

# Variability in Food-Processing Behavior Among White-Faced Capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica

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**ABSTRACT** Observed patterns of variability in the food-processing behavior of white-faced capuchins (*Cebus capucinus*) across populations may reflect foraging traditions. However, there has been relatively little attention given to intrapopulation variability in food processing among groups and age/sex classes, making recent cross-population comparisons difficult to interpret. In this paper, we provide data on patterns of object use in foraging that we observed at Santa Rosa National Park, Costa Rica, for comparison with published data from a neighboring research site, Palo Verde National Park. We also describe the techniques used to process two food items consumed by *Cebus capucinus* at Santa Rosa, and discuss the factors that may underlie observed variability. We conducted a 6-month study on two groups of capuchins in 2001, and collected data on general activity and feeding patterns, rates

and forms of object use, and distinctive processing techniques employed for two specific foods (*Sloanea terniflora* and *Luehea candida*). Rates of object-use behavior at Santa Rosa were considerably higher than those reported for Palo Verde and showed significant variation between groups and age/sex classes, as did patterns of *Sloanea* and *Luehea* processing. Observed differences in feeding rates between groups may reflect food availability or relative profitability, whereas variation between age/sex classes seems to reflect differences in the physical capabilities, foraging strategies, and the relative experience of mature and immature animals. Further research is needed to identify how a social context may influence the acquisition of food-processing techniques in juveniles and the development of foraging traditions in social groups. *Am J Phys Anthropol* 127:000–000, 2005. © 2005 Wiley-Liss, Inc.

Members of the genus *Cebus* are widely recognized as skilled extractive foragers (Izawa and Muzino, 1977; Parker and Gibson, 1977, 1979; Izawa, 1979; Terborgh, 1983; Fragaszy, 1986; Janson and Boinski, 1992; Visalberghi, 1993a,b; Boinski et al., 2000). They are adept at accessing embedded foods and bypassing plant and animal defenses in the wild (Izawa and Muzino, 1977; Struhsaker and Leland, 1977; Panger, 1998; Chevalier-Skolnikoff, 1990; Boinski et al., 2000; Panger et al., 2002). Many patterns of food processing observed in wild capuchins involve forms of object use, or “the manipulation and alteration of a detached object relative to a fixed substrate or medium” (Parker and Gibson, 1977). Panger (1998) grouped forms of capuchin object use into three general categories: “rubbing,” “pounding,” and “fulcrum use.” She also noted the foods processed with such techniques and outlined their apparent functions. More recently, researchers from three long-term *C. capucinus* field sites in north-west Costa Rica (Santa Rosa National Park, Palo Verde National Park, and the Lomas Barbudal Forest Reserve) compiled data on foraging and food processing (Panger et al., 2002). They identified 20 food species and food types that appear to be processed in different ways by capuchins at different sites. All variation in processing techniques fell into six broad categories (“pound,” “rub,” “tap,” “fulcrum use,”

“leaf wrap,” and “army ant following”). Of these categories, three (“pound,” “rub,” and “tap”) were observed at all three sites, although the food items processed using these techniques varied between sites. Patterns of variation in food processing within and across populations may reflect social traditions (Panger et al., 2002; Fragaszy and Perry, 2003). However, foraging and food-processing behavior in nonhuman primates is greatly influenced by environmental factors, different physical capabilities, foraging strategies, and nutrient requirements between age classes and sexes, as well as individual differences in skill and temperament (Izawa and Mizuno, 1977; Collins and McGrew, 1987; McGrew,

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1992; Boesch and Boesch, 1993; Boinski et al., 2000) and variation may simply reflect these factors.

There is a clear need for more detailed information about variability and causes of variability in food-processing behavior within groups, to aid in understanding how social traditions are established in capuchins (Boinski et al., 2000; Panger et al., 2002; Perry et al., 2003). In this paper, we describe patterns of object use in foraging by white-faced capuchins in Santa Rosa National Park, and compare these patterns to those reported for capuchins at the neighboring site of Palo Verde National Park. We also provide details of the food-processing techniques employed for two specific food items at Santa Rosa, and quantify differences in the use of these techniques within and across social groups.

## METHODS

### Study site and subjects

We conducted this research at Santa Rosa National Park (Area de Conservacion Guanacaste), Costa Rica, where several habituated groups of *Cebus capucinus* have been studied since 1983 (e.g., Chapman, 1987, 1988; Chapman and Fedigan, 1990; Fedigan, 1990, 1993; Rose, 1994; MacKinnon, 1995). The 10,800-acre park is a mosaic of former pastureland, dry deciduous forest, and semi-evergreen forest (Chapman and Fedigan, 1990; Fedigan et al., 1996). In addition to white-faced capuchins, the park is home to howler monkeys (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*), and to several potential or known monkey predators (snakes, canids, felids, mustelids, and raptors).

Our study subjects were the Cerco de Piedra (CP) group and the Los Valles (LV) group. The CP group included 13–14 individuals (2 adult males, 4 adult females, 1 subadult male, 1 subadult female, 3 juvenile females, and 2–3 infants), and the LV group numbered 15–18 individuals (5 adult males, 4 adult females, 2 subadult males, 1 subadult female, 2 juvenile females, and 1–4 infants). These two groups' home ranges overlap, and they come into occasional contact. While we did not collect precise data on daily movement patterns as part of this study, the home ranges of the two groups are approximately 1 km<sup>2</sup> each, and have not changed appreciably for at least a decade (Fedigan, unpublished data).

