Diet and Food Choice in Peruvian Red Uakaris (*Cacajao calvus ucayalii*): Selective or Opportunistic Seed Predation?

Mark Bowler · Richard E. Bodmer

Abstract Even primates considered dietary specialists tend to eat a combination of fruit pulp, seeds, other plant parts, or animals. Specialist seed predators could either feed on seeds preferentially, or to avoid competition when ripe pulps are scarce. Pitheciin monkeys have specialized dentition that allows them to feed on seeds protected by hard shells, and the upper limit on the hardness of these is likely to be a function of jaw size. We recorded the diet of Peruvian red uakaris (*Cacajao calvus ucayalii*) on the Yavari River, Peru, to test the prediction that this seed predator would feed on the seeds of hard-shelled fruits preferentially over softer ones in relation to their availability in the forest. We also tested predictions that adult male, adult female, and juvenile diets would differ, with larger individuals eating more hard fruits. Uakaris ate 55.4% seeds, 38.9% pulps and arils, and 5.6% other items, but proportions varied through the year. More pulps, especially from the palm *Mauritia flexuosa*, were eaten when fruit availability was low, and more hard fruits were positively selected for than softer ones. Juveniles did not open the hardest fruit species opened by adults, and adult males ate harder fruits than females. These results provide evidence that seed eating in some primates has evolved beyond a means of avoiding competition for the ripe pulps typically preferred by many primates. Specialist seeding-eating primates therefore occupy divergent niches that require separate consideration from those of similar-sized primates.

Keywords Cacajao · Diet · Pitheciin · Pitheciini · Uacari · Uakari

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Introduction

Although most primates are largely frugivorous, diets are diverse and can include ripe or unripe fruit pulps and seeds as well as leaves, exudates, and other plant parts or animals in various proportions (Rosenberger 1992). Primates that feed predominantly on any particular resource category are considered dietary specialists, but even such specialists tend to use a combination of foods (Rosenberger 1992). The diets of sympatric primates typically overlap considerably when ripe fruit pulp is abundant, and it is during periods of relative ripe fruit pulp scarcity that the diets of sympatric species differentiate (Stevenson *et al.* 2000; Terborgh 1983; Tutin *et al.* 1997).

Several primate species are considered specialists in masticating and digesting seeds. Among the Old World primates, seeds make up a large proportion of the diets of colobine monkeys (subfamily Colobinae: Dasilva 1994; Kool 1993; Maisels *et al.* 1994), mangabeys (*Cercocebus*: Waser 1984), mandrills (*Mandrillus sphinx*: Lahm 1986), orangutans (*Pongo pygmaeus*: Ungar 1995), and sifakas (*Propithecus diadema*: Hemingway 1998; Yamashita 1996). Of the New World primates, brown capuchins (*Cebus paella*: Peres 1991; Terborgh 1983), woolly monkeys (*Lagothrix lagothricha*: Peres 1994), and titis (*Callicebus personatus*: Heiduck 1997) show some dependence on seeds, but the sakis (*Pithecia*), bearded sakis (*Chiropotes*), and uakaris (*Cacajao*), collectively the tribe Pitheciini (Rosenberger *et al.* 1996), are unique among Neotropical primates in that they are specialized seed predators (Aquino 1995, Aquino and Encarnación 1999; Ayres 1986, 1989; Barnett *et al.* 2005; Boubli 1999; Buchanan *et al.* 1981; Cunningham and Janson 2006; Johns 1986; Kinzey and Norconk 1993; Norconk and Conklin-Brittain 2004; Peres 1993; Setz 1994; van Roosmalen *et al.* 1988). Large, palatable seeds are often protected by hard shells (Fischer and Chapman 1993; Norconk *et al.* 1998), and pitheciins are equipped to open such fruits. Their enlarged canines pierce hard shells, and they then remove seeds from the shells with forward-pointing incisors; a process called sclerocarpic harvesting (Kinzey 1992; Kinzey and Norconk 1990). The puncture resistance of fruits eaten by bearded sakis is up to 15 times greater than of those consumed by spider monkeys (*Ateles*), and hardness of fruit pericarps may play a significant role in food choice in sympatric primates (Kinzey and Norconk 1990).

That primate diets tend to converge when ripe fruit pulp is abundant begs the question: Do primates that are specialized to predate seeds feed on them preferentially or do they do so to avoid competition when ripe pulps are scarce? Some primates select food based on nutritional needs; e.g., sympatric howlers (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*) appear to eat proportions of leaves and ripe fruits depending on their abilities to digest these food types and extract the proteins and carbohydrates they require (Milton 1981). However, masked titis (*Callicebus personatus*) feed on higher proportions of seeds during lean periods when fleshy fruits are less abundant and nutrient content does not appear to affect selection (Heiduck 1997). Similar examples, in which food abundance is the main factor in determining food selection, suggest that many primates feed opportunistically on foods available to them (Dasilva 1994; Barton and Whiten 1994; Mowry *et al.* 1996). The proportion of ripe pulps and arils vs. seeds in the diet of white uakaris (*Cacajao calvus calvus*) at Tefé, Brazil increases

when fruit production is high (Ayres 1986). Similarly, in white-faced sakis (*Pithecia pithecia*) and bearded sakis (*Chiropotes satanas*) the ripening of the most-eaten resources brings about a switch from unripe seeds to ripe pulps (Norconk 1996). Contrary to these studies, black uakaris (*Cacajao melanocephalus*) at Pico da Neblina, Brazil, eat proportionally more ripe pulps and arils and fewer seeds when fruits are scarce in the forest (Boubli 1999), and *Pithecia pithecia* at Guri Lake, Venezuela eat fewer seeds and more leaves, insects, and flowers when fruits are scarce (Cunningham and Janson 2006). In all of these studies on pitheciins, the proportions of seeds and pulps in the diet varied seasonally and the authors related this to the relative availability of the plant parts, but they did not measure the selectivity for the fruit species concerned compared to their availability in the environment.

One consequence of a diet of hard-shelled fruits is that the upper limit on the hardness of fruits eaten is likely to be a function of jaw size and muscle mass. Thus smaller individuals may not be able to access harder fruits (Boubli 1999). *Chiropotes* eats harder fruits on average than the smaller *Pithecia* (Kinzey and Norconk 1993), and juvenile black uakaris appear unable to open several fruit species eaten by adults (Boubli 1999), but no researchers have ever directly compared the diets of wild uakaris of different sizes in the same group. High sexual dimorphism in uakaris (Hershkovitz 1987) may mean that males and females, as well as individuals of different age classes, differ in their ability to open hard fruits.

We here examine the diet of one of the most specialized seed predators, the Peruvian red uakari (*Cacajao calvus ucayalii*), to test the prediction that specialized seed predators will feed on the seeds of hard-shelled fruits preferentially over ripe pulps, selecting fruits with harder shells more frequently than softer ones in relation to their availability in the forest. We also test the prediction that adults feed on harder fruits on average than juveniles, and that adult males feed on harder fruits on average than adult females.

Methods

Study Area

We conducted the study in the 9926.19-ha Lago Preto Conservation Concession, Loreto, Peru (S04°27.5′ W071°45.9′), bordered by the Yavarí and Yavarí-Mirín rivers in the south and west, and by the Iquitos-Yavarí logging concessions in the north and east (Fig. 1). The concession contains nonflooding *terra firme* forest, white-water *várzea* forest that floods with silt-laden water between November and May each year, and permanently waterlogged forest known as *aguajal* dominated by the palm *Mauritia flexuosa* and sometimes with a more open canopy similar to the *chavascal* habitat (Boubli 1999). There are 13 primate species including red uakaris.

