Evaluating Social Influences on Food-Processing Behavior in White-Faced Capuchins (*Cebus capucinus*)

Robert C. O'Malley[1] and Linda M. Fedigan[2]*

[1]*Department of Anthropology, University of Alberta, Edmonton, Alberta T6G 0E8, Canada*
[2]*Department of Anthropology, University of Calgary, Calgary, Alberta T2N 1N4, Canada*

ABSTRACT   Interpopulation variability in patterns of food processing, similar to what is described as "traditional" or "cultural" variation in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*), was identified in white-faced capuchins (*Cebus capucinus*). However, recent comparisons of food processing in capuchins were conducted only at the population level, with relatively little attention given to variability among groups, age/sex classes, or individuals. This paper examines variability in the processing of specific food types within the context of various social networks (i.e., patterns of association, rank, and kinship) among free-ranging *Cebus capucinus* at Santa Rosa National Park in Costa Rica. We collected data on two groups of white-faced capuchins in 2001, identifying rates of "food interest" for each individual, as well as forms of processing for specific food types. Juveniles exhibited the most interest in the food-processing behavior of other group members, and food interest was directed most frequently toward adult females. We identified distinctive processing techniques for several food items (*Luehea candida* pods, *Sloanea terniflora* fruits, and caterpillars) that facilitated comparisons among individuals within groups. Food-processing techniques for *Sloanea* fruit and caterpillars appeared to vary independently of the social networks examined in this study. However, we found evidence that variation in *Luehea candida* processing is to some degree linked to both patterns of association and social rank. The potential influence of these variables on observed food processing patterns warrants further scrutiny. Am J Phys Anthropol 127:481–491, 2005.   © 2005 Wiley-Liss, Inc.

As in *Pan* and *Pongo*, behavior patterns of members of the genus *Cebus* may reflect social traditions, or "culture," defined for the purposes of this study as "group-specific behavior that is acquired, at least in part, from social influences" (McGrew, 1998; also see Fragaszy and Perry, 2003). A half-century of chimpanzee and orangutan research across numerous sites has identified a high degree of group- and population-specific variability in courtship and grooming behavior (McGrew and Tutin, 1978; Nishida, 1980; Sugiyama, 1981; Boesch, 1995; Nakamura et al., 2000), in patterns of medicinal plant use (Huffman and Wrangham, 1994; Huffman et al., 1997), and in food-processing and foraging techniques, particularly forms of tool- and object-use (Sugiyama, 1985, 1997; Goodall, 1986; Boesch, 1991, 1996; McGrew, 1992, 1998; Boesch and Boesch, 1993; Boesch et al., 1994; Boesch and Tomasello, 1998; van Schaik et al., 1999, 2003). Despite their apparent cognitive limitations relative to hominoids (Visalberghi, 1997), evidence for similar patterns of social traditions in wild *Cebus* spp. has emerged in studies of grooming behavior and social play (Perry et al., 2003), as well as in medicinal plant and insect use (Baker, 1996; Valderrama et al., 2000). In *Cebus capucinus*, broad variations in processing techniques, including several forms of object-use, for specific food items across ecologically similar sites in northwest Costa Rica were identified in a pattern consistent with "cultural" differences in chimpanzee (Whiten et al., 1999) and orangutan (van Schaik et al., 2003) populations (Panger, 1998; Panger et al., 2002). These preliminary findings from studies of wild *Cebus* spp. call into question both the significance of specific cognitive processes in explaining patterns of complex object manipulation, including those said to be "traditional" or "cultural," and the distinctiveness of such patterns in *Homo* and *Pan* relative to other nonhuman primates (Panger et al., 2002) or other animals. These issues can only be addressed with a more intensive research focus on

food-processing patterns across a broader range of taxa (Boinski et al., 2000). In this paper, we examine distinctive techniques for processing three types of capuchin foods, and whether the use or lack of use of such techniques by different individuals relates to the social networks of kinship, dominance relations, and patterns of physical association.

INTERPRETING PATTERNS OF FOOD PROCESSING

Capuchins' ability to process specific foods is likely subject to numerous physical, cognitive, metabolic, and behavioral constraints (Fragaszy et al., 2004), as well as ecological factors such as food availability (Chapman and Fedigan, 1990) and opportunities to observe conspecifics (Boinski et al., 2000). Therefore, interpreting evidence for social traditions in food processing is a difficult undertaking without detailed information about the methods capuchins use to process specific foods, and the degree (and nature) of variability within and across groups and populations. Panger (1998) described general forms of object-use such as "rub" and "pound" employed by white-faced capuchins, and discussed foods and food types that elicited such processing patterns. More recently, Panger et al. (2002) provided an overview of interpopulation variability in food-processing behavior, and provided evidence for social influences on distinct processing patterns within a social group. However, generalized processing methods such as "pound" are employed by most, or all, wild populations, and are frequently observed in captivity as well (Anderson, 1990; Panger, 1998; Panger et al., 2002), and so the significance of the finding that capuchins have been observed to "pound" different foods at different sites remains unclear. Panger et al. (2002) stressed that more details about processing patterns for specific foods are needed to evaluate the nature and significance of social traditions in capuchin food processing. Such a focus on specific foods has proven valuable in evaluating the significance of variability in ant-dipping (McGrew, 1974; Boesch and Boesch, 1993) and termite-fishing (McGrew and Marchant, 1999) behavior within and across populations of wild chimpanzees.

