THE ONTOGENY OF FORAGING SKILLS IN WILD BROWN CAPUCHINS (*CEBUS APELLA*): DEVELOPMENTAL PERSPECTIVE ON THE ACQUISITION OF ECOLOGICAL COMPETENCE

by

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(Under the Direction of DOROTHY M. FRAGASZY)

ABSTRACT

Extractive foraging refers to the complex food-searching patterns needed to forage on foods that are difficult to locate and obtain, such as invertebrates encased in protective matrices. The study of extractive foraging emphasizes the selective impact of dealing with embedded foods for the evolution of slower development since prolonged immaturity may provide additional learning time to develop adult-level foraging skills.

This research aims to understand the complementary contribution of physical maturation and experiential factors to the ontogeny of an extractive foraging behavior in wild brown capuchins (*Cebus apella*) in Raleighvallen, Central Suriname Nature Preserve: foraging for larvae hidden inside bamboo stalks. I partitioned the processes of foraging for embedded invertebrates into 1) handling components leading to the extraction and consumption of larvae after ripping bamboo stalks apart (Chapter 2), and 2) searching components via specific detection techniques to locate hidden larvae (Chapter 3). I found that the former is mainly explained by age-related morphological changes in size, weight, and dentition, whereas the latter is more dependent upon individual behavioral practice and socially-biased learning allowing immature individuals to gain experience at locating and extracting hard-to-process foods.

In Chapter 2, I found that developing proficiency at obtaining encased larvae extends through several years of juvenescence. Supportive conditions include morphological changes and indirect social influence through foraging artefacts left in the habitat by conspecifics. Chapter 3 shows that young capuchins become efficient foragers through the progressive disappearance of ineffective food-searching behaviors, and the gradual emergence of effective detection techniques applied to appropriate foraging substrates (bamboo stalks likely to contain larvae), which is not fully mastered before the age of six years. This is consistent with the "perception-action" perspective on the development of foraging competence. The behavioral complexities involved in the detection techniques used for locating hidden foods develop over several years of juvenescence and fit the "needing-to-learn" hypothesis. I addressed these issues from a comparative perspective among primates, as a way to provide an evolutionary view on interspecific similarities and differences in the acquisition of complex foraging competence in various primate species.

INDEX WORDS: embedded foods; extractive foraging skills; ontogeny; physical maturation; socially-mediated learning; foraging artefacts; detection techniques; brown capuchin; *Cebus apella*.

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DEDICATION

To all the capuchins of Raleighvallen, Surinam

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Optimal foraging theory as an ecological approach to what and how animals eat

Understanding what and how animals eat is an essential component of addressing many ecological issues such as energy flow, competition and adaptation (Kamil et al., 1987). Acquisition of resources, especially food, is also a central topic in the field of behavioral ecology, partly as a result of the fact that many animals spend much of their active time throughout the year engaged in foraging.

Foraging is defined as all behavioral activities and physiological processes (namely, location, acquisition, and assimilation of food) leading to the satisfaction of a particular set of nutritional needs (Cant & Temerin, 1984). Ecological factors determine the circumstances under which these needs must be met, and these elements combine to produce various problems: spatial and temporal distributions of food patches, variety and arrangement of foods within a patch, physical characteristics of food items, etc. To solve these ecological problems, the foraging animal has to make several decisions such as where and when to forage or give up on a particular foraging area, which food items to include in its diet, as well as how to locate and process particular food items.

Optimal foraging models consider foraging as a decision process and predict an optimal solution for a particular foraging problem (see Pyke et al., 1977 for a review). Optimal foraging theory assumes that costs and benefits of foraging are balanced against each other in order to maximize the net energetic intake, which may be the most important criterion for food choice (MacArthur & Pianka, 1966; Stephens & Krebs, 1986). The fitness of a foraging animal is maximized through its foraging adaptations shaped by natural selection (Schoener, 1971; Charnov, 1976). In optimal foraging models, the foraging process is usually partitioned into two components: first searching patterns, defined as the behaviors exhibited to look for food between encounters of items of the same food type, and second, handling patterns, defined as the skilled manipulation of the food item encountered before it is consumed (MacArthur & Pianka, 1966).

Food embeddedness and evolutionary implications of extractive foraging

A major ecological challenge in foraging is food embeddedness. Food items concealed inside protective matrices such as spines, shells, hard husks or hidden locations that make them hard to detect and extract are referred to as "hard-to-process foods" or "difficult" foods. Faced with such antipredator defenses, some animals use highly flexible, lengthy manipulative and/or tool-based behavioral sequences (e.g. Mc Grew, 1992; Russon, 1998). Extractive foraging is defined as the searching and handling of these foods that are difficult to obtain, such as hard-shelled nuts and fruits, embedded invertebrates, or any encased food sources that need to be located and extracted from a protective matrix through skilled manipulation (Parker & Gibson, 1977; King, 1986). Such food-searching and food-processing behaviors are typically categorized as complex foraging patterns that may necessitate substantial learning time. Locating and getting access to encased foods are thought to demand longer perceptual learning and higher sensorimotor coordination than, for example, collecting surface invertebrates found on leaves and branches, or plucking fruits (Gibson, 1987).

The “needing-to-learn” hypothesis postulates that the timeline for developing adult-level form and efficiency of extractive foraging greatly differs from that predicted by the timeline of physical growth (Ross & Jones 1999; van Schaik et al. 2006). In other words, the development of mature competence in complex foraging activities may be delayed by some components of extractive foraging that are not related to body size and strength (i.e. the need to acquire detection skills). The present research aims at taking an ontogenetic approach to the questions related to extractive foraging.

Developmental perspective on foraging in animals

Comparative findings on the ontogeny of food-related activities in many vertebrate taxa show that immature and mature individuals differ in their food-searching strategy, diet choice, as well as foraging behaviors and efficiency (e.g., Marchetti & Price, 1989; Janson & van Schaik, 1993; Guinet & Bouvier, 1995). In most species of birds, marine mammals, social carnivores, and primates, young individuals devote less time to foraging activities, perform less complex foraging patterns, and as a consequence, are less efficient foragers with a less diverse diet than adults (Whitehead, 1986; Wunderle, 1991; Fragaszy & Boinski, 1995; Holekamp et al., 1997; Mann & Sargeant, 2003; Johnson & Bock, 2004).

Developing adult-level proficiency at obtaining embedded foods is a long process involving gradual behavioral changes and can extend through several years of juvenescence (e.g., Janson & van Schaik, 1993). The ontogeny of foraging competence, and especially the acquisition of extractive foraging skills, are likely to benefit from physical maturation and experiential factors. Physical maturation includes higher body size and mass, increasing strength, as well as the acquisition of powerful jaws and permanent teeth. Experiential factors includes individual behavioral practice of motor patterns belonging to the foraging repertoire of the species through independent food exploration and socially mediated learning via the direct interactions with skilled group members or indirect social influences provided by the foraging artefacts left in the habitat by conspecifics.

Primates are characterized by the longest juvenile period in relation to life span of all mammals (Pereira & Fairbanks, 1993). This extended period of time may allow immature individuals to gain experience at locating and extracting hard-to-process foods. At the level of individual development, the "perception-action" perspective on the ontogeny of food-searching behavior postulates that skilled actions are acquired through the routine generation of species-typical exploratory actions, coupled with learning about the outcomes of actions that generate directly perceptible information (Lockman, 2000; Gibson & Pick, 2003). Young individuals acquired adult-level foraging proficiency through a step-by-step emergence of effective foraging patterns and a gradual disappearance of ineffective food-searching behaviors.

On the other hand, at the level of species or genus, and according to the "needing-to-learn" hypothesis, prolonged juvenility is expected in species showing extractive foraging patterns that necessitate the acquisition of a large amount of information and/or skills to reach adult competence before individuals reach reproductive maturity (Ross & Jones, 1999). In other words, the necessity to learn complex foraging behaviors contributes to slowed life history (Ross & Jones, 1999; van Schaik et al., 2006). In species facing complex foraging challenges (e.g., aye-ayes, *Daubentonia madagascariensis*: Krakauer, 2005; orangutans, *Pongo pygmaeus*: van Noordwijk & van Schaik, 2005; Russon, 2006; chimpanzees, *Pan troglodytes*: Matsuzawa, 1994; humans, *Homo sapiens*: Kaplan et al., 2000), the development of detection and extractive foraging techniques occurs relatively late, compared to other species characterized by non-extractive diets and in which most foraging behaviors appear during infancy (e.g., ruffed lemurs, *Varecia variegata*: Krakauer, 2005; squirrel monkeys, *Saimiri oerstedi*: Boinski & Fragaszy, 1989).

Capuchin monkeys as extractive and social foragers

Capuchin monkeys (*Cebus* spp.) are a generalist genus exhibiting a flexible use of food resources across a broad range of habitats (Fragaszy et al., 1990, 2004a). Capuchins monkeys are primarily frugivorous, although animal prey also constitutes an important part of their diet. They are known for their opportunistic and strenuously destructive, extractive foraging style, which requires manual dexterity, robust teeth and powerful jaws (Janson & Boinski, 1992; Anapol & Lee, 1994; Fragaszy & Boinski, 1995; Fragaszy et al., 2004a; Wright, 2005).

Capuchins are particularly adept at foraging on high-quality foods (e.g., endosperm, invertebrates) protected by hard husks or hidden inside woody substrates that other species can not exploit (e.g., Izawa & Mizuno, 1977; Boinski et al., 2000). To locate embedded invertebrates, they use auditory, olfactory, tactile, and visual cues. A typical detection technique is the tap scanning, consisting of a quick tapping on foraging substrates with fingertips, that may generate acoustic information about the presence of cavities where invertebrates may be sequestred (Izawa, 1978; Janson & Boinski, 1992; Phillips et al., 2003, 2004; Visalberghi & Neel, 2003; Gunst et al., 2008).

Compared to other monkeys, capuchins have an extended life span (to past 50 years in captivity) and a long period of postnatal growth of brain and body (Fragaszy et al., 1990, 2004a). They have relatively large brains and a high level of sensorimotor intelligence. In captive settings, they use and manufacture various types of tools (e.g., Westergaard & Suomi, 1995). In the wild, they can use tools, including stone pounding tools (Fragaszy et al., 2004b).

Capuchin monkeys live in multimale-multifemale groups of 10 to more than 30 individuals, with all age-sex classes represented. Groups are relatively cohesive during the day, although individuals spread out while foraging (Robinson, 1981). Capuchins are highly tolerant of others foraging in close proximity. Young individuals are often allowed to sit in contact with adult foragers, and sniff or even touch the food being processed (for a review, see Panger et al., 2002; Fragaszy et al., 1997, 2004a). Immatures are generally more likely than adults to approach others' foraging sites, and seek out opportunities to learn from others about food location (see also King, 1994; Giraldeau & Caraco, 2000).

Considering the developmental and socioecological features exhibited by capuchins (namely, skilled extractive foraging, dexterous manipulation, tolerant gregariousness, and prolonged juvenescence), this taxon is a good candidate to evaluate the contributions of physical growth, individual behavioral practice, and socially mediated learning on the development of competence in complex foraging. Capuchins should provide diagnostic evidence of lengthy ontogeny of specific extractive foraging behaviors which can be (partially) dissociated from physical maturation, to support the "perception-action" perspective and the "needing-to-learn" hypothesis.

General research goal and specific objectives

The general goal of this research is to understand the complementary contribution of physical maturation and experiential factors to the ontogeny of an extractive foraging skill in wild brown capuchins (*Cebus apella*) in Raleighvallen, Suriname: foraging for larvae hidden inside bamboo stalks via searching and handling behaviors. I will mainly focus on how immature brown capuchins gradually acquire the expertise to solve this particular foraging problem and become efficient foragers. Despite the amount of literature and experimental evidence on the matter (cf. Fragaszy et al., 2004a for a review), I regard as still unresolved the question of the developmental processes involved in the acquisition of extractive foraging competence in wild brown capuchins, including food detection and processing techniques, and how immature individuals gain experience at locating and extracting hard-to-process foods.

In this dissertation, I will take the same approach as used in optimal foraging models (cf. MacArthur & Pianka, 1966), by partitioning the processes of foraging for embedded invertebrates into 1) handling components leading to the extraction of larvae from their protective matrices, and the consumption of this protein and lipid-rich food source (Chapter 2), and 2) searching components via specific detection techniques to accurately locate hidden larvae (Chapter 3). The former is likely to be explained by physical characteristics whereas the latter may depend more on experiential factors. I will address these issues from a comparative perspective among primates, as a way to provide an evolutionary view on interspecific similarities and differences in the acquisition of foraging competence in various primate species.

Chapter 2 (Gunst et al. 2008) explores the relations between morphological changes and the timeline of improving efficiency at obtaining larvae hidden inside bamboo stalks, with an emphasis on conspecifics' foraging artefacts as an indirect social influence. To delineate the scope of skill development and its general time course, I will evaluate the extent to which immature (infants and juveniles) wild brown capuchins are less efficient than older individuals (subadults and adults) in obtaining larvae hidden inside bamboo stalks. I will document variations in foraging efficiency and reliance on encased larvae as opposed to more easily-obtained foods across age classes. I will investigate how these differences may reflect changes in size, weight, dentition, and nutritional requirements. In accord with the social foraging theory assuming that young individuals learn from others about food location by performing foraging actions at potential feeding sites (Giraldeau & Caraco, 2000), I will document variation according to age in attraction and responsiveness to physical traces left by skilled foragers, and test the prediction that immature brown capuchins are more likely than adults to exhibit interest in already-ripped bamboo stalks and direct food-related behaviors toward these foraging spots.