Total annual precipitation is 2,000–3,000 mm, and though the climate is not very seasonal, average rainfall peaks between December and March with drier months between May and August (Pitman *et al.* 2003). Mean temperatures are between 24
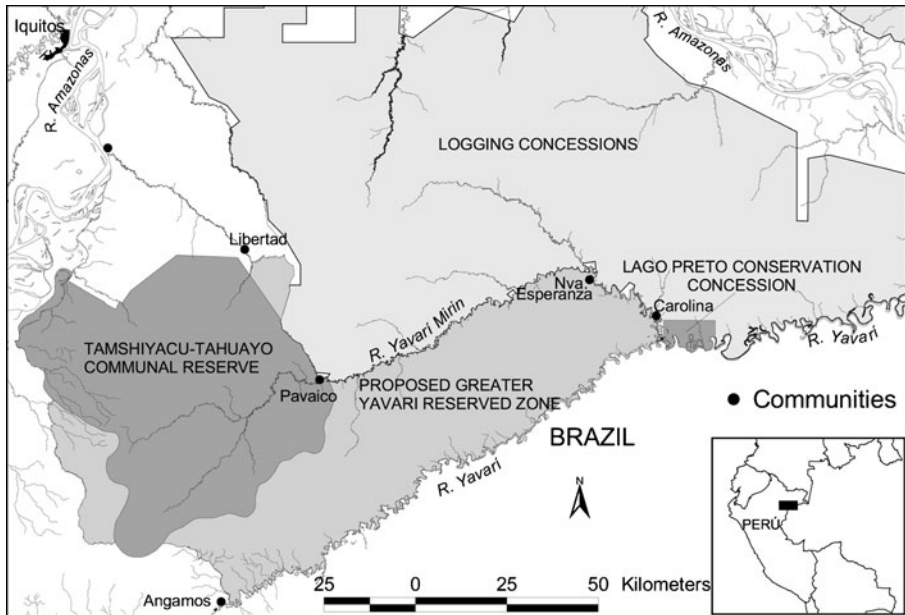
Fig. 1 Map showing the location of the Lago Preto Conservation Concession and surrounding areas. (From Bowler and Bodmer 2009).

and 26°C and are fairly constant throughout the year, aside from rare southerly winds that can produce minimum temperatures of 10°C (Pitman *et al.* 2003).

Fruit Availability

To determine changes in the availability of fruit at Lago Preto, we measured transects on 8 randomly selected trails in each of the main habitats. All transects were 5 m wide except 1, which was created as part of another survey and was 20 m wide (Pitman *et al.* 2003). We tagged and identified every tree of diameter at breast height (DBH) >10 cm within the transects and every vine or liana of DBH >7 cm on all 5-m wide transects (Ayres 1986). To obtain a reasonable sample of the diversity in each habitat, we sampled habitats until the rate of discovery of new species slowed (Sutherland 2000), thus determining the length and area of each transect. We sampled 589 trees and vines in 8,970 m^2 of *terra firme*, 387 trees and vines in 6,135 m^2 of *várzea*, and 386 trees and vines in 5,150 m^2 of *aguajal* habitat. Between March 2004 and February 2005, starting as close to the middle of each month as possible, we examined the canopy of each tagged tree or vine with binoculars and a small telescope, recording the presence of immature fruit (unripe fruits smaller than mature fruits of the species), unripe fruit (full-sized fruits that had not ripened), and ripe fruit.

We used the number of trees bearing fruit per hectare as a measure of fruit availability in each habitat (Ayres 1986; Stevenson *et al.* 1998), and combined these to produce monthly estimates of fruit availability in the uakaris' home range for each plant genus and for immature, unripe, and ripe fruit, adjusting for the proportions of each habitat in home range.

Behavioral Sampling

More than 150 uakaris were present in the study area in groups of variable size (1 to >150 individuals; mean±SD=43.57±24.1) that often fissioned and fused throughout the day (Bowler and Bodmer 2009). We located groups by walking trails or searching flooded *várzea* by canoe, following them until dusk, or we lost the group. Groups sometimes disappeared for up to 5 d, but were more commonly found within 2 d of searching. When we were able to follow the group to its sleeping trees, we often relocated it before dawn the following day. Between April 2003 and July 2005, including all months except February 2004 and April and May 2005, we made 239 contacts with uakari groups during which we collected 945 h and 10 min of behavioural observations (33–123 h of data per calendar month).

We used point scan sampling (Altmann 1974) at 10-min intervals, allowing 1 min to complete the scans. In each scan, we recorded the location of the group using a GPS (Garmin GPS72) and the age–sex class and behavior of each visible monkey, using the following age–sex classes: infant 1 (1–3 mo), infant 2 (3–12 mo), juvenile (12–36 mo), subadult male, unsexed subadult, adult male, and adult female (Bowler and Bodmer 2009; Fontaine 1981). We recorded the following behavioral categories: feed, search, move, social, and rest (Bowler and Bodmer 2009). Feed included masticating, swallowing, processing, or carrying food items. Where possible, we recorded the plant species, parts (seeds, pulp, arils, flowers, leaves, or others), and the maturity of the fruit eaten by the individual through observation and by collecting discarded parts. Search included breaking apart or examining branches or foliage.

Because differing canopy densities between tree species can lead to under- or overrepresentation in the recorded diet through visibility bias, an effect exaggerated by scan sampling, and because insects and fruits with short processing times are disproportionately rare in scan samples, we also used 1–0 sampling (Altmann 1974), recording a 1 for each species used by ≥1 individuals during a 10-min period. This method underestimates the importance of species that were fed on intensively by uakaris, but ensures that all species observed being eaten are recorded. We also recorded the plant parts used for each species on a 1–0 basis.

Professional botanists identified plant species that we recorded on transects or in the diet from photographs and voucher specimens and they deposited the plants at the Herbarium at the Universidad Nacional de la Amazonía Peruana (UNAP), Iquitos.

Fruit Hardness Categories

We gave each fruit species eaten a subjective score for the hardness and puncture resistance of the fruit using criteria similar to those of Boubli (1999), but further subdividing the harder fruits.

Hardness categories:

1) Soft; fruits as soft as grapes, crushable with the fingers
2) Medium; fruits with husks comparable to those of avocados

3) Medium-hard; fruits with tougher skins requiring moderate pressure with a 10-cm penknife blade to open
4) Hard; requiring heavy pressure with a 10-cm penknife blade to open
5) Very hard; requiring heavy hammer action pressure with a 20-cm knife blade or larger to open

We collected samples from those dropped unopened by uakaris, but took care not to test samples that were larger or smaller than samples eaten by uakaris, or samples that were infested with larvae or otherwise in poor condition. Some fruits were eaten at both ripe and unripe stages, at which hardness can vary by several categories. Because samples for many species were limited, we calculated median scores for both species and genera from samples of fruits collected at all stages eaten by uakaris.

Analysis

We used 1–0 feeding records to calculate the percentage of the total diet made up by each species, genus, or family and to determine the proportion of different plant parts in the diet. We calculated proportions for each month, and used these to calculate the total proportions in the annual diet, thus controlling for differing amounts of data collected each month. We used scan samples to look at differences in diet between age–sex classes, comparing hardness scores for the fruits eaten by adult male and adult female uakaris via the Mann-Whitney U-test.