THE SIGNIFICANCE OF SOCIAL NETWORKS

Identifying how specific foraging and food-processing patterns arise, spread, and persist in wild primates can be a difficult task, although such research has been conducted with some success (e.g., Boesch, 1991, 1996; Matsuzawa, 1994; Watanabe, 1994; Inoue-Nakamura and Matsuzawa, 2001; Garber and Brown, 2002). In part because field experiments may risk altering the subjects' food-processing patterns and mechanisms of behavioral diffusion, more indirect means of examining such behavior in a social context were also tried (e.g., Boesch, 1996; Panger et al., 2002). Such indirect evidence can be obtained by identifying potential opportunities for

transmission and determining if such opportunities correspond to specific patterns of behavior. In conjunction with documenting whether an individual directly observes, or is observed in, food-processing behavior by a conspecific, it is possible to use social networks within groups to predict which individuals might be more likely to share a given behavioral pattern. Such analyses do not allow for specific social learning processes to be identified (Whiten and Ham, 1992); instead, they indicate whether social processes could be at work, and if so, the strength of their influence.

A number of intragroup social networks may influence food-processing patterns. The most obvious, and likely the most powerful, are those that influence patterns of physical association, or *proximity*: individuals who spend more time near each other would presumably have greater opportunity to observe and potentially learn from each other's behavior, relative to less proximate individuals (Panger et al., 2002). *Social rank* is known to influence spatial patterns within capuchin groups (Janson, 1990a,b; Hall and Fedigan, 1997), which can in turn influence diet and foraging behavior. In addition, higher-ranking individuals are able to supplant lower-ranking individuals from prized food resources (Di Bitetti and Janson, 2001), which may influence the strategies employed by subordinates when dealing with foods that require some degree of handling time to process effectively. Finally, *kinship* networks may offer opportunities for social transmission, as individuals may monitor their relatives' actions more closely than those of nonrelatives. This is particularly true for mothers and their infants, as capuchin young rarely leave their mothers in the first few months of life (Fragaszy, 1990; Welker et al., 1990), and a great deal of their early explorations of their environment are directed toward their mothers' activities (Fragaszy et al., 1991).

RESEARCH OBJECTIVES

Here, we seek first to determine the degree to which several social networks (specifically proximity, rank, and kinship) are associated with previously identified food-processing patterns for several specific food items consumed by wild capuchin groups. Secondly, we discuss whether such patterns can be taken as evidence for social traditions among wild capuchins.

METHODS

We conducted this research from January–June 2001 at Santa Rosa National Park, Costa Rica. We collected a total of 309.5 hr of quantitative data on members of two habituated *C. capucinus* groups, the "CP" and "LV" groups, which have been studied extensively over the last two decades (Chapman and Fedigan, 1990; Fedigan, 1990; Rose 1994, 1997; Hall and Fedigan, 1997). We focused on patterns of food

TABLE 1. Food processing techniques identified for specific food items

Food item	Technique	Description
Sloanea terniflora	Rub and brush	Moving a fruit or fruits rapidly back and forth against a substrate with one hand, while flailing and brushing against it with other hand. Presumed function of this technique is to facilitate removal of urticating hairs that cover these fruits, and keep them from flying in individual's eyes.
Luehea candida	Pound and catch	Hammering a hard seed pod against a substrate with one hand, while other hand is cupped below, or braced against substrate to catch winged seeds as they come out of pod.
	Skilled pound	Extremely rapid pounding of a pod against a substrate, with no pause in hammering when seeds are slurped or scooped up for consumption.
Caterpillars	Eviscerate	Tearing open one end of a large caterpillar and flicking out gut contents in one smooth motion.