The goal of Chapter 3 (Gunst et al., to be submitted) is to compare age-related morphological changes with the timeline of acquisition of extractive behaviors (i.e. ripping bamboo stalks apart to get access to encased larvae), and those components of extractive foraging that are not strength-dependent (i.e. the acquisition of detection skills to locate hidden larvae) as they may serve as constraints on the development of mature competence (cf. Ross & Jones 1999; van Schaik et al. 2006). Among the foraging behaviors potentially involved in the discovery of larvae, I will determine the relative contribution of different detection methods to a high foraging efficiency. I will also determine the changes with age in the ability to assess the physical properties of appropriate foraging substrates (i.e. bamboo stalks likely to contain larvae). From the "perception-action" theory, I will test the prediction that young capuchins acquire the detection techniques and the ability to select appropriate foraging substrates through a step-by-step emergence of effective detection techniques applied to stalks likely to contain larvae, and a progressive disappearance of ineffective food-searching behaviors directed toward inappropriate substrates. I will discuss the importance of experiential factors on the development of extractive foraging skills through a case study on the foraging behaviors and efficiency of two immigrant naïve adult males, compared to experienced adults and immatures.

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CHAPTER 2

ACQUISITION OF FORAGING COMPETENCE IN WILD BROWN CAPUCHINS (*CEBUS APELLA*), WITH SPECIAL REFERENCE TO CONSPECIFICS' FORAGING ARTEFACTS AS AN INDIRECT SOCIAL INFLUENCE[1]

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Abstract

Wild brown capuchins (*Cebus apella*) in Raleighvallen, Suriname forage on larvae hidden inside bamboo stalks via searching and extractive behaviours. We found that developing proficiency at obtaining larvae from bamboo stalks extends through several years of juvenescence. Older juveniles pass through a transition from a juvenile pattern to an adult pattern of foraging efficiency and diet selection. Whereas most studies have investigated the contribution of direct interactions between a naïve individual and a competent forager on the acquisition of foraging expertise, we focused on indirect social influence through foraging artefacts left in the habitat by conspecifics. Young individuals foraged at bamboo stalks more often shortly after than shortly before encountering bamboo segments previously opened by foragers to extract larvae. We discuss this result in terms of stimulus enhancement and social facilitation. In capuchins, learning how to forage on difficult foods does not necessarily occur in the presence of other group members, and social influences can be delayed in time and separate in space from others. This study provides a view on how the gradual acquisition of foraging competence in brown capuchins is aided jointly by physical maturation and indirect social input that provides opportunities to practice appropriate foraging actions.

Keywords: extractive foraging; age differences; physical maturation; social facilitation; foraging artefacts

Introduction

According to the "needing-to-learn" hypothesis, the prolonged juvenility reported in most primate species (Pereira & Fairbanks, 1993) is associated with foraging patterns that necessitate acquiring a proportionally large amount of information and/or skills to reach adult competence (designated "complex foraging patterns") before individuals reach reproductive maturity (Ross & Jones, 1999). Thus we should find a long developmental trajectory toward mature foraging efficiency (and lengthy periods of juvenescence) in species that exhibit complex foraging patterns. Alternatively, lengthy juvenescence may reflect selection for slow growth, to accommodate limited food resources (Janson & van Schaik, 1993) or some other process. These possibilities are not mutually exclusive, nor are they easy to distinguish in practice. One reason for this difficulty is that comparisons of the relation between life history and foraging patterns across species are constrained by the lack of a principled scale for "complexity" of foraging. Moreover, analysis of the contribution of learning to the achievement of foraging competence by young individuals is complicated by the confound that increasing strength (associated with increasing size) also supports more efficient foraging for those actions that require strength, as many do.

One approach that can help to illuminate the particular contributions of experience and physical growth to the development of foraging competence is to detail the ontogeny of specific foraging elements that are part of the "complex" designation, particularly those that differ in their dependence on physical strength. Components of extractive foraging can be useful for this purpose. 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). The “needing-to-learn” hypothesis produces the general prediction that the timeline for developing mature form and efficiency of extractive foraging varies discernibly from that predicted by the timeline of physical growth and development. A more refined prediction is that those components of extractive foraging that are not strength-dependent will serve as constraints on the development of mature competence. Because skill acquisition may continue even after reaching adult body size, these particular components of extractive foraging requiring refinement of technique and relying on learning may achieve mature form later than the body.

Capuchins serve as a useful taxon to evaluate the contributions of physical growth and development and individual experience on the development of competence in complex foraging. They have a relatively long life span and a prolonged period of body growth and brain maturation (Fragaszy et al., 1990), together with reliance on various extractive behaviours that epitomize “complex foraging patterns” (Janson & Boinski, 1992). Thus, they should provide diagnostic evidence of lengthy ontogeny of specific extractive foraging behaviours which can be (partially) dissociated from physical growth and development, to support the “needing-to-learn” hypothesis. Capuchins also exhibit sexual dimorphism in size and many aspects of behaviour (reviewed below), which can further be expected to have ontogenetic correlates.

In this study we address age and sex differences in a specific extractive foraging skill in brown capuchins (*Cebus apella*), namely, obtaining larvae hidden inside bamboo stalks, and in the distribution of foraging effort to obtain larvae vs. obtain other kinds of foods in the same area. In effect, capuchins in a bamboo patch are presented with dichotomous foraging options: easy, lower-quality foods (pith and leaves) versus difficult, higher-quality foods (embedded larvae). Locating larvae hidden inside the bamboo stalks requires searching actions that are dependent on memorial, perceptual and sensorimotor skills rather than strength. Opening the stalks requires considerable strength. Feeding on bamboo pith and leaves requires no particular searching actions and less strength than opening stalks. Thus variation across individuals in choice of foraging target (leaves, pith, or larvae) and efficiency of foraging with different targets should vary in accord with body size and in accord with skill.

Comparative findings on the ontogeny of diet choice and foraging efficiency

Research on the ontogeny of food-related activities in many vertebrate taxa shows that immature and mature individuals differ in their diet choice and in their foraging efficiency (e.g., Marchetti & Price, 1989; Janson & van Schaik, 1993; Guinet & Bouvier, 1995). Compared to adults, young birds are less efficient foragers and garner a less diverse diet (see Wunderle, 1991 for a review). Among marine mammals, calves show an increase with age in the proportion of time spent foraging and an improvement in foraging skills (Mann & Sargeant, 2003). In social carnivores, immatures develop hunting skills over several years before becoming fully competent adult foragers (Holekamp et al., 1997).

Nonhuman primates are consistent with this broader vertebrate pattern. Immature primates exhibit less diverse diets and/or greater proportion of time devoted to foraging than adults (e.g., Whitehead, 1986; Fragaszy & Boinski, 1995; Johnson & Bock, 2004). One factor contributing to reduced diet breadth is that immatures proportionally select smaller prey, softer fruits, and easier-to-process food items (Janson & van Schaik, 1993). Copious findings also demonstrate that juveniles of many primate species are less efficient foragers than adults (e.g., brown lemurs, *Eulemur fulvus*: Tarnaud, 2004; Japanese macaques, *Macaca fuscata*: Hashimoto, 1991; toque macaques, *Macaca sinica*: Dittus, 1977; yellow baboons, *Papio cynocephalus*: Post et al., 1980; chimpanzees, *Pan troglodytes*: Matsuzawa, 1994; Corp & Byrne, 2002a; Lonsdorf et al., 2004). However, some species exhibit no significant age differences in diet or foraging success (green monkeys, *Cercopithecus sabaeus*: Harrison, 1983; mountain gorilla, *Gorilla gorilla*: Watts, 1985). Reliance on soft fruits and surface invertebrates may account for some primate species exhibiting early foraging competence, resulting in few differences between juvenile and adult foraging efficiency (e.g., squirrel monkeys: Boinski & Fragaszy, 1989), although young toque macaques are less efficient than adults even at picking and ingesting figs (Dittus, 1977).

Capuchins fit the more typical primate pattern: Immature capuchins are less efficient than adults in terms of success rate per time allocated to foraging, especially in those actions requiring skill and strength (Fragaszy, 1986; Fragaszy et al., 1990; Fragaszy & Boinski, 1995). In wedge-capped capuchin monkeys (*Cebus olivaceus*), the percentage of substrates searched that yield invertebrate food items increased from 43% in juveniles to 48% in adult females and 79% for adult males (de Ruiter, 1986; see also Janson & van Schaik, 1993).

Overall, the relatively low foraging efficiency of juvenile primates may force them to devote more time to food procurement, or greater reliance on easily-obtained foods, than adults in order to meet their metabolic demands (Janson & van Schaik, 1993; Johnson & Bock, 2004). Concurrently, 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. Joint consideration of these competing strategies suggests that young capuchin monkeys will spend more time than adults foraging, and usually forage for easier (more reliable) foods, but that they will sometimes forage persistently for high-quality resources eaten by adults without immediate return for their effort.

Sex differences in foraging

Adult male and female primates have contrasting nutritional needs due to differential body size as well as metabolic differences associated with gestation and lactation periods (e.g., Post et al., 1980; Harrison, 1983; Boinski, 1988). In capuchin monkeys, sex differences in foraging may be better explained by the larger size of adult males compared with females (Rose, 1994). Adult female squirrel monkeys, *Saimiri oerstedi*, wedge-capped capuchins and white-faced capuchins, *Cebus capucinus* spend more time than adult males foraging on encased foods, which provide reliable sources of protein, such as small invertebrates (Fragaszy, 1986; Boinski, 1988; Rose, 1994). Chimpanzees show the same pattern in foraging for termites hidden in mounds (McGrew, 1979). Sex differences in chimpanzee termite fishing are well documented, with females being significantly more involved in tool-assisted extractive foraging activity and consuming more termites than males (McGrew, 1979; Pandolfi et al., 2003; Lonsdorf, 2005). According to Lonsdorf (2005), juvenile female chimpanzees attain proficiency in termite-fishing at an earlier age than male chimpanzees, with females spending more time termite-fishing in their early years than do males. In wedge-capped capuchins as well, females differ from males in diet choice, with females exploiting palm materials and dead wood more than males (Fragaszy & Boinski, 1995). The particular extractive skill that we examine here, obtaining larvae from bamboo stalks, requires more strength than the extractive behaviours described by Fragaszy & Boinski (1995) and Lonsdorf (2005). Therefore, in the capuchins studied here, we might expect sex differences to appear later in the course of juvenile period, when a strength threshold is achieved, than in the capuchins studied by Fragaszy & Boinski (1995) or the chimpanzees studied by Lonsdorf (2005).

Foraging strategies also reflect physical development in capuchins

Age-related physical changes that may contribute to improvement in extractive foraging among capuchins involve body mass and dental development (Jungers & Fleagle, 1980; Fragaszy & Adams-Curtis, 1997). The larger its body mass, the more effectively a capuchin is able to perform strenuous foraging actions successfully, such as bashing open hard-husked fruits, and biting open bamboo stalks. Fragaszy & Adams-Curtis (1998) report that captive tufted capuchins (*Cebus 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 three 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 would reach adult mass at 7 years or perhaps even later. Dental development must also be considered. Realized bite force is dependent on the emergence stage of permanent dentition. 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, see Table 2.1 in Methods and Figure 2.3b), and the third premolar and third molar erupt at 2.9 and 3.2 years respectively (which corresponds to the older juvenile age class in this study) (Galliari, 1985; Fragaszy & Adams-Curtis, 1998). Dental development is less affected by variation in nutrition than growth in body mass (Swindler, 2002) and thus we can expect that the published timelines for dental development in *C. apella* apply to our study population. In this report, we examine the relation between physical changes (assessed in captive individuals and reported in the literature) and changes in diet selection and efficiency at obtaining larvae hidden inside bamboo stalks. Given the strenuous nature of foraging for larvae, we expected strong relations for both sets of variables. However, we expected that physical changes would not fully account for changes in foraging for larvae hidden inside bamboo stalks, in accord with the hypothesis that learning contributes substantively to the development of skill in locating larvae.

Behavioural propensities supporting learning

If young individuals' increasing foraging efficiency reflects the contribution of learning as well as physical development (Fragaszy & Visalberghi, 1996; Corp & Byrne, 2002b; Lonsdorf et al., 2004; Krakauer, 2005), young animals should devote time and effort to practicing foraging actions at which they are not yet proficient, even if they do not gain immediate energetic return for doing so, whereas (skillful) adults should not. In this study, we test the prediction that immature wild brown capuchins perform "non-functional" foraging actions at potential feeding sites (bamboo stalks, that may contain larvae) more frequently than do adults. Psychological characteristics of young monkeys would support this pattern: young capuchins' generative exploratory tendencies and high activity levels support their motivation to perform foraging actions. Throughout infancy and juvenescence, capuchins in natural settings display extensive independent food-related behavioural practice through the solitary exploration of various plant substrates and animal prey (Fragaszy, 1990; Agostini & Visalberghi, 2005). Young capuchins in captivity explore objects and surfaces in the absence of immediate gain of food or other discernible consequence. Adults in captivity, on the other hand, perform foraging actions most often in feeding contexts (Fragaszy & Adams-Curtis, 1991). The exploratory behaviours produced by young capuchins reflect behavioural predispositions shared by all members of the species (cf. Huffman & Hirata, 2003), and they are the precursors of components of the foraging repertoire in capuchins. The propensity to perform these behaviours at a rate higher than in adults (Fragaszy & Adams-Curtis, 1991), even in the absence of immediate consequence with respect to foraging, means that young capuchins are highly likely to practice appropriate foraging actions even in the absence of gaining food.