Since fruits from species within a genus are usually quite similar, whereas species within a plant family can be very different, we took the genus as the most useful level at which to examine selectivity. We included any genus eaten by uakaris during the study period, but used only feeding records between March 2004 and February 2005 (463 h and 30 min of observations) for the analysis to coincide with fruit availability data. We used 1–0 data for species eaten to produce similar data for genera (recording a 1 if a genus was used during the 10 minutes). We compared preferences for tree genera using an index calculated by (U–A)/(U+A), where U (use) is a genus' proportion in the diet and A (availability) is its proportion of the total number of fruiting trees on transects (Ivlev 1961), discounting genera with <3 fruiting records from the analysis. This produced an index for each genus of between 1 (total selection) and −1 (total avoidance). To correct for the different areas of each habitat type within the uakaris' home range, we adjusted the number of fruiting trees of each genus in each habitat by the proportion of the habitat within the home range as determined using the minimum-convex polygon method (Stickel 1954). We used a satellite image with a grid superimposed to calculate the proportions of habitat in the home range.

Results

Plant and Animal Parts in the Diet

The diet constituted 55.4% unripe and mature seeds, 38.9% ripe and unripe fruit pulps and arils (including whole fruits of which seeds may also have been

masticated), 3.4% flowers and nectar, 0.7% other plant parts (including leaves, bark, and gums), and 1.5% animal material. Animals eaten included ants, caterpillars, termites, mantids, and katydids, but the majority were not identified beyond family level. Uakaris spent 3.5% of their time searching foliage, presumably for invertebrates, which may suggest they eat more insects than we recorded.

Plant Species in the Diet

We recorded 164 plant species in the diet, including several unidentified morphospecies (electronic supplementary material Table SI) and estimate that feeding records from which insufficient samples could be recovered for identification could add a further 20–40 species. Few species made up >1% of the annual diet, but there are many similar species at Lago Preto, and the importance of some does not become apparent until one examines them collectively as a genus, e.g., *Eschweilera*, or as a family, e.g., Sapotaceae (Table I). Fruit from vines or lianas made up 10.2% of the diet.

Temporal Variation in Fruit Availability

The home range (1,200 ha) consisted 14% *aguajal*, 64% *terra firme*, and 23% *várzea*. The availability of ripe fruit was greatest in March and scarcest between August and October. Availability of unripe fruit was more consistent, and there was no such period of scarcity. The overall availability of fruit was highest from November through March, peaking in February (Fig. 2).

Temporal Variation in the Diet

Between May and August there was a conspicuous switch from high proportions of seeds to relatively high proportions of fruit pulp (Fig. 3). Much of this change can be accounted for by *Mauritia flexuosa*, which was the most eaten species in May (48.0% of records), June (61.4%), July (53.5%), and August (63.7%) coinciding with the availability of ripe pulp of this species (Fig. 4). The proportion of ripe pulp in the diet correlates negatively with the availability of all fruits in the home range (Pearson correlation, $n=12$, $r=-0.64$, $p<0.05$), indicating that the uakaris switched to ripe pulps during times of lower fruit availability. These periods coincide with a high availability of ripe pulps of the palms *Mauritia flexuosa* and *Oenocarpus bataua*, which are important in the diet at these times.

Fruit Protection, Hardness, and Processing

In 2307 1–0 feeding records, 2% were on soft fruits, 47% on medium fruits (of which >50% were *Mauritia flexuosa*), 18% were medium hard, 25% were hard, and 7% were very hard. Uakaris have the adaptations to open fruit of a large range of hardness.

Fruits of many of the species consumed were protected by copious sticky white latex, particularly species in the families Apocynaceae and Sapotaceae, but the uakaris did not appear bothered by this. Fruits from the palm *Astrocaryum chambira*, as well as being in the top hardness category, are also protected by the inaccessibility of

Table 1 Plant species, genera, and families making up ≥1% of the diet of *Cacajao calvus ucayalii* at Lago Preto

	Species making up >1% of the diet			Genera making up >1% of the diet			Families making up >1% of the diet		
Rank	Species	Parts eaten	% diet (weighted by month)	Rank	Genus	% diet (weighted by month)	Rank	Family	% diet (weighted by month)
1	*Mauritia flexuosa*	rp/us	20.0	1	*Mauritia*	20.0	1	Arecaceae	22.3
2	*Licania heteromorpha*	us	5.0	2	*Eschweilera*	6.3	2	Sapotaceae	10.4
3	*Couma macrocarpa*	us	4.1	3	*Licania*	6.1	3	Fabaceae	7.6
4	*Chrysophyllum sanguinolentum*	us	3.2	4	*Couma*	4.1	4	Lecythidaceae	7.0
5	*Hevea* cf. *guianensis*	us	3.1	5	*Pouteria*	4.0	5	Chrysobalanacea	6.2
6	*Oenocarpus bataua*	rp	2.3	6	*Chrysophyllum*	3.2	6	Apocynaceae	5.4
7	*Pouteria guianensis*	us	2.2	7	*Hevea*	3.1	7	Moraceae	5.1
8	*Eschweilera* cf. *albiflora* or *parvifolia*	us	1.9	8	*Inga*	3.0	8	Myristicaceae	4.2
9	*Eschweilera* sp.1	fl	1.8	9	*Pourouma*	2.9	9	Euphorbiaceae	4.2
10	*Salacia impressifolia*	rp, us	1.7	10	*Iryanthera*	2.8	10	Celastraceae	3.8
11	*Paullinia faginia*	rp	1.6	11	*Paullinia*	2.6	11	Cecropiaceae	2.8
12	Species from unidentified family 1 (cf. *Spondias*)	rp, us, up	1.6	12	*Oenocarpus*	2.3	12	Sapindaceae	2.6
13	*Iryanthera tricornis*	us	1.5	13	*Parkia*	2.3	13	Unidentified family 1 (cf. Anacardiaceae)	1.6
14	*Parkia igneiflora*	us, ms	1.5	14	*Salacia*	1.7	14	Clusiaceae	1.4
15	*Pourouma* sp.1	us	1.3	15	*Ficus*	1.4	15	Bombacaceae	1.0
16	*Iryanthera elliptica*	us	1.2	16	Genus from unidentified family 1 (cf. *Spondias*)	1.4	16	Elaeocarpaceae	1.0
17	*Tovomita* sp.2	us, rp	1.2	17	*Brosimum*	1.3	–	–	–
18	*Eschweilera coriacea*	us	1.2	18	*Tovomita*	1.2	–	–	–
19	*Zygia* sp.1	us	1.1	19	*Zygia*	1.1	–	–	–
20	*Eriotheca globosa*	us	1.0	20	*Helicostylis*	1.1	–	–	–
21	*Paranchornia peruviana*	rp, up, us	1.0	21	*Eriotheca*	1.0	–	–	–
–	–	–	–	22	*Paranchornia*	1.0	–	–	–
–	–	–	–	23	*Sloanea*	1.0	–	–	–