TABLE 2. Summary of food-processing patterns for CP (upper set) and LV (lower set) groups[1]

Subject	Rank	Age/sex	"Skilled pound" *Luehea*?	"Pound and catch" *Luehea*?	"Rub and brush" *Sloanea*?	Eviscerate caterpillar?
CP group						
L1	1	AdFem	Yes	Yes	Yes	Yes
NO	2	AdMale	Yes	Yes		Yes
NY	3	AdFem	Yes	Yes	Yes	Yes
TR	4	AdMale	Yes	Yes	Yes	
SI	5	JuvFem				
RA	6	SubMale				
PO	7	AdFem			Yes	
ED	8	JuvFem				
TI	9	SubFem			Yes	
SE	10	AdFem				Yes
ZZ	11	JuvFem				
LV group						
PI	1	AdMale			Yes	
KL	2	AdFem		Yes	Yes	
AO	3	AdMale		Yes	Yes	
CH	4	AdMale			Yes	
DL	5	AdFem		Yes	Yes	
SD	6	AdMale		Yes	Yes	
TO	7	SubMale		Yes		
PR	8	AdMale		Yes	Yes	
AL	9	SubMale		Yes	Yes	
MY	10	JuvFem			Yes	
SL	11	SubFem			Yes	
BL	12	AdFem			Yes	Yes
FI	13	AdFem		Yes	Yes	
SY	14	JuvFem				

[1] Blank cells for specific techniques indicate that processing pattern in question was not observed for that individual in either focal data or in *ad libitum* notes. Ad, adult; Juv, juvenile; Sub, subadult; Fem, female.

processing, including rates of consumption, hand use, and techniques employed for specific foods. In this paper, we examine processing behavior observed for three foods (*Sloanea terniflora*, *Luehea candida*, and caterpillars) that were previously identified as variable or potentially variable across *Cebus* populations (Panger et al., 2002), for which distinctive food-processing techniques were identified, and for which we collected sufficient data for meaningful analysis. We examined these processing techniques in relation to three types of social networks: proximity, rank and kinship. A separate paper discusses variability between groups and among age/sex classes in greater detail (O'Malley and Fedigan, in press).

Analyses

We identified individuals using one of the specific processing techniques described for *Luehea candida*,

Sloanea terniflora, or large caterpillars (Table 1) in the course of previous analyses (Table 2; O'Malley, 2002; O'Malley and Fedigan, in press). We observed the "eviscerate" technique for caterpillars in both groups, but recorded it in focal data for only one individual in the LV group, so we chose to limit analyses of that pattern to the CP group.

Food interest

We tallied the total number of "direct/receive food interest" bouts to see which age/sex classes most often showed interest in others' feeding and processing behavior, and to determine which age/sex classes were most often the focus of interest. "Direct food interest" was defined as actively and closely observing a conspecific engaged in foraging or food-processing behavior without being engaged in other activities, or interfering in the conspecific's activities, at a distance of 3 m or less. "Receive food interest" was

defined as being actively and closely observed by a conspecific under the same conditions. All food items were combined because the data set was too small to examine rates of food interest for specific foods. We adjusted the frequencies of bouts by the number of individuals in each age/sex class, and by the amount of focal time they spent engaged in foraging and food processing. We compared the resulting frequencies of both "direct food interest" and "receive food interest," using chi-square analyses to determine if significant differences existed among age/sex classes.

Proximity

During a scan sample at the beginning of each focal session, we scored the closest three conspecifics within 3 m of the focal animal (if any) as "in proximity." Infants that were not yet moving independently of their mother were not scored. Once offspring began moving independently of their mothers, they were scored normally. Following the methodology of Panger et al. (2002), we calculated "proximity scores" for each dyad of individuals in the group, excluding infants. We calculated these scores by totaling the number of scan samples in which each individual was found in proximity to a specific dyad partner, and dividing that number by the total number of scan samples collected for both individuals in that dyad.

Dyads composed of two individuals who both exhibited a specific processing pattern were identified as "matched dyads," whereas dyads composed of individuals who did not both exhibit a specific technique or processing pattern were identified as "unmatched dyads." Mann-Whitney U-tests (one-tailed) were run for each relevant technique to see if proximity scores of matched dyads were higher than those of unmatched dyads.

Social rank

A dominance hierarchy was established for the members of each group, based on observed frequencies of aggressive behavior, threats, and supplantations among individuals (O'Malley, 2002). To establish rank, we assigned each individual a score based on the number of such acts directed toward each of the other members of the group. Mann-Whitney U-tests (two-tailed) were used to determine if individuals seen to use a given processing technique were, on average, of significantly higher or lower rank than those that did not.

Kinship

The kin relations of most members of the two study groups through both maternal and paternal lines were established through genetic analyses of hair and fecal samples (Jack and Fedigan, 2003; Fedigan, unpublished data), and so r-values could be determined for each dyad (Krebs and Davies, 1993). Matched dyads (those pairs of individuals sharing a given processing pattern) and unmatched dyads (those pairs not sharing a given processing pattern) were compared using Mann-Whitney U-tests (one-tailed) to determine if matched dyads were more closely related than unmatched dyads.

