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Variability in Foraging and Food Processing Techniques Among White-faced Capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica

by

Robert Christopher O'Malley ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Arts

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Variability in Foraging and Food Processing Techniques Among White-Faced Capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica** submitted by Robert Christopher O'Malley in partial fulfillment of the requirements for the degree of Master of Arts.

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DEDICATION

This thesis is dedicated to Dr. William C. McGrew and Dr. Linda F. Marchant.

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ABSTRACT

Capuchins and chimpanzees share a number of socio-ecological characteristics, including an extractive foraging niche and an impressive capacity for skilled object manipulation. Based on documented patterns of foraging variability across populations, they may also share a capacity for social traditions, or 'culture.' This research was an effort to document patterns of foraging variability in two groups of free-ranging *Cebus capucinus*, and to identify the asocial and social factors underlying such variation.

A high degree of variability was observed in foraging patterns and processing techniques for specific foods. Most differences between age/sex classes and groups could be attributed to developmental and environmental factors. However, patterns of food processing observed for one food type, *Luehea candida*, appear to be influenced by patterns of association within groups, and may reflect foraging traditions. This research supports the growing body of evidence suggesting that a capacity for social traditions is not unique to hominoids.

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CHAPTER I: Introduction

"The current attention to the exceptional manipulative abilities of capuchins is not merely because they provide diverting natural history anecdotes...capuchins are now recognized to provide a powerful and independent test of issues fundamental to our understanding of the evolution of intelligence in human and nonhuman primates." **(Boinski *et al.* 2000)**

This thesis was an exploration and interpretation of variability in foraging and food processing techniques among the white-faced capuchins (*Cebus capucinus*) of Santa Rosa National Park, Costa Rica. The research was conducted from January to July of 2001, overlapping with the entire dry season and the beginning of the wet season. The primary focus of this research was to identify patterns of foraging and food processing among wild capuchins, and to determine what variability is present across individuals, age/sex classes, and social groups. I also sought to identify whenever possible the factors that may influence or underlie such variation, and discuss their significance. Of particular interest was an effort to evaluate variability in food processing behaviour as evidence for social traditions, or 'culture', defined as *'group-specific behavior that is acquired, at least in part, from social influences'* (McGrew 1998).

Chapter two discusses variability in general foraging behaviour, including time budgets and dietary comparisons, but focuses on describing the processing techniques identified for several key food items, their patterns of use, and the asocial factors (e.g., environmental, developmental) underlying any observed variability. Chapter three focuses on evidence for social influences on patterns of food processing. In particular, I seek to determine whether social traditions in foraging and food processing techniques are present in the capuchins of Santa Rosa. Chapter four summarizes and discusses the findings of the previous chapters, and attempts to integrate this research into the current body of research on *Cebus* foraging behaviour.

The White-faced Capuchin (*Cebus capucinus*)

The white-faced capuchin (*Cebus capucinus*) is the northernmost of the four species that comprise the genus *Cebus*. They are the only *Cebus* spp. found in Central America, and range from Belize to northern Colombia. *C. capucinus* have prehensile tails, pseudo-opposable thumbs, and are capable of a precision grip (Costello & Fragaszy 1988). Capuchins possess a very large brain to body size ratio (Gibson 1986) and a long period of development (Fragaszy & Bard 1997) relative to other primates. Males are slightly larger and stronger than females (Fedigan 1990). *C. capucinus* live in multi-male, multi-female groups with a discernable dominance hierarchy among adults (Fedigan 1993).

C. capucinus are highly omnivorous. The largest proportion of their diet is usually fruit, followed by insects (Chapman 1987, Chapman and Fedigan 1990). Capuchins also eat a variety of vertebrate prey including eggs, lizards, birds, and small mammals (Fedigan 1990) and only rarely consume leaves and flowers (Chapman and Fedigan 1990). At Santa Rosa National Park, food availability (and thus, diet) varies considerably throughout the year, particularly between the wet and dry seasons (Chapman 1987). Water availability during the dry season is highly restricted and has a powerful influence on troop activity and ranging patterns (Freese 1978, Fedigan *et al.* 1996). There are noticeable inter-group differences in diet, which may be due to varying food profitability or local traditions (Chapman and Fedigan 1990). The *Cebus capucinus* population of Santa Rosa has been increasing steadily over the past 10 years, reflected in a gradual increase in average group size (Fedigan *et al.* 1996).

Extractive Foraging and Food Processing in *Cebus*

Members of the genus *Cebus* are well known for their skill in exploiting embedded foods and bypassing plant and animal defences (Terborgh 1983, Fedigan 1990), one of the many characteristics they share with the genus *Pan* (Visalberghi & McGrew 1997). It has been argued that such skill in extractive manipulation (and by extension, capacity for intelligent object- and tool-use) is an adaptation for exploiting highly variable, seasonally limited, embedded food resources (Parker & Gibson 1977). Such complex object-manipulation is widely argued to have been of particular importance in human evolution (e.g. Darwin 1874, Washburn 1960, Ingold 1993, McGrew 1992), and may be linked to the development of intelligence, language, brain and body morphology, and certain social skills in modern humans (Hamilton 1974, Parker & Gibson 1977, 1979, Westergaard 1995). Exploration of these hypotheses as they relate to the behaviour and ecology of *Cebus* spp. has led to a great deal of research in both captivity and in the wild, particularly in regards to patterns of tool-use ("the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself"; Beck 1980, p10) and object-use ("[when] an individual manipulate[s] (to alter) a detached object relative to a fixed substrate or medium"; Panger 1998, adapted from Parker & Gibson 1977). Capuchin monkeys are among the most prolific nonhuman primate tool-users in captivity, surpassed only by humans and some of the great apes (Anderson 1996, McGrew & Marchant 1997, McGrew 1998). Both tool-use and object-use appear to be part of the normal behavioural repertoire of wild capuchins, primarily in foraging contexts (e.g., Izawa and Mizuno 1977, Chevalier-Skolnikoff 1990, Fernandes 1991, Panger 1998, Phillips 1998, Boinski *et al.* 2000).

Long-term studies of wild *Cebus* have shown that substantial variation exists in the diet and foraging behaviour of different age/sex classes, neighbouring groups, and species. Sex and age differences are generally attributed to differing abilities (physical or cognitive), dietary needs, or metabolic constraints (and thus differing foraging strategies), between such classes (Fragaszy 1987, 1990, Fragaszy & Boinski 1995, Rose 1994, MacKinnon 1995). Differences between neighbouring groups are harder to explain, particularly in overlapping habitat of similar composition, but may be due to differences in food profitability or group-specific dietary traditions (Chapman & Fedigan 1990). Body size has also been argued to be a factor in dietary variation across Cebine species (Janson & Boinski 1992). Intra-group social networks may also play a factor in foraging variability; rank (Janson 1990, Hall 1995) and patterns of individual association within groups (Panger *et al.* 2002) appear to influence the type of foods eaten, and how they are processed, respectively.

Most studies of food processing or manipulation in the wild have focused on fairly broad behavioural or dietary categories, with only occasional discussion of the actual techniques employed for specific food items (but see Izawa & Muzino 1977, Struhsaker & Leland 1977, Panger 1998, Boinski *et al.* 2000). Two studies of *C. capucinus* have specifically examined patterns of tool-use and object-use among wild populations (Chavelier-Skolnikoff 1990, Panger 1998), but did not discuss other food processing techniques. Several studies of *Cebus* spp. have provided excellent qualitative and some quantitative descriptions of foraging and food processing, though usually only in broad terms (Freese 1976, Izawa & Muzino 1977, Fernandes 1991, Janson & Boinski 1992, Panger 1998). The finer details of such behaviour, and discussion of the variation in such behaviours across populations, groups, age/sex classes, individuals, and food types remains largely unexplored beyond anecdotal reports, though this is changing (see Boinski *et al.* 2000, Panger *et al.* 2002).

Capuchin social traditions?

Among the many traits that the genera *Pan* and *Cebus* may share is a capacity for social traditions or 'culture', which can be defined as *"group-specific behaviour that is acquired, at least in part, from social influences."* (from McGrew 1998). Generally speaking, patterns of interpopulation variability in behaviour not readily explainable by genetic or environmental differences are often argued to be the result of social learning processes, and may constitute evidence for social traditions (McGrew 1998, van Schaik *et al.* 1999, Whiten *et al.* 1999, Whiten & Boesch 2001). Such cultural patterns among wild populations of the genus *Pan* may include variations in courtship, grooming behaviour, and social signalling (McGrew & Tutin 1978, Nishida 1980, Sugiyama 1981, Boesch 1995, Nakamura *et al.* 2000), use of medicinal plants (Huffman & Wrangham 1994, Huffman *et al.* 1997), and various food processing techniques, particularly forms of tool- and object-use (Sugiyama 1985, 1997, Goodall 1986, McGrew 1992, 1998, Boesch & Boesch 1993, Boesch 1996) for specific food types. Though study of *Cebus* behaviour has been conducted for a far shorter period of time, researchers have identified similar patterns of variability in grooming behaviour and social play (Perry *et al.* in press.), medicinal plant (and animal) use (Baker 1996, Valderrama *et al.* 2000), as well as broad variations in processing techniques (including several forms of object-use) for specific food item types across ecologically similar research sites (Panger *et al.* 2002).

As outlined by Panger *et al.* (2002), cross-site differences in foraging behaviour identified as social traditions in *Cebus* and *Pan* share a number of parallels. In both genera, some distinct processing techniques are observed at some sites that are absent at others. Other generalized processing behaviours are common to all sites, but the foods targeted with such techniques, or the frequency and prevalence of such techniques, differ consistently between populations. Such a high degree of variability may well be common across taxa (both primate and otherwise), but may also support the widely held theory that certain socio-ecological traits are required, or facilitate to some degree, the establishment of social traditions. Among non-hominoid species only capuchins demonstrate (albeit to a lesser degree than the apes) those traits identified by van Schaik *et al.* (1999) as necessary for the evolution of material culture: extractive foraging, dexterous manipulation, intelligence, and tolerant gregariousness. Other shared characteristics of *Cebus* and *Pan*, such as a high brain-to-body size ratio (Gibson 1986) and a highly omnivorous diet (Fedigan 1990, Rose 1997), have also been identified as potentially important in understanding the evolution of intelligence, complex sociality, and cultural processes in nonhuman primates.

Unresolved Issues

As discussed above, a number of social and asocial influences appear to play a role in explaining variability in foraging and food processing behaviour in *Cebus*, as is the case for the genus *Pan*. Recent studies have indicated that the two genera may also share a capacity for social traditions (Panger *et al.* 2002, Perry *et al.* in press). A more focused study on the processing techniques employed for specific foods is now needed (Boinski *et al.* 2000, Panger *et al.* 2002). That groups, age/sex classes, and individuals differ in their foraging patterns and abilities has long been recognized (Fragaszy 1990, Rose 1994, Fragaszy & Boinski 1995), but how these differences might translate into variability in specific food processing patterns remains an open question. In particular, evidence for social traditions in wild *Cebus* is difficult to evaluate without a more complete understanding of *intra*-population variability, whether due to environmental, developmental, or social factors (Panger *et al.* 2002). Further cross-population studies of *Cebus* foraging traditions will also require more detailed and quantitative data on foraging techniques then what is currently available. Addressing these issues is a necessary step towards a better understanding the evolution and significance of complex manipulative skills in *Cebus*, and their relevance to similar skills among hominoids. It is hoped that this research will make an important contribution to these efforts.

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CHAPTER II: Variability in Foraging and Food Processing Techniques

INTRODUCTION

Members of the genus *Cebus* have long been recognized for their propensity for skilled manipulation and extractive foraging (Izawa & Muzino 1977, Parker & Gibson 1977, Izawa 1979, Terborgh 1983, Fragaszy 1986, Janson & Boinski 1992, Visalberghi 1993a, b, Boinski *et al.* 2000). Their ability to exploit food resources that potential competitors cannot may in part explain their wide distribution in the New World, and is a key factor in their ability to survive in marginal or regenerating habitats (Fedigan *et al.* 1996).

It has been argued that an extractive foraging niche, as well as a capacity for dexterous manipulation and a high degree of social tolerance, are all socio-ecological traits linked to the evolution of material culture (van Schaik *et al.* 1999, Panger *et al.* 2002). As a result, the physical characteristics, cognitive capabilities, and patterns of behaviour of those nonhuman primates exhibiting such traits to some degree [most notably chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and capuchins (*Cebus* spp.)] are topics of considerable importance to researchers interested in the evolution of primate intelligence, and its relevance to the development of culture (material or otherwise) in *Homo sapiens* (Parker & Gibson 1977, McGrew 1992, 1998, Boesch 1996, Boesch & Tomasello 1998, van Schaik *et al.* 1999).

Complex food processing in *Cebus*

Capuchins routinely use hard substrates to access embedded foods or to bypass plant and animal defences in the wild (Izawa & Muzino 1977, Struhsaker & Leland 1977, Panger 1998, Boinski *et al.* 2000, Panger *et al.* 2002). Such frequent 'object-use' [defined as 'the manipulation and alteration of a detached object relative to a fixed substrate or medium' (Parker & Gibson 1977, Panger 1998)] is a defining characteristic of all capuchin species and populations in both the wild and in captivity. In the first study to systematically examine such patterns among wild capuchins, Panger (1998) grouped the forms of object-use she observed among wild capuchins into three general categories- 'rubbing' 'pounding', and 'fulcrum use'- and provided quantitative data on types and rates of object-use, food items targeted, and their presumed functions. Though the latter can usually only be assumed, capuchins appear to employ object-use in foraging contexts to damage or weaken hard shells or coatings, to soften fruits for ingestion, to remove wind-dispersed seeds from fruits, to remove noxious or stinging substances from food items, and to detach fruits from fruit bunches.

There are a handful of anecdotal reports of tool use ["the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself" (Beck 1980:10)] by capuchins in the wild, most often in a foraging or food-processing context (Chevalier-Skolnikoff 1990, Fernandes 1991, Phillips 1998, Boinski *et al.* 2000, Ottoni & Mannu 2001; also see Boinski 1988). Forms of tool-use in captive capuchins have most often been observed (or induced) in a food-processing context, and range from the modification and use of various materials for simple probing or extraction (Westergaard & Fragaszy 1987, Anderson & Henneman 1994, Westergaard & Suomi 1994), to more complex tasks, such as the use of hammers to crack nuts (Antinucci & Visalberghi 1986, Anderson 1990, Westergaard & Suomi 1993) or making and using cutting implements from stone or other material (Westergaard & Suomi 1994, 1995a, b).

The tool-use and tool-making abilities of capuchins surpass that of all nonhuman species in captivity, save perhaps for the chimpanzee and the orangutan (McGrew 1998, van Schaik *et al.* 1999). In the wild, however, chimpanzees exhibit a far greater range of tool- and object-use behaviours than their *Cebus* counterparts or any other nonhuman primate (Visalberghi 1990, McGrew 1992, McGrew & Marchant 1997). Though both object-use and tool-use are within the natural behavioural repertoire of capuchin monkeys, no species, population, or social group of wild *Cebus* spp. can be characterized as *habitual tool users* ("repeated events by several individuals over time"), as defined by McGrew & Marchant (1997) (but see Phillips 1998).

A recent collaborative work between researchers at three long-term *C. capucinus* field sites (Santa Rosa National Park, Palo Verde National Park, and Lomas Barbudal Biological Reserve) in northwest Costa Rica compiled qualitative data on foraging and broad forms of food-processing behaviour in an effort to identify whether a pattern of variability similar to what has been described as 'cultural' differences in chimpanzee and orangutan populations is also present among wild capuchins (Panger *et al.* 2002). 20 food species and types were identified 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, though the food items processed with such techniques varied in consistent patterns. Two of the others ("fulcrum use," and "leaf wrap") were present at two sites. "Army ant following" was observed at only one of the three sites (Santa Rosa), though the authors noted that it has been observed at a fourth site, Curu (Panger *et al.* 2002).

While attempting to document gross patterns of variation across populations is an important first step towards evaluating the presence or absence of social traditions in *Cebus capucinus*, comparisons at a finer level of detail are also necessary, given the strong influence that environmental, developmental, and individual variation is known to have on patterns of object manipulation, tool use, and tool manufacture by primates (Izawa & Muzino 1977, Collins & McGrew 1987, McGrew 1992, Boesch & Boesch 1993, Boinski *et al.* 2000). In particular, it is not yet known how differences in general capuchin foraging behaviour across populations, groups, age/sex classes, and individuals might translate into differences in processing techniques for specific foods. This research was developed in an effort to identify which specific foods or food types require complex processing behaviour to exploit effectively, to quantify the degree of variability in processing techniques across groups, age/sex classes, and individuals, and to identify what factors may underlie such variation.

What (non-social) factors may underlie variability in complex food processing?

Before social explanations for variability in rates and forms of complex food processing are explored, most researchers attempt to rule out purely asocial influences on variability between populations, groups, age/sex classes, and individuals [though separating 'social' from 'asocial' influences on behaviour may be an artificial distinction (Ingold 1998, Fragaszy & Perry in press)]. Such explanations can be grouped into several general categories:

Environmental Factors

Foraging behaviour, particularly food processing behaviour (which is often food-item specific) is obviously greatly constrained by what foods are available. However, minor differences in abundance and food profitability can have a profound effect on foraging patterns, as capuchins are known to feed intensely on food items as they become available (Chapman 1987). Ecological conditions are expected to be particularly relevant in cross-group or cross-population comparisons, even despite similar or overlapping ranges (Chapman & Fedigan 1990). Such factors should play a minimal role in age/sex class or individual differences, since groups are fairly cohesive while foraging and so all individuals in a given group can be presumed to spend most of their time in the same habitat.

Developmental Factors

Diet and foraging activities have been shown to vary significantly across age/sex classes in capuchins (Fragaszy 1990, Rose 1994, Fragaszy & Boinski 1995). The different metabolic demands of adult females (i.e., costs of gestation and lactation, infant carrying after birth) and adult males (i.e., costs of vigilance, higher rates of injury, larger body size) are presumed to have a strong influence on diet (Fragaszy 1986, Rose 1994, Fragaszy &

Boinski 1995). Similarly, differences in body size (most notably between adults and non-adults) affect physical strength, predation risk, and interactions with others, which can in turn affect patterns of foraging (Janson & van Schaik 1993). Different age/sex classes may also be constrained by varying cognitive limitations, which could influence foraging behaviour, particularly extractive or manipulative tasks. Developmental factors should play little or no role in foraging variability between groups, but are expected (by definition) to influence variability across age/sex classes.

Individual Experience & Idiosyncratic Behaviours

For any manipulative task, an individual's skill is presumed to improve with practice and experience, which may be reflected in processing techniques. Young *Saimiri* monkeys (a close relative of *Cebus* spp. also native to Costa Rica) take several months to learn the techniques used by adults to eat caterpillars, including rubbing (to remove stinging hairs), picking up stinging caterpillars with the tips of their tail, and removing the gut contents (Boinski & Fragaszy 1989). Juvenile capuchins will often break (or try to break) any dead twigs they find in search of insects, while adults appear to be more selective, often tapping or feeling them briefly before attempting to open them up (Janson & van Schaik 1993, O'Malley, personal obs.).