Fl flowers/nectar; *ms* mature seeds; *rp* ripe pulp; *up* unripe pulp; *us* unripe seeds
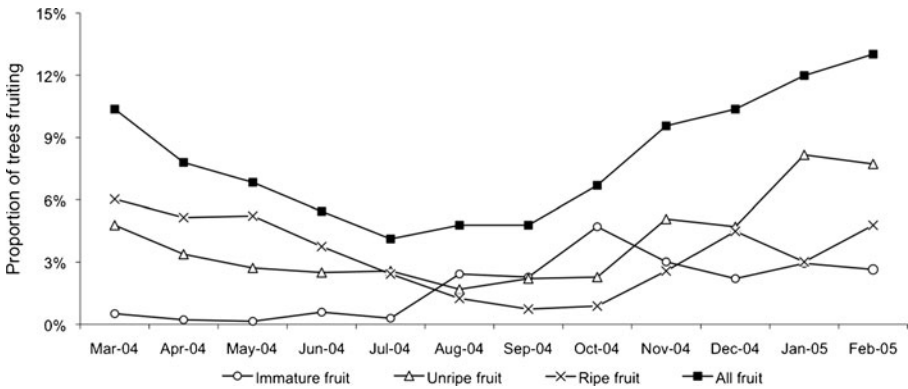
Fig. 2 Monthly variation in the proportions of trees bearing immature, unripe, and ripe fruit at Lago Preto (*n*=1,360).

fruits on trunks covered with long spines. One feeding record demonstrated that at least some uakaris could open the fruits, but the selectivity score for the palm was low.

The pulp of ripe fruits of *Mauritia flexuosa* is covered by dark red scales that can be removed with a fingernail. Uakaris process *Mauritia flexuosa* fruits in the same way as other medium and large-bodied primates, by scraping the scales and mesocarp off with their incisors. The seeds, and frequently part-eaten fruits, are then discarded, sometimes some distance from the palm. The open nature of the *aguajal* habitat and the tall, bare-trunked and slippery nature of the *Mauritia flexousa* themselves may make access for monkeys difficult in some areas. Large male uakaris were sometimes seen leaping onto and climbing hand-over-hand up the trunks of thinner isolated palms, but most were reached by leaping several meters onto the large fronds from adjacent palms and trees.

Selectivity in the Diet

There is a positive correlation between the availability of genera and their proportion in the diet (Pearson correlation, *n*=31, *r*=0.61, *p*<0.05). However, selection rates in
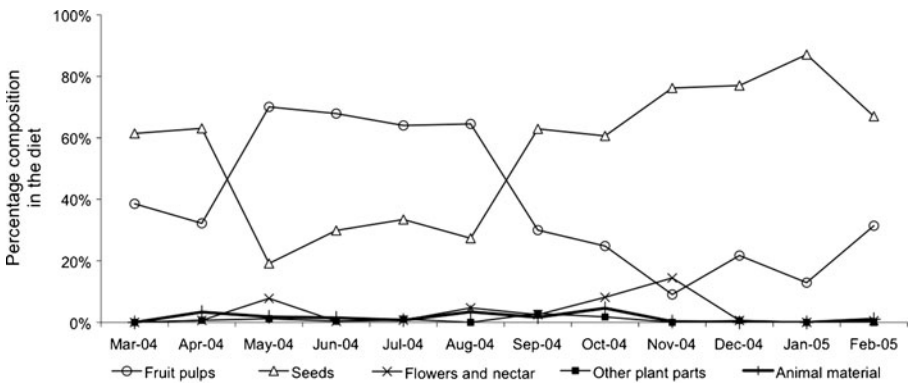
Fig. 3 Monthly variation in the proportions of seeds, pulp, flowers, and other items in the diet of *Cacajao calvus ucayalii*.
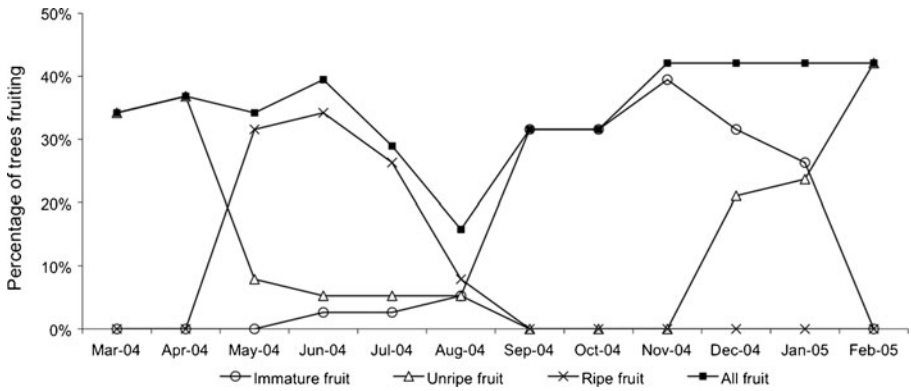
Fig. 4 Monthly variation in palm fruit production for *Mauritia flexuosa* as a percentage of trees bearing immature, unripe, or ripe fruits (*n*=38 trees).

proportion to availability in the environment differed between genera (Fig. 5). Six of the top 10 fruits were hard or very hard, so diet breadth is enhanced by morphological specializations (Fig. 5).

Some species that were important in the diet did not feature in the analysis. For example, *Couma* was fed on in long and intense bouts, making up 4.1% of the diet, but it did not occur on the tree transects. Several genera had particularly high availability in the environment, but were never eaten during the study period. For example, the palm *Euterpe* was not eaten, but had the highest availability of all genera, and was eaten by capuchins (*Cebus apella*) so is probably edible to uakaris.
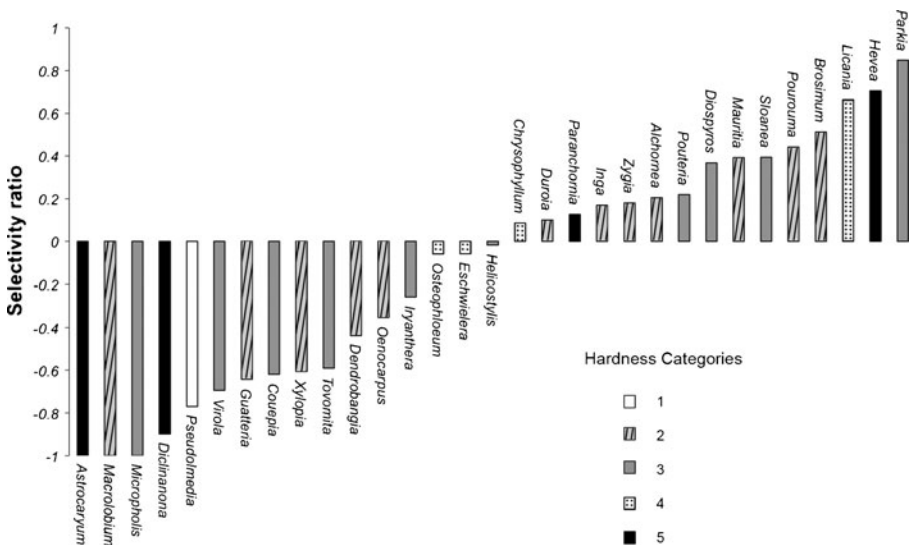
Fig. 5 Preferences for tree genera in the diet of *Cacajao calvus ucayalii* measured via Ivlev's index of selectivity. Values between 0 and 1 indicate increasing positive selection for tree genera, whereas values between 0 and −1 indicate increasing negative selection, use of the genus being at proportions lower than availability.

