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RESEARCH ARTICLE

The Ontogeny of Handling Hard-to-Process Food in Wild Brown Capuchins (*Cebus apella apella*): Evidence From Foraging on the Fruit of *Maximiliana maripa*

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We examined age-related differences in wild brown capuchins' foraging efficiency and the food-processing behaviors directed toward maripa palm fruit (*Maximiliana maripa*). A detailed comparison of the different foraging techniques showed that plucking the fruit from the infructescence constituted the main difficulty of this task. Foraging efficiency tended to increase with age, with a threshold at which sufficient strength allowed immatures by the age of three to reach adult-level efficiency. Youngsters spent more time than older individuals browsing the infructescence and pulling the fruit in an attempt to harvest it. Infants tried to compensate for their inability to pluck fruit by adopting alternative strategies but with low payback, such as gnawing unplucked fruit and opportunistically scrounging others' partially processed food. Although around 2 years of age, young capuchins exhibited all of the behaviors used by adults, they did not reach adult-level proficiency at feeding on maripa until about 3 years (older juveniles). We compared this developmental pattern with that of extractive foraging on beetle larvae (*Myelobia* sp.) hidden in bamboo stalks, a more difficult food for these monkeys [Gunst N, Boinski S, Fragaszy DM. Behaviour 145:195–229, 2008]. For maripa, the challenge was mainly physical (plucking the fruit) once a tree was encountered, whereas for larvae, the challenge was primarily perceptual (locating the hidden larvae). For both foods, capuchins practice for years before achieving adult-level foraging competence, and the timeline is extended for larvae foraging (until 6 years) compared with maripa (3 years). The differing combinations of opportunities and challenges for learning to forage on these different foods illustrate how young generalist foragers (i.e. exploiting a large number of animal and plant species) may compensate for their low efficiency in extractive foraging tasks by showing earlier competence in processing less difficult but nutritious foods, such as maripa fruit. Am. J. Primatol. 72:960–973, 2010.

Key words: hard-to-process food; development; foraging strategies; scrounging; capuchin monkeys

INTRODUCTION

Optimal Foraging Theory and Hard-to-Process Foods

Optimal foraging theory assumes that the most important criterion for diet choices, foraging location and time, is derived from a cost–benefit ratio of foraging efficiency, and animal decisions are made to maximize the net rate of energy intake [Stephens & Krebs, 1986]. Profitability of the energy return rate is dependent on both a food item's energy content and its requisite handling time. Handling time is the amount of time required to handle the food item between the time it is encountered and the time it is consumed, encompassing different actions including capture, killing, processing, chewing, and swallowing.

Appreciating how animals' food-processing expertise is acquired requires understanding the problems their foods pose [Russon, 2003]. Hard-to-process foods are protected by antipredator defenses, such as spines, shells, hard husks, or hidden locations, which make them hard to get. In several primate species, complex foraging techniques are reported, such as removing the seeds and pulp from the hard exocarp of fruits, digging in the ground to obtain underground roots and tubers, and probing mineral or plant substrates for invertebrates. Yellow baboons (*Papio cynocephalus*) and chacma baboons (*P. ursinus*) often perform

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excavations to extract underground plant foods [Altmann, 1998; Byrne et al., 1993]. Chimpanzees (*Pan troglodytes*) and mountain gorillas (*Gorilla gorilla beringei*) deal with plant defenses, such as spiny leaves, by showing complex manual skills [Byrne & Byrne, 1993; Corp & Byrne, 2002a]. Capuchin monkeys (*Cebus* sp.) are known for their opportunistic and strenuously destructive, extractive foraging style, which requires manual dexterity, robust teeth, and powerful jaws [Anapol & Lee, 1994; Fragaszy & Boinski, 1995; Janson & Boinski, 1992; Wright, 2005]. They are particularly adept at foraging on high-quality foods (e.g. endosperm, invertebrates) protected by hard husks or hidden inside woody substrates [e.g. Gunst et al., 2008, in press; Izawa & Mizuno, 1977].

Ontogeny of Foraging Efficiency in Primates

Developmental research on food-related activities in nonhuman primates shows that juveniles of many primate species are less efficient foragers than adults [e.g. chacma baboons: Johnson & Bock, 2004; yellow baboons: Post et al., 1980; chimpanzees: Corp & Byrne, 2002b; Lonsdorf, 2005]. However, some species exhibit no significant age differences in diet or foraging success [mountain gorillas, *G. gorilla berengei*: Watts, 1985; Japanese macaques, *Macaca fuscata*: Hanya, 2003; squirrel monkeys, *Saimiri sciureus*: Stone, 2006; white-faced capuchins, *C. capucinus*: MacKinnon, 2006]. One factor that could contribute to reduced diet breadth is that immatures may proportionally select softer easier-to-process food items and smaller prey [Janson & van Schaik, 1993]. However, this is not uniformly the case. For example, in white-faced capuchins and when considering soft fruits and invertebrates, MacKinnon [2006] showed that the dietary profiles of juveniles and adults were largely similar [see also squirrel monkeys, *S. oerstedii*: Boinski & Fragazsy, 1989].

In other capuchin species, immatures are less efficient than adults in terms of success rate per time allocated to foraging, especially in those actions requiring skill and strength, but they sometimes forage persistently for high-quality resources eaten by adults without immediate return for their effort [wedge-capped capuchins, *C. olivaceus*: Fragaszy & Boinski, 1995; brown capuchins, *C. apella apella*: Gunst et al., 2008, in press]. Investing considerable time foraging on high-quality resources that are difficult to harvest may support acquisition of skills to obtain such valuable resources in the future. Various factors may account for the major age differences in the foraging efficiency reported and the foraging strategies adopted by capuchins, such as nutritional needs, physical maturation, independent foraging practice, and the social context of foraging [Agostini & Visalberghi, 2005; Fedigan, 1990; Gunst et al., 2008; Resende et al., 2008].

Physical maturation and sex differences

Age- and sex-related variation in body size, muscle volume, dental morphology, and development largely predict the strength in manipulating food-bearing substrates, the success in performing strenuous foraging actions, and therefore, access to desired resources in capuchins [Fragaszy & Adam-Curtis, 1997; Fragaszy & Boinski, 1995; Gunst et al., 2008; Jungers & Fleagle, 1980]. The physical strength and control needed to handle hard-to-process foods adeptly increase with body size. In other words, older and larger individuals in some capuchin species are more efficient foragers than younger and smaller individuals. In capuchin monkeys (all species averaged), adult males weigh on average 3.4 kg and females 2.4 kg [Fragaszy et al., 2004], and sex differences in foraging may be better explained by the larger size of adult males compared with females [Rose, 1994].

Independent foraging practice

The low foraging success of some juvenile primates may force them to invest considerably more time and effort in practicing foraging actions at which they are not yet proficient, even if they do not gain immediate energetic return for doing so, compared with the skillful adults [Fragaszy & Visalberghi, 1996; Gunst et al., 2008, in press; Lonsdorf, 2005]. Throughout infancy and juvenescence, capuchins living in natural and captive settings display extensive independent food-related behavioral practice through the solitary exploration of various plant substrates and animal prey, objects, and surfaces, in the absence of immediate gain of food or other discernible consequence [Fragaszy, 1990; Fragaszy & Adams-Curtis, 1991]. Such exploratory behaviors reflect the behavioral predispositions shared by all members of the species and may support learning of effective foraging actions [Gibson & Pick, 2000].

Social context of foraging

Social food-acquisition tactics are acknowledged to play a major role in primate ontogeny [Rapaport & Brown, 2008]. Young primates are intensely curious about what others eat. During synchronous feeding time, infants commonly sniff at tolerant group members' mouths while they feed and touch some of their foods. By regularly scavenging fresh remains of others' foods (i.e. scrounging), immature primates may receive food at little foraging cost [King, 1994; Russon, 2003]. Scrounging may also help young individuals become familiar with the food items eaten and the substrates manipulated by other individuals, stimulate independent food exploration, and learn more rapidly the techniques conspecific adults used to harvest the food [Rapaport & Brown, 2008]. Group members who spend more time in close proximity are likely to have greater opportunity to observe and potentially learn from each other's behavior, relative to less proximate individuals [cf. Coussi-Korbel & Fragaszy, 1995].