Some apparently strong differences within or across social groups or populations may simply be the result of individual variation that appears clumped due to sampling error (Panger *et al.* 2002). Focusing on those patterns of behaviour found to be 'customary' (exhibited by all members of at least one age/sex class), or 'habitual' (if the behaviour has been observed by more than one individual), rather than merely 'present' (a behaviour has been observed, but is neither customary nor habitual), reduces the chance that rare or idiosyncratic behaviours are being misinterpreted as group- or population-specific patterns (Whiten *et al.* 1999, Panger *et al.* 2002).

Complex Food Processing

Foods for which some degree of processing is necessary to exploit effectively are the most likely to show a degree of variation (Panger *et al.* 2002) and so such food items should receive particular focus. Based on the work of other researchers (particularly Panger 1998 and Panger *et al.* 2002) and my own observations during the 2000 field season, several food items were identified which appeared to elicit a degree of manipulation or processing: *Sloanea terniflora* fruits, *Luehea candida* seeds, *Acacia* ant thorns, and large caterpillars (see **Appendix A**).

Research Objectives

The research discussed in this chapter was intended to address several general issues. First, I sought to describe the general diet and foraging patterns of wild white-faced capuchins in Santa Rosa National Park during the 2001 field season. Second, I sought to describe the food processing techniques employed for specific food items. Finally, I attempted to quantify differences in the use of these techniques across social groups, age/sex classes, and individuals, and to identify what asocial factors may underlie such variability.

METHODS

Study site

This research was conducted at Santa Rosa National Park, Guanacaste Province, Costa Rica, where several habituated groups of *Cebus capucinus* have been studied since 1983 as part of an ongoing research project supervised by Dr. L. M. Fedigan of the University of Calgary. The 10,800-acre park is a mosaic of former pastureland, dry deciduous forest, and semi-evergreen forest (Chapman & 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*) (Chapman 1987).

The region normally receives between 800 and 2,600mm of rain per year (mean = 1,472mm), almost entirely in the rainy season. Mean high temperatures range from 21.6° C (September) to 34.4° C (April) (Janzen & Hallwachs 1995). Up to 80% of the trees in tropical dry forests are deciduous, and lose their leaves during the dry season (Frankie *et al.* 1974, cited in Panger *et al.* 2002).

Subjects

The two groups observed for this research were the Los Valles group (LV) and the Cerco de Piedra group (CP). Both groups have become habituated to human observers over the course of nearly 20 years of research (Chapman 1987, 1988, Chapman & Fedigan 1990, Fedigan 1990, 1993, Rose 1994, Hall 1995, MacKinnon 1995, Jack 2001). At the time of this study, the CP group was composed of 13-14 individuals (2 adult males, 4 adult females, 1 immature male, 1 immature female, 3 juvenile females, and 2-3 infants) and the LV group was composed of 15-18 individuals (5 adult males, 4 adult females, 2 immature males, 1 immature female, 2 juvenile females, and 1-4 infants) (See **Appendix B**).

The groups observed in this study have traditionally ranged through the regenerating dry forest around and within the park administration area. Their ranges overlap extensively, and the groups come into occasional contact. While precise data were not collected on daily ranging patterns, the general ranges of the two social groups have not changed significantly for at least a decade (see Chapman & Fedigan 1990).

Data Collection

I conducted a preliminary field season from May to July of 2000, familiarizing myself with the forest and monkeys, developing a research protocol, and identifying complex food processing techniques to focus on during the primary field season. Data collected in 2000 were not analyzed in this study.

309.5 hours of focal data were collected from February to mid-July of 2001 from the Cerco de Piedra and Los Valles social groups on all non-infants (**Appendix C**). Focal sessions were conducted from sunrise to sunset in two-day blocks, alternating between the two groups as much as possible. It was my intention to try to keep the total observation hours roughly equal between groups, but due to occasional difficulties in finding the LV group, the more difficult terrain of the LV range (leading to more aborted focals), and other interruptions, this proved to be unfeasible. Observation times were kept as equivalent as possible across subjects within each group.

Observation conditions were generally very good (within 10m), and subjects would sometimes approach to within 1m. I sought to maintain a distance of at least 3m at all times. Focal data were collected using binoculars (8x25 magnification), a stopwatch, and a Psion Workabout hand-held computer. During periods of extremely rapid activity, I switched to dictaphone, which I then transcribed and inserted into the focal data when necessary. Some *ad-libitum* data were also collected via dictaphone, particularly in the early weeks of the field season.

Data were collected in 15-minute focal animal sessions (Altmann 1974). If the subject was "out of sight" for more than 2.5 minutes of a focal session, that session was excluded from focal analysis (though data from incomplete sessions were still included in comparison of processing techniques across individuals; see below). All data were scored as bouts rather than events. A single bout of food processing often involved a sequence of behaviours (i.e., pound, briefly examine/eat, then pound again) with a single food item. Bouts were distinguished by an intervening behaviour from the ethogram (**Appendix D**), manipulation of a food item by both hands into a new orientation, or a change in hand use during processing. I also conducted a scan sample at the beginning of each focal session, noting the closest three individuals to the focal animal that were also within 10m. Observation conditions did not allow for a strict sampling order, but I made an effort to avoid repeatedly sampling central or conspicuous subjects by frequently moving through the dispersed group between focal sessions, and sampling both clearly visible and more obscured animals. I also sought to collect a focal session from all group members each day before beginning a second session with any subject. Total focal times were tallied continuously across each week and month in order to keep the total observed time for each individual in a group as equal as possible. For those food items for which patterns of variability in food processing were being examined, additional variables were recorded; these were specific to each food item (**Appendix E**).

Data Analyses

All statistical tests were performed using the SPSS 10.0 analytical program. Alpha for all tests was set at $P = .05$. Analyses were conducted in order to compare both differences between groups and age/sex classes (using individual scores), as well as any interaction between group and age/sex class (comparing individual scores by age/sex class between groups). Unless otherwise noted, all comparisons described below were analyzed using two-way Kruskal-Wallis tests, which were conducted via a normal two-factor ANOVA on the ranks of individual scores, rather than the scores themselves. In comparisons of processing bouts employing specific techniques across age/sex classes and groups, it was necessary to correct for sample size, excluding those individuals with less than $n=6$ bouts of the behaviour being analyzed. Among those analyses that proved to be significant, adjusted R^2 values ranged from .128 to .741. Because of the limitations of a small sample size and the statistical tests I chose to use, some strong but non-significant trends in the data are discussed in addition to statistically significant results.

Foraging behaviour and diet

To compare foraging time across groups and age/sex classes, I tabulated for each individual the duration of all bouts of foraging and food processing behaviour from focal observations, and divided this by the total focal observation hours for that individual. To compare general dietary patterns between groups, I tabulated the total focal time that all individuals spent feeding on each food type for each group, and divided the resulting total for each food item by the total observed feeding time for that group.

Object-Use

Analyses of general object-use behaviour were modeled on that of Panger (1998) to allow comparison between the two studies. To determine rate of object-use by each individual, I divided the total number of observed object-use bouts from focal data by the number of focal data hours collected from that individual. To compare the proportion of observation time spent in object-use behaviour by each individual, I tallied the durations of all object-use behaviours by each individual from focal data and divided it by the total focal observation time for that individual.

Processing techniques

For each food item found to show a high degree of variability in processing technique, I tallied the total number of 'process' bouts (those in which some form of complex manipulation or extraction proceeded or occurred during consumption) and 'no-process consumption' bouts (in which no complex manipulation or extraction was observed) from the focal data. This number was then divided by the total focal observation hours to get a rate of "food item 'x'" consumption bouts/hour for each individual. This was not an exact tally, only a close estimation, as a single bout of processing would (rarely) involve more than one individual food item, or an individual food item might be subjected to more than one bout of processing.

For those food items that could be consumed either with or without some form of processing, I tallied for each individual the number of processing bouts from all sources (i.e., focal, incomplete focal, and *ad-libitum* data) and divided that tally by the sum of all processing bouts and 'no process' consumption bouts in order to get a percentage of 'process' bouts for that individual. The exception was *Luehea candida* bouts, for which only bouts from focal data were tallied. This was necessary because *ad-libitum* data collection of *Luehea* focused exclusively on processing bouts.

For *Acacia* ant thorns, for which there was a chance for success or failure for a given processing bout, I divided the number of observed successful bouts (from all data sources) by the total number of observed bouts in order to get a percentage of successful bouts for each individual.

For those food items where distinct processing techniques were identified, I tallied the number of observed bouts for each technique per individual and divided that by the total number of bouts (again from all sources) for that individual in order to calculate the percentage of processing bouts for each technique. I then identified the 'primary' or most commonly used technique, and compared the percentage of bouts employing that technique across individuals of different age/sex classes and groups. For some food items, several different variables were identified (**Appendix E**); these were analyzed independently.

RESULTS

Activity Budgets

The overall activity patterns of the CP and LV groups (as measured by the percentage of observation time spent in social, rest, travel, vigilance, and foraging activities) were very similar (**Figure 2-1**). The proportion of observation time that individuals spent foraging did not differ between groups (F = .311, d.f. = 1, p = .584), but did differ significantly between age/sex classes (F = 4.209, d.f. = 3, p = .021). The proportion of observation time spent foraging by individuals of different age/sex classes did not differ significantly between the two groups (F = .699, d.f. = 3, p = .565).

Dietary comparison

Despite broad overlap in the food types and species consumed during the field season (See **Appendix F**), the dietary composition of the CP and LV groups (as measured by the proportion of total observed feeding time for each food type) were fairly different (**Table 2-1**). Overall, the consumption of plant foods comprised 63.5% of the CP group's feeding time and 77.2% of the LV group's feeding time, while invertebrate prey comprised 32.7% of the CP group's feeding time and 20.5% of the LV group's feeding time. The primary dietary components (i.e., those food species or types that composed at least 5% of total observed feeding time for at least one group) of the CP group and LV group also differed considerably (**Table 2-2**).

The general dietary preferences of the CP and LV groups observed during this study are quite similar to that reported by Chapman & Fedigan (1990) based on data collected between 1984 and 1986. In their study, the 'Sendero' group (Group 'B' in their study, many of whose members joined the LV group when they took over the range) ate considerably more fruit (69.8%) than invertebrate prey (29.0%). In contrast, the CP group (Group 'C' in their study) relied more heavily on invertebrates (44.3%) and ate less fruit (53.0%). However, the proportion of total observed feeding time spent on specific food species was often quite different [e.g., Chapman & Fedigan (1990) report that *Ficus* spp. composed 4.4% of observed feeding time for the 'Sendero' group and 6.3% of the CP group, compared to 17.7% and 6.1% of feeding time for these two groups in this study].

Tool- and Object-use

Tool Use

I observed only one bout of tool-use during the 2001 field season. An adult female in the LV group carefully picked up and carried a spiny (presumably an *Automeris* spp.) caterpillar to a large leaf, which she then wrapped around the caterpillar before rubbing the bundle vigorously against a branch for several seconds. The now-tattered leaf was then discarded and she briefly rubbed the limp and matted caterpillar against the branch for several more seconds before carefully consuming it. I observed similar behaviour on 2 occasions during the preliminary field season in 2000 by individuals in the CP group (O'Malley, unpublished data).

Object-use

All three types of object-use identified by Panger (1998)- "rub", "pound", and "fulcrum-use" – were observed in both groups during the 2001 field season. All object-use behaviour took place in a foraging or food-processing context. I observed a total of 592 object-use bouts, involving 14 identified food items and 2 unidentified food items. 95.1% of object use bouts involved one of three food items: *Sloanea terniflora* (62.8%), *Luehea candida* (28.4%), and *Zuelenia guidonia* (3.9%). I found markedly different rates of object-use between groups and age-sex classes (**Figure 2-2**). The LV group had a significantly higher rate of object-use than the CP group (F = 17.787, d.f. = 1, p = .001), and differences in object-use rates across age-sex classes were also significant (F = 5.165, d.f. = 3, p = .010). Object-use rates by each age/sex class did not differ between groups (F = 1.616, d.f. = 3, p = .223).

The proportion of observation time spent in object-use activities also varied greatly across groups and age/sex classes (**Figure 2-3**). Members of the LV group spent a significantly higher proportion of their total observed focal time in object-use activities than those of the CP group (F = 12.259, d.f. = 1, p = .003). Differences in the proportion of time spent in object-use activities across age-sex classes were also significant (F = 3.646, d.f. = 3, p = .034), though the percentage of time spent in object-use activities by each age-sex class did not differ significantly between groups (F = 1.129, d.f. = 3, p = .365).

The general patterns of object-use observed in Santa Rosa were considerably different than those reported for Palo Verde by Panger (1998). The capuchins at this neighbouring site engaged in 0.19 object-use bouts/hour of observation, compared to 1.63 bouts/hour at Santa Rosa. The monkeys of Palo Verde spent only 0.4% of their time in object-use activities, compared to .63% by the Santa Rosa monkeys. Also in contrast to my results, Panger (1998) reported no significant differences among age/sex classes in either rate of, or percentage of time spent in, object-use activities.

Food Processing Techniques

Sloanea terniflora

Sloanea terniflora fruits (**Figure 2-4**) were a major part of the LV group's diet (9.9% of observed feeding time) and a relatively smaller part of the CP group's diet (1.5% of observed feeding time). Average rates of *Sloanea* consumption bouts/hour are summarized in **Table 2-3**. Rates of *Sloanea* consumption bouts/hour were significantly different between groups (F = 11.610, d.f. = 1, p = .003) but not age/sex classes (F = 1.027, d.f. = 3, p = .405). The rate of *Sloanea* consumption bouts/hour for each age/sex class did not significantly differ across groups (F = .575, d.f. = 3, p = .639).

Capuchins would occasionally attempt to consume *Sloanea* fruits without any attempt to remove the hairs first, which appeared to be quite unpleasant as it was usually involved a great deal of spitting, grimacing, and rubbing their face on the tree bark. It was also often unsuccessful; in 6 of the 14 such bouts, the monkey began a rubbing or pounding bout with the fruit after only a few seconds. Attempts to eat *Sloanea* fruits without processing was observed across all age/sex classes and in both groups (**Table 2-4**). After correcting for sample size, I found no significant difference in the percentage of processing vs. no-process consumption bouts by group (F = .033, d.f. = 1, p = .861), but a significant difference between age/sex classes (F = 9.125, d.f. = 3, p = .006). The percentage of processing bouts vs. no-process consumption bouts in each age/sex class did not differ between groups (F = .261, d.f. = 3, p = .852).

I observed a total of 382 bouts of *Sloanea* processing (including observations from incomplete focals and *ad-libitum* data). General processing techniques could be grouped into three general categories (**Table 2-5**): "rub/roll", "pound", and "body/tail rub". The "rub/roll" behaviour was by far the most frequently observed processing technique (comprising 94.8% of observed *Sloanea* processing bouts). A rubbing bout usually consisted of grasping the fruit in one or two hands (sometimes by the stem, sometimes by the fruit itself) and moving the fruit back and forth on a tree branch vigorously. The monkey would then stop and inspect the fruit with fingers and lips. The entire process might be repeated one or more times over the course of a bout before consumption. "Roll" was distinguishable from "Rub" in that instead of grasping the fruit, the monkey would apply pressure with one or both hands held flat against the fruit as it was moved back and forth across the substrate. Unfortunately, it was often impossible to discern whether a monkey was rubbing or rolling, so I chose to lump these techniques together for analytical purposes. The "pound" technique, observed rarely and only by only two adult male subjects in the LV group, was simply to repeatedly pound a plucked fruit against a substrate, usually immediately after a rubbing bout. The "tail/body rub" technique, also seen rarely, was simply to rub a fruit vigorously over their body fur or tail.

The "rub/roll" technique would sometimes elicit a 'differentiated' hand use pattern (**Table 2-6**), 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' technique presumably served to keep the *Sloanea* hairs from flying up into the subject's face (**Figure 2-5**).

Analyses of Sloanea *processing*

After correcting for sample size, no significant differences in the percentage of "rub/roll" processing bouts vs. all other forms of processing were detected between groups (F= .000, d.f. = 1, p= .989) or age/sex classes (F = .869, d.f. = 3, p = .496). There were no significant differences between age/sex classes across the two groups (F = .137, d.f. = 2, p = .874). I found no significant differences in the percentage of differentiated hand use rubbing bouts between groups (F = .000, d.f. = 1, p = .992) or age/sex classes (F = 1.530, d.f. = 3, p = .280). There were no significant differences in the percentage of differentiated hand-use rubbing bouts between age/sex classes across the two groups (F = .783, d.f. = 2, p = .489).

Luehea candida

Luehea candida (**Figure 2-6**) was a substantial dietary component of both the CP group (2.15% of observed feeding time) and the LV group (3.54% of observed feeding time). There were no significant differences in rate of *Luehea* consumption (**Table 2-7**) between the groups as a whole (F = .850, d.f. = 1, p = .369) or between age/sex classes (F = 2.206, d.f. = 3, p = .125), despite strong apparent differences in the latter. Rate of *Luehea* consumption by age/sex classes did not differ significantly between groups (F = 1.880, d.f. = 3, p = .174).

Because mature *Luehea candida* pods dehisce to release their seeds on their own, the monkeys could often access the seeds without any processing whatsoever, or even detaching the pod from the tree. The monkeys would simply grasp the pod or its stem and pull it towards them, allowing the seeds to be extracted with the tongue, teeth, or fingers. Though no significant difference in the percentage of processing vs. no-process consumption bouts (**Table 2-8**) was detected between groups (F = .026, d.f. = 1, p = .874), I found a significant difference in the percentage of processing bouts between age/sex classes (F = 11.859, d.f. = 3, p < .001). There were no significant differences among age/sex classes by group (F = 1.676, d.f. = 3, p = .210).

Techniques for processing *Luehea candida* pods fell into three broad categories- "pound", "rub/roll", and "hand-pound" (**Table 2-9**). 62.4%, of observed *Luehea* processing bouts were some form of pounding. In a "pounding" bout, the monkey would first detach the pod from the stem with its hands or teeth and carry it over to a nearby branch, then begin hammering the pod against the substrate (usually at about a 45-degree angle), pausing periodically to pick up with fingers or lips the seeds that had fallen out, or to lick or pry at the end of the pod where seeds had accumulated. Though the general technique for "pound" was very similar across age/sex classes and groups, some individuals appeared far more adept than others at manipulating the pods. In particular, I noted one variation of "pound" that while functionally the same as regular pound, appeared to be far more efficient. In this "skilled pound" behaviour, individuals would hammer at a qualitatively more rapid pace, ducking their heads down to pick up seeds off the substrate or from their cupped hands while barely pausing in their hammering. At no point did they need to stop and pick out seeds from the tip of the seed pod with their fingers or teeth. "Skilled pound" bouts composed 26.3% (or 31 of the 118) observed "pound" bouts, and were seen only in the four highest-ranking adults of the CP group- the alpha and beta males, the alpha female, and her eldest surviving daughter.