Dietary Differences Between the Age–Sex Classes

The majority of feeding records in scan samples on fruits classified as very hard were by adult uakaris. We never recorded young uakaris (<12 mo old) successfully opening and feeding on these species. Items with hardness ratings of hard, and especially very hard at the stage during which they were consumed, such *Paranchornia peruviana*, *Hevea* cf. *guianensis*, *Iryanthera elliptica*, and an unidentified species in the family Celastraceae, were often dropped intact with toothmarks indicating that attempts had been made to open them. Adult male uakaris fed on harder fruits more than adult female uakaris did ($U=21,590.0$; $p<0.05$, 2-tailed Mann-Whitney U-test).

Discussion

Specialized dentition allows uakaris to feed on a wider range of foods than other primates, such as *Eschweilera* and *Hevea*, as well as the seeds of unripe fruits of the same species as those exploited for ripe pulps. There were striking similarities between the dietary diversity of uakaris at Lago Preto and that of other pitheciins, supporting findings that Sapotaceae, Lecythidaeceae, Euphorbiaceae, and Chrysobalanaceae are particularly important families, while many of the same genera, e.g., *Eschweilera, Licania, Tovomita*, and *Conceveiba*, are used extensively by pitheciins throughout South America (Norconk *et al.* 1998). Seeds made up a smaller proportion of the diet at Lago Preto than for many other pitheciins, including uakaris (Ayres 1986; Boubli 1999), but this was due mostly to the dominance of the ripe pulp of the palm *Mauritia flexuosa* in the diet between May and August, when there was a period of relative fruit scarcity.

Immature and unripe seeds are available for 3 or 4 times longer than ripe pulps (Leighton and Leighton 1982; Norconk 1996), so seed specialists are likely to be less subject to seasonal food shortages than species dependent on ripe pulp (Norconk 1996). Whereas white uakaris at Lake Teiú fed mainly on immature seeds when few ripe fruits were available, eating more ripe pulp when it was available, and black uakaris did the opposite at Pico da Neblina (Ayres 1986; Boubli 1999), at Lago Preto the seasonal shortage of fruit was less distinct, and coincided with the ripening of *Mauritia flexuosa*. These palms are more nutritious than other diet items; the pulps consist of 53% fat, 43% carbohydrate, and 4% protein (Lopes *et al.* 1980). Outside the fruiting season of *Mauritia flexuosa*, seeds from large-seeded, hard-shelled species dominated the diet.

Differing selectivity ratios show that uakaris prefer some genera over others. Six of the top 10 most selected fruits were categorized as medium-hard to very hard, supporting our prediction that uakaris would feed selectively on hard fruits, rather than turning to them because few ripe fruits are available. Although it is presumably a correlate of pericarp hardness, such as the size or nutrient content of the seeds contained in the fruits, that is selected for rather than hardness *per se*. High selectivity for a few genera for soft ripe pulps may be a result of the lower availability of these fruits in the forest, combined with uakaris' need to balance their nutrient intake, i.e., the 20–35% fruit pulp that they generally include in their

diet may be harder to find than the 55–80% seeds, producing high selectivity ratios. The prominence of the ripe pulps of *Mauritia flexuosa* and other palms in the diet at Lago Preto is unusual for pitheciins. Though this can in part be explained by relative shortages of fruit during the ripening period of these species, the high lipid content relative to that of other ripe fruit pulps may also explain why the uakaris consume this species in such large quantities relative to other ripe fruit pulps.

The relative ability of different pitheciins to open the hardest fruits appears related to the size of the dentition. A semi-free-ranging subadult female Peruvian red uakari at the Pilpintuwasi Amazon Animal Orphanage, Iquitos was able to open all seeds of *Bertholletia excelsa* presented, while a subadult *Pithecia* cf. *monachus* at the same site was apparently unable to open many examples of the seed (M. Bowler *pers. obs.*). Neither juvenile black uakaris at Pico da Neblina (Boubli 1999) nor juvenile red uakaris at Lago Preto were seen opening the hardest species eaten by adults in their groups, and adult male uakaris at Lago Preto fed on harder fruits than adult females, supporting our predictions that the larger age–sex classes would feed on more hard fruits than smaller classes. Sexual dimorphism in the dentition of *Cacajao calvus* is pronounced, perhaps more so than in *Chiropotes* (Kay *et al.* 1988) or *Cacajao melanocephalus* (Hershkovitz 1987); the canines and the jaw are proportionally larger in adult males, and are accompanied by well-developed temporal jaw closure muscle masses overlying the frontal and parietal bones of the skull and attached to a sagittal crest in mature individuals (Hershkovitz 1987). This dentition and musculature is used in fighting and display (Bowler and Bodmer 2009) and may be the result of sexual selection, but is also presumably why male and female diets differentiated at Lago Preto.

References

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour, 48*, 1–41.

Aquino, R. (1995). Concervación de *Cacajao calvus ucayalii* en la Amazonia Peruana. *Neotropical Primates, 3*, 40–42.

Aquino, R., & Encarnación, F. (1999). Observaciónes preliminares sobre la dieta de *Cacajao calvus ucayalii* en el Nor-Oriente Peruano. *Neotropical Primates, 7*, 1–5.

Ayres, J. M. (1986). *The white Uakaris and the Amazonian flooded forests.* Ph.D. thesis, University of Cambridge.

Ayres, J. M. (1989). Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *Journal of Human Evolution, 18*, 697–716.

Barnett, A. A., de Castilho, C. V., Shapley, R. L., & Anicácio, A. (2005). Diet, habitat selection, and natural history of the golden-backed uacari, *Cacajao melanocephalus ouakary*, in Jaú National Park, Brazil. *International Journal of Primatology, 26*, 961–981.

Barton, R. A., & Whiten, A. (1994). Reducing complex diets to simple rules: Food selection by olive baboons. *Behavioral Ecology and Sociobiology, 35*, 283–293.

Boubli, J. P. (1999). Feeding ecology of black-headed uakaris (*Cacajao melanocephalus melanocephalus*) in the Pico de Neblina National Park, Brazil. *International Journal of Primatology, 20*, 719–749.

Bowler, M., & Bodmer, R. E. (2009). Social behavior in fission–fusion groups of red uakari monkeys (*Cacajao calvus ucayalii*). *American Journal of Primatology, 71*, 976–987.

Buchanan, D. B., Mittermeier, R. A., & van Roosmalen, M. G. M. (1981). The saki monkeys, genus Pithecia. In A. F. Coimbra-Filho & R. A. Mittermeier (Eds.), *Ecology and behaviour of Neotropical primates* (pp. 391–417). Rio de Janeiro: Academia Brasileira de Ciencias.

Cunningham, E. P., & Janson, C. H. (2006). *Pithecia pithecia*'s behavioral response to decreasing fruit abundance. *American Journal of Primatology, 68*, 491–497.

Dasilva, G. L. (1994). Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. *International Journal of Primatology, 15*, 655–680.

Fischer, K. E., & Chapman, C. A. (1993). Frugivores and fruit syndromes: Differences in patterns at the genus and species level. *Oikos, 66*, 472–482.

Fontaine, R. (1981). The uakaris, genus Cacajao. In A. F. Coimbra-Filho & R. A. Mittermeier (Eds.), *Ecology and behaviour of Neotropical primates*. Rio de Janeiro: Academia Brasileira de Ciencias.

Heiduck, S. (1997). Food choice in masked titi monkeys (*Callicebus personatus melanochir*): Selectivity or opportunism? *International Journal of Primatology, 18*, 487–502.