Capuchin monkeys are known to display considerable tolerance toward the close proximity of especially younger group members while foraging [Fragaszy et al., 2004]. Young capuchins are allowed to spend time near adult foragers, watch them closely, and sample their food directly, collect debris they drop, or to inspect their foraging artifacts, i.e. the physical traces they leave in the environment after foraging [Fragaszy et al., 1997; Gunst et al., 2008]. They are particularly interested in watching others foraging on novel foods or foods that the young animal cannot obtain itself [Fragaszy et al., 1997; Gunst et al., 2008; Ottoni et al., 2005; Perry & Ordoñez-Jiménez, 2006].

Capuchins Foraging on Maripa Fruit

Brown capuchins at Raleighvallen (RV), Suriname, feed on a vast array of food items, including plants, fruits, flowers, invertebrates, and small vertebrates [Boinski et al., 2000]. In an earlier study, Gunst et al. [2008, in press] found that the food items foraged on by capuchins in bamboo patches naturally fell into a dichotomous categorization: "easy" foods, such as bamboo shoots, bamboo pith, and surface insects, which required nonspecific foraging actions (grasp, pull) and little strength vs. "difficult" foods, such as beetle larvae hidden inside bamboo stalks, which required performance of several sequential specific foraging actions, described below, as well as greater strength. Larvae acquisition begins with searching, selecting an appropriate stalk, and locating the embedded larvae (using various detection techniques, such as tap scanning), followed by handling and ripping the stalk open with teeth and extracting the larvae [Gunst et al., in press].

In this article, we report data on the development of food-processing behaviors by wild brown capuchins when foraging on highly nutritious maripa palm fruits (*Maximiliana maripa*), particularly rich in fatty acids [Bereau et al., 2001], and clumped into large infructescences. The main foraging procedure consisted of performing the following ordered sequence of actions: (1) Browse (i.e. visually and manually inspect) the infructescence to clear one's way to an unplucked fruit by moving adjacent fruit items further apart to facilitate the grasp on one fruit's basal part, (2) attempt to harvest a fruit by grasping, pulling, and twisting a fruit to remove it from the infructescence, (3) harvest a fruit, i.e. pluck it from the infructescence, (4) peel the fruit by holding it in one or both hands and stripping the fibrous epicarp with teeth from the basal cupule to the apex, (5) eat the mesocarp by scraping it off the kernel with teeth, and (6) discard the woody endocarp of the fruit.

From the physical nature of the fruit and description of the behaviors needed to forage on them, it is clear that eating maripa fruit requires pre- and post-harvest handling skills, as well as an essential harvesting step that necessitates physical strength, making this task more complex than feeding on more easily acquired foods.

However, extractive foraging [defined as locating and obtaining food items that must first be removed from plant matrices in which they are embedded or encased; Parker & Gibson, 1977] is typically considered to fit the characterization of a "complex" foraging pattern on the grounds that extraction requires greater sensorimotor coordination and perceptual learning than, for example, harvesting surface insects or plucking fruit [Gibson, 1987]. Therefore, foraging on maripa, whose main difficulty consists of plucking fruit items from the infructescence, can be considered less difficult than preying on invertebrates hidden inside woody substrates. Indeed, foraging on larvae encased in bamboo stalks necessitates (1) substantial time to learn how to select appropriate substrates (i.e. large and intact bamboo stalk internodes more likely to contain larvae) and then performing adequate detection techniques by using auditory, olfactory, tactile, and visual cues, and (2) substantial strength to rip bamboo stalk apart by repetitive biting and tearing actions with hands and teeth and extracting the larva with the fingers, a series of strenuous actions that can take several minutes [Gunst et al., 2008, in press]. By contrast, once a maripa tree with fruit is located, completing the main maripa foraging procedure is contingent upon only two conditions: first, being successful in harvesting a fruit and, second, being successful in keeping the fruit in hand to peel and eat it.

Conversely, if these two conditions are not fulfilled, two alternative foraging strategies can be adopted. The first one can be considered as a default strategy, consisting of gnawing unplucked fruit on the apex, either after failing to harvest a fruit or directly after browsing the infructescence without attempting to harvest. However, because an unplucked fruit cannot be peeled from the basal cupule (attached deep inside the infructescence), only small fragments of epicarp can be torn off. This results in the forager having very limited access to the mesocarp. The second one is an opportunistic strategy consisting of foraging on partially processed food, i.e. picking up already-harvested fruit (i.e. removed from the infructescence by another forager and accidentally dropped) or fruit peelings dropped by other foragers during the foraging process. Picked-up fruit are then peeled and eaten, whereas picked up peelings are licked.

Objectives

The goal of this study is to explore the ontogeny of foraging skills in wild brown capuchins in a strength-dependent task involving a hard-to-process food by (1) examining age and sex-related differences in the foraging efficiency for maripa fruit and (2) explaining age differences, if any, through a detailed comparison of the food-processing techniques as well as the foraging targets and strategies between age classes, including pre- vs. post-harvest handling and social food-acquisition tactics, such as scrounging.

More specifically, we evaluate the five following predictions: Prediction ♯1: Because harvesting maripa fruit from the infructescence is highly dependent on physical strength, foraging efficiency, defined as the total number of fruits harvested and kept in hand divided by the total pre-harvest handling time, should tend to increase with age, with a threshold at which sufficient strength allows immatures by the age of 3 (older juveniles) to reach adult-level efficiency; Prediction ♯2: For an individual embarking on the main foraging procedure, the pre-harvest handling time required to remove each fruit from the infructescence should tend to decrease with age, with a threshold at which sufficient strength allows immatures by the age of 3 (older juveniles) to reach adult-level speed in pre-harvest handling; Prediction ♯3: Owing to differences in body mass and physical strength among mature individuals (subadults and adults), males should be more efficient than females; Prediction ♯4: To compensate for their low foraging efficiency, infants and younger juveniles should attempt to skip the difficult harvesting step by adopting alternative foraging strategies more frequently than older individuals, such as applying inefficient foraging actions to non-harvested fruit, and opportunistically retrieving food remains from already harvested or partially processed fruits; Prediction ♯5: In such a synchronous feeding context, the frequency of scrounging interactions should be positively correlated with the quality of social relationships, such as the affiliation score (defined as the frequency of positive social interactions) and the degree of proximity in maternal kinship.

METHODS

Study Site and Group

Observations took place at the RV site (4°0′N, 56°30′W) within the Central Suriname Nature Preserve, from March to July 2005. The RV landscape is a mosaic of small distinct, patchy habitats. About 40% of habitat used by brown capuchins at RV is liana forest, 25% in and at the edge of bamboo thickets, about 10% in swamp forest, and the remainder in high or plateau forest [Boinski et al., 2003].

The brown capuchin study group (Troop A) had been studied intermittently beginning in 1998 and continuously since 2000, and was habituated to human presence [Boinski et al., 2000]. This research was conducted in compliance with animal care regulations, applicable national laws, and the ASP Principles for the Ethical Treatment of Non-Human Primates. During the 5 months of observation, 26 individuals were sampled, including all age/sex classes. Individual recognition, based on physical features, was well established. Based on the age classes reported in Gunst et al. [2008], the group contained eight adults (aged 7 and more, two males and six females), five subadults (between 5 and 7 years old, two males and three females), five older juveniles (also labeled juveniles 2, between 3 and 5 years old, three males and two females), three younger juveniles (also referred to as juveniles 1, from 1 to 3 years, two males and one female), and five infants (0–1 year, three males and two females). Ages given refer to the monkeys' ages at the start of this study.

Maximiliana maripa Fruit

Among the food items eaten by brown capuchin monkeys at RV, we focused in this report on food sources and foraging techniques observed when the capuchins foraged on *M. maripa* Drude (Arecoideae subfamily), a solitary large subcanopy to canopy palm tree (from 6 to 20 m high at RV) common throughout the Amazon basin [Kahn & de Granville, 1992]. Adult trees produce one to three infructescences from January to June, each weighing 50–80 kg and bearing from several 100s to more than 2,000 clumped fruits [Fragoso et al., 2003]. A fresh maripa fruit is an ovoid drupe, weighing 14–26 g, measuring 5–8 cm in length and 2–3 cm in diameter, with a persistent stigma tapering at the apex and a 2 cm high basal cupule, and composed of a fibrous resistant epicarp, a thick fleshy fatty acid-rich yellow mesocarp, and a hard woody endocarp with one to three seeds [Fragoso, 1997]. At RV, feeding on maripa fruits accounted for 22.9% of capuchins' monthly feeding time during the 6-month maripa fruiting season [Gunst, unpublished data].