During a preliminary field season in 2000, we identified two food species that warranted particular attention because they were often processed using some form of object use, and because they were frequently consumed by members of both groups. *Sloanea terniflora* fruits (Fig. 1) are roughly 1.5 cm long and thickly covered in reddish-purple urticating hairs that can be extremely irritating to the eyes and skin. *Sloanea* is a relatively uncommon tree in Santa Rosa, and is generally confined to intermittent streambeds and other wet areas of the park (Hartshorn, 1983; Enquist and Sullivan,

2001). *Luehea candida* fruits (Fig. 2) are woody pods some 5–8 cm long, which dehisce to release small winged seeds when they are mature. *Luehea candida* is a relatively common tree in Santa Rosa (Haber and Frankie, 1983; Enquist and Sullivan, 2001).

### Data collection

We collected 309.5 hr of quantitative data on all members of the CP and LV groups (except infants) from February–July 2001. We collected data from sunrise to sunset in 2-day blocks, alternating between the two groups as much as possible. We kept observation times as equivalent as possible across subjects within each group. Observation conditions were generally very good (within 10 m), but we sought to maintain a distance of at least 3 m to focal subjects. We gathered data using binoculars, a stopwatch, and a Psion Workabout handheld computer. During periods of extremely rapid activity, we used a dictaphone and later transcribed our observations. We also collected some ad libitum data via dictaphone, particularly in the early weeks of the study.

Our observation conditions did not allow for a strict sampling order, but we avoided repeatedly sampling central or conspicuous subjects by moving through the dispersed group between focal sessions, and by sampling both clearly visible and more obscured animals. We also sought to collect a focal session from all group members each day before beginning a second session with any subject. We tallied total focal times weekly and monthly in order to ensure that the total observed time for each individual in a group remained as equal as possible.

We collected data in 15-min focal animal sessions (Altmann, 1974). If the subject was "out of sight" for more than 2.5 min of a focal session, we excluded that session from focal analysis (though we included data from incomplete sessions in tallies of total observed object-use bouts, and in tallies of processing bouts used for specific foods; see below). We collected detailed data on food-processing techniques (Table 1). We scored all data as bouts rather than events. A single bout of food processing would often involve a very rapid sequence of behaviors (i.e., pound, briefly examine/eat, then pound again) with a food item without significantly changing the orientation of the object, the orientation of the hands, or the orientation and posture of the subject. If the subject performed an intervening behavior from our ethogram, began processing the item using a different technique or orientation, or changed its hand use or position during processing, that would mark the start of a new bout.

### Data analyses

For analytical purposes, we categorized subjects into four classes: adult males, adult females, subadults, and juveniles. We did not separate subadults



**Fig. 1.** *Sloanea terniflora* fruits.

and juveniles by sex due to very small numbers in each category and because prior studies of capuchins (e.g., Frigaszy, 1990; Rose, 1994; MacKinnon, 1995), found no sex differences in foraging prior to adulthood.

We performed all statistical tests using the SPSS 10.0 analytical program. Alpha for all tests was set at  $P = 0.05$ . We conducted analyses to identify significant differences between groups and among age/sex classes, as well as any interaction between group and age/sex class. Our data were not normally distributed, and so all comparisons were made with two-way Kruskal-Wallis tests, conducted via normal two-factor ANOVA on the ranks of individual frequencies, rather than the frequencies themselves.

We modeled our analyses of object-use behavior on those of Panger (1998) to allow comparison between the two studies. To determine the rate of object use for each individual, we divided the total number of observed object-use bouts from focal data by the number of focal data hours collected from that individual. To determine the proportion of observation time spent in object-use behavior by each individual, we totaled the duration of all object-use behaviors by that individual from focal data, and divided this duration by that individual's total focal observation time. We drew on all available data (focals, incomplete focals, and ad libitum data) in calculating totals of object-use bouts by food item.

To obtain rates of consumption for each food, we totaled the number of feeding bouts on that food (regardless of whether any processing was employed) from our focal data for each subject, and divided this



**Fig. 2.** *Luehea candida* pods.

number by the total focal observation hours for that individual. To determine the proportion of *Sloanea* feeding bouts that involved processing, we drew on focal samples as well as incomplete focals and ad libitum sampling. For similar comparisons in *Luehea*, we only drew on focal data and incomplete focal data because ad libitum observations of *Luehea* consumption were recorded only for bouts involving processing. To compare proportions of total bouts for each processing technique used for *Sloanea* and *Luehea* across groups and age/sex classes, we totaled the number of bouts using each technique from all available data (focals, incomplete focals, and ad libitum observations). We included only individuals with at least six feeding bouts in our statistical analyses of processing techniques.