Research design and statistical issues

We realize that the three social networks examined in this study are interrelated. For example, mothers and offspring are likely to spend more time together (Fragaszy, 1990; Welker et al., 1990), and high-ranking individuals tend to be found in certain spatial areas of the group during travel, and therefore may spend more time in proximity with one another than with lower-ranked individuals (Hall and Fedigan, 1997; Di Bitetti and Janson, 2001). Ideally, we would have performed a multiway analysis to control for these interactions among our social networks, but our small sample sizes render such analyses problematic. Furthermore, there are at least two reasons for considering these three social networks separately. For the proximity analyses, we followed the methodology of Panger et al. (2002), which allows some comparison between our proximity results and those of Panger et al. (2002) on capuchins at a neighboring site. Secondly, prior research on the LV and CP groups (MacKinnon, 1995) as well as our own observations showed that patterns of proximity in these monkeys are not always determined by kinship and rank. During foraging as well as daytime rest periods, it is quite common to find members of given age/sex classes (e.g., juvenile males, adult females) foraging in proximity or interacting with one another rather than with their relatives and rank-associates. Thus patterns of physical association may provide an opportunity for lateral transfer of social traditions among peers as well as vertical transfer from adults to offspring or high-ranking individuals to lower-ranked individuals.

Because we conducted Mann-Whitney U-tests for each social network (proximity scores, rank, and kinship) for multiple processing techniques, there is an increased risk of a type I error (Chandler, 1995; Cabin and Mitchell, 2000). To address this issue, we applied a Bonferroni correction to the alpha level used for the intragroup analyses of each individual social network. However, because there is also a high risk of a type II error due to the small sample sizes of this study, we feel justified in discussing results found to be significant ($P < 0.05$) at the unadjusted alpha level as well.

RESULTS

Food interest

Individuals of all age/sex classes showed interest in the foraging and food-processing behavior of others (Table 3), but juveniles engaged in directed bouts of food interest significantly more often than subadults or adults of either sex (n = 36, χ^2 = 36.875, df = 3, $P < 0.001$). Adult females and adult

TABLE 3. *Observed bouts of food interest by age/sex class*[1]

Age/sex class (N)	Direct FI	Receive FI
Juvenile (5)	24	1
Subadult (5)	6	9
Adult female (8)	5	15
Adult male (7)	1	7
Total (15)	36	32

[1] FI, food interest.

males received bouts of food interest significantly more often than juveniles received them (n = 32, $\chi^2 = 9.148$, d.f. = 3, $P = 0.026$). Such interest was most often directed toward individuals consuming vertebrate or invertebrate prey such as squirrel pups, *Acacia*-dwelling ants, or termites, as opposed to plant foods. On occasion, however, we observed nonadults in both groups abandon their food-processing efforts with *Sloanea* fruits and *Luehea* pods, and move to a position where they could observe others processing or consuming the same food. In most of these situations, individuals had run afoul of the food's defenses (e.g., the stinging hairs covering *Sloanea* fruit, or the swarming ants on an *Acacia* plant), or were making no progress in their efforts (e.g., failing to extract any seeds from a *Luehea* pod). Bouts of food interest directed towards individuals with vertebrate prey or prize foods such as eggs or wasp nests were often followed by begging or scrounging attempts, but those directed at individuals processing *Acacia* thorns, *Sloanea* fruits, or *Luehea* pods rarely were.

Proximity

Matched dyads of individuals exhibiting the "rub and brush" *Sloanea* processing pattern did not have a significantly higher mean proximity score than unmatched dyads in either group (Table 4). Proximity scores for matched dyads of individuals seen to use the "pound and catch" *Luehea* processing pattern were found to be significantly higher than those for unmatched dyads in both groups at $P < 0.05$, though after an appropriate Bonferroni correction, these results were not significant. The "skilled pound" *Luehea* technique was seen only in the same four individuals in the CP group who exhibited the "pound and catch" pattern. Thus, proximity scores of matched dyads showing that technique were also significantly higher ($P < 0.05$) than those that did not exhibit it, but not after appropriate Bonferroni correction. Proximity scores for matched dyads of individuals seen to eviscerate caterpillars in the CP group were not significantly higher than those of unmatched dyads.