Data Collection

The observation period included 125 days, between 7:00 am and 5:00 pm. The sampling technique used for this study was the focal-tree method [Vogel & Janson, 2007]. When the study group was ranging within the study area, NG moved to the vanguard of the group and stood under a maripa tree (with currently ripe fruit) that the group was likely to visit. During the observation period, 15 maripa trees were visited and they all produced only one infructescence. NG used a Sony digital video camera (Sony, Tokyo, Japan) (DCR-TRV22) focused on the maripa infructescence to video-record continuously the activity of all individuals present on the infructescence. During each observational session, the entire sequence of events was filmed from start (when the first individual entered the infructescence) to finish (when the last individual had left the infructescence). While filming, NG simultaneously audio-recorded data on individuals leaving the infructescence briefly to pick up dropped food items.

Data Coding and Analysis

We analyzed 67 observational sessions, with an average duration of 52.3 ± 38.5 min per session. The average duration of foraging activity per session was 23.2 ± 11.5 min for infants, 25.5 ± 13.4 min for juveniles 1, 23.7 ± 15.0 min for juveniles 2, 18.0 ± 9.6 min for subadults, and 39.6 ± 20.3 min for adults. While video-scoring, NG transcribed each observational session onto a data sheet to the second, including all occurrences of entering and leaving the infructescence by identified individuals, and all changes in behaviors performed by all individuals present on the infructescence. Behaviors were categorized as ''events'' when they were of short duration (i.e. approximated as points in time) and their frequency of occurrence was of interest, whereas they were categorized as ''states'' when they lasted longer (a minimum of 2 sec) and their duration could be measured [cf. Martin & Bateson, 1993].

The behaviors recorded were divided into non-foraging behaviors (resting, grooming, playing, vigilance, and agonistic interactions), as well as foraging and scrounging behaviors (Table I). Among foraging and scrounging behaviors, we distinguished between pre-harvest handling (browse infructescence, attempt to harvest fruit, gnaw apex) and post-harvest handling (peel fruit, eat and discard endocarp, pick up dropped fruit and peelings, lick peelings). We defined a foraging bout as the display by an individual of foraging behaviors directed toward one maripa fruit, starting from browsing the infructescence for a particular fruit item and finishing when switching to another fruit or leaving the infructescence, after the individual either failed to harvest the fruit item or succeeded in harvesting it, ate the mesocarp, and discarded the endocarp. During synchronous feeding activity on the infructescence, we calculated the time performing scrounging behaviors by adding the durations of the following behavioral states: close interest in others' food, beg, and lick peelings.

From the video records, NG also scored the different conditions of fruit items foraged on the maripa trees, namely unplucked and plucked fruit (attached to and detached from the infructescence, respectively) and fruit/peelings dropped by other foragers. To measure the extent to which a single observer obtains consistent results when transcribing the same video-recorded individual identities and behaviors on different occasions, NG transcribed two times a sample of three observational sessions and obtained good intra-coder reliability κ coefficients [$\kappa = 0.96$ for identities and 0.91 for behaviors; cf. Martin & Bateson, 1993].

In most analyses, we reported percentages on number of events or durations and mean values ± standard deviation (SD). Because our raw and transformed data violated the parametric assumptions,

TABLE I. Maripa Foraging States and Events Scored in This Study

Behavior	Definition	Type
Foraging behaviors		
Browse infructescence	Clear one's way through the infructescence to an unplucked fruit by moving adjacent fruit items further apart to facilitate the grasp on one fruit's basal part	State
Attempt to harvest fruit	Grasp, pull, and twist an unplucked fruit to remove it from the infructescence (two possible outcomes: succeed in removing a fruit or fail)	State
Gnaw apex	Seize with teeth and gnaw an unplucked fruit on the apex	State
Harvest fruit	Pluck/remove a fruit from the infructescence (two possible outcomes: keep the fruit in hand or accidentally drop it)	Event
Peel fruit	Hold a fruit in hand and strip the epicarp (fibrous husk) with teeth from the basal cupule to the apex, tearing off long fragments called peelings	State
Eat mesocarp	Scraping off the fruit mesocarp (creamy, yellow/orange pulp) from the kernel with teeth	State
Discard endocarp	Discard the woody endocarp of the fruit	Event
Unknown	Undetermined foraging behavior	State
Scrounging behaviors		
Close interest in others' food	Closely watch a foraging individual	State
Beg	Actively solicit food from other foragers by either extending one's hand toward others' food or sniffing a feeding individual's mouth (two possible outcomes: succeed in obtaining food artefacts from other foragers or fail)	State
Pick up fruit	Pick up a fruit accidentally dropped by other foragers	Event
Pick up peelings	Pick up fruit peelings dropped by other foragers	Event
Lick peelings	Lick the outer part of mesocarp attached to fruit peelings dropped by other foragers	State

we conducted nonparametric tests. Toanalyze the effect of age on foraging efficiency and the time spent browsing, attempting to harvest, and scrounging, we used Kruskal–Wallis tests followed by multiple pairwise comparisons between age classes based on mean ranks [cf. Siegel & Castellan, 1988].

To test the association between the frequency of scrounging interactions and the quality of social relationships, such as affiliation and kinship, we used matrix correlations [Matman program edited by Noldus Information Technology, 1998]. In the first matrix, we entered for each dyad the frequency of scrounging interactions. In the second matrix, we implemented either the affiliation score within each dyad or the degree of kinship. To measure the affiliation score, we used the frequency of positive social interactions (sitting in body contact, grooming, and playing) collected by focal-animal sampling and presented in Gunst et al. [2008]. We assessed the degree of proximity in maternal kin relationships by distinguishing three types of dyads: non-maternal kin (with a ''0'' proximity value), far kin (maternal siblings, with a ''0.5'' value), and close kin (mother–offspring, with a ''1'' proximity value) dyads. We set the number of automatic permutations of matrices at 10,000 and used the Pearson's correlation coefficient. Statistical significance level was set at $\alpha = 0.05$ (SPSS 13.0 statistical software).

RESULTS

Age and Sex Differences in Foraging Efficiency

We found a significant age effect on the efficiency of foraging on maripa fruit, defined as the total number of fruits harvested and kept in hand divided by the total pre-harvest handling time (Kruskal–Wallis test, $N_{\text{infant}} = N_{\text{juvenile2}} = N_{\text{subadult}} = 5$, $N_{\text{juvenile1}} = 3$, $N_{\text{adult}} = 8$, $H = 17.51$, df $= 4$, $P = 0.002$). Multiple pairwise comparisons showed that the foraging efficiency of juveniles 2, subadults, and adults was significantly higher than that of infants and the foraging efficiency of adults was significantly higher than that of juveniles 1 ($P < 0.05$). Other comparisons did not reach statistical significance. Foraging efficiency tended to increase with age from infants to adults (Fig. 1), with a threshold at which sufficient strength allowed immatures by the age of 3 (older juveniles) to reach adult-level efficiency, thereby verifying Prediction ♯1. The following analyses aim at explaining these differences.

For an individual embarking on the main foraging procedure and when considering the duration of pre-harvest handling per foraging bout, we found a significant age effect on the time spent browsing (Kruskal–Wallis test, $N_{\text{infant}} = 2$, $N_{\text{juvenile1}} = 3$, $N_{\text{juvenile2}} = 5$, $N_{\text{subadult}} = 4$, $N_{\text{adult}} = 8$, $H = 17.72$, $P = 0.001$) and attempting to harvest ($H = 17.71$, $P = 0.001$). Multiple pairwise comparisons showed that infants and juveniles 1 spent significantly more time browsing and attempting to harvest than adults ($P < 0.05$), but not juveniles 2 and subadults. The duration of pre-harvest handling per bout tended to decrease with age from infants to adults (Fig. 2), with a threshold at which sufficient strength allowed immatures by the age of 3 (older juveniles) to reach adult-level speed in pre-harvest handling, thereby verifying Prediction ♯2.