## RESULTS

The overall activity patterns of the CP and LV groups (as measured by the percentage of focal observation time spent in social, rest, travel, vigilance, and foraging activities) were very similar (O'Malley, 2002). The proportion of focal observation time that individuals spent foraging did not differ between groups ( $F_{1,17} = 0.311$ ,  $P = 0.584$ ), but did

TABLE 1. Food processing variables examined for *Sloanea terniflora* and *Luehea candida*

Food item	Technique	Variation	Definition
<i>Sloanea terniflora</i>	No process		Fruit is plucked and brought directly to mouth without any additional manipulation or modification.
	Pound		Fruit is repeatedly hammered against a substrate.
	Body/tail rub	Rub/roll	Fruit is grasped and vigorously moved over body fur and tail.
	Rub	Rub and brush	Fruit is vigorously moved backward and forward across substrate while applying some degree of pressure.
<i>Luehea candida</i>			Like "rub/roll," but one hand flails or brushes at fruit as it moves across the substrate.
	No process	Pick and eat	Seeds are extracted from detached pod with tongue, teeth, or fingers without any additional manipulation or modification.
		Eat attached	Seeds are extracted from pod with tongue, teeth, or fingers without additional manipulation and without detaching pod from tree.
	Pound	(Basic) pound	Pod is grasped and repeatedly hammered against substrate. Subject occasionally pauses to pick up seeds from substrate with its fingers or mouth, or to pick out seeds from tip of pod with its fingers, teeth, and tongue.
		Pound and catch	Like "pound," but one hand is either cupped below or against substrate to catch seeds as they fall out.
		Skilled pound	Like "basic pound" or "pound and catch" but much more rapid and controlled, with no pause in hammering. Subject does not stop to pick seeds from tip of pod. "Skilled pound" bouts in which one hand was cupped below or against substrate were counted as "pound and catch" for analyses of that pattern.
	Rub/roll		Pod is moved backward and forward across substrate while applying some degree of pressure
	Hand pound		Grasping pod with one hand and forcibly upending it into other hand.

differ significantly between age/sex classes ( $F_{3,17} = 4.209$ ,  $P = 0.021$ ), with juveniles spending a greater proportion of their time foraging (58.1%) than subadults (46.9%), adult females (47.9%), or adult males (45.2%). The proportion of observation time spent foraging by each age/sex class did not differ significantly between groups ( $F_{3,17} = 0.699$ ,  $P = 0.565$ ).

### Object use

We observed all three types of object use identified by Panger (1998) ("rub," "pound," and "fulcrum use") in foraging contexts. We recorded a total of 592 object-use bouts involving 13 identified food items and 3 unidentified food items (Table 2): 91.2% of object use bouts involved *Sloanea terniflora* (62.8%) or *Luehea candida* (28.4%). The LV group had a significantly higher rate of object use than the CP group ( $F_{1,17} = 17.787$ ,  $P = 0.001$ ), and differences in object-use rates across age-sex classes were also significant ( $F_{3,17} = 5.165$ ,  $P = 0.010$ ), with juveniles having a much lower rate of object use than all other age/sex classes. Object-use rates by each age/sex class did not differ between groups ( $F_{3,17} = 1.616$ ,  $P = 0.223$ ) (Fig. 3).

Members of the LV group spent a significantly higher proportion of their total observed focal time in object-use activities than did members of the CP group ( $F_{1,17} = 12.259$ ,  $P = 0.003$ ). Differences in the proportion of time spent in object-use activities across age-sex classes were also significant ( $F_{3,17} = 3.646$ ,  $P = 0.034$ ), with juveniles spending a much

lower proportion of their time engaged in object use. The percentage of time spent in object-use activities by each age-sex class did not differ significantly between groups ( $F_{3,17} = 1.129$ ,  $P = 0.365$ ) (Fig. 4).

### *Sloanea terniflora* processing

*Sloanea terniflora* fruits were a larger component of the LV group's diet (9.9% of observed foraging time) than of the CP group's diet (1.5% of observed foraging time). This was largely due to a single *Sloanea terniflora* tree in the LV group's range that produced an enormous fruit crop in mid-February 2001. The group fed in and around this particular tree for several hours a day for nearly 2 weeks. Rates of *Sloanea* feeding bouts/hour were significantly higher in the LV group than in the CP group ( $F_{1,17} = 11.610$ ,  $P = 0.003$ ), but we found no significant differences among age/sex classes ( $F_{3,17} = 1.027$ ,  $P = 0.405$ ), and there was no significant interaction between age/sex class and group ( $F_{3,17} = 0.575$ ,  $P = 0.639$ ) (Table 3).

Though capuchins sometimes attempted to consume *Sloanea* fruits without trying to remove the hairs first, this appeared to be an unpleasant experience for them and usually involved spitting, sneezing, grimacing, and rubbing their faces on tree bark. We observed significant differences in the proportions of "no-process" feeding bouts between juveniles (20.8%, or 5 of 24 bouts), subadults (2.5%, or 2 of 81 bouts), adult females (0.7%, or 1 of 140 bouts), and adult males (4.0%, or

TABLE 2. Capuchin object use behavior observed by food type/species

Food type/species	% rub bouts	% pound bouts	% fulcrum bouts	Total bouts
<i>Sloanea terniflora</i>	97.3%	2.7%	0.0%	372
<i>Luehea candida</i>	29.8%	70.2%	0.0%	168
<i>Zuelania guidonia</i>	4.3%	0.0%	95.7%	23
<i>Tabebuia ochracea</i>	83.3%	0.0%	16.7%	6
<i>Acrocomia vinifera</i>	20.0%	80.0%	0.0%	5
Caterpillar	100.0%	0.0%	0.0%	3
<i>Spondias radlkofri</i>	66.7%	0.0%	33.3%	3
<i>Maniklera chicle</i>	100.0%	0.0%	0.0%	2
<i>Randia</i> spp.	100.0%	0.0%	0.0%	2
<i>Ximeria americana</i>	0.0%	100.0%	0.0%	2
Egg case or cocoon	100.0%	0.0%	0.0%	1
<i>Simaruba olivacea</i>	100.0%	0.0%	0.0%	1
<i>Genipa americana</i>	0.0%	0.0%	100.0%	1
Unknown	66.7%	33.3%	0.0%	3
<b>Total</b>	<b>73.0%</b>	<b>22.8%</b>	<b>4.2%</b>	<b>592</b>