Hemingway, C. A. (1998). Selectivity and variability in the diet of Milne-Edwards' sifakas (*Propithecus diadema edwardsi*): Implications for folivory and seed-eating. *International Journal of Primatology, 19*, 355–377.

Hershkovitz, P. (1987). Uacaries, New World monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): A preliminary taxonomic review with the description of a new subspecies. *American Journal of Primatology, 12*, 1–53.

Ivlev, V. S. (1961). *Experimental ecology of the feeding of fishes*. New Haven: Yale University Press.

Johns, A. (1986). Notes on the ecology and current status of the buffy saki, *Pithecia albicans*. *Primate Conservation, 7*, 26–29.

Kay, R. F., Plavcan, J. M., Glander, K. E., & Wright, P. C. (1988). Sexual selection and canine dimorphism in New World monkeys. *American Journal of Physical Anthropology, 77*, 385–397.

Kinzey, W. G. (1992). Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology, 88*, 499–514.

Kinzey, W. G., & Norconk, M. A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology, 81*, 5–15.

Kinzey, W. G., & Norconk, M. A. (1993). Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology, 14*, 207–227.

Kool, K. (1993). The diet and feeding behavior of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. *International Journal of Primatology, 14*, 667–700.

Lahm, S. A. (1986). Diet and habitat preferences of *Mandrillus sphinx* in Gabon: implications of foraging strategy. *American Journal of Primatology, 11*, 9–26.

Leighton, M., & Leighton, D. R. (1982). The relationship of size of feeding aggregates to size of food patch: Howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado island. *Biotropica, 14*, 81–90.

Lopes, J. P., Albuquerque, H., Silva, Y., & Shrimpton, R. (1980). Aspectos nutritivos de algunos frutos da Amazonia. *Acta Amazonica, 10*, 755–758.

Maisels, E., Gautier-Hion, A., & Gautier, J. P. (1994). Diets of two sympatric colobines in Zaire: More evidence on seed-eating in forests on poor soils. *International Journal of Primatology, 15*, 681–702.

Milton, K. (1981). Food choice and digestive strategies of two sympatric primate species. *American Naturalist, 117*, 496–505.

Mowry, C. B., Decker, B. S., & Shure, D. J. (1996). The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Procolobus badius rufomitratus*). *International Journal of Primatology, 17*, 63–84.

Norconk, M. A. (1996). Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of Neotropical primates* (pp. 403–548). New York: Plenum.

Norconk, M. A., & Conklin-Brittain, N. L. (2004). Variation on frugivory: The diet of Venezuelan white-faced sakis. *International Journal of Primatology, 25*, 1–26.

Norconk, M. A., Grafton, B. W., & Conklin-Brittain, N. L. (1998). Seed dispersal by Neotropical seed predators. *American Journal of Primatology, 45*, 103–126.

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

Peres, C. A. (1993). Notes on the ecology of buffy saki monkeys (*Pithecia albicans*, Gray 1860): A canopy seed-predator. *American Journal of Primatology, 31*, 129–140.

Peres, C. A. (1994). Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagotricha cana*) in central Amazonia: Comparisons with other atelines. *American Journal of Primatology, 15*, 333–372.

Pitman, N., Vriesendorp, C., & Moskovits, D. (2003). *Peru: Yavari. Rapid Biological Inventories Report 11*. Chicago: The Field Museum.

Rosenberger, A. L. (1992). Evolution of feeding niches in New World monkeys. *American Journal of Physical Anthropology, 88*, 525–562.

Rosenberger, A. L., Norconk, M. A., & Garber, P. A. (1996). New perspectives on the pitheciines. In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of Neotropical primates* (pp. 329–333). New York: Plenum.

Setz, E. (1994). Feeding ecology of golden-faced sakis. *Neotropical Primates, 2*, 13–14.

Stevenson, P. R., Quiñones, M. J., & Ahumada, J. A. (2000). Influence of fruit availability on ecological overlap among four Neotropical primates at Tinigua National Park, Colombia. *Biotropica, 32*, 533–544.

Stickel, L. F. (1954). A comparison of certain methods of measuring home range of small mammals. *Journal of Mammology, 35*, 1–15.

Sutherland, W. J. (2000). *The conservation handbook: Techniques in research, management and policy.* Oxford: Blackwell Science.

Terborgh, J. (1983). *Five New World primates: A study in comparative ecology.* Princeton: Princeton University Press.

Tutin, C. E. G., Ham, R. M., White, L. J. T., & Harrison, M. J. S. (1997). The primate community of the Lope Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology, 42*, 1–24.

Ungar, P. (1995). Fruit preferences of four sympatric primates at Ketambe, Northern Sumatra, Indonesia. *International Journal of Primatology, 16*, 221–246.

van Roosmalen, M. G. M., Mittermeier, R. A., & Fleagle, J. G. (1988). Diet of the northern bearded saki (*Chiropotes santanas chiropotes*): A Neotropical seed predator. *American Journal of Primatology, 14*, 11–35.

Waser, P. M. (1984). Ecological differences and behavioral contrasts between two mangabey species. In P. S. Rodman & J. G. H. Cant (Eds.), *Adaptations for foraging in nonhuman primates* (pp. 195–216). New York: Columbia University Press.

Yamashita, N. (1996). Seasonal and site-specific patterns in mechanical dietary properties of Malagasy lemurs. *American Journal of Physical Anthropology, 22*, 249.

Online Resource 1. Plant species eaten by Peruvian red uakaris (*Cacajao calvus ucayalii*) at Lago Preto. Feeding records were collected by one-zero sampling (Altmann 1974) in ten-minute periods during 945 hr and 10 min of observation. Hardness scores are median scores from samples of fruits available at the stages eaten by uakaris.