Among mature individuals (subadults and adults), there was a significant sex difference in foraging efficiency, with males being more efficient than females (foraging efficiency = 2.8 and 2.0 fruits harvested divided by the pre-harvest handling time in minutes, respectively; Mann–Whitney *U* test, one-tailed, $N_{\text{male}} = 4$, $N_{\text{female}} = 9$, $U = 4.0$, $P = 0.034$), thereby verifying Prediction ♯3. Although females tended to spend more time than males browsing the large infructescence and pulling the fruit item they selected in an attempt to harvest it (average duration of pre-harvest handling = 17.3 and 13.3 sec, respectively), this sex difference in duration of pre-harvest handling did not reach statistical significance ($U = 5.0$, $P = 0.073$).

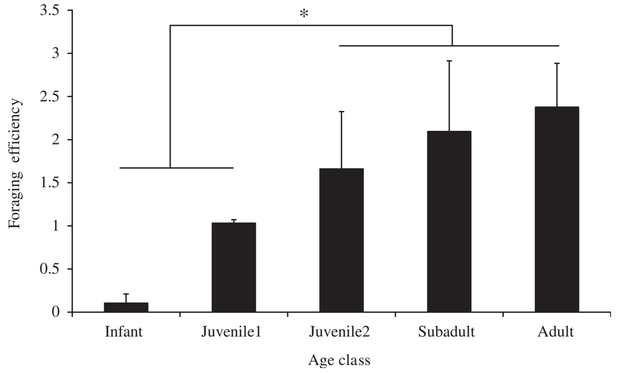

Fig. 1. Age differences in foraging efficiency, defined as the mean number of fruits harvested and kept in hand divided by the pre-harvest handling time in minutes.

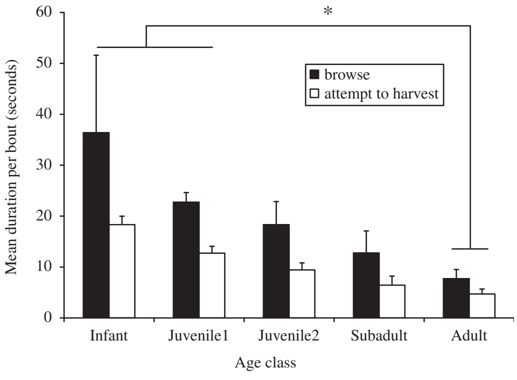

Fig. 2. Age differences in the duration of pre-harvest handling per bout.

Age Differences in Foraging Targets and Strategies

According to the condition of the fruit items targeted, we distinguished three different foraging strategies that corresponded to three different sequences of foraging stages. The main foraging procedure consisted of plucking and processing fruits. Two alternative foraging strategies are ''gnawing'' (consisting of gnawing unplucked fruit on the apex) and ''scrounging'' (consisting of picking up already harvested fruit or fruit peelings dropped by others) (Fig. 3).

Monkeys of different age classes, particularly infants vs. older individuals, varied greatly in their interest in different conditions of fruit items and the time they devoted to different foraging activities and strategies. When considering the total duration of pre-harvest handling, Figure 4 shows that infants spent notably less time browsing (17.3%) and attempting to harvest (3.2%) than other age classes (juveniles 1: 49.2 and 18.7%, juveniles 2: 51.7 and 21.7%, subadults: 58.6 and 22.2%, and adults: 58.1 and 20.4%, respectively). When considering the total duration of post-harvest handling, there was a significant age effect on the total time spent peeling fruit ($H = 9.84$, $P = 0.043$) with infants spending significantly less time peeling than adults (4.1 and 22.6%, respectively; $P < 0.05$), whereas other age differences did not reach statistical significance. There was no significant age effect on the total time spent eating fruit ($H = 7.91$, $P = 0.095$). The effect of age on the total time spent peeling fruit mainly reflected the difference in foraging efficiency between age classes, with infants harvesting many fewer fruits than other age classes. However, when considering the average duration of peeling a fruit per bout, we found a significant age effect ($H = 17.28$, $P = 0.002$), with infants spending significantly more time peeling each fruit than other age classes (mean for infants = 69 sec, juveniles 1 = 25 sec, juveniles 2 = 21 sec, subadults = adults = 19 sec, $P < 0.05$).

Regarding the main foraging procedure, we found a significant age effect on the time spent foraging on plucked fruit ($H = 12.39$, $P = 0.015$), with infants spending significantly less time foraging on plucked fruit than adults (10.8 and 55.5%, respectively,

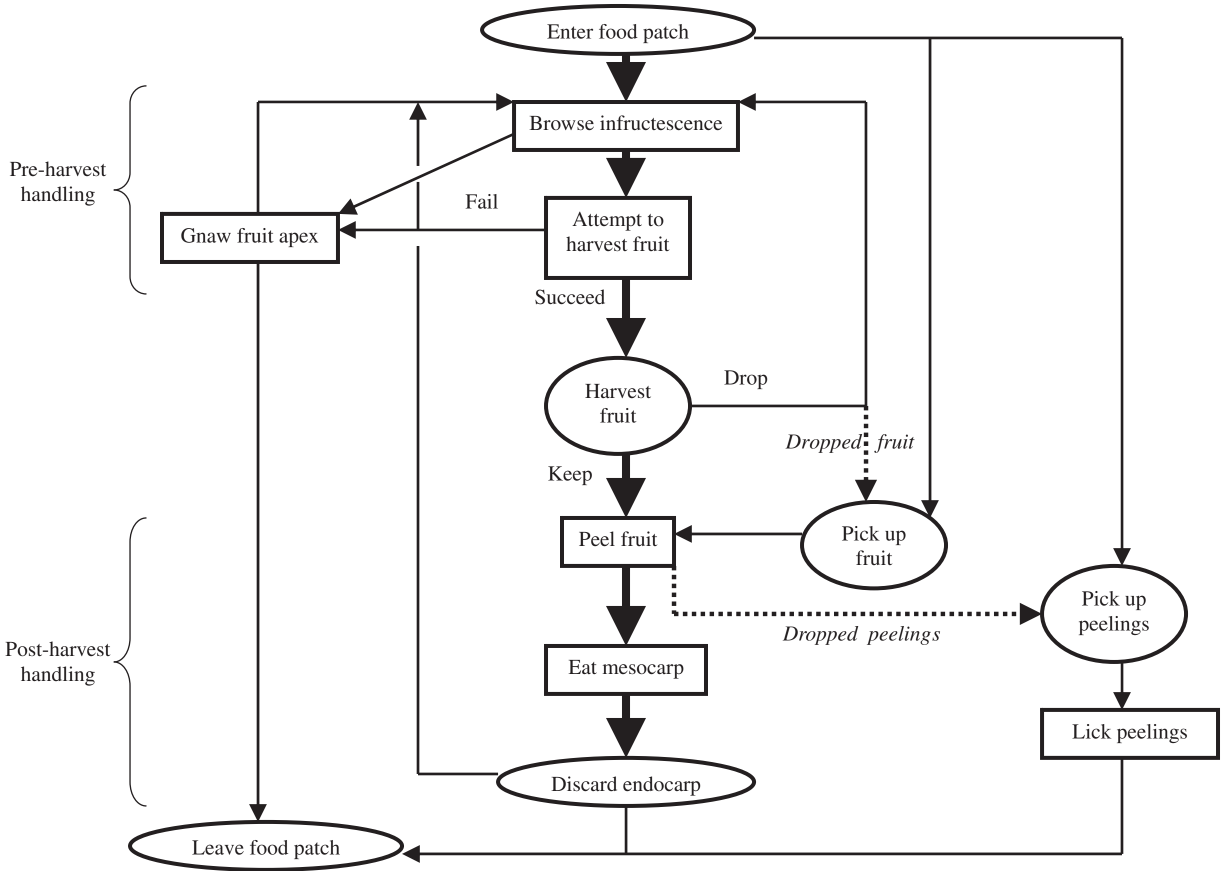

Fig. 3. Flow diagram showing the maripa fruit foraging behaviors performed by brown capuchins. Behavioral events are represented within oval frames and behavioral states within rectangular frames. Plain arrows link two successive behaviors (the large ones indicating the main foraging procedure and the thin ones indicating the gnawing and scrounging strategies) and dotted arrows represent dropped food items that were used in the scrounging strategy.