"Rub/roll" bouts composed 26.5% of observed processing bouts. In a "rub" bout, a detached pod was grasped it firmly and pushed it forward and back across the substrate. In a "roll" bout, the pod was not grasped and the hands were kept flat as the pod was moved back and forth across the substrate, allowing it to rotate. Neither "roll" nor "rub" appeared very efficient and it was rare to see seeds coming out of the pods during such processing bouts. Bouts of "hand pound" composed 11.1% of all observed *Luehea* processing bouts, and involved an individual grasping a detached pod in one hand and rapidly "upending" it into the other hand, as if the pod were a box of candy. Qualitatively, this appeared to be a fairly efficient method of accessing *Luehea* seeds, though not as effective as "pound."

Luehea candida processing often elicited differential hand use in pounding bouts (**Table 2-10**), in which one hand would be used to grasp the pod while the other was held palm-up at an angle beside the substrate to catch seeds as they came out. 81.3% of those pounding bouts where hand use could be distinguished involved this 'pound and catch' hand use pattern (**Figure 2-7**). Only 74.2% of "skilled pound" bouts were differentiated.

Analyses of Luehea *processing*

After correcting for sample size, no significant difference in the percentage of "pound" bouts vs. other forms of processing between groups (F = 4.690, d.f. = 1, p = .083) or age/sex classes (F = 1.805, d.f. = 2, p = .257) was detected, nor did the percentage of "pound" bouts in each age/sex class differ between groups (F = .172, d.f. = 2, p = .847). I found no significant differences in the percentage of "rub/roll" bouts vs. other forms of processing between groups (F = 1.944, d.f. = 1, p = .222) or age/sex classes (F = 1.912, d.f. = 2, p = .242). The percentage of "rub/roll" bouts by age/sex classes did not differ between groups (F = .153, d.f. = 2, p = .862). I found no significant differences in the percentage of differentiated hand use bouts between groups (F = 4.985, d.f. = 1, p = .089) or age/sex classes (F = 4.323, d.f. = 2, p = .100), nor did the percentage of differentiated hand use bouts differ significantly by age/sex class between groups (F = 1.156, d.f. = 1, p = .343).

Acacia *Ant Thorns*

Acacia ants and ant larvae were a substantial dietary component of the CP group (3.69% of observed feeding time), but were almost never consumed by the LV group (0.16% of observed feeding time). I found a significant difference in rates of *Acacia* thorn processing bouts (**Table 2-11**) between groups (F = 39.417, d.f. = 1, p < .001) but not age/sex classes (F = 2.428, d.f. = 3, p = .101). Rate of *Acacia* thorn processing by each age/sex class also differed significantly between groups (F = 3.658, d.f. = 3, p = .034).

Prior to a bout of *Acacia* thorn processing, the monkey would first approach the *Acacia* tree on nearby substrates (sometimes pausing a moment to "size up" the tree) before seizing a branch or stem and pulling the *Acacia* towards them. The monkey would then usually grasp a branch in one or both hands and try to break off a single thorn, a branch of thorns, or a terminal thorn (with attached frond) with hands or teeth, then crack it open to extract the ants or larvae inside with the lips and tongue (**Table 2-12**). Often ants from the host plant were swarming the monkey throughout this process; during such ant attacks (**Table 2-13**), the monkey would rapidly brush or lick the ants out of the monkey's fur during processing as needed (sometimes quite frantically).

In addition to recording information on bouts of *Acacia* ant processing, I noted failed attempts at thorn processing, in which the monkey was unable to detach or feed from any thorns before the attacking ants forced it to withdraw (**Table 2-14**). I was able to compare the number of 'attached' vs. 'detached' processing bouts against the number of 'ant attack' vs. 'no ant attack' bouts (**Table 2-15**), though these results were not analyzed statistically.

Only a few bouts of thorn processing with 'trunk' thorns were observed, so the "thorn type" variable ('branch' vs. 'trunk') was ignored for analysis purposes. I was usually unable to conclusively identify which ant species was being targeted for any given bout, and so what little data on ant species that I was able to collect were not analyzed. The method of thorn acquisition by the monkeys was highly variable, and was likely influenced by a number of factors I did not collect data on, such as the size and orientation of the plant, what substrates were nearby, and the number of ants visible on the plant.

Analyses of Acacia *ant thorn processing*

Because of the extremely low rate of *Acacia* thorn processing in the LV group, I chose not to compare differences in *Acacia* ant thorn processing across groups, only age/sex classes. After correcting for sample size, I found a significant difference in the percentage of "single thorn" bouts between age/sex classes (F = 12.429, d.f. = 2, p = .007). However, I found no significant difference between age/sex classes in the percentage of processing bouts in which the monkey suffered an ant attack (F = .029, d.f. = 2, p = .971), or in the percentage of successful vs. unsuccessful processing bouts (F = .644, d.f. = 2, p = .558).

Large Caterpillars

Caterpillars were a major food item for both groups after the start of the wet season, but composed only a small component of total observed feeding time for both the CP group (1.96%) and LV group (1.08%). Because of the diversity of caterpillar fauna in Santa Rosa during the wet season, the speed at which they were captured and consumed, and the generally poorer observation conditions during the wet season, it was usually impossible to make out any features of the caterpillars beyond size (bite-sized, or larger than bite-sized) and the presence or absence of spines. "Bite sized" caterpillars were almost always consumed whole with little or no handling time; only for large (i.e., "larger than bite-sized") caterpillars was enough variability in processing observed to quantify. Rates of large caterpillar consumption (**Table 2-16**) differed significantly between groups (F = 6.171, d.f. = 1, p = .024) but not between age/sex classes (F = .169, d.f. = 3, p = .916). I found no significant differences in the rate of large caterpillar consumption by age/sex class between groups (F = 1.090, d.f. = 3, p = .380).

Large caterpillars could be consumed without any form of processing (**Table 2-17**); the monkey would simply bite into the caterpillar and begin chewing, occasionally spitting out unpalatable bits or the gut lining as needed, or squeezing the caterpillar in such a way that the guts would burst or spill out the other end as it was consumed (similar to a human eating a pastry and having cream spill out the back end).

All forms of large caterpillar processing (**Table 2-18**) appeared intended to remove the unpalatable parts of the caterpillar (usually the guts and undigested plant material) in an efficient manner before or during consumption. Such processing fell into two broad categories: "drain/pull" and "eviscerate." In "drain/pull", the monkey would bite off one end of the caterpillar and then hold it in its hand for a moment, allowing the guts to spill out. If the guts were particularly firm or stringy, the monkey might attempt to pull them out with its other hand or lips and fling them aside before or during consumption. "Eviscerate" was generally similar to the "drain/pull" technique, but was distinctive in that the monkey would give "flick of the wrist" after one end of the caterpillar was bitten off, resulting in the caterpillar's entire gut sliding out to the ground in one smooth motion. It was not necessary to pull off the guts or even touch them in any way. "Eviscerate" usually took only a fraction of a second to complete (compared to several seconds with the "drain/pull" technique). It also appeared more effective in that a greater percentage of the unpalatable gut contents were removed before consumption. This more qualitatively skilled "eviscerate" was observed in both groups, but only by adult males and adult females.

Analyses of large caterpillar processing

After correcting for sample size, I detected no significant differences in the percentage of processing vs. non-processing bouts between groups (F = .914, d.f. = 1, p = .440) or age/sex classes (F = 1.016, d.f. = 3, p = .531). The percentage of processing bouts across age/sex classes did not differ between groups (F = .229, d.f. = 1, p = .680). Only three individuals met the minimum sample size requirement for processing technique, so no statistical analysis was conducted.

Other Foods

Forms of complex food processing (notably various types of object-use) were observed for a number of other food types, but most were observed too rarely to discuss in the context of variability in food processing, or no obvious variability in techniques were observed between individuals, groups, or age/sex classes.

DISCUSSION

Activity Budgets

Evaluating broad activity patterns across groups or age/sex classes was not the focus of this research, but the general patterns of behaviour observed during this study were largely consistent with previous work (e.g., Rose 1994). Adult males spent a greater percentage of their time in vigilance behaviour than other age/sex classes, spent more time resting, and less time foraging. Relative time spent foraging showed statistically significant differences across age/sex classes, with juveniles spending the highest percentage of their observation time foraging, and foraging times among other age/sex classes relatively equal. Previous studies of differences in foraging across primate age/sex classes have interpreted high rates of foraging among younger animals as a reflection of lower foraging success and higher metabolic demands (Janson & van Schaik 1993) compared to mature animals, which seems sufficient to explain the patterns observed. The proportion of observation time spent in foraging behaviour did not significantly differ between the two groups as a whole, nor did time spent foraging by members of each age/sex class differ significantly between the two groups. These results were not surprising, given that the two groups are of similar size and composition and live in widely overlapping ranges of similar habitat, as they have for more than a decade (Chapman & Fedigan 1990). However, though the general activity patterns of the two groups are very similar, at a finer level, striking differences begin to emerge.

Diet

Though the food lists for the CP and LV groups show considerable overlap, the percentage of overall time spent feeding on different species or food types was often considerably different. How can this difference be accounted for? In their study, Chapman & Fedigan (1990) determined that dietary preferences among these two social groups, as well as a third to the north, did not correlate with food availability. They hypothesized that group dietary preferences may instead reflect food profitability (i.e., capuchins favour more 'profitable' foods available in terms of nutrients, energetics, toxins, and distribution) or group-specific social traditions in diet. Though they reported that the composition of food trees in the two areas were not significantly different, in the 12 years since their study, the regenerating dry forest of Santa Rosa has likely undergone considerable change (Fedigan *et al.* 1996). During the 2001 season the ranges of the two groups appeared qualitatively quite distinct, though it was unfortunately not possible to conduct botanical surveys to assess forest composition.

The CP group's range was almost completely flat, and included a former horse pasture, which had been largely cleared of trees and saplings when the park was established. This area contained numerous saplings and small fruiting trees, but was largely composed of small *Acacia* trees, ranging from ca. 0.25-4m high. While mature trees were numerous, some species that are relatively common elsewhere in the park (such as *Sloanea terniflora*) were quite rare; only one *Sloanea* tree was found within the CP group's usual range. In contrast to the relatively level habitat of the CP group, the defining feature of the LV group's central range was a large, flat plateau, bordered by dry streambeds to the north and east. Intact dry forest lay to the north, and the entire range included far more mature trees, and a greater diversity of species, than the CP group's range.

Though environmental factors undoubtedly played a role in inter-group differences in diet, it is intriguing that the percentage of plant vs. invertebrate prey in each group's diet during the 2001 field season is so similar to what was observed by Chapman and Fedigan (1990) reported over three field seasons (1984 to 1986), despite the substantial and ongoing changes that are underway in the dry forests of Santa Rosa (Fedigan *et al.* 1996). It is also notable that the relative preferences for plant vs. invertebrate prey in these groups appears to have persisted despite changes in the proportion of each group's diet that specific plant foods compose. In other words, though the forests have changed, and the relative importance of different plant species in the diet appears to have changed, the general dietary preferences of these two groups (in terms of the proportion of plant vs. invertebrate prey in the diet) appear to have remained relatively stable, at least in a comparison of the 1984-1986 field seasons and that of 2001. This similarity in diet over a 15-year period may reflect enduring group-specific social traditions in diet, as hypothesized by Chapman & Fedigan (1990). If diet were solely a function of availability and food profitability, one would predict that general dietary patterns should shift with the relative abundance of available food types, yet such changes appear to have been minimal. Alternatively, younger individuals, or those who have emigrated into the group, may be adapting their foraging behaviour to match the foods they have observed older animals to seek and consume. Unfortunately, without up-to-date botanical surveys of the habitats of each group and a larger data set, this question remains unresolved.

Object-Use

Rates and time spent in object-use among the capuchins of Santa Rosa were considerably different than those of Palo Verde as reported by Panger (1998), highlighting the importance of not generalizing patterns of behaviour for a species or group of populations based on relatively short-term studies. The overall higher rate of, and proportion of time spent in, object-use activities that I observed were driven almost entirely by *Sloanea* processing, and to a lesser extent *Luehea* processing, in both study groups. The differences between Santa Rosa and Palo Verde may be partly an artefact of the time and duration of my field season; the study of Palo Verde lasted 11 months, encompassing both the dry season and most of the wet season, while my study lasted only 6 months, encompassing the dry season and only the early wet season. Food availability is greatly reduced in the dry season, which may result in higher rates of extractive food processing because the capuchins target better-defended prey items that might have been ignored in times of greater food abundance. Had my field study lasted for a full year, both the rate of, and time spent in, object-use activities by the Santa Rosa monkeys might more closely resemble those reported for Palo Verde.

One of the most interesting comparisons of object-use patterns between Santa Rosa and Palo Verde that emerged was that neither *Sloanea* processing nor consumption was observed at the latter site during 11 months of study, though *Sloanea* trees are abundant (Panger, personal communication). Individual *Sloanea* trees in Santa Rosa seem to show great variability from year to year in crop size, producing no crop in some years, and particularly abundant crops in others (Fedigan, personal communication). Such annual variation, even in a single tree, can have a huge impact on capuchin feeding behaviour (see below). Given that *Sloanea* is consumed by capuchins at the bordering Lomas Barbudal site (Panger *et al.* 2002), and that capuchins are known to consume other species of *Sloanea* in South America (Terborgh, 1983), it seems likely that *Sloanea* is part of the diet of Palo

Verde monkeys as well, just not during Panger's study. As has been noted before in cross-population comparisons of this sort, "absence of evidence does not constitute evidence of absence" (Panger *et al.* 2002). Future research at Palo Verde (preferably over a multi-year period) is needed to resolve this question.

Processing Techniques

Sloanea terniflora

I observed 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 differences can be attributed largely to environmental factors. A single *Sloanea terniflora* tree in the LV group's range produced a superabundant crop in mid-February of 2001. The group spent several hours feeding in and around the tree nearly every day for more than two weeks. The LV group also had many other *Sloanea* trees within its range that produced normal crops in 2001, while the CP group had only a single *Sloanea* tree in its entire range. I found no significant differences in consumption rates of *Sloanea* between age/sex classes, though adults and immatures consumed *Sloanea* at roughly comparable rates, and juveniles consumed it only rarely. This may in part reflect physical and cognitive limitations of different age/sex classes. While adults, immatures, and juveniles were all observed to have difficulties processing *Sloanea*, juveniles appeared to find the task particularly challenging. It may be that their hands lack the coordination and dexterity needed to manipulate and open the fruits without difficulty, particularly in the 'differentiated' hand-use pattern. This would be consistent with past observations of complex food processing by capuchins in both the wild (Izawa & Muzino 1977, Boinski *et al.* 2000) and in captivity (Anderson 1990).

The lower rate of *Sloanea* processing and consumption in juveniles also likely reflects a form of risk-aversion. While capuchins do not seem as troubled by *Sloanea* hairs as humans are, there are very real consequences if the fruits are processed incorrectly, including irritated skin, sneezing, and impaired vision. Such problems, though temporary, could have a negative impact on an individual's foraging success and ability to evade predators or other threats. Janson & van Schaik (1993) have discussed how juveniles may be more vulnerable to starvation in periods of food scarcity (such as exists during the mid-dry season), lack the physical and cognitive skills of adults, are more vulnerable to predators, and lack experience in choosing and processing foods. They argue that a 'risk averse' strategy of slow development and maturation is an adaptive response to ecological risk, and is reflected in various behavioural and social attributes of juveniles, including dietary choice, foraging behaviour, and patterns of association. My observations of *Sloanea* processing would seem to support such a 'risk averse' strategy. It so happened that less than 20m from the 'superabundant' *Sloanea* tree in the LV group's range was a large *Ficus* tree that came into fruit at roughly the same time. While adults focused primarily on *Sloanea* while in the area, juveniles concentrated on consuming figs.

There was very little variability in *Sloanea* processing techniques across groups or age/sex classes. This lack of variability may simply reflect that there is only one viable way to process *Sloanea*- rubbing it on a substrate to remove the hairs. The "pound" technique was not nearly as effective, and the "body/tail rub" method may bear its own costs in terms of discomfort or irritation from the hairs (though *Sloanea* is among those species for which 'plant rubbing' has been observed independently of consumption; Baker 1994). Rubbing and pounding objects have been commonly observed in both captivity and the wild (Izawa & Muzino 1977, Struhsaker & Leland 1977, Boinski *et al.* 2000), and may reflect a 'default' response when individuals are having difficulties (Panger 1998, Panger *et al.* 2002). While an individual might benefit from seeing other individuals process such a food item (through various social learning processes, i.e., local enhancement, emulation, etc.), I would argue that such benefits would be minimal. An individual physically capable of both 'rubbing' and 'pounding' *Sloanea* fruits would be able to learn relatively quickly on their own that that the former technique is vastly more effective than the latter at removing the stinging hairs.

Still, it would be intriguing to see how captive capuchins with no prior experience with *Sloanea* might respond if presented with it, either alone or in a social setting. I believe it would be fairly simple to find enough captive-born capuchins in Costa Rica alone for a simple observational study along these lines.

Adults of both sexes used the 'rub and brush', or differentiated hand use pattern, more frequently than either immatures or juveniles. As adults processed *Sloanea* at higher rates than non-adults, such differences may simply reflect experience and greater opportunity, but could also reflect knowledge acquired or influenced by social learning processes. This question will be explored more thoroughly in the following chapter.

In summary, asocial factors, such as environmental differences between sites, physical and cognitive limitations of different age/sex classes, foraging strategies of different age classes, and greater experience by adults compared to non-adults seem sufficient to explain most patterns of variation I observed in *Sloanea terniflora* processing. However, some patterns of processing may reflect social influences and warrant examination within the context of social networks.

Luehea candida

Luehea candida was neither particularly abundant nor particularly rare in either group's range (though it seemed somewhat more common in the LV group's range), and so it is not surprising that rates of consumption did not differ significantly between groups. Despite striking differences in *Luehea* consumption rates between age/sex classes, overall these differences were not significant, nor were differences in consumption across age/sex classes between groups. The overall pattern was a high rate of consumption in adult females, immatures, and juveniles compared to adult males. Because *Luehea* pods are a food item that could be consumed without any processing, and one for which younger or smaller individuals, with proportionately smaller hands, might actually have an advantage over older animals, it is not surprising that consumption rates by younger and smaller animals would be fairly high.

Rates of consumption across age/sex classes appear to be inversely linked to the relative frequency of processing bouts. Adult males almost never consumed *Luehea* without processing, while juveniles almost never processed *Luehea* (though they consumed it frequently), and adult females and immatures fell out in between. The most probable explanation for this pattern is the physical and/or cognitive limitations of different age/sex classes. Because *Luehea* pods are attached to their stems quite firmly, it may be that juveniles lacked the strength to pull them off and manipulate the pods effectively, since both immatures and adult females sometimes appeared to have difficulty doing so. Attempting to consume seeds without processing may be a more energetically efficient strategy for these age/sex classes, while adult males can break the stems with ease. This also explains why females engaged in 'hand pound' more than adult males. Another developmental factor that could explain the higher rates 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). Repeated pounding of 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 the site in Suriname where their research was conducted, 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, and so adult females favour the latter technique, even though they are capable of the former.