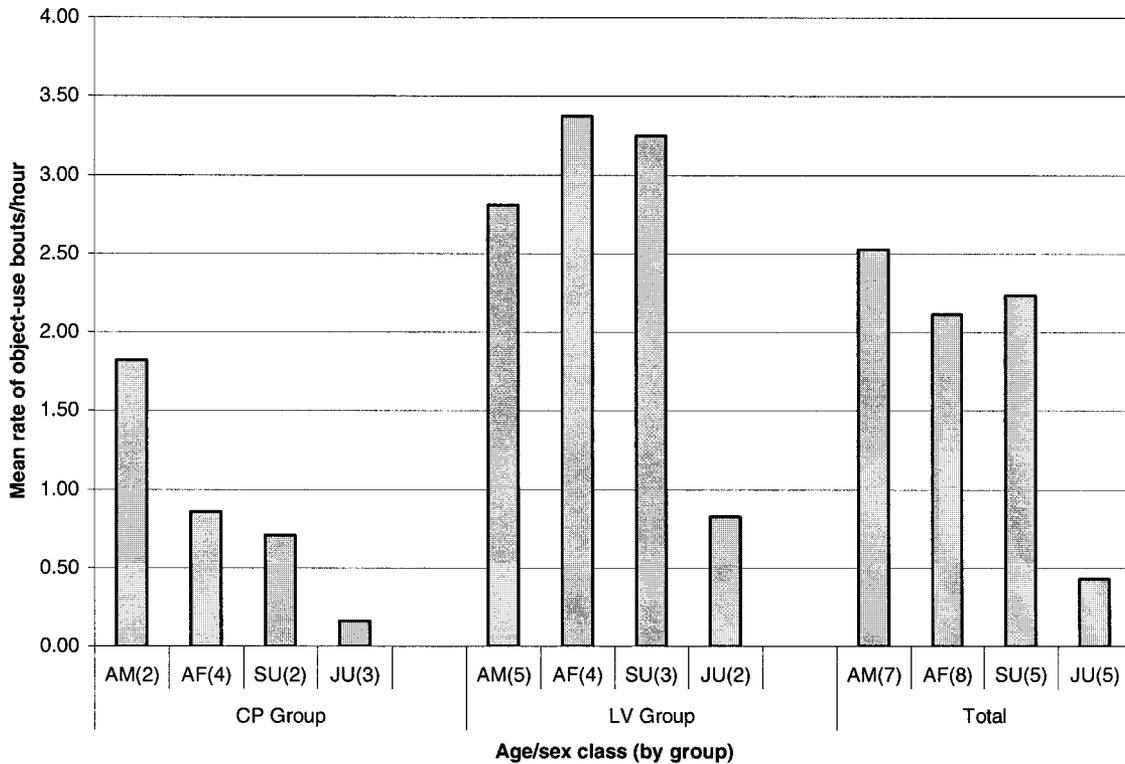
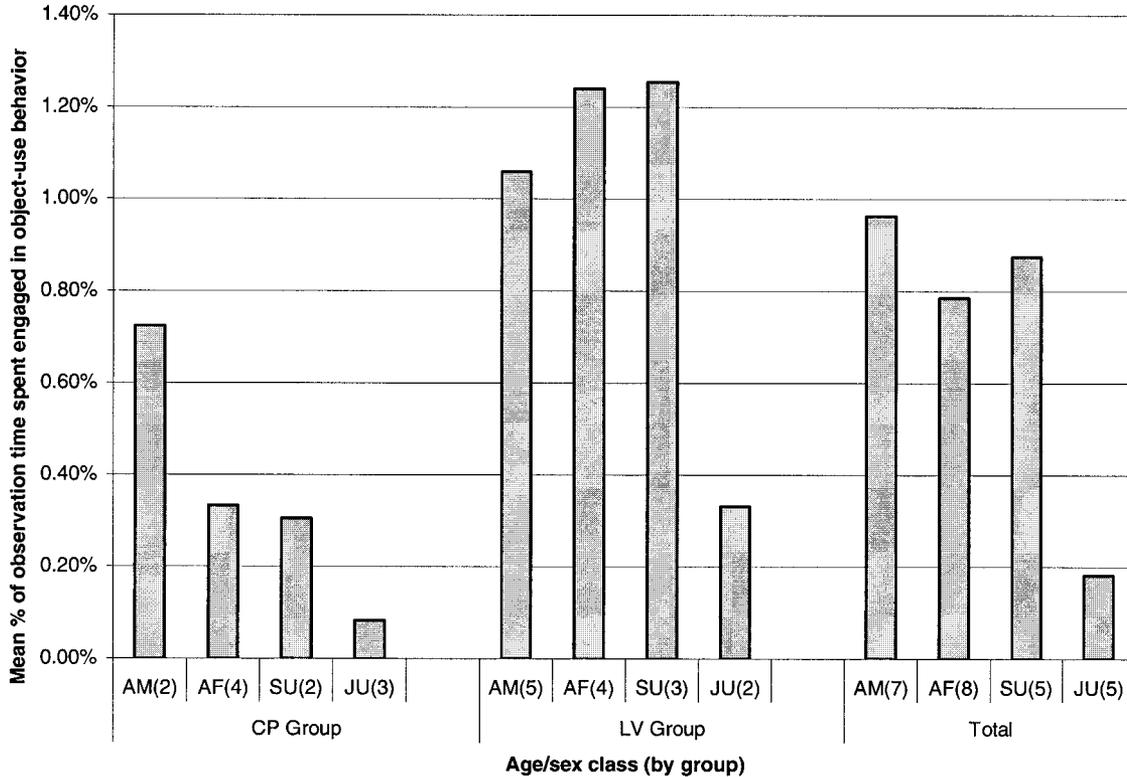