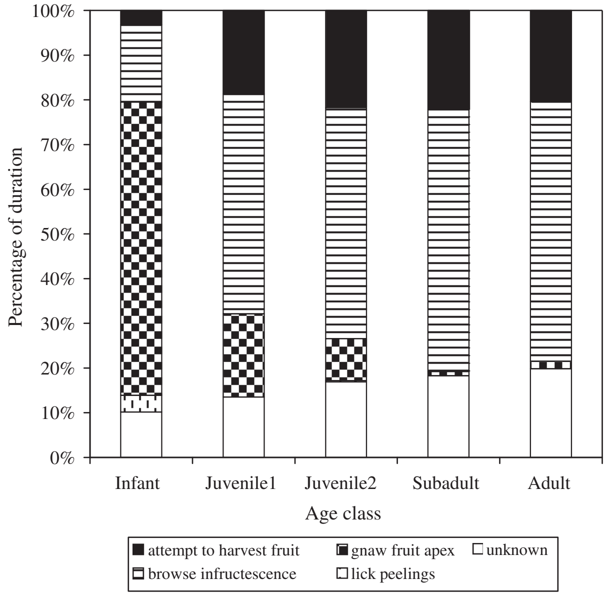

Fig. 4. Age differences in the percentage of duration of maripa foraging states representing pre-harvest handling and scrounging strategy.

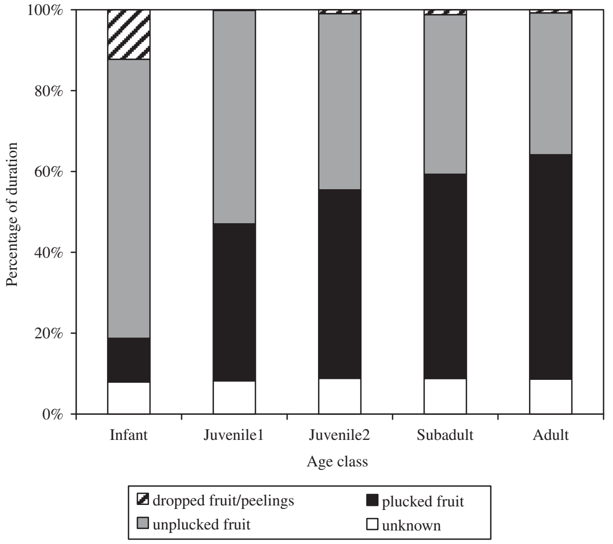

Fig. 5. Age differences in the percentage of time spent foraging on different conditions of fruit items, namely unplucked and plucked fruit, and dropped fruit/remains.

$P < 0.05$), whereas other age differences did not reach statistical significance (Fig. 5). Therefore, infants were less prone than older individuals to adopt the main foraging procedure; the total duration of their attempts to harvest fruit was about four times smaller than that of all other age classes (Fig. 4), and when they did attempt to harvest a fruit, their efficiency was 10–23 times lower than that of older individuals (Fig. 1).

Conversely, the alternative strategies consisting of gnawing unplucked fruit on the apex or picking up partially processed food items were mainly adopted by infants. Figure 4 shows that gnawing unplucked fruit on the apex was mainly performed by infants (65.6% of their time foraging on maripa), whereas it was much less frequent in juveniles (18.6% in juveniles 1 and 9.4% in juveniles 2) and virtually absent in mature individuals (0.9% in subadults and 1.7% in adults). The time spent foraging on unplucked fruit items systematically decreased with age from infants (69.0%) to adults (35.1%) (Fig. 5).

We found a significant effect of age on the time spent scrounging (Kruskal–Wallis test, $N_{\mathrm{infant}} = N_{\mathrm{juvenile2}} = N_{\mathrm{subadult}} = 5$, $N_{\mathrm{juvenile1}} = 3$, $N_{\mathrm{adult}} = 8$, $H = 16.22$, $\mathrm{df} = 4$, $P = 0.003$). Multiple pairwise comparisons showed that infants scrounged significantly more than subadults and adults (total time spent scrounging = 14.4, 0.2, and 0.1 min, respectively, $P < 0.05$) but not than juveniles 1 and 2. Figure 5 shows that foraging behaviors directed toward fruit already harvested or fruit peelings dropped by foragers occurred mainly in infants (12.3% of foraging time), whereas they were virtually absent in other classes (juveniles 1: 0.2%, juveniles 2: 0.9%, subadults: 1.2%, adults: 0.8%). More particularly, infants spent 3.3% of time picking up and licking peelings dropped by skilled foragers, whereas this behavior was (virtually) absent in other age classes (juveniles 1, subadults, adults: 0.0%, and juveniles 2: 0.2%; Fig. 4). A comparison of the percentage of picked up vs. harvested fruit in each age class showed that 13.3% of maripa fruit items obtained by infants were dropped by others and subsequently picked up, whereas older individuals relied considerably less on picked up fruit (2.6% in juveniles 1, 1.4% in juveniles 2, 0.0% in subadults, and 0.3% in adults). Of the 80 begging interactions, infants were successful in obtaining food artifacts from other foragers on 20 occasions (i.e. 25.0%).

In sum, Prediction ♯4 was verified only for infants (not younger juveniles): infants attempted to skip the difficult harvesting step by adopting alternatives foraging strategies more frequently than older individuals.

Social Relationships Promoting Scrounging

We found significant positive correlations between the frequency of scrounging interactions and the quality of social relationships, such as affiliation and maternal kinship (Pearson's correlation coefficient $r = 0.361$ and 0.260, $P = 0.001$ and 0.002, respectively), thereby verifying Prediction ♯5. This result means that infants mainly scrounged from strongly affiliated individuals and close maternal kin. However, the relative importance of affiliation and kinship could not be assessed because these two variables were significantly correlated themselves ($r = 0.552$, $P < 0.001$).

DISCUSSION

We examined age-related differences in foraging efficiency and food-processing behaviors directed toward maripa fruit, an essential food in brown capuchins' diet. We verified that foraging efficiency tended to increase with age from infants to adults, with a threshold at which sufficient strength allowed immatures by the age of 3 (older juveniles) to reach adult-level efficiency, in accord with the assumption that plucking the fruit from the infructescence requires considerable physical strength (Prediction ♯1). Infants and younger juveniles spent more time than older individuals browsing the large infructescence and pulling the fruit item they selected in an attempt to harvest it (Prediction ♯2). We showed that among mature individuals, males were more efficient at foraging on maripa fruit than females, as expected owing to differences in body mass and physical strength (Prediction ♯3). We found that infants (but not younger juveniles) tried to compensate for their lack of foraging success by adopting alternative strategies with low payback, such as gnawing unplucked fruit and opportunistically scrounging others' partially processed food (Prediction ♯4). We also verified that infants scrounged more often from closely affiliated individuals and close kin than other group members (Prediction ♯5).

Our results emphasized that harvesting a fruit was the most difficult step in the foraging procedure and the strength necessary to achieve it was not fully acquired before the age of 3 years. However, other foraging behaviors on maripa, such as the time needed to peel the maripa fruit and time spent foraging on plucked fruit, developed earlier, with juveniles 1 already showing adult-like skills. Interestingly, although juveniles 1 were significantly less efficient than older individuals, they already presented a mature-like profile, in the sense that they dropped the "gnawing" strategy to focus on the individual practice of the main procedure, i.e. performing behaviours, such as browsing and attempting to harvest. Thus, despite their foraging inefficiency, younger juveniles can be considered a transitional status between small-sized infants and fully skilled older foragers in terms of foraging targets and strategies. In sum, some sets of foraging skills develop earlier than others during the ontogeny of capuchins.