Both physical and cognitive limitations likely underlie the higher percentage of 'rub' among immatures and juveniles. Younger individuals may simply lack hands large enough and strong enough to effectively manipulate the pods in one hand. Some non-adults also seemed not to understand that sealed pods couldn't produce seeds. Immature males in each group were observed on separate occasions to detach a pod that had not yet dehisced, rub it for several seconds, then drop it and repeat the process with a new pod over and over (in the case of one individual, this happened more than a dozen times in a row). As noted above, rubbing and pounding seem to be 'default' behaviours employed by capuchins when they encounter difficulties (Panger *et al.* 2002). Such 'non-functional' attempts at food processing suggest some lack of understanding among these individuals about what is necessary for successful extraction of *Luehea* seeds.

Differentiated hand use, or the 'pound and catch' technique, was the standard pattern for individuals pounding *Luehea*, primarily adult males and adult females. The 'skilled pound' behaviour observed in the CP group, though functionally identical to normal pounding, was distinctive and (qualitatively) appeared more efficient. The only four individuals in the CP group observed to use 'skilled pound' were also the only four in that group to practice differentiated hand use. As was the case for *Sloanea*, the relative frequency of differentiated hand use across age/sex classes corresponded to higher rates of pounding, and so may simply reflect greater opportunity and experience on the part of older animals.

In summary, differences in rates of *Luehea* consumption, percentage of processing vs. no processing consumption bouts, and forms of processing can largely be attributed to environmental or developmental factors. However, the qualitative differences in skill observed across age/sex classes and individuals, as well as the percentage of differentiated hand use, could reflect social influences and are worthy of further analyses, to be discussed in **Chapter III**.

Acacia ant thorns

The CP group processed *Acacia* ant thorns significantly more often than the LV group. This could reflect opportunity (since the CP group's range appears to have more

Acacia trees), food profitability (since the LV group's range contains more profitable foods), group-specific dietary traditions, or (most likely) some combination of these factors. Unfortunately, without current botanical data on the ranges of these two groups, there is no way of evaluating these explanations empirically.

Acacia thorns were a food item targeted most frequently by juveniles and adult females, and were almost never consumed by adult males. This is particularly interesting in that one might predict that juveniles would have lower rates of *Acacia* thorn processing, assuming that juveniles should practice a 'risk-averse' foraging strategy as argued by Janson & van Schaik (1993). As is the case for *Sloanea*, inept or careless processing of *Acacia* thorns has negative consequences- an attack by stinging ants. Why might juveniles be the most frequent consumers of *Acacia*?

Juveniles are almost always at a disadvantage compared to adults in foraging success rate, recognition of edible foods, and their ability to acquire and manipulate prey (Boinski & Fragaszy 1989, Janson & Boinski 1992, Janson & van Schaik 1993). Compared to the challenges inherent in acquiring large, mobile prey such as grasshoppers, or accessing the nests of small, cryptic prey such as ants or termites embedded in hard substrates, the ants and larvae in *Acacia* thorns are probably a more plentiful, reliable, and accessible food source for individuals lacking the capabilities of mature or nearly mature animals, despite the painful sting of the ants themselves- which, though painful enough to sometimes deter the monkeys, appear to do no lasting damage. Capuchins in general seem remarkably tolerant of pain (Fedigan, personal communication) and are not deterred from consuming more dangerous stinging prey such as scorpions despite suffering numerous stings in the process (O'Malley, personal observation).

In terms of the manner in which the thorns were detached, the three age/sex classes to process them with any regularity (adult females, immatures, and juveniles) all showed a preference for detached rather than still-attached thorns. All three age/sex classes also showed a preference for detaching a single thorn rather than multiple thorns on a branch, or one with a frond attached. This is presumably a strategy to minimize ant attacks, since the less contact an individual has with the plant itself (or components of the plant), the fewer ants will have an opportunity to attack. The higher percentage of 'attached' thorn processing by immatures and juveniles relative to adult females likely reflects physical strength limitations.

The percentage of processing bouts with an 'ant attack' showed little variation across adult females, immatures, and juveniles, though the two age/sex classes that engaged in thorn processing more often (adult females and juveniles) had *higher* percentages of ant attacks. Differences in percentage of ant attacks between thorn types cannot be evaluated, given how rarely the larger 'trunk' thorns were targeted compared to 'branch' thorns. Though there were strong differences in the percentage of ant attacks in bouts of 'attached' and 'unattached' thorn processing, it was the *more common* technique ('unattached' thorns) that showed a higher percentage of ant attacks. These results suggest that the risk of ant attack is not a crucial factor in determining the whether an individual targets attached or detached thorns. It seems likely that some other variable that was not analyzed in this study (e.g., the number of ants visible on the plant) is a more important consideration to an individual seeking to exploit *Acacia* thorns.

Intriguingly, the general *Acacia* ant thorn processing patterns observed in this study were markedly different from those reported by an earlier study (Freese 1976). This difference will be discussed further in **Chapter III**.

Large Caterpillars

A major problem in evaluating patterns of large caterpillar processing is that this general 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 semi-digested 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 it. Because it was almost always impossible to identify what type of caterpillars were being consumed, any interpretation of the techniques used to process them is problematic at best.

Rates of large caterpillar consumption differed significantly between groups, a pattern that likely reflects the CP group's greater focus on invertebrate prey. The slightly higher rate of consumption by adult females and immatures relative to other age/sex classes is to some degree an artefact of individual variation in rates…two adult females and one immature female in the CP group together accounted for more than half of all large caterpillar consumption bouts.

In general terms, only 'eviscerate' stands out as a distinctive processing technique, as it is seen only in adult males and adult females. However, because it is essentially an extension of the 'drain/pull' technique observed in all age/sex classes, it may simply reflect expertise that can arise solely through individual experience. Non-adults may simply lack the practice necessary to effectively eviscerate large caterpillars. Smaller individuals may also lack hands large enough to effectively grasp and manipulate large caterpillars, though the ability of *Saimiri oerstedii* (which even as adults are considerably smaller than capuchins) to process such prey so skilfully suggests otherwise (Boinski & Fragaszy 1989, Janson & Boinski 1992). The prevalence of the 'eviscerate' technique will be examined within the context of social networks in **Chapter III**.

CONCLUSIONS

The research described in this chapter sought to address three key questions.

What general patterns of foraging and diet are present among wild white-faced capuchins in Santa Rosa National Park?

Though general forms of object-use such as "rub" and "pound," are easily identified food-processing techniques observed frequently in this study, there is extensive variability in such behaviour at a finer level of detail than what has been previously recognized. Much higher rates of, and proportion of time spent in, object-use activities were observed in Santa Rosa than at Palo Verde, due to higher rates of *Sloanea* and *Luehea* consumption. Patterns of complex manipulation in *Cebus* food processing appear to be highly dependent on what food items are being exploited by different populations, groups, and age/sex classes.

What food processing techniques are employed for specific food items?

Details of food processing techniques for specific food items have been provided above. A great degree of variation was observed in such techniques for specific food items, both in rates of consumption and processing, general technique (e.g., 'rub' or 'pound'), and at finer levels of detail (e.g., hand use and skill level) across groups, age/sex classes, and individuals.

What patterns exist in the prevalence of such techniques across social groups, age/sex classes, and individuals, and how can these patterns be explained?

Rates of complex food processing techniques often showed marked differences between groups, though the actual techniques employed were generally comparable. Adults of both sexes engaged in complex food processing behaviours more frequently, and showed greater skill, than immatures or juveniles for most of the specific food items examined in this study, even when the younger age/sex classes consumed the food item in question more frequently. Most differences across groups and age/sex classes could be explained by environmental or developmental factors, but some patterns of variation (differential hand use in *Sloanea* and *Luehea* pounding, 'skilled' *Luehea* pounding, and caterpillar 'evisceration') may reflect social influences, and warrant further analyses. This will be the focus of **Chapter III**.

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TABLES

Table 2-1: Summary of group diets in 2001 (measured by % of observed feeding time).

Food	CP Group	LV Group
Plant	**63.5%**	**77.2%**
Leaves, pith, vine, leaves	*1.0%*	*1.0%*
Flowers	*1.8%*	*5.4%*
Fruit/Seeds	*60.7%*	*70.8%*
Invertebrate	**32.7%**	**20.5%**
Vertebrate	**3.3%**	**1.9%**
Unidentified	**0.4%**	**0.5%**

Table 2-2: Major components of group diets in 2001 (composing >5% of observed feeding time for at least one group).

Food Item	CP Group	LV Group
Acacia spp.	7.1%	0.7%
Sciadodendron excelsum	5.2%	4.8%
Ficus spp.	6.1%	17.7%
Bursera simaruba	7.8%	10.0%
Simaruba olivaceus	7.2%	10.2%
Sloanea terniflora	1.5%	9.9%
Casearia spp.	6.0%	0.3%
Caterpillars	6.8%	3.1%
embedded insects	13.5%	9.5%

Table 2-3: Mean *Sloanea* processing and 'no process' consumption bouts/hour (by group and age/sex class).

Group	Mean bouts/hour
CP	0.41
LV	2.28

Age/sex	Mean bouts/hour
AM	2.05
AF	1.64
IM	1.42
JU	0.39

Table 2-4: Percentage of *Sloanea* processing vs. 'no process' consumption bouts (by group and age/sex class).

Group	# processed	Total bouts	% processed
CP	88	90	97.8%
LV	294	306	96.1%

Age/sex	# processed	Total bouts	% processed
AM	145	151	96.0%
AF	139	140	99.3%
IM	79	81	97.5%
JU	19	24	79.2%

Table 2-5: Percentage of *Sloanea* processing bouts for each technique (by group and age/sex class).

Group	Total	#pound	#rub/roll	#body/tail rub	% pound	% rub/roll	% 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	# pound	#rub/roll	# body/tail rub	% pound	% rub/roll	% 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%
IM	79	0	75	4	0.0%	94.9%	5.1%
JU	19	0	18	1	0.0%	94.7%	5.3%

Table 2-6: Percentage of differentiated hand use, or 'rub and brush' *Sloanea* rubbing bouts (by groups and age/sex class). Bouts of unclear hand use were excluded.

Group	# differentiated	Total ID'd	% ID'd
CP	52	81	64.2%
LV	141	269	52.4%

Age/sex	# differentiated	Total ID'd	% ID'd
AM	73	126	57.9%
AF	101	133	75.9%
IM	17	74	23.0%
JU	2	17	11.8%

Table 2-7: Mean *Luehea* processing and 'no process' consumption bouts/hour (by group and age/sex class).

Group	mean bouts/hour
CP	1.00
LV	1.25

Age/sex	mean bouts/hour
AM	0.31
AF	0.93
IM	2.43
JU	1.34

Table 2-8: Percentage of *Luehea* processing vs. 'no process' consumption bouts (by group and age/sex class). These tallies include focal data only.

Group	# processed	Total bouts	% processed
CP	65	182	35.7%
LV	64	157	40.8%

Age/sex	# processed	Total bouts	% processed
AM	24	25	96.0%
AF	65	108	60.2%
IM	37	125	29.6%
JU	3	81	3.7%

Table 2-9: Percentage of *Luehea* processing bouts for each technique (by group and age/sex class).

Group	# pound	# rub	# handpd	Total	% pound	% rub	% handpd
CP	55	32	16	103	53.4%	31.1%	15.5%
LV	63	18	5	86	73.3%	20.9%	5.8%

Age/sex	# pound	# rub	# handpd	Total	% pound	% rub	% handpd
AM	37	7	3	47	78.7%	14.9%	6.4%
AF	56	1	17	74	75.7%	1.4%	23.0%
IM	24	39	1	64	37.5%	60.9%	1.6%
JU	1	3	0	4	25.0%	75.0%	0.0%

Table 2-10: Percentage of differentiated hand use, or 'pound and catch', *Luehea* pounding bouts (by group and age/sex class). Bouts of unclear hand-use are excluded.

Group	#differentiated	Total ID'd	% differentiated
CP	40	53	75.5%
LV	51	59	86.4%

Age/sex	#differentiated	Total ID'd	% differentiated
AM	36	37	97.3%
AF	38	52	73.1%
IM	17	22	77.3%
JU	0	1	0.0%

Table 2-11: Mean *Acacia* thorn processing bouts/hour (by group and age/sex class). This includes both successful and failed attempts.

Group	Mean bouts/hour
CP	1.23
LV	0.06

Age/Sex	Mean bouts/hour
AM	0.11
AF	0.71
IM	0.49
JU	1.09

Table 2-12: Percentage of successful *Acacia* ant processing bouts for each technique (by age/sex class).

Age/Sex	Total	# thorn	# thorn & frond/br	# attached	% thorn	% thorn & frond/br	% attached
AM	9	2	5	2	22.2%	55.6%	22.2%
AF	87	57	24	6	65.5%	27.6%	6.9%
IM	36	14	13	9	38.9%	36.1%	25.0%
JU	72	31	24	17	43.1%	33.3%	23.6%

Table 2-13: Percentage of successful *Acacia* thorn processing bouts with ant attacks (by age/sex class). Bouts in which it could not be determined if there was an attack were excluded.

Age/Sex	Total	# attacked	% attacked
AM	6	1	16.7%
AF	67	33	49.3%
IM	28	10	35.7%
JU	67	31	46.3%

Table 2-14: Percentage of failed bouts of *Acacia* ant thorn processing (by age/sex class).

Age/Sex	Total	# failed	% failed
AM	9	0	0.0%
AF	94	7	7.4%
IM	41	5	12.2%
JU	86	14	16.3%

Table 2-15: Comparison of ant attack vs. type of *Acacia* thorn targeted. Those bouts where it could not be determined if there was an attack or not were excluded.

	Total	Detached	attached
Attack	57	54	2
No attack	88	62	26

Table 2-16: Mean large caterpillar consumption bouts/hour (by group and age/sex class).

Group	Mean bouts/hour
CP	0.79
LV	0.35

Age/Sex	Mean bouts/hour
AM	0.47
AF	0.68
IM	0.54
JU	0.44

Table 2-17: Percentage of large caterpillar processing vs. 'no-process' consumption bouts (by group and age/sex class).

Group	Total	process	no process	% process
CP	116	68	48	58.6%
LV	29	13	16	44.8%

Age/Sex	Total	process	no process	% process
AM	25	15	10	60.0%
AF	78	35	43	44.9%
IM	27	20	7	74.1%
JU	15	11	4	73.3%

Table 2-18: Percentage of large caterpillar consumption bouts for each technique (by group and age/sex class).

Group	Total	# eviscerate	# drain/pull	no process	% evisc	% drain/pull	% no proc.
CP	116	11	57	48	9.5%	49.1%	41.4%
LV	29	2	11	16	6.9%	37.9%	55.2%

Age/Sex	Total	# eviscerate	# drain/pull	no process	% evisc	% drain/pull	% no proc.
AM	25	2	13	10	8.0%	52.0%	40.0%
AF	78	11	24	43	14.1%	30.8%	55.1%
IM	27	0	20	7	0.0%	74.1%	25.9%
JU	15	0	11	4	0.0%	73.3%	26.7%

FIGURES

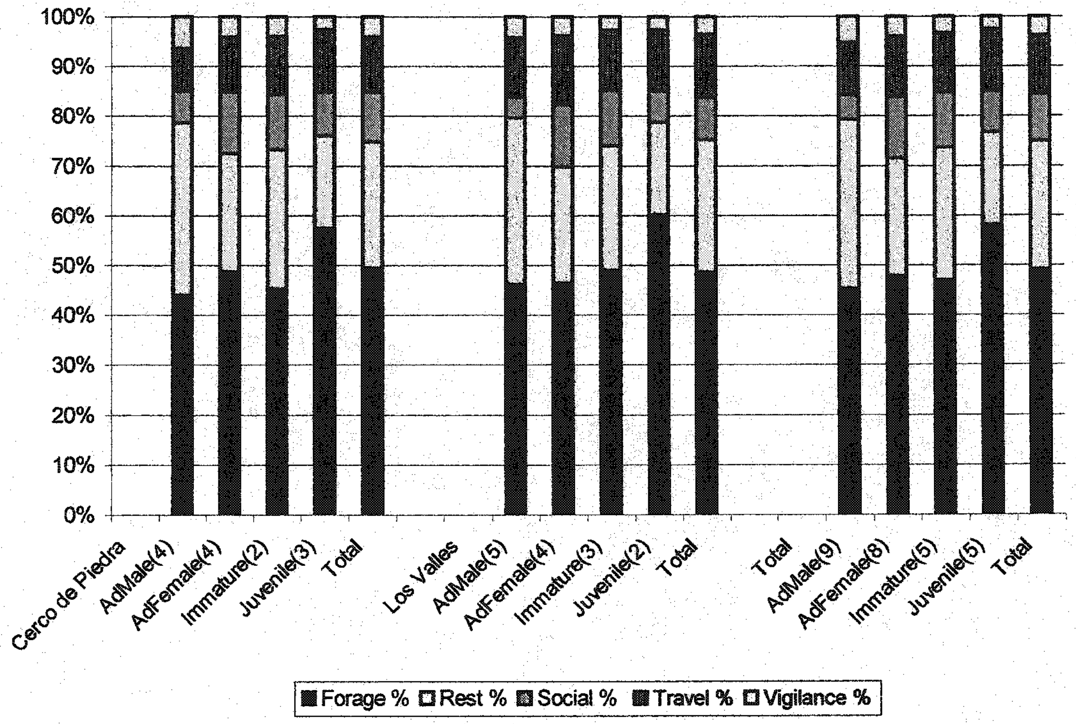

Figure 2-1: Activity budgets for the CP and LV groups (by age/sex class).