Fig. 3. Mean rates of object use bouts. Numbers in parentheses indicate number of individuals in each age/sex class (AM, adult male, 8+ years old; AF, adult female, 8+ years old; SU, subadult, 4–8 years old; JU, juvenile, 0.5–4 years old). CP group: AM, mean 1.82, SD 1.52; AF, mean 0.86, SD 0.56; SU, mean 0.71, SD 0.58; JU, mean 0.16, SD 0.12; LV group: AM, mean 2.81, SD 1.11; AF, mean 3.37, SD 1.36; SU, mean 3.25, SD 1.10; JU, mean 0.83, SD 1.17; Total: AM, mean 2.53, SD 1.20; AF, mean 2.11, SD 1.65; SU, mean 2.23, SD 1.62; JU, mean 0.43, SD 0.69.

6 of 151 bouts) ( $F_{3,8} = 9.125, P = 0.006$ ). We found no significant differences in proportions of “no-process” feeding bouts between groups ( $F_{1,8} = 0.033, P = 0.861$ ); nor did we find a significant difference across age/sex classes between groups ( $F_{3,8} = 0.261, P = 0.852$ ).

We observed three general processing techniques for *Sloanea* (Table 4): “rub,” “pound,” and “body/tail rub.” “Rub” was the most frequently observed technique in all age/sex classes (comprising 94.8% of observed *Sloanea* processing bouts). Only two adult males (both in the LV group) used the

“pound” technique. The “tail/body rub” technique was used rarely in both groups and in all age/sex classes, by a total of 6 individuals. Capuchins using the “rub” technique would sometimes use a two-handed variation in which the fruit was rubbed against a substrate with one hand, while the other hand brushed or slapped at the fruit. This “rub and brush” variation appeared to reflect an effort to keep the *Sloanea* hairs from flying up into the subject’s face. Among those “rub” bouts where we could distinguish hand-use patterns, this “rub and brush” variation was used more often by



**Fig. 4.** Mean proportions of foraging time spent in object use activities. CP group: AM, mean 0.72%, SD 0.005; AF, mean 0.33%, SD 0.002; SU, mean 0.30%, SD 0.002; JU, mean 0.08%, SD 0.000; LV group: AM, mean 1.06%, SD 0.005; AF, mean 1.24%, SD 0.004; SU, mean 1.23%, SD 0.007; JU, mean 0.33%, SD 0.005; Total: AM, mean 0.96%, SD 0.005; AF, mean 0.79%, SD 0.006; SU, mean 0.87%, SD 0.007; JU, mean 0.18%, SD 0.003.

**TABLE 3.** Mean rate of consumption bouts/hour by food type

<i>Sloanea terniflora</i>			<i>Luehea candida</i>		
Group	Mean bouts/hour	SD	Group	Mean bouts/hour	SD
CP	0.41	0.77	CP	1.00	0.79
LV	2.28	1.33	LV	1.26	1.37

Age/sex		Age/sex			
AM	2.05	1.04	AM	0.32	0.19
AF	1.64	1.81	AF	0.94	0.75
SU	1.42	1.61	SU	2.43	1.60
JU	0.39	0.71	JU	1.34	0.88

adult males (57.9%, or 73 of 126 bouts) and adult females (75.9%, or 101 of 133 bouts) than subadults (23.0%, or 17 of 74 bouts) or juveniles (11.8%, or 2 of 17 bouts). However, there were no significant differences among age/sex classes or between groups (and no significant interaction between age/sex class and group) in either the proportion of “rub” bouts or in the proportion of “rub and brush” bouts.

#### *Luehea candida* processing

The CP group spent 2.15% of its total foraging time on *Luehea candida*, compared to 3.54% of total foraging time for the LV group. We detected

no significant differences in rates of *Luehea* feeding bouts between groups ( $F_{1,17} = 0.850$ ,  $P = 0.369$ ) or age/sex classes ( $F_{3,17} = 2.206$ ,  $P = 0.125$ ); nor did we find a significant interaction between group and age/sex class ( $F_{3,17} = 1.880$ ,  $P = 0.174$ ) (Table 3).

*Luehea candida* pods dehisce as they mature. Monkeys could access seeds from dehisced or partially dehisced pods with their teeth, tongue, or fingers, sometimes without even detaching the pod from the tree. We found significant differences in the proportions of “no-process” feeding bouts among juveniles (96.3%, or 78 of 81 bouts), subadults (70.4%, or 88 of 125 bouts), adult females (39.8%, or 43 of 108 bouts), and adult males (4.0%, or 1 of 25 bouts) ( $F_{3,17} = 11.859$ ,  $P < 0.001$ ). We found no significant differences in the proportion of “no-process” feeding bouts between groups ( $F_{1,15} = 0.026$ ,  $P = 0.874$ ), or among age/sex classes across groups ( $F_{3,17} = 1.676$ ,  $P = 0.210$ ).