For capuchins, pulling and twisting a maripa fruit to remove it from the infructescence seems to be a typical strength-dependent foraging action. Age-related physical changes in capuchins, including increase in body size and mass, muscle volume, and the timing of the eruption of adult dentition, are likely to contribute to improvement in those foraging tasks that require considerable strength, such as plucking fruits from a substrate, bashing open hard-husked fruits, and biting open bamboo stalks [Fragaszy & Adam-Curtis, 1997; Gunst et al., 2008; Jungers & Fleagle, 1980]. Fragaszy and Adams-Curtis [1998] report that captive tufted capuchins (*C. apella* spp.) weigh 9% of the mother's weight at birth, 50% by 1 year of age, 53% at 1.2 years (average weaning age), and take 3 more years to gain the last 47% of adult weight, by about 5 years of age. We assume that wild monkeys may gain body mass more slowly than captive monkeys, given the deviation from optimal nutrition encountered by some wild populations [cf. Altmann & Alberts, 1987; Strum, 1991], and thus could reach adult mass at 7 years or perhaps later.

The quasi-null foraging success of infants is likely to be explained by the lack of strength and experience in their attempts to harvest maripa fruit. Their very rare successful attempts may simply reflect the relative ripeness of the fruit, with overripe items being easier to pluck. Older and larger individuals are more efficient in most foraging tasks (and therefore, have a higher rate of nutrient collection) than younger and smaller individuals. However, our results on foraging efficiency show that an adult-size body is not necessary to pluck maripa fruits from the infructescence. Infants and younger juveniles may be less proficient than older individuals at harvesting maripa fruits because they have not reached the necessary threshold body size. A second constraint on infants' proficiency could be their immature dentition. When capuchins rip bamboo stalks apart with teeth [mainly canines, i.e. the last permanent teeth to erupt at around 4–5 years; Galliari, 1985] and hands to extract embedded larvae, physical strength and dental development are major constraints. In ripping bamboo stalks, the maximum foraging efficiency was attained by subadults, the youngest age cohort in which full and permanent dentition was present [Gunst et al., 2008]. By contrast, this study shows that younger juveniles can peel maripa fruit effectively. Therefore, dentition was a likely constraint only in infants, who spent significantly more time peeling fruit than other age classes. In brown capuchins, the first and second molars emerge at 1.2 and 2.2 years, respectively, which in this study corresponds to the younger juvenile age class [Galliari, 1985].

Whereas our first result, concerning overall efficiency of foraging on maripa, considered the total time spent performing all pre-harvest handling behaviors (browse infructescence, attempt to harvest fruit, and gnaw fruit apex), our second result focused on the time necessary to pluck one fruit by performing the first two actions characteristic of the main foraging procedure (browse and attempt to harvest). The decrease with age, from infants to adults, in the duration of these two behaviors per foraging bout confirmed the strength-dependent nature of the pre-harvest handling components. Older, and we assume, larger and stronger individuals were able to pluck a fruit item faster than younger and smaller individuals. By reducing their pre-harvest handling time, mature individuals increase the net rate of energy intake. In accord with sex differences in body mass and physical strength, we found that mature males were significantly more efficient and, on average, 30% faster than mature females in plucking fruits. Sex differences in pre-harvest handling time (browsing and attempting to harvest) were in the same direction, but did not reach statistical significance.

Compared with similar-sized Old World primates and many (but not all) other New World monkey species, capuchins' physical growth is slow and their major life history stages occur later [Fragaszy, 1990]. Brown capuchins show a long developmental trajectory toward mature efficiency in highly complex extractive foraging behaviors, such as preying on embedded invertebrates and cracking nuts using stone hammers and anvils [Gunst et al., 2008, in press; Resende et al., 2008]. For example, developing foraging competence for larvae hidden in bamboo stalks continues throughout juvenescence; this foraging task is not fully mastered before age 6 [Gunst et al., in press]. Such an extended timeline reflects two types of challenges: the monkeys must know where and how to locate the larvae as well as being able to open the stalk. Extracting the larvae encased inside tough substrates requires at least the physical strength and morphological features (body mass and dentition), characteristic of older juveniles. However, selecting the appropriate foraging substrate and locating hidden foods require sensorimotor coordination and perceptual learning, foraging skills that benefit from prolonged practice and whose acquisition is only completed in subadults [Gunst et al., 2008, in press]. Therefore, reaching adult-level proficiency at obtaining embedded larvae is not only constrained by physical maturation, but also by learning how to detect them. The capuchins' timeline for mastering complex extractive foraging activities incorporating detection of hidden prey and/or managing multiple spatial relations among objects and surfaces extends beyond the onset of juvenility and has been argued to resemble that of apes and humans for similar extractive activities [cf. Gunst et al., 2008; Resende et al., 2008].

As opposed to such difficult foods, foraging on maripa fruit requires no detection skills, described in the case of foods encased inside concealing matrices [see Di Bitetti & Janson, 2001; Garber, 2000, for sensory and cognitive searching skills, such as spatial memory and integrating spatial-temporal information]. Moreover, the strength needed to reach a mature-like efficiency at harvesting a fruit is acquired as early as 3 years old and full adult dentition is not necessary to peel the fruit. The lesser challenge faced by capuchins dealing with such hard-to-process food may explain why adult competence develops faster in this task than in foraging on larvae hidden inside bamboo stalks [Gunst et al., 2008, in press].

In our study, the quasi-null foraging efficiency of infant capuchins engaged in the main procedure may lead them to skip the harvesting step by gnawing unplucked fruit from the apex, a strategy that never resulted in removing fruit from the infructescence and gave the forager very limited access to the mesocarp. Despite the low immediate payback with respect to food acquisition, the persistence in performing such compensatory foraging actions may reflect young capuchins' generative exploratory tendencies, help them familiarize with the foraging substrate, and lead them to individually practice appropriate foraging behaviors in the future [cf. Fragaszy & Adams-Curtis, 1991; Gunst et al., in press]. Gunst et al. [in press] found major age differences in substrate selection identical to those reported here, when capuchins foraged on prey embedded in bamboo stalks. Lacking permanent canines and powerful jaws, infants mainly ripped soft bamboo pith (that cannot contain any larvae) instead of more appropriate plant material, such as hard and large bamboo stalks, likely to contain larvae. Working on softer material could allow them to practice opening bamboo, even though it does not result in gaining a larva [Gunst et al., in press].

The poorer success of infants at harvesting maripa fruit by themselves or gnawing unplucked fruit may account for their adopting a second alternative strategy during synchronous feeding, consisting of feeding on fruit already harvested by other foragers and accidentally dropped or licking off fruit peelings discarded by others during the foraging process. The scrounging strategy was quasi exclusively adopted by infants whose presence near other foragers was tolerated. Although gnawing fruit apex can be considered an individual foraging tactic, scavenging partially processed fruit is a socially mediated way for infants to feed at little pre-harvest handling cost. For an infant, picking up a fruit item plucked by a skilled forager and accidentally dropped represents an opportunistic means to bypass the harvesting of a fruit, a foraging step difficult to achieve at this stage of development. Licking off fresh fruit peelings left by others is also an easier way to gain access to pieces of fruit mesocarp than through gnawing the apex of unplucked fruit.

The strong dependency of infants on others' proficiency at harvesting maripa fruit emphasizes that the social environment may have an important role in learning. By retrieving a fruit item accidentally dropped or fruit peelings discarded by other foragers, an immature individual may not only gain energetic benefits through extra nutrients, but also informational benefits through the opportunity to learn about diet breadth, food locations, or food-processing skills, i.e. what, where, and how to eat

[Rapaport & Brown, 2008]. As a consequence of feeding synchronously with mature individuals, young primates may thus learn more rapidly, if they can actually obtain some of the food being harvested by skilled conspecifics. For example, King [1994] reported that young and naïve yellow baboons selectively approached and interacted with adults feeding upon favored and difficult foods, such as corms impossible for infants to pull from the ground, and suggested that this early interest might benefit immatures' future foraging success. In our study, the scrounging strategy became rare in younger juveniles, suggesting that by 1 year of age, capuchins had learned how to harvest maripa fruit but only had the strength to do it efficiently by the age of 3. Because they focused more on practicing the main foraging procedure and had a higher harvesting rate than infants, younger juveniles might not need to keep on adopting alternative foraging strategies with a very low payback.