Social support for learning

Stimulus or local enhancement (of interest in an object or a place associated with positive outcome of the behaviour of conspecifics toward that object or in that place) is widely documented among vertebrates (Clayton, 1978; Galef, 1988). Stimulus enhancement may contribute to young animals learning the characteristics of appropriate substrates through drawing their attention to a particular foraging spot, leading to familiarization with the food items and substrates. Theoretically, local enhancement can support exploration and perceptual learning (Gibson, 2000) and in general promote learning how to solve a particular foraging problem.

The extent of tolerance exhibited among individuals is thought to influence social support for learning: individuals are more likely to learn with others in a tolerant social context (Coussi-Korbel & Fragaszy, 1995). Capuchin monkeys are known to display considerable tolerance towards the close proximity of especially younger group members while foraging (Boinski et al., 2003; Fragaszy et al., 2004). Young capuchins are allowed to spend time near adult foragers, to watch them closely, and to sample their food directly or to collect debris they drop (Fragaszy et al., 1997). These behavioural patterns are called scrounging (Giraldeau et al., 1994). Young capuchins, in turn, are highly motivated to watch others foraging, particularly when the others are foraging on novel foods or foods that the young animal cannot obtain itself (King, 1994; Fragaszy et al., 1997; Ottoni et al., 2005; Perry & Ordoñez Jiménez, 2006). These findings with capuchins are congruent with Giraldeau & Caraco's (2000) suggestion that young individuals generally seek out opportunities to learn from others about food location i.e., immatures are more motivated than adults to approach others' foraging sites (see also King, 1994).

Social context may aid an individual to learn in another way, namely, by facilitation of actions. In the situation considered here, observing others performing particular actions (e.g., tapping and biting) during bamboo foraging may stimulate these specific actions in the observer. In this way, young monkeys will produce "search" and "extraction" behaviours like those produced by the adults with which they are physically associated, whether or not they are likely to find food by doing so.

In the typical situation discussed in the literature, social facilitation of action occurs at the time one individual observes another, that is, during the simultaneous presence of a naïve individual and a competent forager at the same foraging spot (e.g., Aisner & Terkel, 1992; Fragaszy et al., 1997; Ottoni et al., 2005; Perry & Ordoñez Jiménez, 2006). Here, we consider if these social influences can also be detected when the naïve forager encounters foraging artefacts, i.e. the physical traces left in the habitat by skilled foragers, after their departure. Boesch (1991) suggests that the hammers and nut debris left by other chimpanzees at and near an anvil used to crack nuts can trigger a young chimpanzee's activities with nuts and stones at theses sites. Immature orangutans (*Pongo pygmaeus*) may also be attracted to extractive damage to palms exploited by others and forage at these sites (Russon, 2003). Similarly, Fragaszy (1986) notes that juvenile capuchins exploit palm fronds for pith that have been ripped open by adults, immediately following the event of adults' departure. However, the effect of indirect social input on foraging has not been studied in capuchins.

By altering their physical world, niche-constructing organisms also modify the environment of their community members (Odling-Smee, 1996). As extractive and destructive foragers, capuchins can be labelled as “ecosystem engineers” (Fragaszy et al., 2004). When a group of capuchins searches for food in a bamboo patch, and more specifically forages on invertebrates embedded in bamboo stalks, they leave physical traces such as numerous holes in bamboo segments previously ripped apart for larvae (Gunst et al., 2006). A capuchin monkey takes from 30 seconds to several minutes to select a spot on a bamboo stalk, rip it open, and then extract the larvae (if one is present). The ripping process is quite noisy. Visual and auditory stimuli during ripping and visual characteristics afterwards may attract others’ attention toward particular foraging spots, stimulating them to engage in foraging activity there. When the monkey leaves the site, the bamboo stalk has visually distinctive features: an opening approximately 2 cm x 15 cm, and a spray of whitish stalk fragments prized up from the side of the hole distal to the growth node (Gunst et al., 2006). These visual characteristics can become associated in memory with observation of action and perhaps olfactory traces of the larvae in the stalk. If an opened stalk cues other monkeys that a monkey previously searched there for larvae, it could trigger interest in the site and actions associated with foraging for larvae. Therefore, we investigated whether young capuchin monkeys are more likely than adults to exhibit interest in opened bamboo stalks and to exhibit behaviours associated with obtaining larvae at sites where others have left the remains of such foraging. This should be the case even though only one larva inhabits each segment of bamboo (Gunst, unpublished data). Because the first forager reliably retrieves the larva, later individuals on the scene may smell the larva, but exploratory actions cannot garner food. Thus “practice” at an already-ripped stalk cannot lead to success by obtaining a direct reward (i.e. a larva).

Objectives of this study

The overarching goal of this study is to understand the complementary contribution of physical and experiential factors, including social factors among the latter, to the ontogeny of an extractive foraging skill: foraging for larvae hidden inside bamboo stalks. First, to delineate the scope of skill development and its general time course, we evaluated the extent to which immature (infants and juveniles) wild brown capuchins were less efficient than older individuals (subadults and adults) in detecting and extracting larvae hidden inside bamboo stalks. Second, we tested three predictions concerning individual variation in the reliance on easy foods versus difficult foods in the bamboo patches: (a) individual foraging efficiency for difficult but highly nutritious foods (larvae) should covary with the time spent foraging on these difficult foods, (b) adults should spend more time foraging on difficult foods than on easy foods, whereas the converse is expected in younger individuals, and (c) females should engage in more frequent extractive actions than males.

Finally, we predicted that infants and juveniles should be more attracted than subadults and adults to the physical traces (ripped bamboo segment) left in foraging spots by skilled foragers, in accord with the social foraging theory assuming that young individuals seek out opportunities to learn from others about food location (Giraldeau & Caraco, 2000). This work examines the hypothesis that encountering physical traces of previous activity affects subsequent foraging activity by young capuchins.

Material and methods

Study site

Observations took place at the Raleighvallen (RV) site (4°0’N, 56°30’W) within the Central Suriname Nature Preserve (CSNR), which comprises 1.6 million ha of primary tropical forest of west-central Suriname and protects the upper watershed of the Coppename River. The RV landscape is a mosaic of small distinct, patchy habitats, to a degree exceptional throughout the Guianan Plateau. About 40 % of habitat use 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 unpub. data; Boinski et al., 2003). Brown capuchins at RV feed on a vast array of food items, including plants, fruits, flowers, invertebrates, and small vertebrates. Further descriptions of habitat use and diet of *Cebus apella* at this site can be found elsewhere (Fleagle & Mittermeier, 1980; Mittermeier & van Roosmalen, 1981; Boinski et al., 2000). The aerial and terrestrial predator fauna of RV is intact (Reichart, 1993).

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 in bamboo patches. The species of bamboo present at the study site is *Guadua latifolia* (*Graminae*). Of the three bamboo patches regularly exploited by the study troop, the largest one was approximately 350 m x 150 m (see Figures 1A and 1B in Boinski et al., 2005). Because the bamboo patch was impenetrable by human observers, three trails (about 2 m wide) were cut across the bamboo patch to allow observers to follow the monkeys.

In the bamboo patches, brown capuchins feed on bamboo shoots, stalk pith, and larvae hidden inside bamboo stalks. They also drink water contained inside bamboo stalks. The larvae (*Myelobia sp.*, Family of *Pyralidae*: Britton, 1984) feed and are hidden inside the internodes of the bamboo stalk, attaining a maximum size of 10 cm and 7 g. The larvae are prototypical ‘encased’ foods (Britton, 1984) that can be extracted by capuchins only after they use their hands and teeth to break into the stalk (1 to 9 cm diameter). Larvae are evenly distributed throughout bamboo patches, in the same way as surface insects, and therefore can be considered a dispersed food source for capuchins. Capuchins at Raleighvallen ate larvae across the year, with a decrease during the months of October and November (Gunst, unpub. data).

Study group

The *Cebus apella* study group (Troop A) had been studied intermittently beginning in 1998 and continuously since 2000, and is well habituated to human presence (Boinski et al., 2003). Boinski et al. (2000) present additional ecological and social contexts for the Troop A. All age/sex classes were included in the current observations. During the 28 months of observation we report, the group varied from 25 to 29 individuals, as a result of births, presumed deaths, and male transfers. A total of 33 individuals were sampled during the entire study period (Table 2.1). Individual recognition, based on physical characteristics, was well established. For individuals from 0 to 5 years, exact age was known. For some individuals, particularly adults and subadults, ages were estimated, based on body size and behavioural features. To delineate adults from subadults, based on the literature currently available on wild capuchins, we used the average age at first delivering an infant for females (7 years) and the average age of emigration from the natal group for males (7 years) (Di Bitetti & Janson, 2001; Fragaszy et al., 2004). Visibility of social, foraging, and manipulative behaviours was good in the bamboo patch; group members were easily approached within 2 meters along the trails.

Data collection

Data were collected by N.G. and several other observers continuously from March 2003 to June 2005. The inter-observer reliability for animal identification was verified to meet or exceed an 80% kappa coefficient (Cohen, 1960). While learning identities, observers apprenticed with N.G. or another trained observer until they could confidently and reliably code behaviours. Reliability was achieved more quickly for behaviour coding than for identities. The daily observation period lasted 10 hours, between 7:00 am and 5:00 pm. We used a hybrid "focal-animal sampling" method (after Altmann, 1974), consisting of continuous observations on the activity of the focal animal taken during consecutive 30-sec intervals, and one-zero coding for behavioural occurrence within each interval. One-zero pen and paper focal data were collected during each interval, noting behaviours related to several classes of activity (eat/drink, forage, rest, travel or social behaviour). That is, each unique behaviour that occurred within a 30-sec interval was coded once. The specific foraging patterns are listed in Table 2.2. The duration of focal samples varied from 3 to 15 minutes, depending on the visibility conditions and the feasibility of following the focal individuals. Focal samples lasting less than 3 min were discarded. The focal individual was selected, independently of its activity, from an ordered list of focal individuals. The list was prepared in advance and assured that all individuals had equal sampling opportunities every month. The same focal individual could not be selected twice in the same 60 minutes block of time.

Data coding

For individuals changing age classes during the study period (e.g. infant to juvenile), we used in the analysis the focal samples only for the age class with the greater number of intervals.

In the following analyses, we focused on food sources and foraging techniques in bamboo patches. The minimum, maximum, and mean number of intervals collected in bamboo patches per age class and per study subject are presented in Table 2.1 and Table 2.3, respectively.

The bamboo patches presented a limited array of food items which naturally fell into a dichotomous categorization: ‘easy’ foods that required non specific actions (grasp, pull) and little strength, versus ‘difficult’ foods that required performance of several sequential specific actions described below, as well as greater strength. Based on these definitions, we classed bamboo shoots, bamboo pith, and insects found on surfaces as easy foods, and larvae embedded in bamboo stalks as difficult foods. Although foraging on bamboo pith requires more strength than foraging on bamboo shoots, it is not comparable with foraging on larvae, which not only necessitates detection skills to locate the larva hidden inside the stalk, but also dental equipment to process the bamboo stalk itself (by ripping apart a very hard and thick woody material) to extract the larva. In contrast, foraging on bamboo pith requires no detection skills and much less strength than foraging on larvae hidden inside bamboo stalks. Based on these considerations and in an effort of classification, we ascribed bamboo shoot and pith and surface insects to the same broad category, referred to as ‘easy’ foods.

We defined specific detection patterns as follows: olfactory inspecting (put one’s nose to bamboo stalk and sniff), auditory inspecting (put one’s ear to bamboo stalk), visual inspecting (visually scan bamboo stalk), manual inspecting (touch bamboo stalk with hand, probe into a hole), tap scanning (a quick tapping on bamboo stalk with fingertips, apparently generating acoustic information about the content of cavities, see Visalberghi & Neel, 2003; Phillips et al., 2004). Extraction patterns consisted of ripping bamboo stalk apart by repetitive biting and tearing actions with hands and teeth, and extracting the larva with the fingers. Ripping bamboo appears to be a very strenuous action (see Figure 2.1).

Description of variables

Our observation time was 321 hours, representing a total of 38,520 intervals in bamboo patches, and encompassing all age and sex classes over a 2-year period. These data were not used to describe frequencies or durations, but to estimate the probability that a behaviour will occur at least one time if an animal is observed for a 30-sec interval. We used these data to calculate percentages or proportions of intervals in which a specific behaviour occurred. The figures show the percentages or proportions of intervals. To do so, raw frequency of intervals were collated by individual. We tabulated the number of intervals in which specific foraging patterns related to finding larvae occurred. Foraging efficiency for larvae was calculated as the number of larvae found per hour allocated to search for larvae. For other analyses, we used number and proportion of intervals. The stimulating effect of bamboo segments ripped by others was evaluated by comparing the frequency of larvae-related foraging behaviours performed by the focal individuals shortly (two minutes) before and shortly (two minutes) after inspecting a ripped bamboo segment.