We observed three general techniques for processing *Luehea candida* pods: “pound,” “rub,” and “hand pound” (Table 5). Of all observed *Luehea* processing bouts, 62.4% were “pound” bouts. “Pound” bouts were observed more often in adult males and females than in either subadults or juveniles. In a variation of the “pound” technique that we called “pound and catch,” one hand would be used to grasp the pod while the other was held palm-up at an

TABLE 4. Percentage of *Sloanea* processing bouts for each general technique

Group	Total	No. pound	No. rub	No. body/tail rub	% pound	% rub	% body/tail rub
CP	88	0	85	3	0.0%	96.6%	3.4%
LV	294	10	277	7	3.4%	94.2%	2.4%
Age/sex	Total	No. pound	No. rub	No. body/tail rub	% pound	% rub	% body/tail rub
AM	145	10	132	3	6.9%	91.0%	2.1%
AF	139	0	137	2	0.0%	98.6%	1.4%
SU	79	0	75	4	0.0%	94.9%	5.1%
JU	19	0	18	1	0.0%	94.7%	5.3%

TABLE 5. Percentage of *Luehea* processing bouts for each general technique

Group	Total	No. pound	No. rub	No. hand pound	% pound	% rub	% hand pound
CP	103	55	32	16	53.4%	31.1%	15.5%
LV	86	63	18	5	73.3%	20.9%	5.8%
Age/sex	Total	No. pound	No. rub	No. hand pound	% pound	% rub	% hand pound
AM	47	37	7	3	78.7%	14.9%	6.4%
AF	74	56	1	17	75.7%	1.4%	23.0%
SU	64	24	39	1	37.5%	60.9%	1.6%
JU	4	1	3	0	25.0%	75.0%	0.0%

angle beside the substrate to catch seeds as they came out. Of those “pound” bouts where we could distinguish hand-use patterns, 81.3% involved this “pound and catch” variation. We observed “pound and catch” bouts more often among adult males (97.3%, or 36 of 37 bouts) than among adult females (73.1%, or 38 of 52 bouts) or subadults (77.3%, or 17 of 22 bouts). Juveniles were never observed to use this variation (0 of 1 bout). In a “skilled pound” variation (which was not mutually exclusive with “pound and catch”), an individual would hammer the pod at a qualitatively more rapid pace, ducking its head down to pick up seeds while barely pausing in its hammering. At no point would the subject need to stop and pick out seeds from the tip of the pod with its fingers or teeth, as was often the case with regular “pound” bouts. These “skilled pound” bouts composed 26.3% (or 31 of 118) of all observed “pound” bouts, and were seen only in four adults (the alpha and beta male, and the alpha and beta female) of the CP group. “Rub” bouts composed 26.5% of observed *Luehea* processing bouts. We observed “rub” bouts more often in juveniles and subadults than in adult females or adult males. This pattern did not appear to be very effective at removing seeds from seed pods. Bouts of “hand pound” composed only 11.1% of all observed *Luehea* processing bouts, and involved an individual grasping a detached pod in one hand and forcefully upending it into the other hand. We observed this pattern in both groups and in adult males, adult females, and subadults, but not juveniles. This appeared to be an effective method of accessing *Luehea* seeds, though not as effective as “pound.” We found no significant differences across age/sex classes or between groups in the proportion of “pound” or “rub” bouts, or in the proportion of “pound and catch” processing bouts;

nor did we find any significant interactions between age/sex class and group.

## DISCUSSION

We found significant differences in the proportion of time spent foraging among age/sex classes but not between groups. Juveniles spent the highest proportion of their time foraging, and other age/sex classes spent relatively equivalent proportions of their time foraging. High rates of foraging among younger primates are generally interpreted to reflect their lower foraging success and higher metabolic demands compared to mature animals (e.g., Janson and van Schaik, 1993). The close similarity between the two groups’ activity budgets presumably reflects that the two groups are of similar size and composition and live in widely overlapping ranges, as they have for more than a decade (Chapman and Fedigan, 1990).

## Object use

Panger (1998) reported that the capuchins at the neighboring site of Palo Verde engaged in 0.19 object use bouts/hour of observation during her 11-month study, compared to 1.63 bouts/hour at Santa Rosa for this 6-month study. The monkeys of Palo Verde spent 0.4% of their time in object-use activities, compared to 0.63% by the Santa Rosa monkeys. Also in contrast to our results, Panger (1998) reported no significant differences among age/sex classes in either rate of, or percentage of time spent in, object-use activities.

The higher rates of object use that we found in our study may in part reflect that capuchins are more likely to target better-defended food items in the dry season that might be ignored in times of

greater food abundance. In a full-year study, object-use patterns by the Santa Rosa monkeys might have more closely resembled those reported for Palo Verde. The overall higher incidence of object-use activities at Santa Rosa were driven largely by *Sloanea* processing in the LV group, and to a lesser extent by *Luehea* processing in both study groups. As previously noted, one *Sloanea* tree in the LV group's range produced a particularly abundant crop. Boinski et al. (2000) and others (Izawa and Mizuno, 1977; Parker and Gibson, 1977) noted that rates and patterns of complex food processing are highly dependent on local conditions, including the availability of foods that can or must be processed, the relative profitability of such foods relative to what else is available, and the availability of skilled models. Interestingly, Chavalier-Skolnikoff (1990) observed 20 bouts of tool use in her 5-month study at Santa Rosa, though Panger (1998) did not observe any in 11 months at Palo Verde. Local conditions may favor a greater degree of tool and object use in foraging by capuchins at Santa Rosa relative to other Costa Rican research sites, though this hypothesis remains untested. The striking differences in frequencies of tool and object use reported for these two research sites highlight the difficulty in making broad generalizations about capuchin manipulative tendencies in the wild, even between groups living in ecologically and geographically similar habitats.