Foraging artifacts, such as partially processed maripa fruits and peelings left behind by skilled foragers, are visual and olfactory cues that can become associated in memory with feeding, and possibly trigger naïve individuals' interest in these particular foraging sites. Immature brown capuchins (infants, younger and older juveniles) are often attracted to bamboo stalks that have been ripped open by adults and direct specific foraging behaviors toward this damaged substrate, even after the adults' departure, a socially mediated learning process called stimulus/local enhancement [Gunst et al., 2008]. Fragaszy [1986] reported another example of opportunistically scrounging others' partially processed food in wedge-capped capuchins, where infants, younger and older juveniles were not strong enough to open green frond stalks from palms by themselves and instead used fronds already opened by skilled foragers. Likewise, observing their mothers forage on *Saba florida* might help young chimpanzees select the appropriate physical characteristics of the fruit, acquire new foraging techniques, and learn the more efficient processing sequence [Corp & Byrne, 2002b].

Our fifth result, showing that infants often scrounged from closely affiliated group members, is consistent with the predictions generated by a model relating social learning to social dynamics within groups of animals, and stating that the more tolerant partners are to each other, the more spatial proximity and behavioral coordination they exhibit, the more social attention they pay to each other, the more opportunities for social learning they provide, and the more similar the behavioral patterns are [Coussi-Korbel & Fragaszy, 1995]. Young primates tend to feed at the same time and on the same food items as their mothers, and such synchronous feeding may influence the development of food selection or feeding habits [e.g. Hauser, 1993; Hikami et al., 1990]. Close and peaceful proximity to a feeding individual, namely co-feeding, has been proposed as a major factor in the transmission of feeding innovations because it is assumed to enhance opportunities for social learning [Ueno, 2005; van Schaik et al., 1999]. In a socially tolerant species, such as brown capuchins, infants and young juveniles are allowed to spend time near adults while they are foraging, watch them closely, sample some of the food they discard, and even receive food directly from adults' hands or mouth [Fragaszy et al., 2004]. Such a tolerated co-feeding context is likely to enhance in infants the use of similar food processing patterns as the adults to which they are physically associated [Agostini & Visalberghi, 2005; Fragaszy & Visalberghi, 2004].

However, it should be noted that the gnawing and scrounging strategies are not very efficient in terms of immediate energetic payoff. Individuals relying only on these tactics cannot garner sufficient amount of food to sustain themselves for the following reasons: (1) tearing off small pieces of epicarp from the apex of unplucked fruit and licking off the outer part of mesocarp attached to fruit peelings only give a limited access to the pulp; (2) fruit plucked and accidentally dropped by other foragers is an unpredictable food source; and (3) picking up fruit dropped on the ground is highly unlikely when the infructescence is more than 10 m high and can be hazardous in terms of predation risk. In the case of shorter maripa trees with lower infructescence (about 5 m high), capuchins were very vigilant while climbing down the trees to pick up fruit items dropped on the ground, looking out for potential terrestrial predators before jumping off the trunk, running to pick up the fruit, and rushing back to the tree [Gunst, personal observation]. Most fruit peelings were collected by infants on the surface of the large infructescence and in the close vicinity of older foragers while peeling their fruit and discarding food debris around them. Even with low payback, sampling these foraging artifacts provide infants with some access to the food, as opposed to already-ripped bamboo stalks around which young scroungers' exploratory actions cannot garner food [Gunst et al., 2008]. Thus, for infants, scrounging others' partially processed maripa fruit can generate limited but immediate reward (i.e. pieces of fruit mesocarp), whereas practicing at an already-opened stalk does not lead to short-term success by obtaining a direct reward (i.e. larva).

Squirrel monkeys (*S. sciureus*) also forage extensively on maripa [Stone, 2006; Boinski, unpublished data], despite adult squirrel monkeys having no more than half the body mass of adult capuchins [0.7–1 kg vs. 2–4 kg, respectively: Fragaszy et al., 2004; Smith & Jungers, 1997]. According to Stone [2006], by 1 year of age, squirrel monkeys are able to forage efficiently on maripa fruit and their foraging behaviors and efficiency are comparable to those of adults. By 1 year of age, a brown capuchin weighs on average 1.2 kg [Fragaszy & Adams-Curtis, 1991] and is thus about as big and heavy as an adult squirrel monkey. How is it that much smaller squirrel monkeys are more efficient at harvesting maripa than young capuchins? The answer may be the timing of their feeding on these fruits. Capuchins foraged on maripa fruit even before they were fully ripe and thus were still firmly attached to the fruiting stalk. In contrast, squirrel monkeys (*S. sciureus*) at RV fed on fully ripe fruit items that were much easier to remove from the infructescence than the partially ripe fruit taken by capuchins. Moreover, when competing for maripa with capuchins, squirrel monkeys had little access to the infructescence and opportunistically focused on already harvested and partially processed fruit items dropped on the ground by capuchins. By doing so, they could skip the difficult harvesting step [Gunst, personal observation].

Our results revealed an overall picture of the ontogeny of foraging on maripa fruit with several complementary developmental trends: (1) an increase in foraging efficiency with age from infants to adults mainly explained by a decrease in pre-harvest handling time, (2) a rapid decline in gnawing from infants to young juveniles followed by a decrease with age until fading in mature individuals, and (3) an early disappearance of the scrounging strategy from young juveniles. The main behavioral patterns of foraging on maripa were already in place from around 2 years (i.e. young juveniles). However, proficiency was mainly predicted by the timeline of physical growth and adult levels of proficiency were achieved by older juveniles (greater than 3 years of age). For capuchin monkeys, developing mature form and efficiency in preying on embedded invertebrates had a more extended timeline: the abilities to select appropriate substrates and to master adequate detection and extraction techniques were not fully completed before the subadult stage, around 6 years [Gunst et al., in press]. We suggest that learning to search effectively for hidden food items may take longer than growing large enough to process them. These findings on two different foraging tasks parallel those in chimpanzees, for which the timeline of acquisition of processing *S. florida* fruit was faster [between 2 and 4 years; Corp & Byrne, 2002b] than the timeline of mastering an extractive and tool-using foraging task like nut-cracking, which extends far beyond the onset of juvenility [up to 10 years; Matsuzawa, 1994]. We predict the same pattern for other generalist foragers (i.e. exploiting a large number of animal and plant species) that search for embedded prey, such as *Leontopithecus rosalia*, the golden lion tamarin [Bicca-Marques, 1999], which exhibits more direct social support for young monkeys learning to locate prey than do brown capuchins [reviewed in Rapaport & Brown, 2008].

Given that capuchins are weaned before age 2, they must find adequate quantities of foods that are easier to process than are maripa fruits in their second year. How capuchins obtain adequate nutrition during and just after weaning, when they are not strong enough to process hard-to-process foods as efficiently as adults (such as maripa), remains to be determined. Developmental changes in foraging choices by young capuchin monkeys (and others that are weaned well before adult dental and skeletal development is completed) must reflect changing options for processing foods presenting varying physical challenges.

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REFERENCES

Agostini I, Visalberghi E. 2005. Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigrittus*). American Journal of Primatology 65:335–351.

Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press.

Altmann J, Alberts S. 1987. Body mass and growth rates in a wild primate population. Oecologia 72:15–20.

Anapol F, Lee S. 1994. Morphological adaptation to diet in Platyrrhine primates. American Journal of Physical Anthropology 94:239–261.

Bereau D, Benjelloun-Mlayah B, Delmas M. 2001. *Maximilian maripa* drude mesocarp and kernel oils: fatty acids and total tocopherols compositions. Journal of the American Oil Chemists' Society 78:213–214.

Bicca-Marques JC. 1999. Hand specialization, sympatry, and mixed species associations in callitrichines. Journal of Human Evolution 36:349–378.

Boinski S, Fragazsy DM. 1989. The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedi*. Animal Behaviour 37: 415–428.

Boinski S, Quatrone R, Swarts H. 2000. Substrate and tool-use by brown capuchins in Suriname: ecological context and cognitive basis. American Anthropologist 102:741–761.