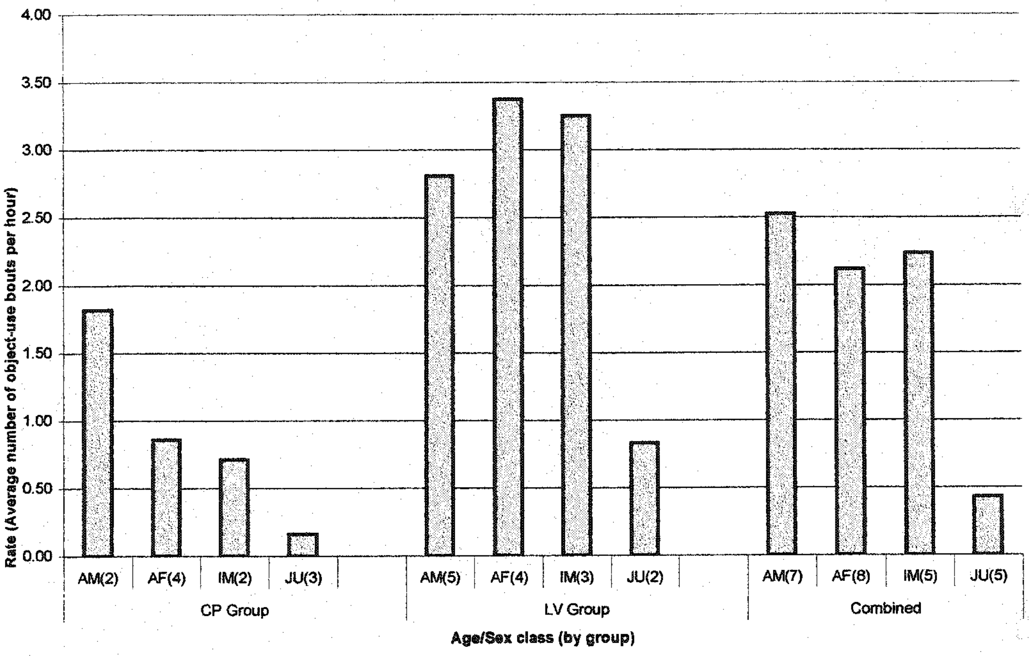

Figure 2-2: Rates of object-use among age/sex classes and groups.

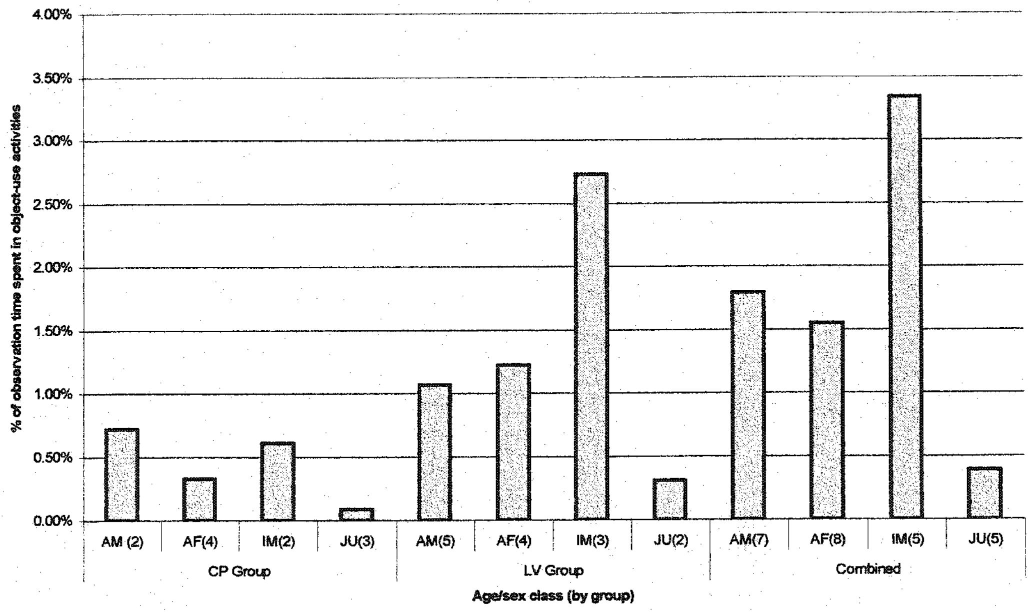

Figure 2-3: Percentage of observation time spent in object-use activities among age/sex classes and groups.

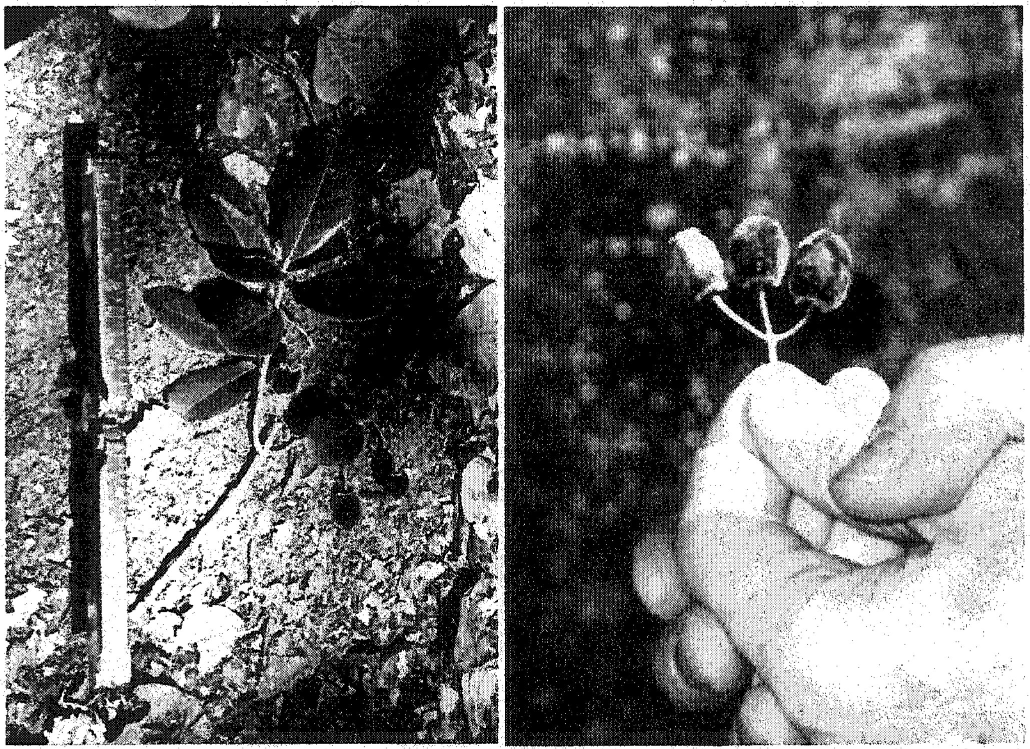

Figure 2-4: *Sloanea terniflora*. Note the urticating hairs that cover the surface of each fruit.

Figure 2-5: Adult male capuchin processing *Sloanea terniflora.* Note the use of the 'rub and brush' pattern.

Figure 2-6: *Luehea candida.* Note the structural differences between the more mature pods in the upper photo and the immature pods in the lower photo.

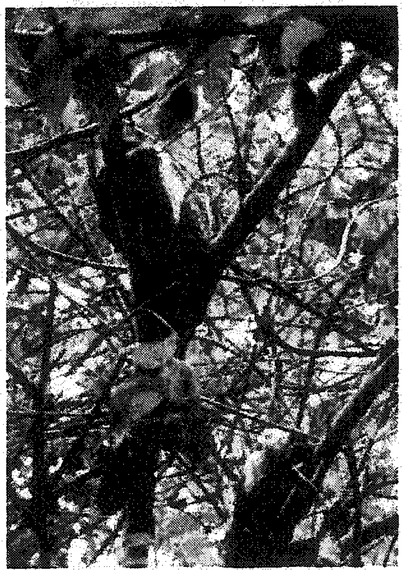

Figure 2-7: Capuchins processing *Luehea candida* pods. Note how the individual in the foreground has cupped its right hand against the branch to catch seeds as they emerge (the 'pound and catch' technique).

CHAPTER III: Social Influences on Food Processing Behaviour

INTRODUCTION

Patterns of complex object manipulation, particularly forms of tool- and object-use, have long held significance in studies of human evolution (Darwin 1874, Ingold 1993, Washburn 1960). Such complex manipulation may be linked to the development of other key characteristics of modern humans, including language, morphology, and complex social skills (Hamilton 1974, Parker and Gibson 1977, 1979, Westergaard 1995).

As the closest living relations of modern humans, members of the genus *Pan* have received particular attention in efforts to understand early human socio-ecology and behaviour (e.g., Wynn & McGrew 1989, McGrew 1992, Toth *et al.* 1993, Boesch & Tomasello 1998). Chimpanzees in the wild habitually make and use tools for a variety of tasks, most often in a foraging or food-processing context, but also for grooming and various patterns of social signalling (McGrew 1992, 1998, Whiten *et al.* 1999). There is a growing consensus among primatologists that the high degree of variability in such patterns of behaviour across chimpanzee populations, apparently independent of asocial factors such as environmental or genetic variation, reflects patterns of cultural variation (McGrew 1992, 1998, Boesch & Tomasello 1998, van Schaik *et al.* 1999, Whiten *et al.* 1999, Whiten & Boesch 2001).

Members of the Neotropical genus *Cebus*, though evolutionarily quite distant from both *Homo* and *Pan*, nonetheless share many socio-ecological characteristics with their hominoid relatives, including a long period of development, a large brain relative to their body size, frequent hunting and consumption of vertebrate prey, tolerance of others in proximity during foraging, and an extractive foraging niche (Parker & Gibson 1977, Gibson 1986, Fedigan 1990, Fragaszy & Bard 1997, Visalberghi & McGrew 1997, Panger 1998a). In particular, the capuchin capacity for complex object manipulation and tool use is virtually unrivalled in the animal kingdom, surpassed only by humans, chimpanzees, and orangutans.

Identifying the similarities and differences between such patterns of manipulative behaviour in the genus *Cebus* and the tool-using hominoids is thus of particular importance in evaluating the distinctiveness and significance of such traits in the evolution of *Homo sapiens*.

Cognitive Issues

Despite the impressive range of *Cebus* tool- and object-use in a staggering array of tasks (i.e., Izawa & Muzino 1977, Struhsaker & Leland 1977, Visalberghi 1987, Westergaard & Fragaszy 1987a, b, Boinski 1988, Visalberghi & Trinka 1989, Anderson 1990, Fernandes 1991, Westergaard & Suomi 1993a, b, 1994a, b, c, d, Anderson & Henneman 1994, Westergaard 1995, Westergaard & Suomi 1995a, b, Westergaard *et al.* 1995, 1997, Panger 1998a, Phillips 1998, Urbani 1999, Boinski *et al.* 2000, Ottoni & Mannu 2001, Panger *et al.* 2002), such behaviour is said to be fundamentally different from similar behaviour among the great apes on a cognitive level (Visalberghi 1990, 1993a,b, 1997, Visalberghi & Fragaszy 1990). Unlike tool-using apes, capuchins apparently fail to develop an understanding of the tool tasks presented, and are successful tool-users through "persistent and vigorous trial-and-error attempts" (Visalberghi 1990) rather than through an understanding of the goals and mechanics of a given task, as is argued to be the case for tool-using apes (Visalberghi 1993a,b, 1997).

However, it is important to note that a great deal of this research with capuchins has been conducted with fairly small sample sizes, and in some cases with the same individuals over and over again (see table 7.1 in Visalberghi 1993b, Westergaard & Suomi 1993a, b, 1994a, b, c, d, 1995a,b). Such intensive exposure to manipulative tasks in a captive environment is likely to influence the strategies employed by these individuals. While studies of captive animals are obviously vital to understanding animal behaviour, wide disparities often emerge between captive and wild studies of the same phenomenon, particularly among primates (e.g., handedness; McGrew & Marchant 1997, Panger 1998b).

Ultimately the capabilities of capuchins must be evaluated in their natural environment as well as in the laboratory.

Social Learning in *Cebus*

In addition to their more limited cognitive abilities relative to the great apes, capuchins appear to have only a limited capacity for social learning in cooperative and tool-use tasks (Visalberghi 1987, 1997, Fragaszy & Visalberghi 1989, Visalberghi & Fragaszy 1990, Adams-Curtis & Fragaszy 1995). When evidence for social learning has emerged, less robust forms of learning such as local enhancement ('activity directed towards a place or object by others that enhances interest') and social facilitation ('activity by others that encourages activity by observers') are usually sufficient to explain observed patterns of social transmission (Fragaszy & Visalberghi 1989, 1990). In particular, the lack of evidence for imitation ('modelling another's actions to achieve the same goal') in capuchins is argued to be a key difference between their abilities and those of tool-using great apes (Visalberghi 1993a; 1997, van Schaik *et al.* 1999).

Van Schaik *et al.* (1999) argue that capuchins lack a capacity for insight, emulation, and imitation, which explains the lack of population-wide patterns of tool-use in the wild. The presence of other key variables (an extractive foraging niche, manual dexterity, and social tolerance) allow capuchins to acquire complex manipulative techniques such as tool-use in a captive setting, where observation and manipulative opportunities are numerous and frequent. However, the incapacity of capuchins for simple imitation has been challenged (Custance *et al.* 1999), and so such arguments seem premature, at least until the body of knowledge on wild *Cebus* populations begins to approach that of *Pan*. And indeed, as more researchers in recent years have focused on specific patterns of foraging and food processing in wild *Cebus* populations, the distinctions between complex manipulative behaviour in *Cebus* and *Pan*, (particularly those said to reflect social traditions, or patterns of 'culture'), have been called into question (i.e., Boinski *et al.* 2000, Panger *et al.* 2002; also see Perry *et al.* in press).

Culture in *Cebus*?

Like the genus *Pan*, members of the genus *Cebus* may possess a capacity for social traditions, or 'culture', defined for the purposes of this study as *"group-specific behaviour that is acquired, at least in part, from social influences."* (from McGrew 1998). A half-century of chimpanzee research across numerous sites have identified a high degree of group- and population-specific variability (apparently independent of genetic or environmental differences) in courtship and grooming behaviour (McGrew & Tutin 1978, Nishida 1980, Sugiyama 1981, Boesch 1995, Nakamura *et al.* 2000), patterns of medicinal plant use (Huffman & Wrangham 1994, Huffman *et al.* 1997), and a number of food-processing and foraging techniques, particularly forms of tool- and object-use (Sugiyama 1985, 1997, Goodall 1986, Boesch 1991, 1993, 1996, McGrew 1992, 1998, Boesch & Boesch 1993, Boesch *et al.* 1994, Boesch & Tomasello 1998) among chimpanzee populations. Despite their apparent cognitive limitations relative to hominoids, evidence for similar patterns of social traditions, or culture, in the genus *Cebus* has emerged, in grooming behaviour and social play (Perry *et al.* in prep.) as well as medicinal plant (and animal) use (Baker 1996, Valderrama *et al.* 2000) in the wild. In *Cebus capucinus*, broad variations in processing techniques (including several forms of object-use) for specific food item types across ecologically similar sites in NW Costa Rica have been identified (Panger *et al.* 2002) in a pattern consistent with 'cultural' differences in chimpanzee populations (Whiten *et al.* 1999). These preliminary observations from the wild call into question both the significance of specific cognitive processes in explaining patterns of complex object manipulation (including those said to be 'cultural'), and the distinctiveness of such patterns in *Homo* and *Pan* relative to other nonhuman primates (Panger *et al.* 2002). Only with a more intensive research focus on food processing patterns across a broader range of taxa can these issues be addressed.

As noted by Fragaszy & Perry (in press), many biologists find the issue of 'culture' in nonhuman animals of little interest, preferring to focus on the impact that individual-, group-, or population-specific traditions have on behavioural ecology, fitness, and evolution. I concur that the latter approach is valuable, particularly in terms of understanding the evolution of modern human behaviour, and the research described in the following pages seeks to address these issues to a degree. However, as part of a discipline that straddles the paradigms of anthropology, zoology, and psychology (McGrew 1998), primatologists cannot ignore the implications of their research for the numerous qualitative and quantitative distinctions drawn between human societies and those of their closest living relations. Nearly a half-century of research on wild chimpanzees has eroded many of the long-standing distinctions held to exist between *Homo* and *Pan*. Whether the behavioural, cognitive, and social distinctions (including a capacity for social traditions, or 'culture'), that are said to exist between these two closely related hominoids and the rest of the Order Primates, particularly the genus *Cebus*, will survive comparable scrutiny remains an open question.

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, though such research has been conducted with some success (e.g. Boesch 1991, 1993, 1996, Matsuzawa 1994, Watanabe 1994, Inoue-Nakamura & Matsuzawa 2001, Garber & Brown 2002). Short of conducting intrusive field experiments (which risk altering the patterns of behaviour one seeks to examine), a more indirect means of examining such patterns in a social context is to identify *opportunities* for transmission, and determine if such opportunities correlate with specific patterns of behaviour (e.g. Boesch 1996, Panger *et al.* 2002). This does not usually allow for specific social learning processes (Whiten & Ham 1992) to be identified, only whether social processes could be at work, and the strength of their influence.

A number of social networks operate within and between groups that may influence foraging and food processing patterns. The most obvious (and likely the most powerful) are 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 behaviour, relative to less proximate individuals (Panger *et al.* 2002). *Social rank* is known to influence spatial patterns within capuchin groups (Janson 1990a, b, Hall & Fedigan 1997), which can in turn influence diet and foraging behaviour. In addition, higher-ranking individuals are able to supplant lower-ranking individuals from prized food resources (Di Bitetti & 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 be more likely to associate with relatives, and may monitor their actions more closely than those of non-relatives. 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 towards their mothers' activities (O'Malley personal obs.).

Research Objectives

The research discussed in this chapter addressed several key issues. First, I sought to determine the degree to which several social networks (specifically proximity, rank, and kinship) correlate with foraging or food processing patterns for specific food items within wild capuchin groups. Second, I sought to determine if such correlations reflect social influences on foraging and food processing patterns. Finally, I attempted to determine if such patterns should be taken as evidence for social traditions, or patterns of 'culture', among wild capuchins.

METHODS

A detailed description of the study site, subjects, data collection methods, and other analyses conducted as part of this research have been provided elsewhere (**Chapter II**).

Analyses

Individuals who were seen to use one of the specific processing techniques (**Table 3-1**) identified for *Luehea candida, Sloanea terniflora,* or 'large caterpillars' were identified as such during the course of previous analysis (see **Chapter II**). The 'eviscerate' technique for 'large caterpillars' was seen in both groups, but is only recorded in focal data for one individual in the LV group, and so analyses of that pattern were limited to the CP group.

Food Interest

I tallied the total number of 'direct/receive food interest' bouts ('actively observing the foraging or food processing behaviour of a conspecific without interfering in their activities') to see which age/sex classes most often showed interest in others' feeding and processing behaviour, and which age/sex classes were most often the focus of interest. The data set was too small to examine rates of food interest for specific food items.

Proximity

Modeling the methodology of Panger *et al.* (2002) and using the proximity data gathered at the beginning of each focal session, I calculated 'proximity scores' for each dyad of individual group members, excluding infants. These scores were calculated by tallying 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 bouts of aggressive behaviour, threats, and supplantations among individuals (**Table 3-2).** I scored each individual based on the number of such bouts towards each of the other members of the group to establish social rank (**Table 3-3**). Mann-Whitney U-tests (one-tailed) were used to determine if individuals seen to use a given processing technique were, on average, of higher rank than those that did not.

Relatedness

The degree of relatedness, or 'kinship', between two individuals in the same group, as measured by the percent of their genetic material they would on average share with relatives, were assigned for each dyad (**Table 3-4**) in a manner comparable to that described for 'proximity scores' above, producing a 'relatedness score.' '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 had higher mean relatedness scores than unmatched dyads.