Statistics

In the statistical tests, we used the raw frequencies of intervals, not the percent intervals. Data were screened for normality, independence, and homogeneity of variances, using Levene's test (SPSS). When these assumptions were verified, we used parametric tests (ANOVAs and Student's t-tests). When these assumptions were not verified, we used non-parametric tests to compare behavioural frequencies in the five age classes (Kruskal-Wallis tests) and between two periods (Wilcoxon signed ranks tests). General linear models (GLM) were used to assess the effects of age and sex on foraging efficiency and types of foods foraged. The model used foraging efficiency or the proportion of intervals spent foraging on difficult foods (larvae), respectively as the dependent variable, age and sex as fixed factors, and LSD for post-hoc multiple comparisons. We used a cross-sectional design to investigate age differences in foraging efficiency and diet selection. We used Student's t-tests to investigate sex differences within each age class in foraging efficiency and the proportion of intervals spent foraging on difficult foods. We used Kruskal-Wallis tests to investigate the effect of age on attraction to physical traces, followed by multiple paired comparisons between mean ranks of age classes. To evaluate the relationships between body weight and foraging efficiency, and between dental equipment and foraging efficiency as individuals age, we used Kendall rank-order correlation tests (one-tailed, based on the directional hypothesis that immatures are less efficient foragers than fully-grown individuals). A Spearman's rank correlation test (one-tailed) was used to test our predicted positive correlation between individual foraging efficiency and the number of intervals spent foraging on larvae. Only individuals recorded searching for larvae during at least 60 intervals were used in this analysis. We used Wilcoxon signed ranks tests to investigate the difference in the frequency of foraging patterns before and after coming to physical traces (one-tailed). SPSS 12.0 (SPSS, Inc., Chicago, Illinois, U.S.A.) was used for all statistics. Statistical significance level was set at $\alpha = 0.05$.

Results

Variation in efficiency of foraging for larvae across ages and sexes

Capuchins were observed foraging on larvae in 15,360 interval samples, which represents 40% of the 38,520 intervals collected in bamboo patches. The main effect of age on efficiency was significant, whereas the main effect of sex and the interaction of age and sex were not significant (GLM: adjusted $R^2 = 0.77$, $N = 29$; age: $F_{4, 19} = 17.75$, $p < 0.001$; sex: $F_{1, 19} = 0.75$, $p = 0.397$; age * sex: $F_{4, 19} = 1.56$, $p = 0.226$).

Figure 2.2 shows that foraging efficiency (i.e. the average number of larvae successfully harvested per hour spent foraging on larvae) consistently increased with age from infants to subadults. It should be noted that even though the data were collected during one-zero scoring, the number of larva found may be a true frequency, because finding two larvae in one 30-sec interval is very unlikely. Post-hoc multiple paired comparisons between age classes showed that infants were significantly less efficient than older juveniles, subadults, and adults ($p < 0.001$) but did not significantly differ from younger juveniles ($p = 0.053$). Younger juveniles were significantly less efficient than older juveniles ($p = 0.004$), subadults and adults ($p < 0.001$). Older juveniles were significantly less efficient than subadults ($p = 0.039$) but did not differ significantly from adults ($p = 0.133$). Foraging efficiency in subadults and adults did not differ significantly ($p = 0.342$). A series of t-tests showed no statistically significant sex differences in foraging efficiency within each age class ($p > 0.05$ for younger juveniles, older juveniles, subadults, and adults). Variation within each age class is quite modest (Figure 2.2). Coefficients of variation (CV) range from 0.18 in older juveniles to 0.74 in younger juveniles. In subadults, CV = 0.26 and in adults, CV = 0.31.

To investigate the relationship between foraging efficiency and age-related morphological changes, we compared our data on foraging efficiency with published data on body weight (Fragaszy & Bard, 1997; Fragaszy & Adams-Curtis, 1998) and dentition (Fleagle & Schaffler, 1982) in captive capuchins. We plotted for each age class the mean value of foraging efficiency against body weight and dental development score, respectively (Figures 2.3a and 2.3b). We found positive correlations between body growth and foraging efficiency, and between the acquisition of dental equipment and foraging efficiency across age classes (Kendall rank-order tests, $N = 5$, $T = 0.800$, $p = 0.025$, and $T = 0.949$, $p = 0.011$, respectively).

Variation in type of foods foraged according to age and sex

As predicted, we found a significant positive correlation between the proportion of intervals spent foraging on larvae and the efficiency of foraging for larvae (Spearman's rank correlation test: $N = 29$, $r_s = + 0.856$, $p < 0.001$; Figure 2.4).

For each sampled individual, we measured the proportion of intervals spent foraging on easy foods (bamboo shoots, bamboo pith, and non-embedded insects) and difficult foods (larvae). The investigation of the relationships among age and sex classes and the proportion of intervals spent foraging on difficult foods showed that the main effect of age was significant, whereas the main effect of sex and the interaction of age and sex were not significant (GLM: adjusted $R^2 = 0.78$, $N = 29$; age: $F_{4,\,19} = 21.13$, $p < 0.001$; sex: $F_{1,\,19} = 0.35$, $p = 0.561$; age * sex: $F_{4,\,19} = 0.906$, $p = 0.480$).

Figure 2.5 shows that the proportion of intervals spent foraging on difficult foods consistently increased with age from infants to subadults. Post-hoc multiple paired comparisons between age class means showed that infants and younger juveniles spent significantly fewer intervals foraging on difficult foods than older juveniles, subadults, and adults ($p < 0.001$). These results are in agreement with our prediction. Moreover, subadults spent significantly more intervals foraging on difficult foods than adults ($p = 0.008$). Proportions did not differ significantly between infants and younger juveniles ($p = 0.077$), older juveniles and subadults ($p = 0.159$), or older juveniles and adults ($p = 0.286$).

Regarding sex differences in the proportion of intervals spent foraging on difficult foods, we found similar proportions in females and males within younger juveniles ($t = 0.587$, $df = 4$, $p > 0.05$), older juveniles ($t = -0.053$, $df = 2$, $p > 0.05$), and subadults ($t = -1.370$, $df = 3$, $p > 0.05$). In adults only, females displayed significantly greater proportion of intervals foraging on difficult foods than males (mean ± SD = 0.66 ± 0.13 and 0.47 ± 0.12, respectively, $t = 2.368$, $df = 7$, $p < 0.05$). We did not test sex differences in infants because of insufficient data.

Variation according to age in attraction and responsiveness to physical traces left by foragers

To investigate age differences in attraction to the physical traces due to destructive foraging activity by others, we calculated the number of intervals spent per age class manually and visually inspecting ripped bamboo stalks left by other group members (Figure 2.6). We found a statistically significant effect of age on the attraction to physical traces (Kruskal-Wallis test: $H = 25.5$, $df = 4$, $p < 0.001$). Infants, younger juveniles, and older juveniles spent respectively 12.4, 9.7, and 8.0% of their time manually and visually inspecting already ripped bamboo stalks, whereas this percentage dropped to 1.1 and 0.3% in subadults and adults respectively (Figure 2.6). Multiple paired comparisons between mean ranks showed that infants were significantly more attracted to the physical traces than subadult and adult individuals ($p < 0.05$). Infants, younger juveniles and older juveniles did not differ significantly. Likewise, differences among younger juveniles, older juveniles, subadults and adults did not reach statistical significance ($p > 0.05$).

To evaluate age differences in the stimulating effect of physical traces left in the environment by skilled foragers, we compared the frequency of foraging behaviours two minutes before and two minutes after being attracted to physical traces. We found that immature individuals (infants, younger juveniles, and older juveniles) performed significantly more larvae-related foraging behaviours (tap scanning, manual inspecting, olfactory inspecting, biting into, and ripping bamboo stalks apart) within two minutes after than in the two minutes before being attracted to a ripped bamboo stalk left by a skilled forager (mean frequency ± SD, before: 1.1 ± 1.0 and after: 4.8 ± 5.0, Wilcoxon test: $N = 10$, $z = -2.5$, $p = 0.012$). In mature individuals (subadults and adults), we did not find a statistically significant difference in the frequency of larvae-related foraging behaviours between the two periods (mean frequency ± SD, before: 2.1 ± 1.9 and after: 2.5 ± 1.5, Wilcoxon test: $N = 12$, $z = -1.2$, $p = 0.236$). Experienced foragers briefly inspected ripped bamboo stalks but did not follow inspection with foraging.

Discussion

Capuchins at Raleighvallen are faced with complex foraging challenges, including searching for a hidden, rich food requiring extraction from a tough, concealing substrate (larvae living inside bamboo stalks). Various hypotheses have been presented linking the development of proficient foraging on embedded foods with physical growth, with substantial contributions of learning to foraging proficiency, and with substantial contributions of social context to learning how to forage for these foods (Ross & Jones, 1999; Gibson, 2000; van Schaik et al., 2006). Our findings support all of these hypotheses. We found that young capuchin monkeys achieved adult levels of proficiency at finding and extracting larvae from bamboo stalks at 5 years or older, several years after weaning and about the same time as they reach reproductive maturity. Young monkeys devote more time than adults to foraging on foods that are easy to obtain, but from one to five years of age they also devote increasing effort to foraging for larvae (from 37% to 68% of time spent foraging). They do so even though they rarely obtain larvae from these efforts. Our results on the stimulating effect of physical traces left in the environment by skilled foragers indicate that social partners indirectly facilitate young monkeys' practice of the components of searching for and extracting larvae, even before they are physically capable of opening stalks themselves. In essence, older individuals leave the landscape littered with prepared "practice" sites that appeal to younger monkeys. These findings are consistent with the role of social partners in the development of foraging competence through the alteration of the physical environment by animal societies, also referred to as "niche construction" (Odling-Smee, 1996; Laland et al., 2000).

Variation in foraging efficiency according to age and physical growth

Linked changes in size, weight, and dentition parallel differences in foraging efficiency and time allocation in one difficult type of food foraged in bamboo patches across the first seven years of development in brown capuchins. Ideally, one would have growth data as well as behavioural data with which to make quantitative comparisons among these variables. However, most quantitative data available on body weight and all data on acquisition of dental equipment are based on captive capuchins (reviewed in Fragaszy et al., 2004). Fortunately, there is no consistent effect of captivity on dental development of primates (Swindler, 2002), providing confidence that data for this aspect of development derived from captive samples can be generalized to wild monkeys. Generalization of growth patterns in body mass is more problematic. Studies on growth of body mass in baboons showed that the growth rates of wild primates can be lower (perhaps by one half to one third) than the values obtained in well-provisioned captive animals. However, the variation in rate of growth in body mass among wild groups from different populations can be as great as variation between captive and wild animals (Altmann & Alberts, 1987). Our data are drawn from one wild group, increasing the probability that individuals within that group experienced similar nutrition. With respect to the comparisons that we draw across age groups, we point out that the magnitude of the difference in growth rate between wild and captive individuals is likely to be the same across age classes of monkeys, and in this sense, the shape of the growth curve is likely to be consistent between captive and wild monkeys. Therefore, it is reasonable to use data from captive animals to evaluate the relations between growth and foraging efficiency, keeping in mind that the rate of growth might be substantially lower and the age at attainment of full adult mass might be later.

We found substantial variability in foraging efficiency and diet selection according to age of the capuchins foraging in bamboo patches. Foraging efficiency consistently increased from infancy (0.0 larvae per hour) to seven years of age (subadults: 6.6 larvae per hour). Our result expands preliminary findings obtained in a group of wild brown capuchins observed in Peru, where subadults and adults succeeded in retrieving larvae from bamboo segments in 81% of attempts, whereas younger individuals as a whole successfully extracted larvae in 42% of attempts (same genus of bamboo as here: *Guadua* sp.: Phillips et al., 2003). However, these authors' definition of 'attempts' was not clear enough for us to compare our findings more precisely. We can only conclude that these two populations of capuchins share an age difference in the efficiency of foraging on embedded larvae. Similar age-related differences in finding hidden invertebrates are evident in other populations of wild capuchins (e.g., Agostini & Visalberghi, 2005) and in other taxa (e.g., baboons: Johnson & Bock, 2004; aye-ayes: Krakauer, 2005).

Previously published studies on the ontogeny of foraging have typically considered all immatures as one age class (e.g., Boinski & Fragaszy, 1989; Hanya, 2003; Johnson & Bock, 2004). In order to assess how foraging expertise gradually emerges during juvenescence, further subdivisions linked to physical states and social status should be considered (Rhine & Westlund, 1978; Post et al., 1980). Accordingly, we distinguished more precisely among immatures by ascribing individuals less than seven years to four different age classes. As predicted, we found that infants and younger juveniles were considerably less proficient than subadults and adults (less than a tenth and less than half as proficient, respectively) in finding and extracting hidden larvae by ripping bamboo stalk apart. No individual aged less than one year was successful in finding larvae on its own. The efficiency of younger juveniles was relatively low, with less than two larvae found per hour allocated to larvae foraging. Older juveniles (about 4 year-old) obtained roughly 4 larvae per hour; subadults and adults roughly six larvae found per hour searching. Thus, older juveniles appeared to be intermediate between small-sized inefficient youngsters and almost full-grown and fully skilled subadults in their foraging abilities.