Rank

Matched dyads of individuals seen to use the "rub and brush" *Sloanea* processing technique did not differ significantly in rank from those that did not show the pattern in either group (Table 5). Individ-

TABLE 4. *Mann-Whitney U-tests comparing proximity scores of "matched" dyads (between individuals seen to use a specific technique) and "unmatched" dyads (between all other dyads)*

Group	Food item	Technique	Dyad type	N	Mean	SD	Range	U-score	z-score	P-value (one-tailed)
CP	*Sloanea terniflora*	Rub and brush	Matched	10	0.084	0.06	0.022–0.233	182.00	−0.938	0.174
			Unmatched	45	0.092	0.046	0.015–0.209			
	Luehea candida	Pound and catch	Matched	6	0.129	0.062	0.066–0.233	85.00	−1.674	0.047*
			Unmatched	49	0.086	0.045	0.015–0.209			
		Skilled pound	Matched	6	0.129	0.062	0.066–0.233	85.00	−1.674	0.047*
			Unmatched	49	0.086	0.045	0.015–0.209			
	Caterpillars	Eviscerate	Matched	6	0.119	0.076	0.015–0.233	109.00	−1.026	0.153
			Unmatched	49	0.087	0.043	0.015–0.209			
LV	*Sloanea terniflora*	Rub and brush	Matched	66	0.061	0.05	0.000–0.233	767.00	−0.516	0.303
			Unmatched	25	0.061	0.039	0.000–0.139			
	Luehea candida	Pound and catch	Matched	28	0.075	0.049	0.000–0.175	663.00	−1.884	0.030*
			Unmatched	63	0.055	0.046	0.000–0.233			

* Indicates statistical significance in predicted direction with alpha of $P < 0.05$, but no statistical significance after Bonferroni correction is applied (resulting in alpha of $P < 0.013$ for CP group, and $P < 0.025$ for LV group).

TABLE 5. *Mann-Whitney U-tests comparing social rank with processing techniques used by each individual*

Group	Food item	Technique	Used technique?	N	Mean	SD	Range	U-score	z-score	*P*-value (two-tailed)
CP	*Sloanea terniflora*	Rub and brush	Yes	5	4.8	3.194	1–9	9.00	−1.095	0.273
			No	6	7.0	3.347	2–11			
	Luehea candida	Pound and catch	Yes	4	2.5	1.291	1–4	0.00	−2.646	0.008*
			No	7	8.0	2.16	5–11			
		Skilled pound	Yes	4	2.5	1.291	1–4	0.00	−2.646	0.008*
			No	7	8.0	2.16	5–11			
	Caterpillars	Eviscerate	Yes	4	4.0	4.082	1–10	6.00	−1.512	0.131
			No	7	7.14	2.41	4–11			
LV	*Sloanea terniflora*	Rub and brush	Yes	12	7.0	4.068	1–13	6.00	1.095	0.273
			No	2	10.5	4.95	7–14			
	Luehea candida	Pound and catch	Yes	8	6.63	3.503	2–13	17.00	−0.904	0.366
			No	6	8.67	5.046	1–14			

* Indicates statistical significance after appropriate Bonferroni correction (resulting in alpha of *P* = 0.013 for CP group, and 0.025 for LV group).

uals seen to use the "pound and catch" *Luehea* processing pattern did have a significantly higher rank than those that did not use the technique in the CP group (even after an appropriate Bonferroni correction), but not in the LV group. Individuals in the CP group seen to "eviscerate" caterpillars did not differ significantly in rank from those individuals that did not.

Kinship

Dyads of individuals exhibiting the "rub and brush" *Sloanea* processing pattern did not have significantly higher r-values (i.e., were not more closely related) than unmatched dyads in either the CP or LV groups (Table 6). R-values for matched dyads of individuals seen to use the "pound and catch" *Luehea* processing pattern were not significantly higher than those of unmatched dyads in either group. R-values for matched dyads of individuals seen to eviscerate caterpillars in the CP group were not significantly higher than those of unmatched dyads.

DISCUSSION
Food interest

Research on wild capuchin populations showed that intragroup diets and foraging patterns are not homogeneous (Fragaszy, 1986; Rose, 1994; Fragaszy and Boinski, 1995; Hall, 1995), that groups living in similar habitats do not necessarily have similar diets (Chapman and Fedigan, 1990; Panger et al., 2002), and that the acquisition of complex processing techniques for specific foods does appear to be socially influenced to some degree (Boinski et al., 2000; Panger et al., 2002). Observed patterns of food interest across age/sex classes in this study suggest that opportunities for social learning in capuchin foraging or food-processing contexts occur among individuals of all age/sex classes, but are instigated significantly more frequently by juveniles than older individuals. Food interest bouts are directed toward adult females and males significantly more often than other age/sex classes. Adults are likely to be better or more skilled models than nonadults. Being able to observe which foods are consumed by conspecifics would presumably be of particular importance to younger animals, who must otherwise rely on trial-and-error to learn what can and cannot be eaten, a strategy that could have negative consequences if toxic or unpalatable foods are consumed (Janson and van Schaik, 1993). The social learning processes involved in the acquisition of dietary knowledge may be fairly simple, i.e., social facilitation (an increased probability of performing a behavior in the presence of others performing the same behavior). Nonetheless, observation of how others eat, as well as what they eat, may provide important opportunities for social transmission of information.