Neither *Sloanea* processing nor consumption was observed at Palo Verde during the 11 months of study by Panger (1998), though *Sloanea* trees are abundant (Panger, personal communication). Individual *Sloanea* trees in Santa Rosa show great variability from year to year in crop size, producing no crop in some years, and particularly abundant crops in others (Janzen, personal communication). Given that *Sloanea* is consumed by capuchins at the nearby Lomas Barbudal site (Panger et al., 2002), and that capuchins are known to consume other species of *Sloanea* in South America (Terborgh, 1983), it is possible that *Sloanea* is part of the diet of Palo Verde monkeys but that no trees produced abundant crops during the time of the study by Panger (1998). Future research at Palo Verde is needed to resolve this issue.

### ***Sloanea terniflora* processing**

Chapman and Fedigan (1990) found that the group that occupied what is now the LV group's range spent more than twice as much of their total observed feeding time on *Sloanea terniflora* (14.7%) than the CP group did (6.9%). These dietary differences were still apparent in our study, as we found significant differences in *Sloanea* consumption rates across groups, with the LV group's overall rate more than five times greater than that of the CP group. These findings may reflect differences in food availability between the two home

ranges. In Santa Rosa, *Sloanea* trees are sufficiently rare and clustered that they often fail to show up in random quadrat surveys of our groups' home ranges (e.g., Chapman and Fedigan, 1990; Sorensen, 1998; Aureli, personal communication). Chapman and Fedigan (1990) estimated the density of *Sloanea* trees in the range of the CP group as 0.6/ha (or 53.9 cm diameter at breast height (DBH)/ha), and in the LV group as 0.0/ha (or 0.0 cm DBH/ha), respectively. However, the major source of variation in *Sloanea* availability is not the number of trees but the idiosyncratic and stochastic nature of the fruit crop. As previously noted, one large *Sloanea terniflora* tree in the LV group's range produced an enormous crop in mid-February 2001, and the group spent several hours feeding in and around the tree nearly every day for more than 2 weeks. There are also other *Sloanea* trees within the LV group range that produced standard-sized crops in 2001. In contrast, only one of the *Sloanea* trees within the CP group range was observed to produce a fruit crop in 2001, though other such trees were present.

Although we did not document significant differences in consumption rates of *Sloanea* between age/sex classes, juveniles consumed *Sloanea* only rarely compared to adults (of either sex) or subadults. While adults, subadults, and juveniles all had difficulties processing *Sloanea*, juveniles appeared to find the task particularly challenging, and would frequently break off their processing behavior to rub their face, sneeze, or discard the fruit they were working with. It may be that juveniles are unable to manipulate the fruits as easily as more mature animals, particularly in the "rub and brush" hand-use pattern. This interpretation is consistent with past observations of food processing by capuchins in both the wild (Izawa and Muzino, 1977; Boinski et al., 2000) and in captivity (Anderson, 1990), where younger individuals often appear to lack the strength, manual coordination, or understanding of a task's requirements to tackle it effectively.

The rare consumption of *Sloanea* by juveniles may also reflect a form of risk-aversion. There can be negative consequences if these fruits are handled carelessly, including irritated skin and impaired vision if the hairs get into the eyes (O'Malley, personal observation). Such problems, though temporary, could have a negative impact on an individual's foraging success and ability to evade predators or other threats. Janson and van Schaik (1993) characterized the juvenile period in primates as one of ecological risk, and discussed their greater vulnerability (relative to adults) to both starvation during periods of food scarcity and to predation due to their lower physical strength and inexperience in choosing and processing appropriate foods. These authors argued that a "risk averse" strategy of slow development is intended to minimize mortality risk. This adaptation is predicted to have a strong influence on juvenile dietary choice, foraging behavior, and

patterns of association within groups. Our observations of *Sloanea* processing support a risk-averse strategy in juvenile capuchin foraging behavior. Despite its apparent value as a food resource, and despite being capable (with some difficulty) of processing *Sloanea* using the same technique favored by adults, the potential costs of *Sloanea* fruit processing may deter juveniles from feeding on it as frequently as other age/sex classes. A large *Ficus* tree that was less than 20 m from the particularly abundant *Sloanea* tree in the LV group's range came into fruit at roughly the same time. When the adults were feeding on *Sloanea*, juveniles were often in this tree consuming figs.

We found little variability in *Sloanea* processing techniques across groups or age/sex classes. This lack of variability suggests that rubbing *Sloanea* fruits on a substrate is the only viable way to process this food for safe consumption. The "pound" technique did not appear to be very effective, and the "body/tail rub" technique may bear its own costs in terms of discomfort or irritation from the hairs. Rubbing and pounding objects were commonly observed in both captivity and the wild (Izawa and Muzino, 1977; Struhsaker and Leland, 1977; Boinski et al., 2000), and may reflect a default response when individuals are having difficulties (Panger, 1998; Panger et al., 2002). Adults of both sexes used the "rub and brush" variant more frequently than either subadults or juveniles. Since adults processed *Sloanea* at higher rates than nonadults, such differences may simply reflect physical ability, experience, and greater opportunity on the part of older animals. However, immature capuchins would presumably need to learn that *Sloanea* is edible by watching conspecifics, and it seems likely that observing others processing these fruits might serve to channel their own efforts. The potential role of the social context in the development of *Sloanea* processing techniques is explored more thoroughly in a companion paper (O'Malley and Fedigan, 2005).