Let us consider the transitional status of older juveniles (about 4 year-old) in terms of foraging efficiency. The dental developmental score of older juveniles has reached the subadult and adult level (Fleagle & Schaffler, 1982). In older juveniles, two additional permanent teeth emerge, the third premolar and third molar (Galliari, 1985). The canines (the last permanent teeth to erupt at around 4-5 years; Galliari, 1985) also appear during the older juvenile period. The appearance of these morphological features in older juveniles may account for their higher success, compared with younger juveniles, in extracting hidden larvae by ripping bamboo stalks apart with teeth. Greater body mass may also contribute to the older juveniles' success. In captivity, older juveniles (4 years) weighed 1 kg more than younger juveniles (2 years) (Fragaszy & Bard, 1997). However, although older juveniles and subadults have similar dentitions and body weights, the former are still significantly less proficient than the latter in finding embedded larvae. Since this difference in foraging efficiency is not likely to be explained by physical characteristics, we deduce that older juveniles may simply be poorer in locating larvae hidden inside bamboo than subadults. Our results suggest that the acquisition of specific detection skills is not fully completed before reaching the subadult level. Searching and locating hidden foods require sensorimotor coordination and perceptual learning. These aspects of foraging skill benefit from practice. The monkeys must know where and how to locate the larvae, as well as being able to open the stalk.

Foraging efficiency, diet choice, and nutritional requirements

The age class differences in foraging efficiency on larvae strictly parallel those obtained in the time spent foraging on difficult foods by each age class. On the one hand, the inability of infants and younger juveniles to obtain hard-to-process foods is likely to account for their marked preference for easy food items. On the other hand, subadults were not only the most efficient foragers but also the age class showing the highest interest in difficult foods. Interestingly, the tendency to devote more time to difficult foods switched at about the age of 3 years, between younger juveniles and older juveniles, reemphasizing the period from 3 to 5 years as key in terms of the acquisition of foraging competence and diet selection. As weaning is completed before the second birthday, this means juveniles between 2 and 3 years of age are “scraping by”, in the sense that they are less efficient than older individuals and rely on easier foods. It may be that the appearance of the last permanent molar and premolar (P3 and M3) at about 3 years of age supports increasing effort by young monkeys to open bamboo stalks.

Given their body size and age, one could wonder why adult males were less efficient foragers than adult females and subadults. There might be a link between variation in metabolic needs according to age and physiological state, relative interest in reliable sources of protein, possible differences in the practice of detection techniques, and resulting foraging efficiency. Because subadults are large-sized but still growing individuals, they may need to focus more on difficult foods with higher levels of protein in their diet than adults (Richards, 1985). Similarly, due to the costs of pregnancy and lactation, adult females have higher metabolic needs than adult males, requiring more protein intake (Clutton-Brock, 1977). Only in adults did females allocate more time to forage on embedded larvae than males. Juvenile and subadult females showed no significant differences from same-aged males in time spent foraging on larvae. This is consistent with previous findings in other capuchin congeners and chimpanzees showing that adult females focus more than adult males on protein-rich food obtained via extractive foraging activities (McGrew, 1979; Fragaszy, 1986; Rose, 1994). Small invertebrates hidden inside substrates provide reliable sources of protein (Fragaszy, 1986; Boinski, 1988; Rose, 1994). Therefore the difference in foraging efficiency between age and sex classes may reflect differences in the practice of detection techniques resulting from differential diet choice based on nutritional requirements. In any case, our findings indicate that males, with larger body mass and larger canines than females, do not experience a significant advantage in finding or obtaining bamboo larvae. We suggest that whereas opening bamboo stalks requires a threshold body mass and dental equipment to accomplish at all, achievement of high levels of skill depends on individual experience.

Food competition and foraging strategies

Social constraints should also be considered to account for differences in diet choice between age and sex classes. Food competition could be an alternative explanation as to why adult females and subadults devote more time to foraging on larvae than other age and sex classes. Brown capuchins adjust their spatial positions to decrease the risk of direct food competition from other group members (Janson, 1990). When foraging on a dispersed food source, such as larvae in a bamboo patch, non-tolerated or subordinate animals (e.g., certain subadults and adult females) may lower the probability of being displaced by increasing inter-individual distances. Such a foraging strategy is more likely to emerge in dispersed than in clumped food patches. For example, a single fruiting cluster (in the palm *Maximiliana maripa,* Family of *Arecaceae*), is easily monopolizable by high-ranking individuals. Competition for access to fruit clusters is limiting and subordinate individuals may defer to dominant group members (Gunst, unpub. data; cf. squirrel monkeys: Boinski et al., 2002). In contrast, within the dense cover of bamboo, subordinate individuals tend to become peripheral, i.e. stay in the outskirts of the troop to locate, harvest and ingest desirable larvae with reduced risk of displacement by older and/or more dominant troop members. We argue that avoiding direct competition may account for subadults and adult females focusing more on more dispersed food sources such as larvae than do higher-ranking individuals, such as adult males. In another group of brown capuchin monkeys, social rank was found to affect the spatial positions occupied by individuals during foraging activities. By maintaining large inter-individual distances when foraging on dispersed food sources, animals are expected to increase their total amount of food consumed (‘finder’s share’: Di Bitetti & Janson, 2001).

In sum, larvae intake in subadult and adult female capuchins may depend not only on foraging skills but also on spatial strategies (e.g., social spacing, adopt peripheral position in the group: Di Bitetti & Janson, 2001). Focusing on larvae may be an adaptive foraging strategy for these individuals since larvae represent reliable, high quality food items in a dispersed food patch.

Physical traces

Infants showed significantly more interest than subadults and adults in the physical traces left by skilled foragers (i.e., ripped bamboo segments) (12.4% of intervals during focal observation in infants vs. 1.1 and 0.3% in subadults and adults, respectively). This is consistent with findings that primate infants exhibit more interest than adults in others’ activities and possessions, particularly food items (e.g., King, 1994; Fragaszy & Visalberghi, 1996). To a lesser extent, we found that younger juveniles (9.7% of intervals) and older juveniles (8.0%) were also more interested in ripped bamboo stalks than were subadults (1.1%) and adults (0.3%). Although the latter differences did not attain statistical significance, there was a general downward trend in the attraction to physical traces as individuals age. We have the impression that there may also be age-related changes in the behavioural sequences related to such attraction, although we did not have enough data for analyses here. Infants persist in exploring a ripped bamboo segment with their hands, trying to find very improbable leftovers (only one larva can be harvested from each bamboo segment). This tendency seems to decrease consistently over time as younger juveniles tend to exhibit detection behaviours (e.g., tap scanning) toward an already ripped bamboo segment, whereas older individuals are more inclined to shift their attention to the adjacent segment that may more likely contain a larva (Gunst et al., 2007). These findings may reveal the gradual development of abilities to shift attention from one activity to another, to engage in sequences of action, and other aspects of cognition.

The propensity for infants to display high interest in others' foods may reflect an intrinsic attentional difference across ages, as suggested by Adams-Curtis & Fragaszy (1995), and/or differences in social constraints (i.e., infants are less subject to competitive exclusion than older group members). In wild chimpanzees, only infants had free access to the stones and nutshells remains left after nut-cracking activities by others (Inoue-Nakamura & Matsuzawa, 1997). In our case, however, competition around physical traces left by skilled foragers is unlikely since there are no leftovers inside a ripped bamboo segment. Therefore, age-related changes we observed in the attraction to physical traces are likely not due to differential social constraints in young monkeys in access to foraging artefacts.

We found that immatures most consistently showed foraging actions after encountering the physical traces left in bamboo stalks by other foragers. The interest in a particular object or area spatially associated with a valuable object (in our case, a larva previously extracted from a ripped bamboo segment) triggers an appropriate object-related behaviour (here, larvae foraging patterns). This process is referred to as stimulus or local enhancement, and it incorporates an aspect of what many authors identify as social facilitation (increased performance of a particular behaviour following a socially-provided cue; cf. Galef, 1988). Significantly, facilitation occurred in the absence of the other forager. The motivation in young individuals to engage in foraging activity shortly after encountering foraging artefacts may produce learning opportunities (Fragaszy & Visalberghi, 1989). Occasionally, immatures were observed tapping and continuing to rip apart a bamboo stalk previously ripped apart by another individual (Gunst et al., 2007). Although another larva is not likely to be found inside a ripped bamboo segment, the simple performance of these appropriate foraging actions in a place with residual odours may be a first step to learning the relations among certain food items (larva), substrates (bamboo stalk), and the behavioural patterns required to forage efficiently on this type of food (e.g., tap scanning and ripping the stalk).

A bamboo stalk altered by another forager provides a good site for learning how to forage for larvae. Practicing ripping on already opened bamboo stalks provides an easier initial form of the problem, supporting the gradual development of more effective actions. A similar process occurs in young black rats (*Rattus rattus*) learning to strip seeds from pine cones (Terkel, 1996). In the case of black rats, experienced mothers allow pups to take partially processed cones. Experiments showed that pups that were exposed to such already opened cones acquired the pine cone-opening technique, but the most efficient learning occurred in the mother's presence, as she processed cones (Aisner & Terkel, 1992). Thus both attraction and opportunities to practice played a role. Although similar, the process seems looser in capuchin monkeys, since immatures approached and directed foraging actions towards physical traces, even after the original forager had left the site. In capuchins, it appears that learning to find an obtain larvae may not specifically occur with the mother or any other group member, and can be delayed in time and separate in space from others. In this sense, niche construction in capuchins has an extended time frame and lesser dependence on co-presence with others. The others provide "tools" for learning, *sensu* socio-cultural learning theory, developed to explain human development in social context (e.g., Forman et al., 1993). In general, situations in which artefacts of others' activity promote practice of relevant behaviours can foster learning effectively, as shown by experimental studies of birds learning to open the lids on milk bottles (Sherry & Galef, 1984, 1990), a behaviour observed to occur spontaneously (Fisher & Hinde, 1949). Exploring this theory in nonhuman animals could yield insights into the range of skills that may be aided by socially-provided "tools" independent of language (as formulated in socio-cultural learning theory).

Comparative perspective

Among primates, interspecific differences in the acquisition of foraging competence may reflect the varying complexity and difficulty of foraging tasks and developmental timing. In species characterized by a relatively simple diet that does not require extractive foraging skills, most foraging behaviours appear during infancy (e.g., 3 to 6 months in ruffed lemurs, *Varecia variegata rubra:* Krakauer, 2005; 4.5 months in squirrel monkeys, *Saimiri oerstedi*: Boinski & Fragaszy, 1989). According to the "needing-to-learn" hypothesis, the necessity to learn complex foraging behaviours contributes to slowed life history (Ross & Jones, 1999; van Schaik et al., 2006). In species that face complex foraging challenges, the development of food-processing and extractive foraging techniques occurs later, either during early juvenescence (e.g., 15 to 17 months in aye-aye, *Daubentonia madagascariensis*: Krakauer, 2005), or extends far beyond the onset of juvenility (e.g., up to 10 years in orangutans: van Noordwijk & van Schaik, 2005; Russon, 2006; up to 10 years in chimpanzees: Matsuzawa, 1994). The latter pattern is thought to characterize humans (Kaplan et al., 2000). We found that developing foraging competence for larvae hidden in bamboo stalks continues throughout juvenescence in wild brown capuchins. This form of foraging clearly presents both physical challenges and challenges for sensorimotor coordination to find and process the larva (Gibson, 1987). The prolonged acquisition of foraging expertise in capuchins reflects both of these challenges. The timeline of developing adult competence in this foraging task in capuchins follows that of apes and humans, in that it is not complete until close to the onset of reproduction (in females). This is quite different from the pattern in aye-ayes, which achieve adult competence in tap foraging about two years before reaching reproductive maturity (for females, i.e., at about 4 years; Krakauer, 2005). This may reflect an important difference in life history between aye-ayes and simians, and it raises interesting questions about how the aye-ayes become efficient at the sensorimotor and cognitive aspects of extractive foraging so much more quickly than monkeys, apes, and humans.

Conclusion and future direction

The present study provides a view on how the gradual acquisition of foraging competence in brown capuchins is aided jointly by physical growth and experiential processes supporting learning. Capuchins alter the environment in a way that supports learning by others of a specific foraging skill via two mechanisms that have differing temporal properties: not only through action, with a timeline on the order of seconds to minutes (e.g., Fragaszy et al., 1997; Ottoni et al., 2005), but also through artefacts of activity, with a much extended timeline of days to weeks (this study). Both can be considered forms of niche construction (Laland et al. 2000), a process that can link socially-aided learning to biologically significant outcomes at the level of groups and populations (Fragaszy & Perry, 2003).

Further analyses are underway to identify the emergence of techniques in young capuchins to locate larvae hidden in bamboo stalks. Longitudinal analyses are also in progress to evaluate the impact of seasonal availability of larvae, as well as the opportunities for learning through direct social influence, and the possible effect of inter-individual competition on the development of foraging competence. However, it is already clear that capuchins afford an interesting view of how physical, social, and experiential factors contribute to the development of foraging competence in a long-lived primate.