The very intent interest shown by juveniles toward individuals engaged in complex processing behavior (such as with *Acacia* thorns, *Sloanea* fruits, or *Luehea* pods) is consistent with observations of capuchins in similar contexts, both in captivity (i.e., Anderson, 1990; Adams-Curtis and Fragaszy, 1995) and the wild (Boinski et al., 2000). Such focused interest may precede an attempt to scrounge food, but may also serve to facilitate social learning of edible foods or specific processing techniques. Given the lowered foraging efficiency of juveniles, their greater vulnerability to food scarcity, and their greater risk of predation (Janson and van Schaik, 1993), such intense monitoring of conspecifics is likely to be of some benefit to the observer.

Studies of capuchins in captivity have usually found only weak evidence for social influences on diet and feeding behavior (Visalberghi and Fragaszy, 1995; Fragaszy et al., 1997; Visalberghi et al., 1998; Visalberghi and Addessi, 2000, 2001; but see Custance et al., 1999). However, because the consequences of food choice in a natural setting are quite different than those in captivity, study of free-ranging groups is an important venue for evaluating the development of dietary knowledge and food-processing techniques, despite the inherent challenges of a wild setting. Experiments evaluating response to novel foods or extractive problems by wild or semi-wild capuchins in social settings are needed as a way to bolster, or counter, the results of previous studies

TABLE 6. Mann-Whitney U-tests comparing r-values of "matched" dyads (between individuals seen to use a specific technique) and "unmatched" dyads (between all other dyads)

Group	Food Item	Technique	Dyad type	N	Mean	SD	Range	U-score	z-score	P-value (one-tailed)
CP	Sloanea terniflora	Rub and brush	Matched	10	0.1	0.175	0.000–0.500	138.00	-2.027	0.022
			Unmatched	45	0.25	0.213	0.000–0.500			
	Luehea candida	Pound and catch	Matched	6	0.167	0.258	0.000–0.500	121.00	-0.749	0.227
			Unmatched	49	0.23	0.209	0.000–0.500			
		Skilled pound	Matched	6	0.167	0.258	0.000–0.500	121.00	-0.749	0.227
			Unmatched	49	0.23	0.209	0.000–0.500			
	Caterpillars	Eviscerate	Matched	6	0.167	0.258	0.000–0.500	121.00	-0.749	0.227
			Unmatched	49	0.23	0.209	0.000–0.500			
LV	Sloanea terniflora	Rub and brush	Matched	66	0.028	0.109	0.000–0.500	721.50	-1.696	0.045
			Unmatched	25	0.08	0.173	0.000–0.500			
	Luehea candida	Pound and catch	Matched	28	0.054	0.157	0.000–0.500	879.50	-0.04	0.484
			Unmatched	63	0.038	0.118	0.000–0.500			

(Ottoni and Mannu, 2001; Garber and Brown, 2002; O'Malley, 2002).

Sloanea terniflora

Sloanea terniflora is a relatively rare tree in Santa Rosa, and is generally confined to intermittent streambeds, riverine forest, and other wet areas of the park (Hartshorn, 1983; Enquist and Sullivan, 2001). Chapman and Fedigan (1990) found relatively low densities of mature *Sloanea terniflora* in the ranges of the CP group (0.6/ha, or 53.9 cm DBH/ha) and the range of what is now the LV group (0.0/ha, or 0.0 cm DBH/ha). However, they also found *Sloanea* to be a substantial dietary component for both groups. More recent botanical surveys confirmed that the density of mature *Sloanea* trees remains very low in both ranges (Sorensen, personal communication; Aureli, personal communication), though the LV group's range in 2001 did include a streambed with several mature *Sloanea* trees (one of which produced a particularly abundant crop during the 2001 field season). During the 2001 field season, the LV group spent significantly more of their total observed foraging time on *Sloanea* than did the CP group (9.9% and 1.5%, respectively). Rates of *Sloanea* consumption did not differ significantly across age/sex classes.

Chapman and Fedigan (1990) found that the availability of *Sloanea* in the range of their study groups did not correspond to time spent feeding on *Sloanea*, and concluded that these findings reflected either learned group traditions in diet or differences in relative food profitability. None of the social networks examined here had a significant relationship with the expression of the "rub and brush" processing technique used for *Sloanea* fruit. Proximity patterns, social rank, and relatedness were not significant factors in predicting whether or not an individual would exhibit the "rub and brush" processing pattern, which was observed in the majority of the LV group and almost half of the CP group. The lack of diversity in *Sloanea* processing patterns may reflect that there is only one "right" way to process *Sloanea* fruits (i.e., rub), since attempting to use other techniques appears to incur a high price from the urticating hairs on each fruit (O'Malley and Fedigan, in press). Though the "rub and brush" pattern requires a degree of manual coordination, the fruits are small enough to be easily manipulated by monkeys of all age/sex classes, and the flailing hand motions involved are not likely to be particularly challenging. The presence of this processing pattern across all age/sex classes and in both groups, with no discernible influence from intragroup social networks, indicates that the acquisition of the "rub and brush" processing pattern for *Sloanea* is likely relatively rapid for young monkeys, though skill at such patterns would increase with practice.

