient composition or presence of toxic oils or resins in unripe seeds has not been examined. If toxic, macaws may counter the effects of ingesting seeds of these species by ingesting clay. MUNN (1992) suggested that ingestion of clay may ameliorate the effects of digesting fruit high in secondary compounds. We did not locate clay licks used by red and green macaws in Guri Lake, Venezuela, although one of us (C.W.) did note whitish discoloration on the beaks that could have been residual clay deposits. We have never observed bearded sakis to ingest soil or clay.

Fruit with mechanical protection in the form of hard or thick husks, and hard or brittle seed coats do not deter macaws or bearded sakis from seed predation. Preliminary evidence also suggests that there might be considerable overlap in the seed species ingested, although some variation appears to exist in the stage of maturation at which seeds are used. Yet to be determined is the role of chemical protection in fruit choice for these two large-bodied canopy level seed predators. Taste and/or digestibility may limit primate access to some fruits and seeds that are ingested and apparently can be digested by macaws. Using colobines as a point of comparison for the sakis, KAY and DAVIES (1994) suggest that the digestion of complex starches in seeds may be facilitated by complex forestomach and slow transit through the gut. The anatomical correlates of seed predation by bearded sakis have been explored in the dental anatomy (KINZEY, 1992), but the physiology of digestion and gut anatomy of bearded sakis is poorly known. CHIVERS (1994) remarked that colobines and ceboids have converged with pitheciines and *Alouatta* sp. in the evolution of capacious gut segments, but this conflicts with the only feeding experiment conducted on an individual of closely related *Chiropotes albinasus*. MILTON (1984) found that markers first appeared after only 5 hr in the white-nosed saki where KAY and DAVIES (1994) estimated 38 hr retention time of lignin for captive *Colobus guereza*. An increase in interdisciplinary research between field ecologists and animal nutritionists with the use of feeding experiments and comparisons between species with convergent adaptations will be needed if we are to ask more informative questions about primate diets and primate feeding ecology.

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