Boinski S, Quatrone RP, Sughrue K, Selvaggi L, Henry M, Stickler CM, Rose LM. 2003. Do brown capuchins socially learn foraging skills? In: Fragaszy DM, Perry S, editors. The biology of tradition: models and evidence. Cambridge: Cambridge University Press. p 365–390.

Byrne RW, Byrne JME. 1993. Complex leaf-gathering skills of mountain gorillas (*Gorilla gorilla beringei*): variability and standardization. American Journal of Primatology 31:241–261.

Byrne RW, Whiten A, Henzi SP, McCulloch FM. 1993. Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. Behavioral Ecology and Sociobiology 33:233–246.

Corp N, Byrne RW. 2002a. Leaf processing by wild chimpanzees: physically defended leaves reveal complex manual skills. Ethology 108:673–696.

Corp N, Byrne RW. 2002b. The ontogeny of manual skill in wild chimpanzees: evidence from feeding of the fruit *Saba florida*. Behaviour 139:137–168.

Coussi-Korbel S, Fragaszy DM. 1995. On the relation between social dynamics and social learning. Animal Behaviour 50:1441–1453.

Di Bitetti MS, Janson CH. 2001. Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour 62:47–56.

Fedigan LM. 1990. Vertebrate predation in *Cebus capucinus*: meat eating in a Neotropical monkey. Folia Primatologica 54:196–205.

Fragaszy DM. 1986. Time budgets and foraging behavior in wedge-capped capuchins (*Cebus olivaceus*): age and sex differences. In: Taub DM, King FA, editors. Current perspectives in primate social dynamics. New York: Van Nostrand. p 159–174.

Fragaszy DM. 1990. Early behavioral development in capuchins (*Cebus*). Folia Primatologica 54:119–128.

Fragaszy DM, Adams-Curtis LE. 1991. Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology 105:387–397.

Fragaszy DM, Boinski S. 1995. Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). Journal of Comparative Psychology 109:339–348.

Fragaszy DM, Visalberghi E. 1996. Social learning in monkeys: primate "primacy" reconsidered. In: Heyes CM, Galef Jr BG, editors. Social learning in animals: the roots of culture. Toronto: Academic Press. p 65–84.

Fragaszy DM, Adam-Curtis LE. 1997. Developmental changes in manipulation in tufted capuchins from birth through two years and their relation to foraging and weaning. Journal of Comparative Psychology 111:201–211.

Fragaszy DM, Adams-Curtis LE. 1998. Growth and reproduction in captive tufted capuchins (*Cebus apella*). American Journal of Primatology 44:197–203.

Fragaszy DM, Visalberghi E. 2004. Socially biased learning in monkeys. Learning and Behavior 32:24–35.

Fragaszy DM, Feuerstein JM, Mitra D. 1997. Transfers of food from adults to infants in tufted capuchins. Journal of Comparative Psychology 111:194–200.

Fragaszy DM, Visalberghi E, Fedigan LM. 2004. The complete capuchin: the biology of the genus *Cebus*. Cambridge: Cambridge University Press.

Fragoso JMV. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. Journal of Ecology 85:519–529.

Fragoso JMV, Silvius KM, Correa JA. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology 84:1998–2006.

Galliari CA. 1985. Dental eruption in captive-born *Cebus apella*: from birth to 30 months old. Primates 26:506–510.

Garber PA. 2000. Evidence for the use of spatial, temporal, and social information by primate foragers. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. p 261–298.

Gibson KR. 1987. Cognition, brain size and the extraction of embedded food resources. In: Else JGF, Lee PC, editors. Primate ontogeny, cognition and social behaviour. Cambridge: Cambridge University Press. p 93–103.

Gibson EJ, Pick AD. 2000. An ecological approach to perceptual learning and development. Oxford: Oxford University Press.

Gunst N, Boinski S, Fragaszy DM. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. Behaviour 145:195–229.

Gunst N, Boinski S, Fragaszy DM. In press. Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (*Cebus apella apella*). Journal of Comparative Psychology.

Hanya G. 2003. Age differences in food intake and dietary selection of wild Japanese macaques. Primates 44:333–339.

Hauser MD. 1993. Ontogeny of foraging behavior in wild vervet monkeys (*Cercopithecus aethiops*). Journal of Comparative Psychology 107:276–282.

Hikami K, Hasegawa Y, Matsuzawa T. 1990. Social transmission of food preferences in Japanese monkeys (*Macaca fuscata*) after mere exposure or aversion training. Journal of Comparative Psychology 104:233–237.

Izawa K, Mizuno A. 1977. Palm fruit cracking behavior of wild black-capped capuchins (*Cebus apella*). Primates 18:773–792.

Janson CH, Boinski S. 1992. Morphological and behavioral adaptations for foraging in generalist primates: the case of the Cebines. American Journal of Physical Anthropology 88:483–498.

Janson CH, van Schaik CP. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. Oxford: Oxford University. p 57–74.

Johnson SE, Bock J. 2004. Trade-offs in skill acquisition and time allocation among juvenile chacma baboons. Human Nature 15:45–62.

Jungers WL, Fleagle JG. 1980. Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: a longitudinal and comparative study. American Journal of Physical Anthropology 53:471–478.

Kahn F, de Granville JJ. 1992. Palms in forest eco-systems of Amazonia. New York: Springer-Verlag.

King BJ. 1994. Primate infants as skilled information gatherers. Pre- and Perinatal Psychology Journal 8:287–307.

Lonsdorf EV. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii* of Gombe National Park, Tanzania. Animal Behaviour 70:673–683.

MacKinnon KC. 2006. Food choice by juvenile capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. In: Estrada A, Garber PA, Pavelka MSM, Luecke L, editors. New perspectives in the study of Mesoamerican primates. New York: Springer. p 349–365.

Martin P, Bateson P. 1993. Measuring behaviour: an introductory guide. Cambridge: Cambridge University Press.

Matsuzawa T. 1994. Field experiments on use of stone tools by chimpanzees in the wild. In: Wrangham RW, McGrew W, de Waal FBM, Heltne P, editors. Chimpanzee culture. Cambridge: Harvard University Press. p 351–370.

Noldus Information Technology. 1998. Matman reference manual. Version 1.0 for Windows. Wageningen, The Netherlands: Noldus Information Technology.

Ottoni EB, de Resende BD, Izar P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. Animal Cognition 24:215–219.

Parker S, Gibson K. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in *Cebus* monkeys and great apes. Journal of Human Evolution 6:623–641.

Perry S, Ordoñez-Jiménez JC. 2006. The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics. In: Hohmann G, Robbins M, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press. p 203–234.

Post DG, Hausfater G, McCuskey SA. 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. Folia Primatologica 34:170–195.

Rapaport LG, Brown GR. 2008. Social influences on foraging behavior in young non-human primates: learning what, where, and how to eat. Evolutionary Anthropology 17:189–201.

Resende BD, Ottoni EB, Fragaszy DM. 2008. Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a perception-action perspective. Developmental Science 11:828–840.

Rose LM. 1994. Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 15:95–114.

Russon AE. 2003. Developmental perspectives on great ape traditions. In: Fragaszy DM, Perry S, editors. The biology of tradition: models and evidence. Cambridge: Cambridge University Press. p 329–364.

Siegel S, Castellan NJ. 1988: Nonparametric statistics. London: McGraw-Hill.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. Journal of Human Evolution 32:523–559.

Stephens DW, Krebs JR. 1986. Foraging theory. Princeton: Princeton University Press.

Stone AI. 2006. Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (*Saimiri sciureus*). Ethology 112:105–115.

Strum SC. 1991. Weight and age in wild olive baboons. American Journal of Primatology 25:219–237.

Ueno A. 2005. Development of co-feeding behaviour in young wild Japanese macaques (*Macaca fuscata*). Infant Behavior and Development 28:481–491.

Vogel ER, Janson CH. 2007. Predicting the frequency of food-related agonism in white-faced capuchin monkeys (*Cebus capucinus*), using a novel focal-tree method. American Journal of Primatology 69:533–550.

van Schaik CP, Deaner RO, Merrill MY. 1999. The conditions for tool use in primates: implications for the evolution of material culture. Journal of Human Evolution 36:719–741.

Watts D. 1985. Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla beringei*). American Journal of Primatology 8:1–10.

Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. Journal of Human Evolution 48:473–492.