Opportunities to practice *Sloanea* processing or to observe others doing so were presumably higher in the LV group, given that almost 10% of their feed-

ing/foraging time was spent on *Sloanea*, which may also explain why the majority of individuals in this group exhibited the "rub and brush" pattern (Table 2). Though individual preferences as well as the physical constraints and dietary strategies of different age/sex classes may also underlie the variability in *Sloanea* processing we observed (O'Malley and Fedigan, in press), observations of conspecifics engaging in such behavior could still be of benefit to an unskilled monkey and serve to channel its efforts (Boinski et al., 2000).

Luehea candida

Chapman and Fedigan (1990) found that densities of mature *Luehea candida* trees were considerably higher 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). Nonetheless, during the 2001 field season, the proportions of total foraging time spent on *Luehea candida* (2.15% and 3.54% of total observed foraging times, respectively) did not differ significantly between groups (O'Malley and Fedigan, in press). Rates of *Luehea* consumption were much higher among juveniles, subadults, and adult females than among adult males, though overall differences among age/sex classes were not statistically significant. These results suggest that the density of *L. candida* trees plays a minimal role in variation between groups, though developmental factors (such as physical and cognitive constraints of younger animals) may well influence how *Luehea candida* pods are processed (for a more detailed discussion of these issues, see O'Malley and Fedigan, in press).

Variation in forms of processing of *Luehea candida* appears to be associated to some extent with social networks. Individuals using the "pound and catch" and "skilled pound" techniques spent more time in proximity to one another in both the CP and LV groups relative to those that did not use these techniques, although these results were not significant after a Bonferroni correction to the alpha level. Rank is a significant factor in predicting *Luehea* processing patterns within the CP group, with the four highest-ranking individuals being the only ones to exhibit the "pound and catch" and "skilled pound" patterns. Relatedness had no significant relationship with the presence or absence of the "pound and catch" variant of *Luehea* pounding in either group.

Why might our results suggest that rank and proximity patterns are associated with techniques of *Luehea* processing, when such factors do not appear to be associated with processing patterns for *Sloanea* fruit? A major variable in *Luehea* processing, and one that could not be quantitatively examined in this study, was the stage of maturity of the pods processed. Fruits of different *Luehea* trees do not mature synchronously, and even pods on the same tree often dehisce several weeks apart (O'Malley, personal observations). Seeds can be extracted from a *Luehea* pod that has only just begun to open, but

this is far more difficult than extraction from more mature pods. Adult and subadult capuchins seemed to target pods that were more fully dehisced, often inspecting several pods in sequence, both visually and with their fingers and tongue, before abandoning it, attempting to extract seeds, or detaching it from the tree for processing. Juveniles appeared far less discriminating. The alpha male of the CP group was also observed to actively supplant another individual from an apparently "choice" pod, though many other pods were available. Because mature pods are easier to process, focusing on such pods in preference to others is probably the more energetically efficient strategy, even if such pods have fewer seeds, and so higher-ranking individuals might be expected to supplant subordinates from such pods regularly.

Both the "pound and catch" processing pattern seen in both groups, and the "skilled pound" pattern seen in the CP group, may simply be a reflection of high-ranking animals' ability to target more mature *Luehea* fruits. More mature pods likely require less force to dislodge seeds, and rarely require monkeys to pause in their pounding activity to pull out seeds with their tongue and fingers, perhaps resulting in the more rapid and efficient "skilled pound" pattern. Mature pods also allow those monkeys capable of manipulating the pod in one hand (i.e., adults and subadults) to free up their other hand for catching seeds instead of for postural support, leading to the "pound and catch" pattern. Dominant capuchins readily supplant subordinates from valued food items (Hall and Fedigan, 1997; Di Bitetti and Janson, 2001; O'Malley, personal observations); fully dehisced *Luehea* pods may be such a prize. However, this does not mean that the "pound and catch" technique is not socially transmitted. The presence of higher-ranking individuals was shown to suppress the expression of socially learned behavior in low-ranking macaques, even when it can be shown that such individuals have learned the behavior in question (Drea and Wallen, 1999). A low-ranking animal may know how to use the "pound and catch" processing technique for fully dehisced pods, but may have few opportunities to use it if higher-ranking individuals monopolize such pods.

Our findings on *Luehea* processing support the work of Panger et al. (2002), who also found that processing patterns within a social group correlated with patterns of association. However, given that social rank may also play a role in determining whether certain processing patterns are expressed, a degree of caution is warranted in interpreting patterns of food processing that may reflect social *constraints* as well as, or instead of, social *traditions*.