Family	Species	FEEDING RECORDS													Habit	Parts eaten	Hardness
		TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
ANACARDIACEAE	*Anacardium* cf. *Gigantium*	3											3		t	us	2
ANNONACEAE	*Diclinanona tessmannii*	1		1											t	us	5
ANNONACEAE	*Guatteria* sp.1	6											2	4	t	rp	2
ANNONACEAE	*Guatteria* sp.2	1											1		t	rp	2
ANNONACEAE	*Tetrameranthus laomae*	3		1			1	1							t	rp, us	2
ANNONACEAE	Unidentified *Xylopia*	2		2											t	us, rp	2
ANNONACEAE	*Xylopia* sp.1	3										1		2	t	us	2
APOCYNACEAE	*Couma macrocarpa*	86	7	30	16	6	1		23	1	2				t	us, rp	4
APOCYNACEAE	*Paranchornia peruviana*	19				1	4							14	t	rp, up, us	5
APOCYNACEAE	*Rhigospira quadrangularis*	10					1		2	1	4	1	1		t	us, rp	3
ARECACEAE	*Astrocaryum chambira*	1											1		p	us	5
ARECACEAE	*Mauritia flexuosa*	572				11	82	164	151	149	10	3	2		p	rp, us	2
ARECACEAE	*Oenocarpus bataua*	67								1	43	19	2	2	p	rp	2
BOMBACACEAE	*Eriotheca globosa*	20				7	13								t	us	3
CECROPIACEAE	*Pourouma bicolor*	28										3	25		t	us	2
CECROPIACEAE	*Pourouma* cf. *tomentosa*	10	2	4							2		1	1	t	us	2
CECROPIACEAE	*Pourouma* sp.1	28											6	22	t	us	2
CECROPIACEAE	*Pourouma* sp.2	17											17		t	us	2
CELASTRACEAE	Unidentified Celastraceae spp.	4	4												v	us	n/a
CELASTRACEAE	Unidentified Celastraceae 1	8	1	1		2			4						v	rp, us	4
CELASTRACEAE	Unidentified Celastraceae 2	10	1						1			4	4		v	up, rp, us	5
CELASTRACEAE	*Salacia impressifolia*	42				14		25		2				1	v	us, rp	2
CHRYSOBALANACEAE	Unidentified Chrysobalanaceae 1	1										1			t	us	n/a
CHRYSOBALANACEAE	*Couepia paraensis*	1											1		t	us	3
CHRYSOBALANACEAE	*Couepia* sp.1	1						1							t	us	3
CHRYSOBALANACEAE	Unidentified *Licania*	2											1	1	t	us	n/a
CHRYSOBALANACEAE	*Licania heteromorpha*	153		2					22	29	31	36	24	9	t	us	4
CHRYSOBALANACEAE	*Licania hypoleuca*	10	5	5											t	us	5
CHRYSOBALANACEAE	*Licania micranthra*	11											11		t	us	4
CHRYSOBALANACEAE	*Licania octandra*	2			2										t	us	3
CHRYSOBALANACEAE	*Licania* sp.1	2	1		1										t	us	4
CLUSIACEAE	*Moronobea coccinea*	5	2	1								1	1		t	fl, us	4
CLUSIACEAE	*Rheedia* sp1.	1										1			t	us	3
CLUSIACEAE	*Symphonia globulifera*	19				1	13	1	1	3					t	fl, us	1
CLUSIACEAE	*Tovomita* sp.1	3											1	2	t	us	3
CLUSIACEAE	*Tovomita* sp.2	23	17	6											v	us, rp	3
CLUSIACEAE	Unidentified Clusiaceae 1	5									5				t	us	3
COMBRETACEAE	Unidentified *Combretum* spp.	2						1		1					v	us	3
COMBRETACEAE	*Combretum* sp.1	1												1	v	us	3
COMBRETACEAE	*Combretum* sp.2	2											2		v	us	3

Family	Species	FEEDING RECORDS													Habit	Parts eaten	Hardness
		TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
CONNARACEAE	*Rourea camptoneura*	6					2	4							v	rp, us	2
CONVOLVULACEAE	*Maripa* sp.1	13				3		5	5						v	us, rp	2
CONVOLVULACEAE	*Maripa* sp.2	1							1						v	us, rp	2
EBENACEAE	*Diospyros poeppiguiana*	9				8	1								t	us	3
ELAEOCARPACEAE	*Sloanea* sp.1	5					5								t	us	3
ELAEOCARPACEAE	*Sloanea* sp.2	7			7										t	us	3
ELAEOCARPACEAE	*Sloanea* sp.3	5			5										t	ar	3
ELAEOCARPACEAE	*Sloanea tuerckheimii*	1		1											t	us	3
EUPHORBIACEAE	Unidentified Euphorbiaceae sp.1	2		1										1	t	us	3
EUPHORBIACEAE	Unidentified Euphorbiaceae sp.2	2	1	1											t	us	4
EUPHORBIACEAE	*Alchornea triplinervia*	20									4	16			t	us	2
EUPHORBIACEAE	*Conceveiba rhytidocarpa*	2		1									1		t	us	2
EUPHORBIACEAE	*Glycydendron amazonicum*	4												4	t	us	2
EUPHORBIACEAE	*Hevea* cf. *guianensis*	79	4	1	6	5	5	24	4				18	12	t	us, le, fl	5
FABACEAE	Unidentified Fabaceae sp.1	3		1			2								t	us	n/a
FABACEAE	*Albizia* sp.1	2				2									t	us	2
FABACEAE	*Dussia* spp.	8			3	3		2							t	us	3
FABACEAE	*Enterolobium barnebianum*	11				1	2		5	3					t	us, ms	3
FABACEAE	*Hymenaea* sp.1	3							3						t	rp	4
FABACEAE	*Inga* spp.	44	3	10	1				1		2	1	22	4	t	us, ar	n/a
FABACEAE	*Inga capitata*	2	2												t	us	2
FABACEAE	*Inga* cf. *semialata*	7	6	1											t	us	2
FABACEAE	*Inga gracilifolia*	12	1	7	4										t	us, ar	2
FABACEAE	*Inga* sp.1	1												1	t	us	2
FABACEAE	*Inga* sp.2	3			2							1			t	us, ar	2
FABACEAE	*Inga* sp.3	1										1			t	us	2
FABACEAE	*Inga* sp.4	1									1				t	us	2
FABACEAE	*Macrolobium angustifolium*	1			1										t	us	2
FABACEAE	*Parkia* spp.	18					3	2	2		6	5			t	us, gu	n/a
FABACEAE	*Parkia igneiflora*	45						7	14	9	9	6			t	us, ms	3
FABACEAE	*Parkia nitida*	2					1							1	t	gu, fl	3
FABACEAE	*Parkia* sp.1	2				1			1						t	gu, ms	3
FABACEAE	*Pterocarpus* sp.1	1										1			t	us	3
FABACEAE	*Zygia* sp.1	20												20	t	us	2
HERNANDIACEAE	Unidentified *Sparattanthelium* spp.	3				3									v	us	n/a
HERNANDIACEAE	*Sparattanthelium* sp.1	1			1										v	us	2
HUMIRIACEAE	Unidentified Humiriaceae 1	9	1	2							3			3	t	us, up	5
HUMIRIACEAE	Unidentified Humiriaceae 2	1									1				t	us	4
ICACINACEAE	*Dendrobangia multinervia*	3							3						t	rp	2
LECYTHIDACEAE	*Couroupita guianensis*	5						5							t	us	4
LECYTHIDACEAE	*Eschweilera* spp.	24	5				1			1		1	16		t	us	4
LECYTHIDACEAE	*Eschweilera coriacea*	24	8	6	3					3		2		2	t	us	4
LECYTHIDACEAE	*Eschweilera* sp.1	70										20	50		t	fl	4
LECYTHIDACEAE	*Eschweilera* sp.2	12											12		t	us	4
LECYTHIDACEAE	*Eschweilera tessmannii*	8			5						3				t	us	4