### *Luehea candida* processing

Chapman and Fedigan (1990) found that *Luehea* trees were far more common in the range of what is now the LV group (5.6/ha, or 255.6 cm DBH/ha) than in the range of the CP group (0.6/ha, or 34.6 cm DBH/ha). The group that occupied the LV group's range at that time spent more than twice as much of their total feeding time on *Luehea candida* (5.8%) than did the CP group (2.3%). In the present study, we found that rates of *Luehea* consumption did not differ significantly between the two groups or between age/sex classes. Chapman and Fedigan (1990) concluded that the dietary choices of capuchin groups may be determined as much by food profitability (how nutritious foods are and how long it takes to consume them compared to other items simultaneously available) as by food abundance. Relative food profitability seems likely to play a role

in the rate of consumption of *Luehea* seeds, a dietary item that can require considerable time and effort to extract and that is only seasonably available. However, in their study, Chapman and Fedigan (1990) did not rule out the possibility that group differences in diet reflect local traditions in food choice. The degree of stability in the proportion of foraging time spent feeding on *Luehea* by the CP group over a 15-year period (2.3% in 1986 vs. 2.15% in 2001), despite changes in forest maturity and structure (and presumably food availability and profitability) due to ongoing forest regeneration (Fedigan et al., 1996), suggests that group dietary preferences may be traditional.

Adult males had the lowest rate of *Luehea* feeding bouts, and subadults the highest, though differences among age/sex classes were not significant. Adult males almost always used some form of processing when feeding on *Luehea*, while juveniles almost never processed *Luehea*, and adult females and subadults fell out in between. One explanation for this pattern relates to the physical limitations of different age/sex classes. *Luehea* pods are attached to their stems quite firmly, and both subadults and adult females sometimes appeared to have difficulty removing them. Juveniles may lack the strength to pull them off with any regularity, or to manipulate the pods effectively. Adult male capuchins are both larger and stronger than adult females (Fedigan, 1990), who in turn are larger and stronger than immature animals. At the same time, smaller animals may have an advantage over larger animals in retrieving *Luehea* seeds without any processing due to their smaller fingers. Attempting to consume seeds without processing the pods may be a more energetically efficient strategy for these age/sex classes, whereas adult males can break the stems with ease. Differences in physical strength might also explain why females engaged in "hand pound" more than adult males.

Another factor that could relate to the higher rate of "pound" in adult males relative to other age/sex classes would be avoidance of predation risk, particularly on the part of adult females, as hypothesized by Boinski et al. (2000) in their discussion of capuchin food processing in Suriname. Repeatedly pounding a woody pod on a substrate produces considerable noise, and could signal the presence of a capuchin to potential predators. Boinski et al. (2000) reported that at their site, both researchers and local hunters were easily able to locate capuchin groups by listening for the sound of pounding activities. Because of the need to visually monitor the food being processed (thus reducing vigilance), *Luehea* "pounding" may involve greater predation risk than simply consuming seeds without processing, or using the "hand pound" technique, and so adult females favor the latter techniques, though they are capable of the former.

The relatively high percentage of "rub" bouts in *Luehea* processing among subadults and juveniles

may reflect that younger individuals lack hands large and strong enough to effectively manipulate the pods for pounding. They may also fail to comprehend the requirements for successful seed extraction (e.g., appropriate use of a substrate, pod maturity, and pod orientation). We often observed juveniles and subadults trying to remove seeds from immature (not yet dehisced) pods without success, whereas adults were never observed to process immature pods, and would usually briefly inspect a pod before trying to break it off its stem.

Individuals (primarily adult males and females) used the "pound and catch" variation frequently while pounding *Luehea*. The "skilled pound" variation observed in the CP group was only subtly different from other variations of "pound," but appeared to be considerably more efficient. The only four individuals in the CP group observed to use "skilled pound" were also the only members of that group to use the "pound and catch" variation. As with *Sloanea*, the relative frequency of the "pound and catch" variation across age/sex classes corresponded to a higher use of the "pound" technique, and so may simply reflect greater opportunity and experience on the part of older animals. That the "skilled pound" and "pound and catch" variations were seen only in the highest-ranking individuals in the CP group suggests that the social context may be important in explaining the expression of these patterns. This issue is addressed more thoroughly in a companion paper (O'Malley and Fedigan, 2005).

In conclusion, we found significant differences in rates and time spent in object-use activities between groups and age/sex classes at Santa Rosa. Capuchins engaged in object-use activities more frequently at Santa Rosa than at the nearby site of Palo Verde, and such activities were overwhelmingly directed toward only two food species. These differences may reflect differences in food availability, but may also reflect relative food profitability or local traditions in foraging. Differences in *Luehea candida* and *Sloanea terniflora* processing among age/sex classes may reflect variation in physical abilities, experience, or foraging strategies, but a social component to the development of processing techniques is also likely. We concur with other researchers (e.g., Boinski et al., 2000; Panger et al., 2002) that further research on variability in food processing for specific foods should be undertaken within groups and populations, ideally in conjunction with more rigorous documentation of ecological variation as well as the social context of complex food processing. Such research will become particularly valuable, given the growing interest in *Cebus* as a model for understanding the development of non-human social traditions (Fragaszy and Perry, 2003).

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