Statistical issues

Because Mann-Whitney U-tests for each social network (proximity scores, rank, and relatedness) were conducted for multiple processing techniques, there is an increased risk of a Type I error (i.e., incorrectly rejecting the null hypothesis) (Chandler 1995, Cabin & Mitchell 2000). To address this issue, an appropriate Bonferroni correction was applied to the alpha used for the intra-group analyses of each social network. However, because there is also a high risk of a Type II error (i.e., incorrectly failing to reject a null hypothesis) due to the small sample sizes of this study, I feel I am justified in discussing results found to be significant at the unadjusted alpha level ($P = .05$) as well. It should also be noted that the analysis of dyads employed by Panger *et al.* (2002) may be of questionable statistical validity due to an issue of pseudoreplication (Hurlburt 1984). Because each individual contributes more than one data point to the data set, data points may not be independent. Future studies attempting to examine variation in processing patterns within the context of social networks may need to consider exploring alternative analytical methods.

RESULTS

Food Interest

Individuals of all age/sex classes (including infants) showed interest in others' foraging and food processing behaviour (**Table 3-5**), but juveniles engaged in bouts of food interest far more frequently than infants, immatures, or adults. Bouts of food interest were directed at adult females and adult males most frequently, and usually towards individual consuming vertebrate or invertebrate prey (including *Acacia* ants in thorns) as opposed to plant foods. On numerous occasions, I observed non-adults in both groups abandon their own food processing efforts with *Sloanea* fruits or *Acacia* thorns when they appeared to be having difficulty, and move to a position where they could observe adults processing or consuming the same food (my impression was that this was usually the closest such individual). In most such situations, individuals had appeared to run afoul of the food items' defences (in the case of *Sloanea*, the stinging hairs, and in the case of *Acacia* thorns, being swarmed by ants). No attempt was made by the observer to beg for food or interfere with the processing behaviour of the other animal. The animal being observed usually appeared comfortable with the observer's presence, even at close range (<1m). Such intent observation appeared quite different from more directed efforts that were observed on other occasions to beg or scrounge food (such as when the food was vertebrate prey), which often included attempts to touch or taste the food item, pull it away from its possessor, or tear portions away.

The prevalence of the various food processing techniques discussed below were summarized before analysis (**Table 3-6**).

Proximity

Matched dyads of individuals exhibiting the differentiated hand use (or 'rub and brush') *Sloanea* processing pattern did not have a significantly higher mean proximity score than unmatched dyads in either group (**Table 3-7**). Proximity scores for matched dyads of individuals seen to use the differentiated hand use (or 'pound and catch') *Luehea* processing pattern were found to be significantly higher than those for unmatched dyads in both groups at P = .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, and so proximity scores of matched dyads showing that technique were also significantly higher than those that did not at the P = .05 level, but not after appropriate Bonferroni correction (this correlation between 'pound and catch' and 'skilled pound' in CP obviously holds true for later analyses as well). 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 differentiated hand use (or 'rub and brush') *Sloanea* processing technique did not have a significantly higher rank than those that did not show the pattern in either group (**Table 3-8**). Individuals seen to use the differentiated hand use (or 'pound and catch') *Luehea* processing pattern did have a significantly higher mean rank than those that did not in the CP group (even after an appropriate Bonferroni correction), but not in the LV group. Individuals in the CP group seen to 'eviscerate' large caterpillars did not have a significantly higher mean rank than those individuals that did not.

Relatedness

Dyads of individuals exhibiting the 'rub and brush' *Sloanea* processing pattern did not have a significantly higher mean relatedness score (i.e., were not more closely related) than all other dyads in either group (**Table 3-9**). Relatedness scores for matched dyads of individuals seen to use the differentiated hand use (or 'pound and catch') *Luehea* processing pattern were not significantly higher than those of unmatched dyads in either group. Relatedness scores for 'matched' dyads of individuals seen to eviscerate large caterpillars in the CP group were not significantly higher than those of 'unmatched' dyads.

DISCUSSION

Food Interest

Observed patterns of food interest bouts across age/sex classes in this study suggest that situations conducive to social learning in foraging or food processing contexts occur among individuals of all age/sex classes, but are most frequently instigated by juveniles and immatures. 'Food interest' bouts are most frequently directed towards adult females and adult males, who are likely to be better or more skilled models relative to non-adults. Being able to observe what 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 which could have consequences if toxic or unpalatable foods are consumed (Janson & van Schaik 1993). Though social learning processes involved in the acquisition of dietary knowledge are presumed to be fairly simple (i.e., social facilitation, or 'an increased probability of performing a behaviour in the presence of others performing the same behaviour'), observing how others eat, as well as what they eat, nevertheless may provide important opportunities for social transmission of information.

A series of experiments spearheaded by Visalberghi & Fragaszy (1995; also see Fragaszy *et al.* 1997, Visalberghi *et al.* 1998, Visalberghi & Addessi 2000, 2001) have found that a social setting may reduce neophobia towards unfamiliar foods among captive capuchins (Visalberghi & Fragaszy 1995, Visalberghi & Addessi 2000), though younger individuals appeared to show less caution about novel foods than older animals, and do not selectively seek information from adults about such foods (Fragaszy *et al.* 1997). These researchers also argue that social transfer of information is not required for the development of group-homogeneous diet (at least in captivity), though it might speed the process. In contrast to these findings, research on wild populations has shown that intra-group diets and foraging patterns are not homogeneous (Fragaszy 1986, Rose 1994, Fragaszy & Boinski 1995, Hall 1995), that groups living in similar habitats do not necessarily have very similar diets (Chapman & Fedigan 1990, Panger *et al.* 2002), and that the acquisition of complex processing techniques for specific foods do appear to be socially influenced to some degree (Boinski *et al.* 2000, Panger *et al.* 2002). It may therefore be premature to downplay social influences on the development of dietary preferences, at least without further research on free-ranging groups, or from a more diverse set of groups in captivity.

The very intent interest shown by juveniles towards individuals engaged in complex processing behaviour (such as with *Sloanea* fruits or *Acacia* thorns) is reminiscent of similar observations of capuchins in similar contexts, both in captivity (i.e., Anderson 1990, Adams-Curtis & Fragaszy 1995) and the wild (Boinski *et al.* 2000). Even if scrounging food is the primary motivation behind such intense visual monitoring, such attention could still 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 & van Schaik 1993), it seems likely that such observation of conspecifics must be of some benefit to the observer. An obvious explanation is that the observer is seeking to learn something about the task.

Because the consequences of food choice in a natural setting are quite different than those in captivity, study of free-ranging groups seems a more appropriate 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 captive studies thus far (Ottani & Mannu 2001, Garber & Brown 2002, also see **Chapter IV**).

Sloanea terniflora

None of the social networks examined here appeared to have any relationship to the expression of the only complex processing technique ('rub and brush') in *Sloanea* for which enough variability was observed to quantify. 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. As explained in **Chapter II**, the lack of diversity in *Sloanea* processing patterns may reflect that there is only one 'right' way to process *Sloanea* fruits (i.e., rub). 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 discernable influence from intra-group social networks, indicates that the acquisition of the 'rub and brush' processing pattern in *Sloanea* rubbing is likely relatively rapid for young monkeys, though skill at such patterns would increase with practice. Asocial influences (i.e., individual preferences, dietary strategies in different age/sex class, physical constraints, etc.) appear sufficient to explain variability in *Sloanea* processing (see **Chapter II**), though observations of conspecifics engaging in such behaviour could still be of benefit to an unskilled observer and serve to channel their efforts.

Luehea candida

Variation in forms of processing of *Luehea candida*, previously shown to vary across age/sex classes (**Chapter II**), also appears to be influenced by social networks. Relatedness had no significant relationship with the presence or absence of differentiated hand use in *Luehea* pounding in either group. Though individuals using the 'pound and catch' and 'skilled pound' techniques spent more time in proximity in both the CP and LV groups relative to those that did not, these results were not significant after a Bonferroni correction to the alpha. Rank did appear to be significant factor in predicting *Luehea* processing patterns within the CP group, with the four highest-ranking individuals the only ones to exhibit the 'pound and catch' and 'skilled pound' patterns.

Why might both rank and patterns of association influence forms of *Luehea* processing, when such factors have no apparent influence in the other food processing patterns examined in this study? 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 would not mature synchronously, and even pods on the same tree showed would often dehisce several weeks apart (O'Malley, personal obs.). Seeds can be extracted from a *Luehea* pod that has only just begun to open, but this is far more difficult than in more mature pods. Adult and immature 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 either 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 on one occasion, though many others 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. When pods dropped by the capuchins were examined, pods that were more fully dehisced usually contained few or no seeds, while immature pods usually still had many seeds wedged inside.

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 'better' (i.e., more mature) *Luehea* fruits (see **Fig 2-6** in **Chapter II**). More mature pods likely require less force to dislodge seeds, and rarely require the monkey 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), as well as allowing those monkeys capable of manipulating the pod in one hand (i.e., adults & immatures) to free up their other hand for catching seeds instead of for postural support (leading to the 'pound and catch' pattern). Dominant capuchins will readily supplant subordinates from valued food items (Di Bitetti & Janson 2001, O'Malley, personal observation); fully dehisced *Luehea* pods may be such a prize.

That rank may play a major role in explaining the *expression* of *Luehea* processing patterns that I observed does not conflict with the finding that patterns of association (i.e., proximity) may also have an influence on the acquisition and maintenance of processing patterns. Dyads of individuals exhibiting the more complex 'pound and catch' and 'skilled pound' processing patterns spent more time with each other than with those who did not exhibit these techniques in both study groups. This supports the work of Panger *et al.* (2002) who examined patterns of processing for different foods, although their analyses were at a broader level. Regardless of the social learning processes involved (Whiten & Ham 1992), it seems likely that the acquisition and persistence of these patterns in individuals is to some degree socially mediated.

Large caterpillars

None of the social networks examined had a significant influence on the presence of this processing pattern among members of the CP group. The more parsimonious explanation would be that it is experience (presumably greater among older animals) that leads to the development of this qualitatively more skilled technique.

Capuchins are not the only Cebine species to show a high degree of manipulative skill in processing caterpillars or other invertebrates (Janson & Boinski 1992). Boinski & Fragaszy (1989) collected data on the ontogeny of foraging behaviour 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, though they did so more overtly than older animals. Though they provide some anecdotal evidence that young squirrel monkeys may learn which caterpillar species to avoid (because of particularly poisonous spines, for example) through observation of conspecifics, the authors 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. This research has found no evidence to suggest that the development of caterpillar processing techniques in *Cebus capucinus* is any different from that reported by *Saimiri*. 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 observation).

Evidence for Social Traditions?

The foraging behaviours described here appear, for the most part, to vary independently of social networks. However, processing patterns for one food item (*Luehea candida*) appeared to be consistently influenced by social networks to some degree. The finding that individuals in both groups who spend more time in proximity appear 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. This would meet the definition of a social tradition: "*group-specific behaviour that is acquired, at least in part, from social influences*" (McGrew 1998). However, that rank also plays a role could indicate that the use of these patterns reflects opportunity for expression rather than knowledge. For example, a low-ranking adult female may know of 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. The presence of higher-ranking individuals has been shown to suppress the expression of socially learned behaviour in low-ranking macaques, even when it can be shown that such individuals have learned the behaviour in question (Drea & Wallen 1999); a similar effect may be at work here. Future research exploring patterns of intra-group variability in processing patterns in *Cebus* would do well to consider rank as a potential influence in predicting individual foraging techniques, in addition to patterns of association, variability across age/sex classes, or other factors discussed here.

No robust inter- or intra-group patterns of variability in *Acacia* ant thorn processing were observed that warranted examination within the context of social networks (See **Chapter II**). However, the qualitative differences in patterns of *Acacia* thorn predation by capuchins as described by Freese (1976) and those observed in this study are noteworthy, and may be worthy of more in-depth research. As discussed in detail in the previous chapter, the capuchins observed in this study overwhelmingly targeted single, 'detached' thorns for processing. In contrast, the two common processing techniques described by Freese (1976) in his study of capuchins in Santa Rosa involved the detachment and processing of multiple thorns at once, and the processing of thorns still attached to the tree. Even without quantitative details on thorn processing techniques across individuals and age/sex classes, it is difficult to imagine a developmental or environmental explanation for the differences in the processing methods used in the 1970's compared to those used in 2000-2001. That Santa Rosa capuchins appear to be processing *Acacia* thorns using fundamentally different techniques today then what were reported twenty years ago may reflect intra-group social traditions. Such intra-group differences may still be present within Santa Rosa or across other research sites in Costa Rica, but without detailed descriptions on *Acacia* thorn processing techniques for other groups and sites, this remains only speculation.

Both Panger *et al.* (2002) and Perry *et al.* (in press) note that distinctive behavioural patterns, such as 'tapping' sticks and branches in search of embedded insects, or certain grooming or play conventions, appear to rise, spread, and disappear relatively quickly in capuchin populations. Temporal differences in *Acacia* thorn processing may simply reflect the fluid and impermanent nature of capuchin foraging strategies, but this should not be assumed. It would be informative to study the behaviour of other, more distant capuchin groups in Santa Rosa or elsewhere in order to compare *Acacia* thorn processing techniques.

Understanding Nonhuman Social Traditions

In recent years, a number of authors have challenged current views on the relevance of the genus *Cebus* in understanding the evolution and significance of social traditions in nonhuman primates (Boinski *et al.* 2000, Panger *et al.* 2002, Perry *et al.* in press). What implications do these findings, and those presented in this study, have for studies of nonhuman culture?

As noted by Panger *et al.* (2002), a high degree of cross-population variability in foraging patterns, previously described in chimpanzees and orangutans, appear to be present in *Cebus capucinus* as well. In all three genera, distinct processing techniques have been observed at some sites but not at others. Other food processing patterns are observed at all sites but are employed for different foods, and at different frequencies. That capuchins demonstrate such a degree of socially influenced variability in the wild calls into question the importance of specific cognitive abilities or social learning processes in understanding the development of social traditions (e.g., Galef 1992, Visalberghi 1997). Likely of greater importance are the shared socio-ecological characteristics of capuchins, chimpanzees, and orangutans identified by van Schaik *et al.* (1999) as necessary precursors to the evolution of material culture.

Despite these similarities, it is important not to lose sight of the differences that remain. In both chimpanzees and orangutans, many social traditions in foraging behaviour incorporate the manufacture and use of tools (McGrew 1992, 1998, Whiten *et al.* 1999). The lack of habitual tool use and manufacture in wild capuchins means that any variability in foraging and/or food processing for specific foods is likely to be fairly subtle (e.g., in patterns of manipulation, hand use patterns, etc.) and so research focusing on such details (in the manner described in this chapter, and in **Chapter II**) will be necessary. This should not be seen as a handicap; in fact, exploring these 'finer points' of foraging and food processing has led to some of the most thought-provoking studies of wild chimpanzees. It has been demonstrated, for example, that the 'pull through' technique employed at the Gombe research site is a far more efficient means to fish for driver ants than the simpler techniques used by chimpanzees of the Tai forest (McGrew 1974, Boesch & Boesch 1990). Similarly, McGrew & Marchant (1999) have shown that individuals who show a right- or left-hand preference in termite fishing are more efficient than those that do not demonstrate such lateralization.

Boinski *et al.* (2000) suggest that the manipulative abilities of wild capuchins weakens the argument for the proposed link between the evolution of intelligence, tool use, language, and complex sociality (Washburn 1960, Hamilton 1974, Parker & Gibson 1977, 1979, Westergaard 1995), arguing that despite their propensity for skilled object manipulation, capuchins do not show markedly more complex vocal behaviour or patterns of sociality relative to other monkeys. I would argue that the latter, at least, is highly questionable. Other researchers (e.g., Perry *et al.* in press) have noted that capuchins spend an inordinate amount of time maintaining social relationships, and engage in complex social interactions such as food sharing (de Waal 1997, Rose 1997, O'Malley personal obs.) that are rare in most nonhuman primates other than the genus *Pan*. Wild capuchins have also been observe to engage in social games that incorporate social interactions such as 'turn-taking' (Perry *et al.* in press), believed to be a difficult 'cognitive leap' for most primates to make.

Resolving these differences of opinion within the discipline seems likely to become an important issue in future capuchin research efforts.

The growing evidence for social traditions, or 'culture', in wild capuchins brings with it a note of caution, as well. It may be that a high degree of cross-population behavioural variability in wild chimpanzees (in a foraging context or otherwise), and the strong degree of social influence on such variability, may not be particularly rare characteristics in the primate order, or among animals in general (Whiten *et al.* 1999, Panger *et al.* 2002). There is an impressive (and still growing) body of work on social traditions across non-primate genera (e.g. Diamond 1987, Terkel 1996, Rendall & Whitehead 2001, Galef in press) that primatologists and anthropologists should not fail to acknowledge in discussions of the evolution of nonhuman culture (McGrew 1998).

In summary, the growing evidence for social traditions among wild capuchins calls into question many long-standing distinctions drawn between the degree of behavioural variability of hominids and that of other nonhuman primates (and perhaps other animals as well). In particular, recent work by a number of authors, as well as that presented here, has raised new questions regarding the relative significance and uniqueness of 'cultural' variability across wild populations, and will hopefully serve to spur future research efforts on this topic.

CONCLUSIONS

The research discussed in this chapter sought to address several key questions. *To what degree do social networks (patterns of proximity, rank, and kinship) correlate with foraging or food processing patterns for specific food items within groups?*

Intra-group differences in *Sloanea* and large caterpillar processing techniques do not appear to be related to rank, proximity, or relatedness. Individuals seen to employ specific *Luehea* processing techniques collectively spent more time in association than those that did not (in both groups), and (in the CP group) tended to be of higher rank, though only the latter finding was significant after an appropriate statistical correction.

Do such correlations reflect social influences on foraging and food processing patterns?

Differences in *Luehea* processing techniques within and between groups may reflect some degree of social influence. In particular, rank is likely to influence pod choice in *Luehea* consumption, which in turn may influence the processing techniques employed. Patterns of association appear to influence whether complex processing techniques are employed or not, which suggests that some form of social influence may be at work in the maintenance of these behaviour patterns.

Do such influences represent evidence for social traditions?'

Evidence for social traditions in foraging and food processing techniques presented in this study is largely absent or inconclusive. However, processing patterns employed for *Luehea candida* appear to qualify as social traditions, and should be examined further. Though I observed no strong inter- or intra-group differences in *Acacia* ant thorn processing patterns in this study, difference in the general techniques observed in 2001 compared to those reported in an earlier study may also reflect social traditions in food processing, and also warrant further inquiry.

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TABLES

Table 3-1: Complex food processing techniques identified for specific food items.