		FEEDING RECORDS															
Family	**Species**	TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Habit	Parts eaten	Hardness
LECYTHIDACEAE	*Eschweilera* sp.3	**1**	1												t	us	4
LECYTHIDACEAE	*Eschwielera albiflora* or *parvifolia*	**49**	5								2	15	11	16	t	us	4
LECYTHIDACEAE	*Gustavia hexapetala*	**6**				1		1			1	2	1		t	us	4
LECYTHIDACEAE	*Gustavia* sp.1	**1**								1					t	fl	4
MALPIGHIACEAE	*Byrsonima* sp.1	**4**			4										?	rp	2
MARCGRAVIACEAE	*Souroubea* sp.1	**4**			3								1		v	us	2
MELASTOMATACEAE	*Miconia* sp.1	**2**										2			t	rp	2
MELIACEAE	*Guarea* sp.1	**4**									1	3			t	us	4
MENISPERMACEAE	Unidentified Menispermaceae	**2**										2			v	rp	n/a
MENISPERMACEAE	*Anomospermum reticulatum*	**8**									3	4		1	v	us, rp	2
MENISPERMACEAE	*Odontocarya* spp.	**2**							2						v	rp	2
MENISPERMACEAE	*Odontocarya floribunda*	**12**		1					4			3	1	3	v	rp	2
MORACEAE	*Brosimum* spp.	**2**										2			t	us	2
MORACEAE	*Brosimum lactescens*	**6**										5	1		t	us	2
MORACEAE	*Brosimum rubescens*	**2**										2			t	us	2
MORACEAE	*Brosimum* sp.1	**4**										1	3		t	us	2
MORACEAE	*Brosimum* sp.2 *(but cf. utile)*	**9**	6	1	1							1			t	us	2
MORACEAE	*Brosimum utile*	**10**											10		t	us	2
MORACEAE	*Ficus* spp.	**8**			4	1	1	1				1			t	rp	n/a
MORACEAE	*Ficus* cf. *guianensis*	**13**							2		6		5		t	wf	1
MORACEAE	*Ficus mathewsii*	**3**												3	t	rp	2
MORACEAE	*Ficus* sp.1	**1**								1					t	rp	2
MORACEAE	*Ficus* sp.2	**2**	2												t	rp	2
MORACEAE	*Helicostylis scabra*	**12**	5										2	5	t	us	3
MORACEAE	*Helicostylis tomentosa*	**9**		9											t	us, rp	3
MORACEAE	*Maquira* spp.	**1**				1									t	us	n/a
MORACEAE	*Maquira* cf. *guianensis*	**21**		2							12	7			t	us, rp	2
MORACEAE	*Naucleopsis mello-barretoi*	**6**										1	5		t	rp, us	2
MORACEAE	*Perebea* sp.1	**4**											4		t	us	2
MORACEAE	*Pseudolmedia laevigata*	**1**	1												t	rp	1
MORACEAE	Unidentified Moraceae 1	**11**									1	10			t	us	3
MORACEAE	Unidentified Moraceae 2	**6**												6	t	up	2
MORACEAE	Unidentified Moraceae 3 (cf. *Brosimum*)	**4**										4			t	us	2
MYRISTICACEAE	Unidentified Myristicaceae	**2**						1					1		t	us	n/a
MYRISTICACEAE	*Iryanthera* spp.	**3**							2				1		t	us	n/a
MYRISTICACEAE	*Iryanthera elliptica*	**34**		2	4						14	9	5		t	us	5
MYRISTICACEAE	*Iryanthera tricornis*	**40**	8	5	3				1		3	1	17	2	t	us	3
MYRISTICACEAE	*Osteophloeum platyspermum*	**11**			3	6					2				t	us, ar	4
MYRISTICACEAE	*Virola pavonis* (but cf. *surinamensis*)	**11**	4								1			6	t	us, ar	3
MYRISTICACEAE	*Virola* sp.1	**1**			1										t	us	n/a
MYRISTICACEAE	*Virola* sp.2	**2**	1	1											t	ar	1
MYRISTICACEAE	Unidentified Myristicaceae 1	**2**	1	1											t	us	4
MYRISTICACEAE	Unidentified Myristicaceae 2	**1**									1				t	us	4

| | | FEEDING RECORDS | | | | | | | | | | | | | | | |
Family	Species	TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Habit	Parts eaten	Hardness
MYRISTICACEAE	Unidentified Myristicaceae 3	1											1		t	us	4
MYRTACEAE	*Eugenia* sp.1	2			2										t	rp	1
MYRTACEAE	*Eugenia* sp.2	7				7									t	rp, us	1
PASSIFLORACEAE	*Passiflora ligularis*	3			1	2									v	rp	1
POLYGALACEAE	*Moutabea* sp.1	7	2	3			1			1					v	rp, us	2
POLYGALACEAE	*Moutabea* sp.2	1					1								v	rp	2
POLYGONACEAE	*Coccoloba* sp.1	6							6						v	rp	2
RUBIACEAE	*Duroia triflora*	5			2	3									t	rp	2
SAPINDACEAE	*Paullinia faginia*	32				9	23								v	rp	2
SAPINDACEAE	*Paullinia pachycarpa* or *grandifolia*	29									2	14	13		v	us	3
SAPINDACEAE	*Paullinia* sp.1	2	2												v	rp	2
SAPINDACEAE	*Paullinia* sp.2	1				1									v	rp	2
SAPINDACEAE	Unidentified Sapindaceae spp.	2							1	1					v	rp, us	n/a
SAPOTACEAE	*Chrysophyllum sanguinolentum*	68	10	19	20				1		6	2	10		t	us	4
SAPOTACEAE	*Ecclinusa lanceolata*	1		1											t	us	3
SAPOTACEAE	*Manilkara* sp.1	13	8		1			1		2	1				t	us	3
SAPOTACEAE	*Micropholis venulosa*	13									6	3	4		t	us	3
SAPOTACEAE	*Micropholis guyanensis*	8									4		4		t	us	4
SAPOTACEAE	Unidentified *Pouteria* sp.	1			1										t	us	3
SAPOTACEAE	*Pouteria cuspidata*	14	1	3	2				1		5		1	1	t	us	3
SAPOTACEAE	*Pouteria gomphiifolia*	11	5			3							1	2	t	us	3
SAPOTACEAE	*Pouteria guianensis*	42	28	11		3									t	us	3
SAPOTACEAE	*Pouteria oblanceolata*	2											2		t	us	3
SAPOTACEAE	*Pouteria* sp.2	5			2	3									t	us	3
SAPOTACEAE	*Pouteria* sp.3	2				2									t	us	3
SAPOTACEAE	*Pouteria* sp.4	2				2									t	us	3
SAPOTACEAE	*Pouteria* sp.5	1				1									t	us	3
SAPOTACEAE	*Pradosia grisebachii*	11	1		1	9									t	us	3
SAPOTACEAE	Unidentified Sapotaceae 1	4	2	1									1		t	us	3
SAPOTACEAE	Unidentified Sapotaceae 2	6			3	3									t	us	2
SAPOTACEAE	Unidentified Sapotaceae spp.	18	1		2	2		5		4	1		2	1	t	rp	n/a
unidentified family 1 vine	Unidentified 1 (cf. *Spondias* in Anacardiaceae)	49			4						9	36			v	rp,us,up	2
unidentified family 2	Unidentified 2	5							2	1	1		1		?	us	5
unidentified family 3	Unidentified 3	11							1		8	1	1		?	us	4
unidentified family 4	Unidentified 4	4										4			?	us	4
unidentified family 5	Unidentified 5	5	2										3		t	us	4
Invertebrate	Invertebrate	37		2		5	3	4	2	3	4	13	1		inv	in	n/a
Invertebrate	Commensal ants and sweet sap in *Couroupita guianensis*	5								5					inv	in	n/a
ITEM NOT IDENTIFIED	ITEM NOT IDENTIFIED	122	3	2	28	13	5	12	14	12	14	9	7	3	n/a	n/a	n/a
	Totals	2583	170	149	149	145	171	267	282	234	232	280	348	156			

Abbreviations: rp, ripe pulp; up, unripe pulp; us, unripe seeds; ms, mature seeds; fl, flowers/nectar; ar, aril; wf, whole fruit; gu, gums; le, leaves; in, invertebrates; v, vine or liana; p, palm; t, tree

Hardness: 1 = very soft, 2= soft, 3= medium, 4= hard, 5=very hard