Caterpillars

None of the social networks we examined had a significant relationship with the presence of the caterpillar "eviscerate" pattern among members of the CP group. The most parsimonious explanation of

this finding is that personal experience, presumably greater among older animals, drives the development of this qualitatively more skilled technique.

A major problem in evaluating patterns of large caterpillar processing is that this type of prey may comprise dozens of different species, which in turn forage on a variety of different plants of varying toxicity or palatability to the monkeys. The characteristics of the semidigested plant material within a single caterpillar is likely a major factor in predicting the degree of care and thoroughness a monkey will exhibit in removing its gut contents, as are the presence of urticating hairs, spines, or other defenses. Because it was impossible to consistently identify what species of caterpillar was being consumed, any interpretation of the techniques used to process them must be circumspect.

Capuchins are not the only Cebine species to show a high degree of manipulative skill in processing caterpillars or other invertebrates (Janson and Boinski, 1992). Boinski and Fragaszy (1989) collected data on the ontogeny of foraging behavior among squirrel monkeys (*Saimiri oerstedii*). Despite the relative complexity of the processing techniques they observed, analyses of proximity data found that infants spent little time monitoring more experienced foragers in close proximity, but they did so more overtly than older animals. Although they provided some anecdotal evidence that young squirrel monkeys may learn which caterpillar species to avoid (e.g., because of poisonous spines) through observation of conspecifics, the researchers concluded that juveniles do not learn specific motor acts or specialized handling techniques through observing others. Such techniques appear to be acquired largely through individual experience, with little or no social influence. The present research found no evidence to suggest that the development of caterpillar-processing techniques in *C. capucinus* is any different from that reported for *S. oerstedii*. Like their squirrel monkey counterparts, however, young capuchins may learn which poisonous or stinging caterpillars to avoid based on observing the intense vocalizations and threats directed by conspecifics at such potential hazards (O'Malley, personal observations).

Evidence for social traditions?

The evidence for social traditions in food processing we have presented here is promising, but inconclusive. The use of specific food-processing techniques that we identified for *Sloanea* and caterpillars varied independently of the social networks we examined. However, processing patterns for one food item (*Luehea*) appeared to be associated with two of the three social networks examined. The finding that individuals in both groups who spend more time in proximity are also more likely to use the same complex techniques suggests some degree of social influence on the acquisition and maintenance of these techniques, as concluded by Panger et al. (2002) in similar analyses. Though variability in food-processing behavior among wild capuchins may indeed reflect social traditions, the finding that social rank also plays a role could indicate that the use of these patterns reflects opportunity for expression rather than knowledge. Future research exploring patterns of intragroup variability in processing patterns for specific foods should attempt to account for the influence of rank as well as patterns of association.

The most robust "cultural" patterns of variation in food-processing behavior among chimpanzee populations often involve distinctive forms of tool use, such as cracking nuts with stone hammers and anvils, that are observed at some sites but not at others (Whiten et al., 1999). Other patterns are of a more subtle nature, e.g., population-level differences in tool materials and techniques used to dip for driver ants (McGrew, 1974; Boesch and Boesch, 1990) or to dig for and capture termites or ants in nests (Sugiyama, 1993, 1997). Through long-term study of habituated chimpanzees in a number of different research sites, it has been possible to identify patterns of variability across individuals, age/sex classes, groups, and populations, and to evaluate the ecological, developmental, cognitive, or social factors that may underlie such variation (McGrew, 1992; Boesch and Boesch, 1993; Sugiyama, 1993; van Schaik et al., 1999). It has also been possible to conduct more focused analyses, e.g., to compare efficiency of different foraging or food-processing patterns for specific foods within and across sites (McGrew, 1974; Boesch and Boesch, 1990; McGrew and Marchant, 1999), and to consider the potential benefits and consequences for individuals who adopt, or fail to adopt, more efficient or effective techniques.

We have described complex processing techniques for three specific food items (each requiring a high degree of manipulative skill) for a wild population of *Cebus capucinus*. Having identified such patterns, it will be possible to develop more focused research questions in order to evaluate their significance. For example, is the "pound and catch" pattern in *Luehea* processing more efficient than a one-handed pattern (in terms of rate of seed intake, or time required to extract all the seeds from a given pod)? Does efficiency increase with practice? Is it a technique universal to all capuchin groups in Santa Rosa? Do other populations in Costa Rica that were observed to "pound" *Luehea* pods employ similar techniques? Are there other levels of variation (such as hand grip, or maturity of the pods targeted) present within or across sites? Preliminary studies on foraging variability in wild *Cebus* (Boinski et al., 2000; Panger et al., 2002), including the research presented here, suggest that these and other questions are worthy of further study.

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