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Table 2.1. Definition of age classes, number of sampled males, females, and total individuals, and minimum, maximum, and mean number of 30-sec intervals sampled per individual in bamboo patch during the study. In the text, juveniles 1 and juveniles 2 were referred to as younger and older juveniles, respectively.

	Infants 0 – 1 yr	Juveniles 1 1 – 3 yrs	Juveniles 2 3 – 5 yrs	Subadults 5 – 7 yrs	Adults From 7 yrs
N_{Males}	6	3	2	4	4
N_{Females}	1	3	2	2	6
$N_{\text{Total individuals}}$	7	6	4	6	10
Number of 30-sec intervals sampled					
Min	53	157	391	853	186
Max	819	1708	1489	3297	2056
Mean	350	1007	911	1454	1017

Table 2.2: Specific foraging patterns

Pattern	Description
Finding food:	
Auditory inspect	Put one’s ear to plant material
Clear away	Pull a food item clear of a branch tangle
Dig into hole	Enlarge a tree hole by digging into it
Manual inspect	Touch a food item with one’s hand
Olfactory inspect	Put one’s nose to plant material and sniff
Probe with fingers	Insert fingers into a hole
Probe with hand	Insert hand into a hole
Remove dead leaves	Search through a tangle of dead leaves
Tap-scan	Tap a branch slightly with fingertips
Visual inspect	Visually scan for food
Processing food:	
Bite	Bite into a substrate
Break into pieces	Break a dead stick into pieces
Extract	Extract a larva with fingers from a bamboo stalk
Lick	Lick a food item
Scoop water	Scoop water from a tree hole using hand as a cup
Rip apart with hands	Rip plant material apart with hands
Rip apart with teeth	Rip plant material apart with teeth

Table 2.3. Number of 30-sec intervals sampled per study subject (represented by their identification codes) categorized by age classes.

Individual	No. intervals	
	ID code	sampled
Infants	1,37	562
	1,43	819
	1,47	130
	1,48	186
	1,49	53
Juveniles 1	1,18	1708
	1,27	950
	1,29	815
	1,33	157
	1,34	1355
	1,36	1058
Juveniles 2	1,11	1489
	1,16	1132
	1,45	632
	1,46	391
Subadults	1,13	3297
	1,4	977
	1,5	1126
	1,6	853
	1,8	1016
Adults	1,1	838
	1,2	186
	1,21	1467
	1,23	796
	1,3	2056
	1,31	1451
	1,32	741
	1,35	461
	1,41	637
	1,42	1532

Figure 2.1. Brown capuchin monkey ripping a bamboo stalk apart.

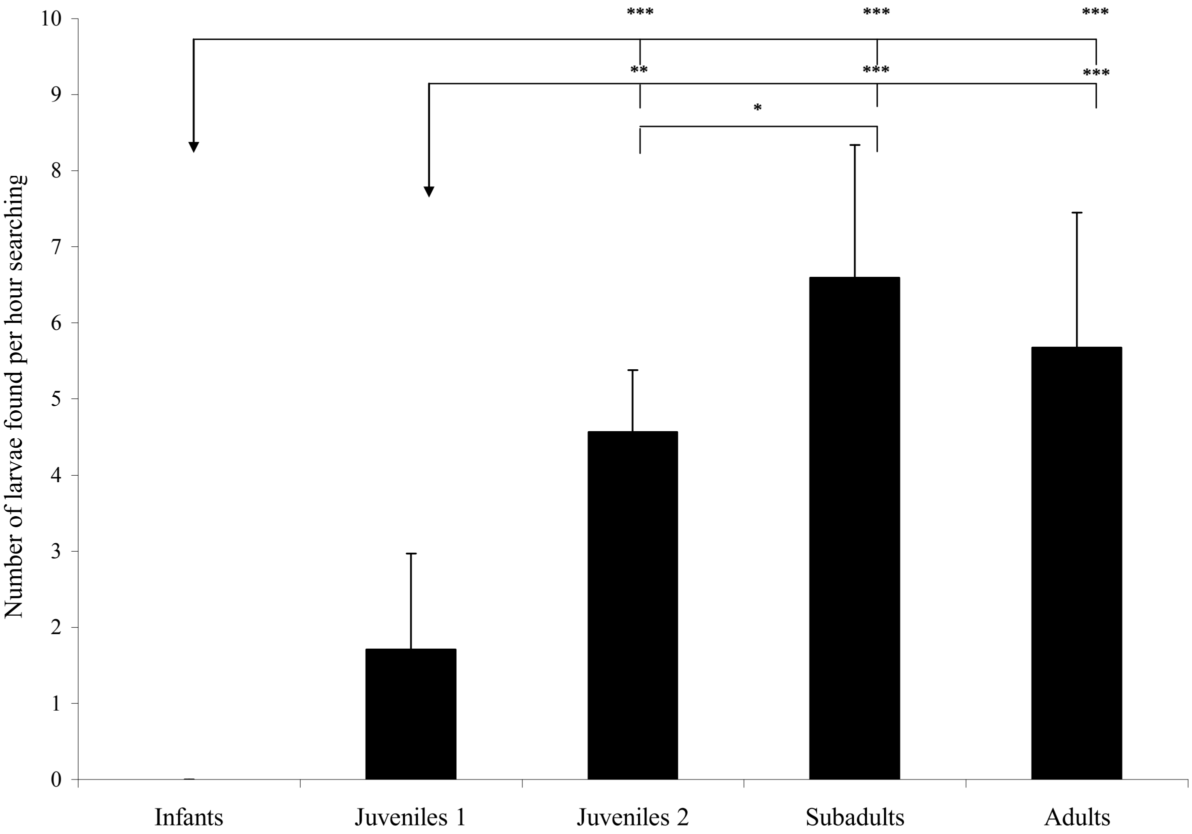

Figure 2.2. Foraging efficiency on larvae according to age class; Bars represent the mean number of larvae found per hour spent foraging on larvae ± SD; The number of individuals sampled per age class were: $n_{infants} = 5$, $n_{juveniles1} = 6$, $n_{juveniles2} = 4$, $n_{subadults} = 5$, $n_{adults} = 10$; Asterisks indicate statistically significant paired differences between arrowed and plain lines (**: $p < 0.01$, ***: $p < 0.001$) or between two plain lines (*: $p < 0.05$).

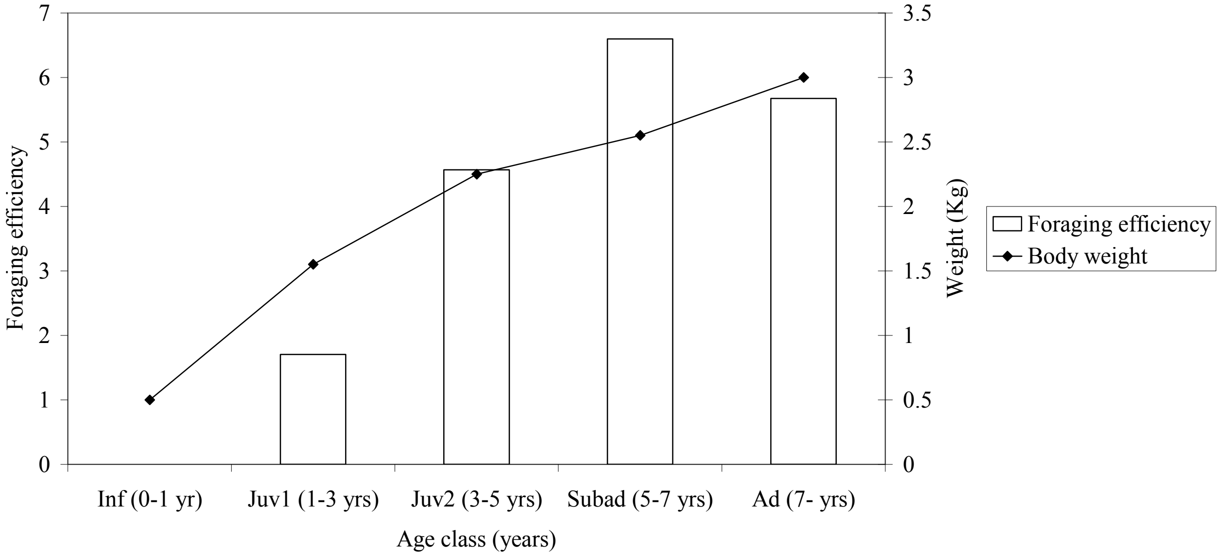

Figure 2.3a. Relationship between foraging efficiency and body weight (after Fragaszy & Bard, 1997) across age classes.

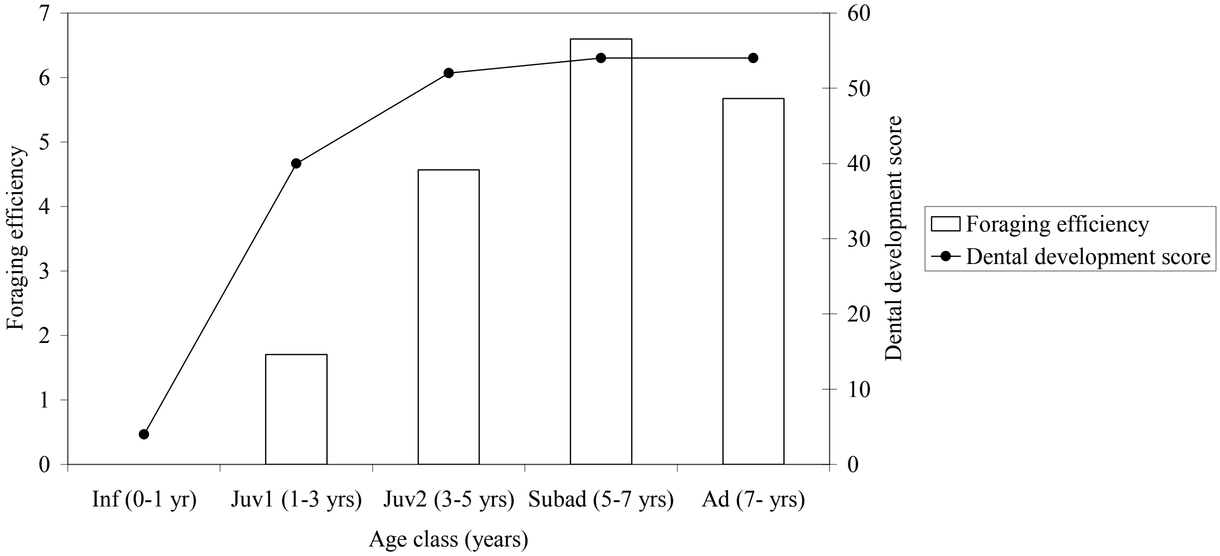

Figure 2.3b. Relationship between foraging efficiency and dental development score (after Fleagle & Schaffler, 1982) across age classes.

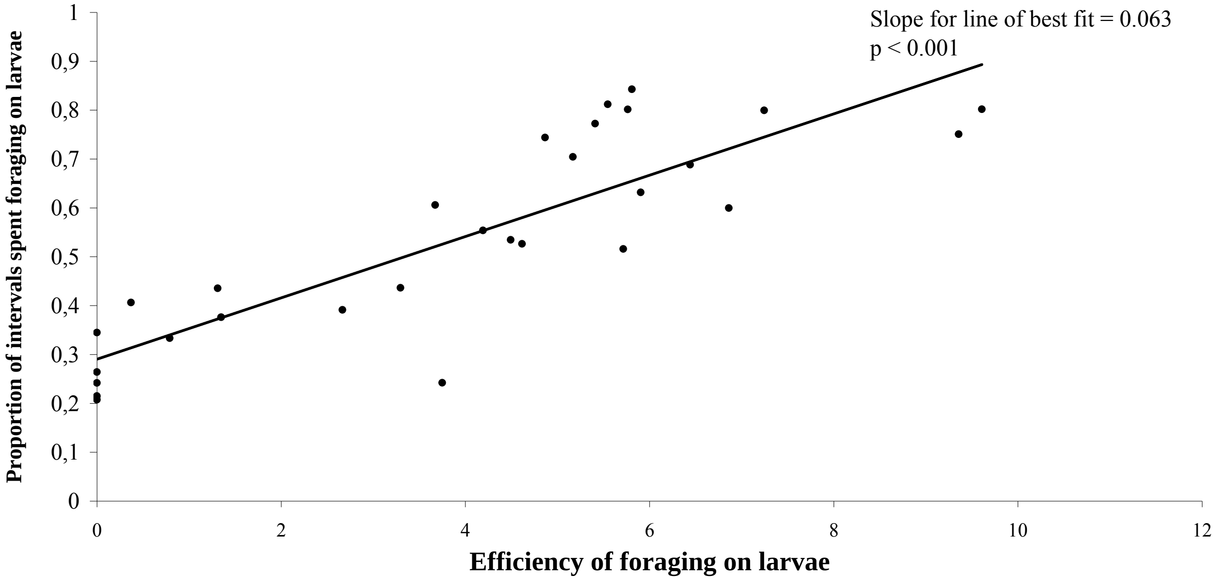

Figure 2.4. Relationship between the proportion of intervals spent foraging on larvae and the efficiency of foraging for larvae (defined as the number of larvae found per hour searching). Each dot represents one individual.