Sloanea terniflora	
"Rub & Brush"	Moving a fruit or fruits rapidly back and forth against a substrate with one hand while flailing and brushing against it with the other hand. The presumed function of this technique is to facilitate the removal of the urticating hairs, and keep them from flying in the individual's eyes. Also referred to as 'differentiated hand use' in Chapter II.
Luehea candida	
"Pound & Catch"	Hammering a seed pod against a substrate with one hand, while the other hand is cupped below, or braced against the substrate, to catch seeds as they come out. Also referred to as 'differentiated hand use' in Chapter II.
"Skilled Pound"	Extremely rapid pounding of pods against a substrate, with no pause in hammering when the seeds are slurped or scooped up for consumption.
Large caterpillar	
"Eviscerate"	Tearing open one end of a caterpillar and flicking out the gut contents in one smooth motion.

Table 3-2: 'Directed' or 'received' behaviours used to establish dominance matrixes

Behaviour type	**Description**
Low-grade agonism	non-contact agonistic interaction, such as chase, screams, etc.)
Medium-grade agonism	contact agonistic interaction, such as slapping, grabbing, etc.)
High-grade agonism	agonistic interaction resulting in obvious injury, bleeding, etc.)
Display	rapid leaping and vocalizing while piloerected
Branch drop	detaching or dislodging branches over a subject so that they fall
Threat	open-mouth 'threat face' with teeth bared
Double-threat	a 'threat' as above in conjunction with one or more other individuals nearby, directed at the same individual
'Overlord' threat	a 'double threat' as above, with the individuals involved 'stacking' themselves so that two or more monkeys are threatening together
Supplantation	actively or passively causing another animal to move or abandon a position or object by approaching

Table 3-3: Dominance matrixes for the CP and LV groups

	Rank	CP	LI	NO	NY	TR	SI	RA	PO	ED	TI	SE	ZZ	
	1	LI		1	0	1	1	2	2	5	3	2	8	25
	2	NO	0		0	1	1	1	1	0	0	1	1	6
	3	NY	0	0		0	1	0	2	7	0	1	3	14
	4	TR	0	0	0		0	1	0	1	2	0	1	5
	5	SI	0	0	0	0		0	2	3	6	6	4	21
director	6	RA	0	0	0	0	0		0	1	0	1	2	4
	7	PO	0	0	0	0	0	0		0	1	5	8	14
	8	ED	0	0	0	0	0	0	0		3	0	3	6
	9	TI	0	0	0	1	0	1	1	2		2	0	7
	10	SE	0	0	0	0	0	0	0	1	0		1	2
	11	ZZ	0	0	0	0	0	0	0	0	0	0		0
		Total	0	1	0	3	3	5	8	20	15	18	31	

	Rank	LV	PI	KL	AO	CH	DL	SD	TO	PR	AL	MY	SL	BL	FI	SY	
	1	PI		0	0	0	0	0	0	0	1	0	1	0	1	0	3
	2	KL	0		3	2	0	0	1	0	0	0	1	1	0	6	14
	3	AO	0	1		0	1	0	0	2	1	0	0	0	1	0	6
	4	CH	0	0	0		0	0	0	0	0	0	0	0	0	0	0
director	5	DL	0	0	0	0		0	0	0	0	1	0	0	2	6	9
	6	SD	0	0	0	0	0		1	0	0	1	0	0	1	0	3
	7	TO	0	0	0	0	0	0		0	2	0	0	0	0	0	2
	8	PR	0	1	0	0	2	0	0		3	0	0	1	0	0	7
	9	AL	0	0	0	0	0	0	0	1		2	0	1	0	1	5
	10	MY	0	0	0	0	0	0	0	1	0		0	3	0	0	4
	11	SL	0	0	0	0	0	0	0	0	1	0		0	0	1	2
	12	BL	0	0	0	0	0	0	0	0	0	0	0		0	0	0
	13	FI	0	0	0	0	0	0	0	0	0	0	0	0		0	0
	14	SY	0	0	0	0	0	0	0	0	0	0	0	0	0		0
		Total	0	2	3	2	3	0	2	4	8	4	2	6	5	14	

Table 3-4: Kinship scores for individual dyads based on coefficients of relatedness (Krebs & Davies 1993: 266-67).

Parent-offspring	.50
Grandparent-grandkid	.25
Full sibling	.50
Half-sibling	.25
Aunt-niece/nephew	.25
Cousin-cousin	.125
No known relationship	.00

Table 3-5: Observed bouts of food interest (by age/sex class)

		receive food interest					
		Infant	Juvenile	Immature	AdFemale	AdultMale	
	Infant	0	7	3	3	2	15
direct	Juvenile	0	7	9	21	1	38
food	Immature	0	0	0	6	9	15
interest	AdultFemale	1	0	3	2	4	10
	AdultMale	0	0	1	5	4	10
		1	14	16	37	20	88

Table 3-6: Summary of food processing patterns for the CP (upper set) and LV (lower set) groups. Blank cells for specific techniques indicate that the processing pattern in question was not observed for that individual.

Subject	Rank	Age/Sex	Skilled pound *Luehea*?	Pound and catch' *Luehea*?	Rub and brush' *Sloanea*?	Eviscerate caterpillar?
LI	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	ImMale				
PO	7	AdFem			yes	
ED	8	JuvFem				
TI	9	ImFem			yes	
SE	10	AdFem				yes
ZZ	11	JuvFem				

Subject	Rank	Age/Sex	Skilled pound *Luehea*?	‘Pound and catch' *Luehea*?	‘Rub and brush' *Sloanea*?	Eviscerate caterpillar?
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	ImMale		yes		
PR	8	AdMale		yes	yes	
AL	9	ImMale		yes	yes	
MY	10	JuvFem			yes	
SL	11	ImFem			yes	
BL	12	AdFem			yes	yes
FI	13	AdFem		yes	yes	
SY	14	ImFem				

Table 3-7: 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). "*" indicates statistical significance in the predicted direction with an alpha of P = .05, while "**" indicates statistical significance after an appropriate Bonferroni correction (resulting in an alpha of P = .013 for the CP group, and .025 for the LV group).

		Dyad type	N	mean	S.D.	range	z-score	p-value (1-tailed)
CP Group	***Sloanea terniflora***							
	rub & brush	matched	10	0.084	0.060	.022-.233	-0.938	0.174
		unmatched	45	0.092	0.046	.015-.209		
	Luehea candida							
	pound & catch	matched	6	0.129	0.062	.066-.233	-1.674	**0.047** *
		unmatched	49	0.086	0.045	.015-.209		
	skilled pound	matched	6	0.129	0.062	.066-.233	-1.674	**0.047** *
		unmatched	49	0.086	0.045	.015-.209		
	Large caterpillars							
	eviscerate	matched	6	0.119	0.076	.015-.233	-1.026	0.153
		unmatched	49	0.087	0.043	.015-.209		
LV Group	***Sloanea terniflora***							
	rub & brush	matched	66	0.061	0.050	.000-.233	-0.516	0.303
		unmatched	25	0.061	0.039	.000-.139		
	Luehea candida							
	pound & catch	matched	28	0.075	0.049	.000-.175	-1.884	**0.030** *
		unmatched	63	0.055	0.046	.000-.233		

Table 3-8: Mann-Whitney U-tests comparing social rank with processing techniques used by each individual. "*" indicates statistical significance in the predicted direction with an alpha of P = .05, while "**" indicates statistical significance after an appropriate Bonferroni correction (resulting in an alpha of P = .013 for the CP group, and .025 for the LV group).

		Used technique?	**N**	**mean**	**S.D.**	**range**	**z-score**	**p-value (1-tailed)**
CP Group	***Sloanea terniflora***							
	rub & brush	Yes	5	4.80	3.194	1 - 9	1.095	0.137
		No	6	7.00	3.347	2 - 11		
	Luehea candida							
	pound & catch	Yes	4	2.50	1.291	1- 4	-2.646	**0.004** **
		No	7	8.00	2.160	5 - 11		
	skilled pound	Yes	4	2.50	1.291	1- 4	-2.646	**0.004** **
		No	7	8.00	2.160	5 - 11		
	Large caterpillars							
	eviscerate	Yes	4	4.00	4.082	1 - 10	-1.512	0.065
		No	7	7.14	2.410	4 - 11		
LV Group	***Sloanea terniflora***							
	rub & brush	yes	12	7.00	4.068	1 - 13	1.095	0.137
		No	2	10.50	4.950	7 - 14		
	Luehea candida							
	pound & catch	Yes	8	6.63	3.503	2 - 13	-0.904	0.183
		No	6	8.67	5.046	1 - 14		

Table 3-9: Mann-Whitney U-tests comparing relatedness scores of 'matched' dyads (between individuals seen to use a specific technique) and 'unmatched' dyads (between all other dyads). "*" indicates statistical significance in the predicted direction with an alpha of P = .05, while "**" indicates statistical significance after an appropriate Bonferroni correction (resulting in an alpha of P = .013 for the CP group, and .025 for the LV group).

		Dyad type	N	mean	S.D.	range	z-score	p-value (1-tailed)
CP Group	***Sloanea terniflora***							
	rub & brush	matched	10	0.100	0.175	.000-.500	-2.027	0.022
		unmatched	45	0.250	0.213	.000-.500		
	Luehea candida							
	pound & catch	matched	6	0.167	0.258	.000-.500	-0.749	0.227
		unmatched	49	0.230	0.209	.000-.500		
	skilled pound	matched	6	0.167	0.258	.000-.500	-0.749	0.227
		unmatched	49	0.230	0.209	.000-.500		
	Large caterpillars							
	eviscerate	matched	6	0.167	0.258	.000-.500	-0.749	0.227
		unmatched	49	0.230	0.209	.000-.500		
LV Group	***Sloanea terniflora***							
	rub & brush	matched	66	0.028	0.109	.000-.500	-1.696	0.045
		unmatched	25	0.080	0.173	.000-.500		
	Luehea candida							
	pound & catch	matched	28	0.054	0.157	.000-.500	-0.040	0.484
		unmatched	63	0.038	0.118	.000-.500		

CHAPTER IV: Conclusions

"Our principal aim is to understand traditions as biological phenomena."
(Fragaszy & Perry, in press)

In the wild, capuchin monkeys show a high degree of variability in foraging and food processing patterns across species (Janson & Boinski 1992), populations (Panger *et al.* 2002), and even neighbouring groups in similar habitat (Chapman & Fedigan 1990). Within groups, rates, types, and forms of foraging and food processing behaviour vary between age/sex classes (Fragaszy 1986, 1990, Fragaszy & Boinski 1995, Rose 1994), and are influenced by rank (Hall 1995) and patterns of association (Panger *et al.* 2002).

The research I have presented here provides the first detailed quantitative data on inter- and intra-group variability in processing techniques for specific foods consumed by white-faced capuchins (*Cebus capucinus*) in the wild. As expected, much of this variability appears to reflect ecological differences in the habitats of different groups, and differences in the physical abilities, cognitive abilities, and foraging strategies of different age/sex classes. However, I have also presented evidence that patterns of variation in foraging and food processing are (to some degree) socially influenced. Most notably, the expression of distinct complex food processing techniques in *Luehea candida* pods appears to correlate with patterns of association: individuals who spend more time in proximity appear more likely to share common patterns of behaviour than those who are less affiliative. In other words, the *expression* of specific complex behaviours appears to correlate with *opportunities to observe* such behaviour in others. This research bolsters the recent claim by Panger *et al.* (2002) and others (Boinski *et al.* 2000, Perry *et al.* in press) that patterns of behavioural variability said to reflect social traditions in chimpanzees and orangutans (van Schaik *et al.* 1999, Whiten *et al.* 1999) may be present in capuchin monkeys as well. However, because of the small sample size and the relatively weak patterns that I observed, these conclusions should be considered preliminary.

Cebus *and* Pan *compared*

The most robust 'cultural' patterns of variation in food processing behaviour among chimpanzees 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; for example, population-level differences in tool materials and techniques used to dip for driver ants (McGrew 1974, Boesch & Boesch 1990) or to dig for and capture termites or ants (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 & Boesch 1993, Sugiyama 1993, van Schaik *et al.* 1999). It has also been possible to conduct more focused analyses; for example, to compare efficiency of different foraging or food processing patterns for specific foods within and across sites (McGrew 1974, Boesch & Boesch 1990, McGrew & Marchant 1999), and to consider the potential benefits and consequences for individuals who adopt, or fail to adopt, more efficient or effective techniques.

With this study, complex techniques for specific food items (involving coordinated hand use and requiring a high degree of hand-eye coordination and manipulative skill) have for the first time been presented 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? Are their other levels of variation (such as grip, or maturity of the pods targeted) present within or across sites? Preliminary studies on foraging variability in wild *Cebu*s (Boinski *et al.* 2000, Panger *et al.*

2002) including the research presented here, suggest that these and other questions are worthy of further study.

'Towards A Biology of Traditions'

Fragaszy & Perry (in press) highlight a number of major problems that hamper discussion of social traditions in nonhuman primates and other animals. They challenge a number of common perceptions among researchers of social traditions, such as whether specific forms of social learning are required for social traditions to be considered (Galef 1992, Whiten & Ham 1992, Heyes 1993), whether it is necessary for a behavioural pattern to persist across generations to be 'traditional' (e.g. McGrew 1998, Whiten *et al.* 1999), whether attempting to rule out purely asocial influences (such as environmental factors) on behavioural variability before considering social ones is sensible, or even possible (Ingold 1993, 1998, McGrew 1998), and whether the special status afforded those taxa most closely related to humans (particularly *Pan*) in discussion of social traditions is warranted (Fragaszy & Visalberghi 1996). They seem to view the many disagreements over these and other issues, and the extent to which they have been or can be addressed in studies of social traditions, as drawing focus away from what should be the real issue: understanding traditions as biological phenomena. In response, they call for a new perspective, grounded more firmly in ethological explanations of behaviour, in terms of mechanism, ontogeny, evolution and function (Tinbergen 1963).

I do not believe it will be possible for those researchers interested in 'the biology of traditions' to set aside the implications (and ongoing controversy) that studies of 'nonhuman culture' have for studies of *human* learning and culture, given the spirited and long-standing disagreements that persist within psychology, sociology, and anthropology regarding their nature and significance (see McGrew 1998 for a relevant discussion). That being said, I support a shift in focus towards more ethological explanations for variability in behaviour. As noted by Fragaszy & Perry (in press), the socio-ecological traits of capuchins make them particularly well suited for such an approach of traditions or potential traditions. I hope that the research presented here has made a useful contribution to this effort.

Directions for future research

What contributions can field researchers make to the study of social traditions? Fragaszy & Perry (in press) note that field research, particularly with nonhuman primates, can never hope to approach the rigorous experimental protocols possible in captivity, and that the "most effective use of information from naturalistic observations is to analyze patterns of behaviour across sites." I would add, based on the results of this research, that patterns of variation within sites could be equally important, and should not be ignored in favour of broader comparisons.

I would also suggest that an experimental approach should not be left entirely to those researchers working in a captive setting, particularly in regards to nonhuman primates, which often show profound differences between captive and wild settings (e.g., handedness; McGrew & Marchant 1997). As noted by Boinski *et al.* (2000), capuchins in the wild are presented with fundamentally different ecological, energetic, dietary, social, and cognitive challenges than their captive counterparts. To the degree that it is possible to do so, results from captive experimental studies should be confirmed independently in wild populations (e.g., wild capuchins' response to a tool use task; Garber & Brown 2002). To do otherwise seems counterproductive if we are seeking to understand traditions as biological phenomena.

Response by Wild Capuchins to an Extractive Task

Researchers who conduct experiments on primate behaviour in the wild (e.g., Matsuzawa 1994, Garber & Brown 2002), particularly those involving complex manipulation, must take care not to alter the very patterns of behaviours they seek to examine (McGrew 1998). With care, however, I believe it is possible to develop and conduct informative experimental protocols that nonetheless have a minimal impact on the general behaviour patterns of the subjects involved. To explore this possibility, a simple pilot study was conducted during the 2001 field season with the Cerco de Piedra capuchin group.

Over the course of April and early May, when water is a particularly limited resource in Santa Rosa (Freese 1978), I presented the CP group with a novel source of water during the late dry season. The water source (a sturdy plastic container) was established at the same location as the group's normal water source (an artificial spring), so as to have a minimal impact on their daily ranging behaviour. After allowing the group to grow accustomed to this water tube (**Figure 4-1**), blocks were put in that severely hampered the capuchins' ability to access the water inside (**Figure 4-2**). The first such block was a plastic bolt that had to be uncapped and drawn out the side of the tube. The second was a wooden block with a thin metal bar running through it; the wooden block could not be pulled out until the bar was removed. The goal of this research was not to provide conclusive evidence for or against specific social learning processes in capuchins, or to evaluate the comprehension of the task requirements on the part of the capuchins, but only to see whether (a) wild capuchins were capable of the sustained manipulative interest observed in captive capuchins presented with similar extractive tasks, and (b) to observe the degree to which the capuchins were monitoring and/or modeling each others' attempts to solve the task.

The capuchins showed immediate interest in the water tube, and within a week of their initial exposure, all group members were observed to drink from it at least once. Even after the 'blocks' were added, their interest continued, with individuals of all age/sex classes attempting to manipulate, remove, or bypass the blocks to access the water (**Figure 4-3**). Individuals showed keen interest in the efforts of their fellow group members, and some appeared to monitor the efforts of their group mates even if they had already gotten their fill of water from the artificial spring. Before the rains returned in late May (effectively terminating the experiment), two individuals had solved the task (**Figure 4-4**), though they did so independently while no others were observing them, so there was no opportunity to observe how other group members might have benefited from observing their successful efforts. Given these results of this preliminary study, I would suggest that the possibilities for experimental studies of manipulation in the wild have been underestimated. Such research need not have a large impact on the groups' foraging and ranging behaviour, nor would it require the introduction of novel foods or new forms of behaviour. Though it will never be possible to achieve the same degree of control in a wild experimental study as is possible in captivity, there is clearly potential for extractive experiments involving water with capuchins in a dry forest habitat that remains unexplored.

While experimental research on the manipulative and cognitive abilities of capuchins and other primates will always rely primarily on studies from captivity, opportunities to examine such abilities in the wild should not be ignored, particularly if these abilities and their relationship to the phenomenon of social traditions are to be understood from an ethological perspective.

Conclusions

This research has bolstered the growing body of evidence that members of the genus *Cebus* demonstrate a capacity for social traditions in the wild in foraging patterns and food processing techniques (Boinski *et al.* 2000, Panger *et al.* 2002), and in other contexts (Perry *et al.* in press) consistent with what has been observed in the great apes (McGrew 1998, van Schaik *et al.* 1999, Whiten *et al.* 1999). Further research on the issues addressed in this thesis, particularly regarding variability among groups and populations of *Cebus* in the wild, will serve to further illuminate the nature and significance of such complex manipulation patterns.

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Figure 4-1: Capuchins drinking from the water tube. The individuals are 'Li' (an adult female with dependent infant 'Sz') and 'Ra' (an immature male). On the second day of exposure, several individuals used the water tube for the first time. Within a week, all group members were using the water tube regularly.