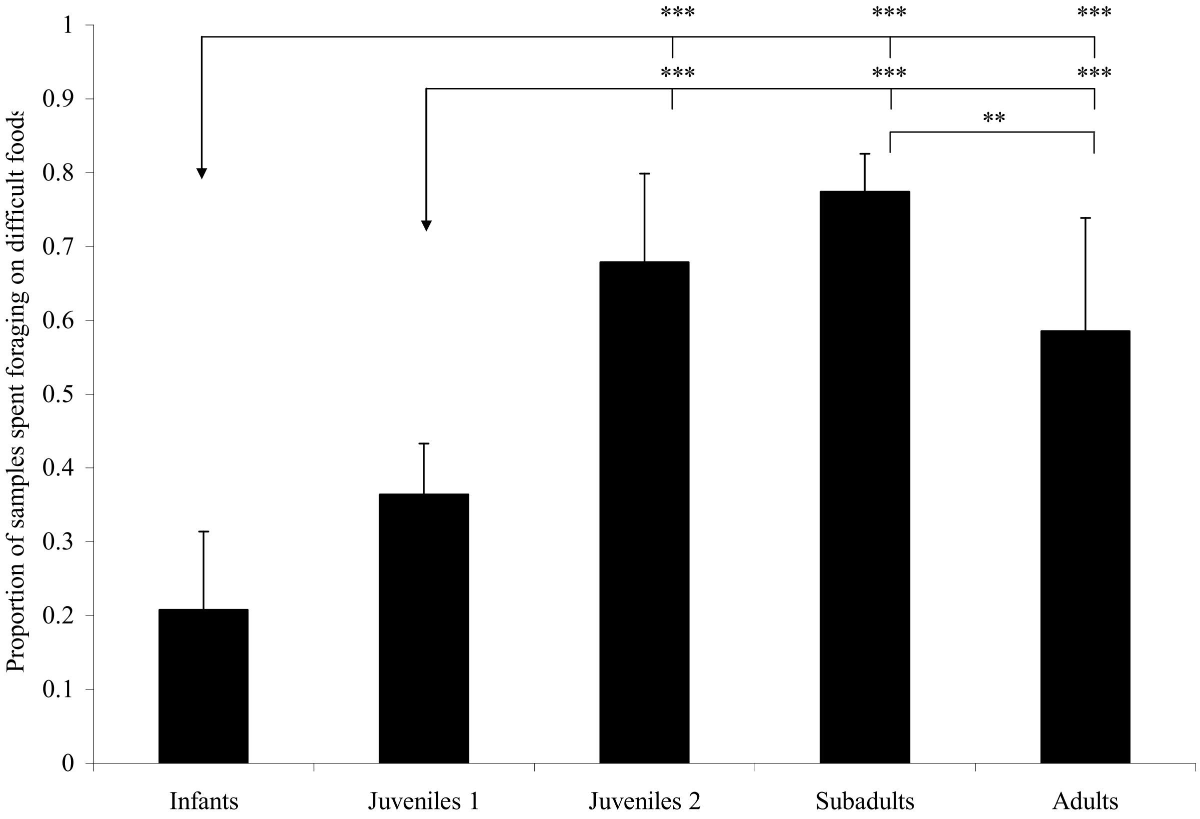

Figure 2.5. Proportion of intervals spent foraging on difficult foods (larvae) according to age class; Bars represent the mean proportion ± SD; The number of individuals sampled per age class were: $n_{infants} = 5$, $n_{juveniles1} = 6$, $n_{juveniles2} = 4$, $n_{subadults} = 5$, $n_{adults} = 10$; Asterisks indicate statistically significant paired differences between arrowed and plain lines (***: $p < 0.001$) or between two plain lines (**: $p < 0.01$).

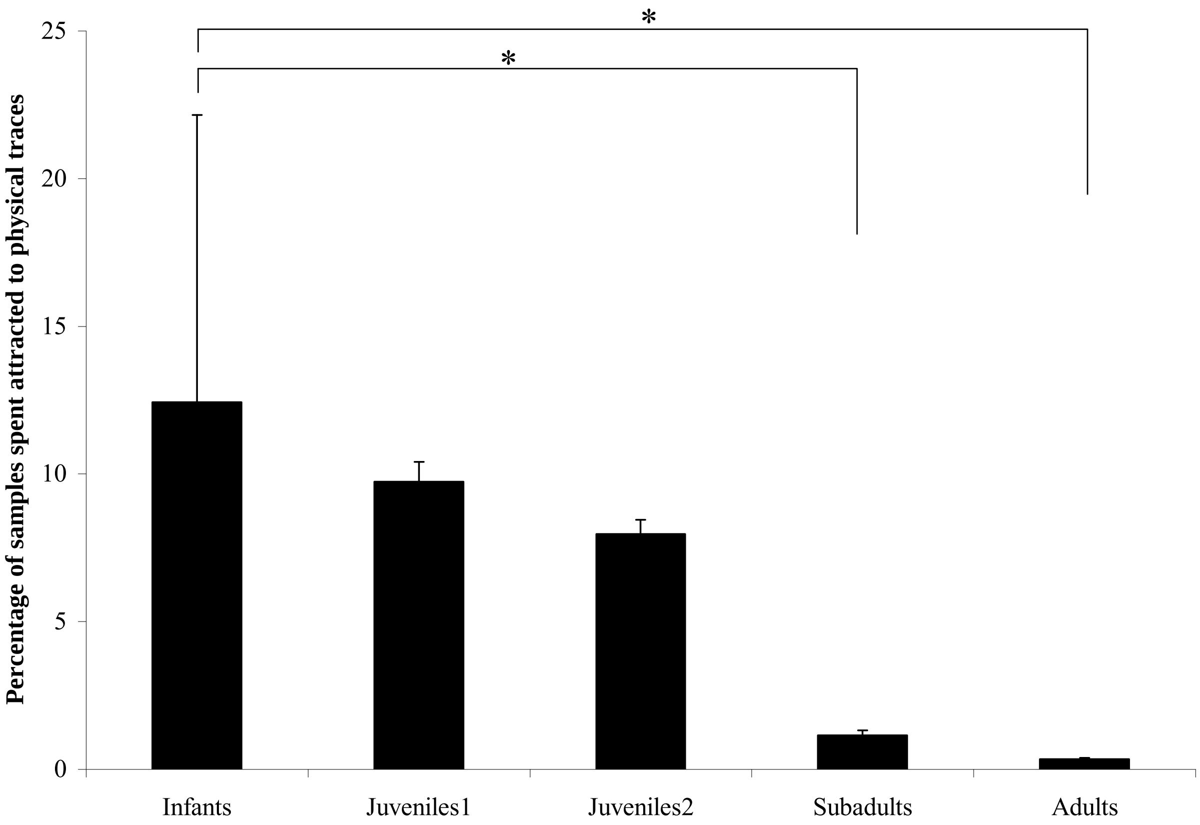

Figure 2.6. Attraction to physical traces (ripped bamboo stalks left by other group members) according to age classes; Bars represent the mean percentage of intervals spent attracted to physical traces ± SD; Asterisks indicate statistically significant differences ($p < 0.05$).

CHAPTER 3

DEVELOPMENT OF SKILLED DETECTION AND EXTRACTION OF EMBEDDED INVERTEBRATES BY WILD CAPUCHIN MONKEYS [1]

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[1] Gunst, N., Boinski, S. & Fragaszy, D.M. To be submitted to *Behavioral Ecology*.

Abstract

Optimal foraging models recognize search and handling as separate components of foraging effort. This formulation applies well to the manner in which brown capuchins monkeys (*Cebus apella*) in Suriname forage on larvae embedded in healthy bamboo stalks. Obtaining larvae requires selecting an appropriate stalk and locating the larvae within the stalk, both components of searching. Ripping the stalk open and extracting the larvae are the final (handling) components. Although extraction behaviors were present at low rates in infant capuchins' repertoire, we found that the acquisition of adequate detection techniques was fully completed in subadults, i.e. around six years of age. Selecting appropriate foraging substrates, requiring accurate assessment of the physical properties of bamboo stalks, gradually increased with age and experience. Juveniles 3 – 5 years old and two immigrant adult males, the latter apparently naïve about foraging for larvae in bamboo stalks, were equally inefficient at locating and extracting larvae compared to proficient adults and subadults, although the immigrant males were proficient at ripping open stalks. We conclude that both components of searching require extended practice beyond that required to master the handling components (opening the stalks and removing the larva). This example illustrates that searching components can present greater challenges than handling components in extractive foraging. We suggest that specifying the searching components of foraging more precisely will improve our ability to understand the variations across species in the timeline of foraging skill development.

Keywords: extractive foraging; searching and handling components; detection techniques; ontogeny; *Cebus apella*

Introduction

Optimal foraging theory and extractive foraging

Optimal foraging theory assumes that costs and benefits of foraging are balanced against each other in order to maximize the net energetic intake, which may be the most important criterion for food choice (MacArthur & Pianka, 1966; Stephens & Krebs, 1986). In optimal foraging models, the time spent foraging is usually partitioned into two components: first searching time, defined as the time devoted looking for food between encounters of items of the same food type, and second, handling time, defined as the amount of time required to handle the food item between the time it is encountered to the time it is consumed (MacArthur & Pianka, 1966).

Extractive foraging refers to searching for and handling foods that are difficult to obtain, such as hard-shelled nuts and fruits, embedded invertebrates, or other encased food sources that need to be located and extracted from a protective matrix through skilled manipulation (Parker & Gibson, 1979; King, 1986). Such food-related behaviors are typically considered to fit the characterization of complex foraging patterns that may necessitate substantial learning time. Detecting and extracting embedded food present greater cognitive challenges than, for example, harvesting surface insects or plucking fruit (Gibson, 1987).

Capuchins forage on larvae in bamboo stalks

Wild brown capuchins in Raleighvallen, Suriname forage on larvae embedded in healthy (non-rotten) bamboo stalks. The main handling problem they face is to extract the larva from its tough protective matrix. This is accomplished by ripping the stalk apart with the teeth and hands, and pulling out the larva with the fingers. However, first the monkey has to identify an appropriate stalk of bamboo, and it has to identify the segment of the stalk to open. If it mismanages these components of the task, opening the stalk is futile. To locate embedded larvae within a stalk, capuchins might use auditory, olfactory, tactile, and visual cues. A detection technique typically reported in capuchins is tapping quickly on a substrate with the fingertips ("tap scanning"), apparently generating acoustic information about the existence of cavities, or more generally about the density of the material (Izawa, 1978; Janson & Boinski, 1992; Phillips et al., 2003, 2004; Visalberghi & Neel, 2003; Gunst et al., 2008). Some authors mention sniffing, as well as manual and visual inspection of bamboo stalks, as potential detection patterns (Izawa, 1978; Phillips et al., 2004; Gunst et al., 2008). We have little information about how capuchins might select stalks. Izawa (1978) reported that brown capuchins in Colombia capture and feed on frogs and grasshoppers hidden in bamboo stalks (*Bambusa guadua*). The author noticed that the internodes containing a frog were physically very different from others, since frogs were systematically found in the medullary cavities which presented one or two slits and had changed color, being brownish instead of green. However, at our field site in Suriname, the internodes of bamboo that contain larvae did not differ in appearance from internodes lacking larvae – they did not contain slits and they were the same green color (Gunst, pers. obs.). Detecting embedded larvae may be more difficult for the capuchins than detecting embedded frogs because the former leave less physical cues on the bamboo substrate than the latter.

Becoming proficient at finding and extracting larvae from bamboo stalks

If the handling component constrains proficiency at obtaining larva, then monkeys with given size and dental equipment would be equally proficient in this task. But this is not the case. Gunst et al. (2008) report that although older juveniles and subadults have similar dentitions and body weights, the former were still significantly less proficient than the latter in finding embedded larvae. These findings suggest that ineffective search components, more than ineffective handling components, constrain young monkeys' foraging efficiency for larvae in the bamboo. Locating an appropriate stalk and an appropriate site on the stalk depend more on perceptual skills than physical strength. Therefore these aspects of bamboo larvae foraging may be mastered on a different time frame than opening the stalks. In particular, they may be mastered later than the handling components.

Objectives

This study addresses how young monkeys become proficient at foraging for larvae in bamboo stalks. We are particularly interested in how they become skilled at selecting appropriate stalks and how they search these stalks to determine if, and where, to rip them open. We assume that these skills are acquired through the routine generation of species-typical exploratory actions, coupled with learning about the outcomes of actions that generate directly perceptible information (Lockman, 2000; Gibson & Pick, 2003). In accord with this framework, we hypothesize that young capuchins become proficient at locating larvae by two complementary processes: (a) gradual increase in the performance of actions effective in this context, including selection of appropriate stalks, and (b) gradual diminution of actions ineffective in this context, including actions directed at inappropriate stalks. We hypothesize that young individuals are attracted to stalks they can break more easily (i.e. thin diameter and rotten bamboo stalks). Previous work has shown that young capuchins at Raleighvallen are attracted to stalks ripped open by others (Gunst et al. 2008). Neither of these classes of stalks (thin, rotten, and already-ripped) contain larvae.