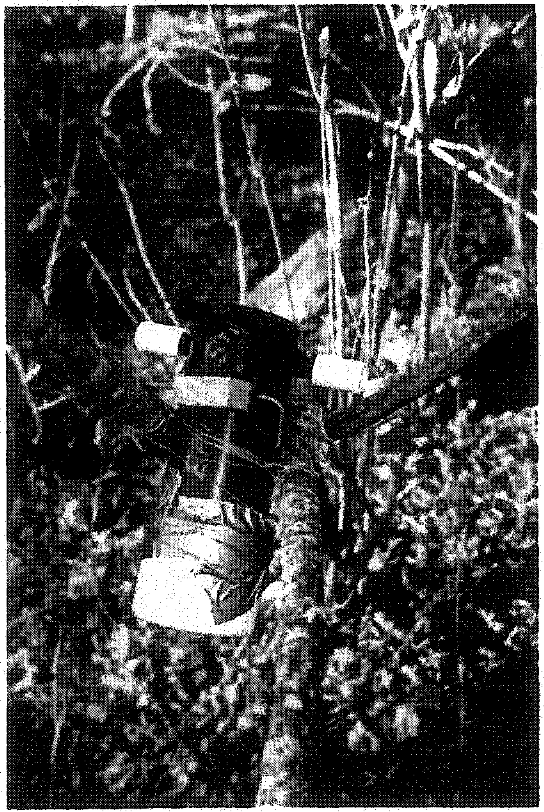

Figure 4-2: The water tube (with blocks added).

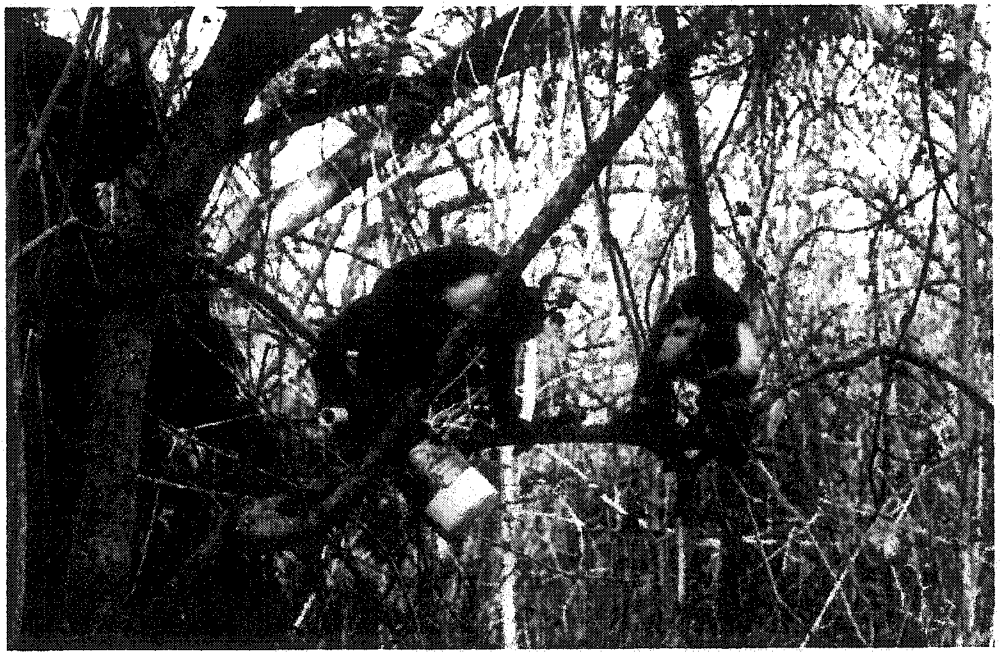

Figure 4-3: Capuchins investigating the water tube (with blocks added). After several weeks of unimpeded access to the water, the blocks are put in place for the first time. Efforts to remove or bypass the blocks (i.e., pulling, pushing, shaking, biting, and rolling) are made by all age/sex classes and by almost all group members. Group members monitor each other's efforts closely.

Figure 4-4: Solution to the water tube task. 'Se' (an adult female), successfully removes the plastic bolt and gains access to the water through the upper opening on the third day of exposure to the blocked water tube. She solved the task again the following day, as did 'Tr' (an adult male) the day after that. In all three cases, the 'solver' was alone, and no other individuals were present to observe their success.

APPENDIX A: Food items for which variation in food processing behaviour was identified.

***Sloanea terniflora* fruits**

Sloanea terniflora is an evergreen tree that favours wet areas, and in Santa Rosa is most often found along streambeds or ravines (O'Malley, personal obs.). Its fruits are roughly 1.5cm long and are covered in a coat of fine urticating hairs that are irritating to the skin and eyes. The fruits usually mature mid-dry season (Enquist & Sullivan 2001).

During the 2000 field season, I observed numerous bouts of *Sloanea* processing, which normally involved rubbing a fruit on a branch to remove the hairs so the fruit could be consumed safely. At the time, Panger's (1998) work was the only published paper to examine such food processing behaviour in capuchins, and she reported no *Sloanea* rubbing or consumption by capuchins at Palo Verde in 11 months of study.

***Luehea candida* seeds**

Luehea candida is common in the tropical dry forest habitat of Guanacaste and the Central Pacific regions of Costa Rica. Mature trees reach a height of 10-15m. The tree is leafless from January to April, with the first leaves flushing out in May with the onset of the first rains of the season (Haber & Frankie 1983).

The large, woody fruits of the tree range from 5-8cm long, are exceptionally hard, and are coated with a golden brown pubescence as they develop. The fruits begin to mature in February and March, with the woody pod dehiscing along its five longitudinal ridges, allowing the winged seeds to fall out when jostled by winds (Haber & Frankie 1983).

Luehea candida seeds are consumed by white-faced capuchins at Santa Rosa, Lomas Barbudal, and Palo Verde (Panger *et al.* 2002). Panger (1998) reported both 'pound' and 'rub' object-use bouts in *Luehea* processing at Palo Verde, in which the pod was grasped in one hand and repeatedly hit or rubbed against a tree branch or rock to extract the seeds. No differences in general processing techniques were noted across the three sites she compared

(Panger *et al.* 2002). During my preliminary study in 2000 at Santa Rosa, it was noted that members of different age/sex classes seemed inclined to employ different strategies for extracting seeds, with adults usually pounding the pods, while younger individuals were more likely to rub them or simply lick or pry out seeds without any processing (O'Malley, personal observation).

***Acacia* ant thorns**

Several species of swollen-thorn *Acacia* plants, particularly *A. collensii*, are home to obligate *Pseudomyrmex spp.* ants in Costa Rica, who defend the plant from herbivores in return for food and shelter (Janzen 1966, 1967 reported by Freese 1976). While a number of arthropods, lizards, birds, and mammals consume parts of *Acacia* plants, capuchin are the only mammal known to intentionally target the ants themselves in Costa Rica (Freese 1976).

Both type 'A' (branch) and type 'B' (trunk) thorns (identified by Janzen 1967 in Freese 1976) are consumed. *Cebus* predation on *Acacia* ant thorns is highly seasonal, confined largely to the early to mid-dry season. The ants aggressively swarm over the plant at any disturbance, and all species possess a painful sting (O'Malley, personal obs.). During the preliminary field season from May to July of 2000, *Acacia* thorn predation was observed only rarely. However, it was noted that neither of the two techniques described by Freese (1976) appeared to be in frequent use. Since the food being processed was the same, I though that this might reflect group-specific patterns in processing.

Large caterpillars

Santa Rosa is home to roughly 3,000 species of caterpillars over the course of the year (Janzen 1988). In the months after the first rains hit, capuchins gorge themselves on such prey for hours on end (O'Malley, personal observation). Many of the host plants consumed by these caterpillars are apparently unpalatable to the monkeys, as they take care to remove the digestive tract before (or during) consumption, most commonly by spitting it out as the caterpillar is consumed, or by biting an end off and either pulling or draining the gut out before consuming it. During the 2000 field season, it was noted that some individuals seemed more skilled at removing the gut, and would bite the caterpillar open and flick out the digestive material in one smooth motion rather than in the messy fashion that was more commonly seen.

Some caterpillar species (notably *Automeris* spp.) bear irritating or urticating hairs or stinging spines. Capuchins have been observed to process such prey items by rubbing them on a branch, sometimes with a leaf wrapped around them (Panger *et al.* 2002), while adults of the closely related *Saimiri oerstedii* use the tip of their tails as a sort of 'oven mitt' to protect their hands while rubbing such prey on a substrate (Boinski & Fragaszy 1989, Janson & Boinski 1992). Sympatric non-primate predators use similar techniques; Janzen (1988) reported that squirrel cuckoos eat such caterpillars after first smashing the spines on a tree branch. There is not yet enough data available to evaluate whether such processing might be socially learned in wild capuchin populations (but see Boinski & Fragaszy 1989).

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APPENDIX B: Group Membership in 2001 Field Season

CP Group	ID	Age	Sex	Maternity (if known)	Member since	Comments
Nose	NO	Adult	M		1993	alpha male
Trickle	TR	Adult	M		1998	beta male; member of LV group from 1996-1998
Limp	LI	Adult	F		birth	alpha female
Seria	SE	Adult	F		birth	
Pumba	PO	Adult	F	Tuft	birth	
Nyla	NY	Adult	F	Limp	birth	
Rafiki	RA	Immature	M	Limp	birth	
Timone	TI	Immature	F	Seria	birth	
Simba	SI	Juvenile	F	Limp	birth	
Zazu	ZZ	Juvenile	F	Seria	birth	
Ed	ED	Juvenile	F	Pumba	birth	
Sarabi	SB	Infant	F	Limp	birth	
Shenzi	SZ	Infant	F	Nyla	birth	
Mowgli	MW	Infant	M	Seria	birth	

LV Group	ID	Age	Sex	Maternity (if known)	Member since	Comments
Picante	PI	Adult	M		2000	alpha male
A-1	AO	Adult	M		2000	beta male?
Chili	CH	Adult	M		2000	beta male?
Side	SD	Adult	M		1997	former beta male, briefly alpha
Prego	PR	Adult	M		2000	
Kathy Lee	KL	Adult	F	Gringa	birth	
Dos Leches	DL	Adult	F	Gringa	birth	
Fiesty	FI	Adult	F		1997	joined group with Side
Blanquita	BL	Adult	F		1990	
Tobasco	TO	Immature	M	Fiesty	birth	
Alien	AL	Immature	M	Carmen	birth	
Salsa	SL	Immature	F	Blanquita	birth	
Mayo	MY	Juvenile	F	Kathy Lee	birth	
Chutney	SY	Juvenile	F	Blanquita	birth	
Mostaza	MZ	Infant	M	Kathy Lee	birth	
Tahini	TA	Infant	M	Fiesty	birth	
Caramelo	CA	Infant	F	Blanquita	birth	
Queso	QU	Infant	???	Dos Leches	birth	disappeared in May 2000

Adult Male: male 8+ years old
Adult Female: female 8+ years old
Immature: 5 - 8 years old
Juvenile: 6 months - 4 years old
Infant: 0 - 6 months old

APPENDIX C: Focal tallies and total observation hours for the 2001 field season

CP Group	#Focals	Obs Hours
NO	70	17.5
TR	69	17.25
LI	67	16.75
SE	70	17.5
PO	66	16.5
NY	66	16.5
RA	68	17
TI	66	16.5
SI	69	17.25
ZZ	63	15.75
ED	63	15.75
TOTAL	**737**	**184.25**

LV Group	#Focals	Obs Hours
PI	34	8.5
AO	32	8
CH	35	8.75
SD	34	8.5
PR	35	8.75
KL	44	11
DL	36	9
FI	38	9.5
BL	43	10.75
TO	34	8.5
AL	38	9.5
SL	35	8.75
MY	29	7.25
SY	34	8.5
TOTAL	**501**	**125.25**

APPENDIX D: Ethogram for 2001 Field Season

SOCIAL (grooming, agonism, play, etc.)
VOCALIZATION (lost calls, alarm calls, etc.)
DRINKING (drinking water with hands, mouth, tail, etc.)
TRAVEL
REST

FORAGING
process & eat acacia thorn- opening acacia thorns and consuming the ants/larvae within
failed attempt at acacia thorn- attempt to access acacia thorn(s) thwarted by swarming ants
break wood (>5cm diameter)- breaking open branches or rotten wood with fingers/teeth
break branch (1-5cm diameter)- breaking open medium-sized branches with fingers/teeth
break twig (>1cm diameter)- breaking open thin branches/vines with fingers/teeth
failed attempt to break- a failed attempt to break open a woody substrate (note size)
catch and eat- rapid seizure of a prey item, which is immediately consumed
catch & move- rapid seizure of a prey item, which is then carried away
carry object- carrying an object, food item, or prey.
chew- mastication of leaves or other substance without consuming it.
food interest- intently observing the foraging or food processing behaviour of a conspecific without interference
food theft (resisted)- seizure of a food item from an unwilling conspecific
resist food theft- successfully preventing the seizure of a food item by a conspecific
tolerated theft- allowing a conspecific to take some or all of a food item without resistance
food sharing- actively distributing a food item or portions of a food item to one or more conspecifics
eating- mastication and consumption of a food or prey item not integrated into an ongoing bout of food processing.
eat unplucked fruit- consumption of fruit without handling (right off the vine)
search arboreal leaf litter- sifting arboreal leaves gathered in tree branches or crooks
sift ground leaf litter- sifting ground litter with hands
gnaw- mastication of hard object without effect (usually seed pods)
hand pound- hammering an object with one hand into the other hand in order to dislodge something (usually food) within
eat insects from fur- licking or plucking insects from fur and consuming them
lick- licking the surface of a substrate (usually leaves) or food item
grab & miss- failed attempt to seize a fast-moving prey item
open seed pod/legume- opening woody pod or legume with hands/mouth
search palm crown- sifting through crevices and leaf litter collected in palm crown
pick and eat- seizing an immobile or nearly immobile food item (fruit, caterpillar, etc.) with one or two hands and immediately consuming it
pick & move- seizing an immobile or nearly immobile food item (fruit, caterpillar, etc.) object and then carrying it for a distance of one meter or more
remove bark- pulling or stripping bark from large woody branches with hands and mouth
sample- briefly licking, biting, tasting, or otherwise sampling a food item without (or before) consuming it outright
search foliage- manipulating arboreal leaves, vines, and branches in search of invertebrate prey
search hole- thrusting one or both hands into tree bole, beneath rock, etc.
smell- pressing face against an object and inhaling deeply
search nest- accessing or tearing open a bird nest in search of eggs or nestlings
tap- repeated taps with a finger or fingers against a substrate or item, usually with the head cocked to listen more clearly
unfurl leaves- unrolling curled leaves in search of invertebrates
object use- manipulation and alteration of a detached object relative to a fixed substrate or medium (provide details)
fulcrum use (object use)- applying force on an object working against a substrate without moving the object in the process
pound (object use)- hitting an object against a substrate with some degree of force
rub (object use)- sliding an object against a substrate while applying some degree of force
tool use- the external employment of an unattached object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself (provide details)
visual forage- visually scanning the immediate area for prey items, often while moving
unspecified foraging- the subject is clearly engaged in foraging behaviour (moving, putting objects in mouth, etc.) but no details can be identified.

APPENDIX E: Food Processing Variables for Specific Food Items of Interest

Sloanea terniflora

- Hand use
  - *unimanual (right or left)
  - *bimanual
  - *bimanual differentiated (right or left dominant)
  - *unclear
- Technique
  - *Rub
  - *Roll
  - *Unclear (roll or rub)
  - *Body/tail rub
  - *Pound
  - *No-process consumption
- Fruits processed
  - *Single fruit
  - *Multiple fruits
  - *Unclear
- Leaves attached
  - *No leaves
  - *One leaf/2 or more leaves
  - *Unclear

Luehea candida

- Hand use (as above)
- Technique
  - *Rub
  - *Roll
  - *Pound
  - *Hand pound
  - *Pick and eat (no-process consumption)
  - *Eat undetached *Luehea* (no-process consumption)

***Acacia* ant thorns**

- Thorn type
  - Type A- "branch thorns", found on branches and fronds
  - Type B- "stem thorns", found on main stem
- Method
- thorn only
  - thorn and frond or branch (Type A only)
  - thorn still attached to tree
- Ant attack?
  - None (no licking or brushing of ants on body)
  - Some (some licking or brushing of ants on body)
  - Fierce (frantic licking/brushing of ants on body, animal is in distress)

Large Caterpillars

- Processing (if any)
  - -None (eaten whole, guts spit out during consumption)
  - -Rub
  - -Guts spill or squeezed out while eating
  - -Guts pulled out with hands/lips
  - -Guts allowed to drain out in hand
  - -'Eviscerated', end bitten off and guts flicked out in one smooth motion
  - -Unclear- could not tell what processing (if any) occurred

APPENDIX F: Food Lists for CP and LV Groups During the 2001 Field Season

	CP Group	LV Group
Leaves, pith, etc.		
Bursera simaruba pith	X	
green acacia thorn (no ants inside)	X	
Tabebuia ochracea leaves		X
Flowers		
Bromeliad flower	X	
Byrsinoma crassifolia	X	
Cochlospermum vitifolium	X	
Combretum farinosum		X
Cydistia aequincictialis	X	
Malvaviscus arboreus	X	
Maniklera chicle	X	X
Fruits/seeds/legumes		
Acacia spp.	X	X
Acrocomia vinifera		X
Alibertia edulis		X
Alpeiba tibourbau	X	
Ardisia revoluta	X	
Bromeliad	X	X
Bursera simaruba	X	X
Byrsonima crassifolia	X	
Casearia spp.	X	X
Castilla elastica		X
Cercropia peltata	X	X
Dilodendron costaricense	X	X
Ficus spp.	X	X
Genipa americana	X	X
Hymenea courbaril?		X
Jacquinia nervosa		X
Karwinskia calderonii	X	X
Krugiodendron ferreum		X
Luehea candida	X	X
Luhea speciosa	X	X
Maniklera chicle	X	X
Muntingia calabura	X	
Phoradendron quadrangulare	X	X
Psidium sartorianum	X	
Quercus costaricensis		X
Randia subcordata	X	X
Randia thurberi	X	X
Sapranthus palanga	X	X

Sciadodendron excelsum	X	X
Simaruba olivaceus	X	X
Sloanea terniflora	X	X
Spondias radlkofri	X	X
Tabebuia ochracea	X	X
Trichilia spp.	X	
Xylosma flexuosa	X	
Zuelania guidonia	X	X
Invertebrate prey		
acacia ants & larvae	X	X
other ants	X	X
bee		X
butterflies/moths	X	X
caterpillars	X	X
cicadas	X	X
egg case or cocoon	X	X
embedded insects	X	X
forest roach	X	X
grasshoppers	X	X
katydid	X	X
mantis	X	
scorpion		X
snail	X	X
walking stick	X	X
wasp or bee hive	X	X
Vertebrate prey		
bird or bird nestling	X	X
coati pup	X	
egg	X	
frog	X	
mouse	X	
squirrel or squirrel pup	X	X