To learn how to forage efficiently on embedded foods, immature capuchins may initially apply the full repertoire of species-typical perception-action routines to various types of foraging substrates, in the process detecting the affordances of each action, and finally direct actions in a correct sequence on the appropriate foraging substrate (Resende et al., 2008). Therefore, we predict that 1) the behavioral patterns that in adults are associated with effective detection exist in the repertoire of immature capuchins from the outset, 2) frequency of performing these behaviors will increase from infancy to adulthood (i.e., by around 6 years), and 3) performance of all behaviors during foraging for bamboo larvae, including selection of inappropriate stalks and search actions that are not common in proficient adults, will be more frequent in young juveniles than infants, as juveniles take up foraging activity, but will be increasingly less frequent in older age groups, although they will remain in the repertoire at a very low rate. Immigrant adults, if they are naïve about this form of foraging, should be as efficient as animals of equal size at opening stalks, but, like younger individuals, they will produce inappropriate behaviors proportionally more frequently than proficient resident adults.

Material and methods

Study site

Observations took place at the Raleighvallen site (4°0’N, 56°30’W) (hereafter, RV) within the Central Suriname Nature Preserve (CSNR), which comprises 1.6 million ha of primary tropical forest of west-central Suriname and protects the upper watershed of the Coppename River. About 40 % of habitat use 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). Brown capuchins at RV feed on a vast array of food items, including plants, fruits, flowers, invertebrates, and small vertebrates (Mittermeier & van Roosmalen, 1981; Boinski et al., 2000). 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 in a large bamboo patch. The species of bamboo present at the study site is *Guadua latifolia* (*Graminae*). Because the bamboo patch was impenetrable by human observers, three trails (about 2 m wide) were cut across the bamboo patch visited by the study group to allow observers to follow the monkeys.

In bamboo patches, brown capuchins feed on bamboo shoots, stalk pith, and larvae hidden inside bamboo stalks. The larvae (*Myelobia sp.*, Family of *Pyralidae*: Britton, 1984) feed and are hidden inside the internodes of the bamboo stalk, attaining a maximum size of 10 cm and 7 g. The larvae are prototypical 'encased' foods (Britton, 1984) that can be extracted by capuchins only after they use their hands and teeth to break into the stalk (1 to 9 cm diameter). Larvae are evenly distributed throughout bamboo patches, in the same way as surface insects, and therefore can be considered a dispersed food source for capuchins (Gunst, unpub. data).

Study group

The *Cebus apella* study group (Troop A) had been studied intermittently beginning in 1998 and continuously since 2000, and is well habituated to human presence (Boinski et al., 2003). During the 8 months of observation we report, a total of 31 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 10 adults (aged 7 and more), among which two immigrant males living within the group for less than six months, six subadults (between 5 and 7 years old), four older juveniles (also labeled juveniles 2, between

3 and 5 years old), six younger juveniles (also referred to as juveniles 1, from 1 to 3 years), and five infants (0-1 year). Ages given refer to the monkeys' ages at the start of this study.

Data collection

The observation period was from March 2004 to July 2004, and from March 2005 to July 2005, between 7:00 am and 5:00 pm. When the study group was ranging within the bamboo patch, N.G. collected focal-animal samples (Altmann, 1974) with continuous video-recording using a digital video camera. The duration of focal samples varied from 1 to 15 minutes, depending on the visibility conditions and the feasibility of following the focal individuals. Focal samples lasting less than 1 min were discarded. The focal individual was selected, independently of its activity, from an ordered list of focal individuals. The list was prepared in advance and assured that all individuals had equal sampling opportunities every month. The monkeys could be seen well up to 3 meters into the bamboo from the edge of the trail.

Data coding

Videotaped data were scored using The Observer version 5.0 by Noldus Information Technology (Wageningen, The Netherlands), a software package for behavioral analysis. The list of all the behaviors recorded was divided into non-foraging (e.g., resting, locomoting, grooming, playing) and foraging behaviors, which in turn was divided into larvae-related foraging behaviors and foraging behaviors directed to other foods. We used The Observer to score ten larvae-related foraging behaviors (Table 3.1). Behaviors were categorized as 'events' when they were of relatively short duration (i.e. approximated as points in time) and their frequency of occurrence was of interest, whereas they were referred to as ‘states’ when they lasted longer, and their duration could be measured (cf. Martin & Bateson, 1993).

We also scored the different types of food items foraged in the bamboo patch (e.g., bamboo shoots, pith, larvae hidden inside bamboo stalks, surface insects), and the different types of bamboo stalks processed by the capuchins during larvae foraging according to thickness (thin stalk: less than 2 cm of diameter, medium stalks: 2-4 cm, and large stalks: more than 4 cm), condition (rotten vs. healthy stalks), and integrity (intact vs. already-ripped stalks). In a preliminary study, we investigated which types of bamboo stalks were more likely to contain larvae by cutting open each internode of all stalks found in five 5m^2-quadrats randomly delimited within the bamboo patch. We found no larvae inside rotten stalks with light brown epidermis, inside internodes already-ripped apart by capuchins, and inside thin stalks. In contrast, large and medium healthy stalks with green epidermis contained an average of 0.05 larva per intact internode. These values were based on 274 internodes sampled from the patch visited by the study group as well as two other bamboo patches present in the study area, in order to avoid depleting the supply of larvae during the study.

Data analysis

A total of 45.5 hours of focal data was analyzed, with a minimum of 0.6 hour and a maximum of 3.1 hours per individual. We used The Observer to calculate the durations and frequencies of the larvae-related foraging behaviors directed to the different types of bamboo substrates. When foraging on larvae hidden inside bamboo stalks, Visual Inspect, Manual Inspect, Tap Scan, Bite, and Sniff were categorized as detection patterns, whereas Rip Apart was referred to as an extraction pattern. We defined the time performing larvae-related foraging behaviors by adding up the durations of the behavioral states, namely Visual Inspect, Manual Inspect, and Rip Apart. Behavioral frequencies were defined as hourly rates or total number of occurrence of behavior per hour spent foraging. Behavioral durations were expressed as the percentage of time performing a particular behavior over the total time devoted to foraging. We used data presented in Gunst et al. (2008) to evaluate the foraging efficiency for larvae per individual, defined as the number of larvae found per hour allocated to searching for larvae.

To evaluate age differences in the abilities to discriminate the physical properties of foraging substrates, we measured the interest in rotten and already-ripped bamboo stalks, where no larvae can be found. The variable named ‘interest in already-ripped bamboo stalks’ was defined as the sum of the time spent visually and manually inspecting, ripping apart, and exploring the hole left in these particular stalks. We used two variables to assess ‘interest in rotten bamboo stalks’, the first one, based on foraging states, was defined as the sum of the time spent manually inspecting and ripping apart these stalks, and the second one, based on foraging events, was defined as the sum of frequencies of Tap Scan and Sniff behaviors directed toward these particular stalks.

After verifying the assumptions of data normality, independence, and homogeneity of variances by using Levene’s test, we used general linear models (GLM) to test the effect of age on the duration and frequency of different foraging behaviors. The least significant differences (LSD) were used for post-hoc multiple paired comparisons among the five age classes. To determine the relative importance of particular behaviors that precede the discovery of a larva, we conducted a stepwise linear regression, with foraging efficiency as the dependent variable and either the duration of three foraging states (Visual Inspect, Manual Inspect, and Rip Apart), or the frequency of three foraging events (Tap Scan, Sniff, and Bite) as independent variables, since these six behaviors represented a large proportion of all the behaviors performed during foraging for larvae. SPSS 12.0 was used for all statistics. Statistical significance level was set at $\alpha = 0.05$.

Results

Time devoted to foraging in the bamboo patch

When observed in the bamboo patch, capuchins devoted a total of 40.2 hours to foraging activities, which represents 88.4 % of the time spent collecting data in this patch. We found a statistically significant effect of age on the percentage of time devoted to foraging (GLM: $N = 31$, $F_{4,26} = 19.11$, $p < 0.001$), that consistently increased with age from infants to subadults. Post-hoc multiple paired comparisons between age classes showed that infants spent significantly less time foraging than individuals belonging to all older age classes (infants: 63.3% ±11.3, younger juveniles: 84.6±6.6, older juveniles: 94.5±0.3, subadults: 96.0±2.3, and adults: 91.4±7.6), and younger juveniles spent significantly less time foraging than older juveniles and subadults ($p < 0.05$).

The time devoted to foraging specifically on larvae hidden inside bamboo stalks significantly differed according to age (GLM: $N = 31$, $F_{4,26} = 39.47$, $p < 0.001$). Figure 3.1 shows that the percentage of time performing larvae-related foraging behaviors (i.e. detection and extraction patterns, see Methods for details) consistently increased with age from infants (9.5%±6.6) to adults (83.0±8.0). Post-hoc comparisons showed that infants spent less time than younger juveniles foraging for larvae, and infants and younger juveniles spent less time foraging for larvae than older juveniles, subadults, and adults ($p < 0.001$).

Behaviors contributing to foraging efficiency for larvae

Foraging states. Among the three state predictor variables (durations of Visual Inspect, Manual Inspect, and Rip Apart) that may explain a significant portion of the variance in the foraging efficiency, the first independent variable selected in the regression model was Visual Inspect. This variable explained the most variance in the foraging efficiency and resulted in the largest increase in the overall R^2 (Model #1a: Visual Inspect as predictor, adjusted $R^2 = 0.449$, $F_{1,29} = 25.43$, $p < 0.001$). At the next step, the two remaining variables were evaluated to see if they could explain any additional variance in the dependent variable, and the first predictor that had already been selected was also examined to see if it continued to contribute significantly to the overall R^2. A second regression model was created by entering the first predictor and a second variable (Model #2a: Visual Inspect and Rip Apart as predictors, adjusted $R^2 = 0.624$, $F_{1,28} = 14.47$, $p = 0.001$).

The variable Manual Inspect was excluded from both models, as it could not explain any additional variance in the foraging efficiency (Model #1a, $p = 0.580$; Model #2a, $p = 0.684$). Contrary to Visual Inspect, the variables Manual Inspect and Rip Apart were not selected alone as predictors in models that would also explain a significant portion of variance of the foraging efficiency. Therefore, Visual Inspect can be considered a sufficient detection technique, whereas Manual Inspect and Rip Apart are insufficient techniques in the discovery of larvae.

Foraging events. Among the three event predictor variables (frequencies of Tap Scan, Bite, and Sniff) that may explain a significant portion of the variance in the foraging efficiency, the first independent variable selected in the regression model was Tap Scan, as the one that explained the most variance in the foraging efficiency and resulted in the largest increase in the overall R^2

(Model #1b: Tap Scan as predictor, adjusted $R^2 = 0.275$, $F_{1,29} = 12.35$, $p = 0.001$). A second regression model was created by entering the first predictor and a second variable that explained additional variance in the dependent variable, and also contributed significantly to the overall R^2 (Model #2b: Tap Scan and Bite as predictors, adjusted $R^2 = 0.364$, $F_{1,28} = 5.06$, $p = 0.033$). Finally, a third regression model was generated by considering the first two predictors and the third variable (Model #3b: Tap Scan, Bite, and Sniff as predictors ranked in decreasing importance, adjusted $R^2 = 0.542$, $F_{1,27} = 11.91$, $p = 0.002$).

Contrary to Tap Scan, the variables Bite and Sniff were not selected alone as predictors in models that would also explain a significant portion of variance of the foraging efficiency. Therefore, Tap Scan can be considered a sufficient detection technique, whereas Bite and Sniff are insufficient detection techniques.

Age differences in detection and extractive behaviors when foraging for larvae

To investigate the ontogeny of the foraging patterns selected above, we analyzed the differences between the five age classes in the frequency and duration of detection (Visual Inspect, Manual Inspect, Tap Scan, Bite, and Sniff) and extractive behaviors related to foraging for larvae (Rip Apart).

We found a significant effect of age on the percentage of time spent visually inspecting bamboo when foraging in the bamboo patch (GLM: $N = 31$, $F_{4,26} = 22.92$, $p < 0.001$). Post-hoc multiple paired comparisons between age class means showed that infants devoted significantly less time to Visual Inspect than younger juveniles, and infants and younger juveniles spent less time in Visual Inspect than older juveniles, subadults, and adults ($p < 0.01$). Figure 3.2 shows that the percentage of time devoted to Visual Inspect by infants was negligible (0.4±1.0%), in comparison with the other age classes (from younger juveniles: 23.1% ±11.2 to adults: 56.0±13.5). The percentage of time devoted to Manual Inspect also differed significantly according to age (GLM: $F_{4,26} = 5.11$, $p = 0.004$), but contrary to Visual Inspect, the values consistently decreased with age from infants to adults (Figure 3.3). Post-hoc analyses showed that infants (5.4% ±4.5), younger and older juveniles (5.1±2.1 and 4.5±1.9, respectively) were more engaged in manual inspection of bamboo stalks than adults (0.7±0.7) ($p < 0.01$).

When considering more specific detection techniques, there was a significant age effect on the frequency of Tap Scan (GLM: $F_{4,26} = 4.42$, $p = 0.007$) and Sniff (GLM: $F_{4,26} = 5.60$, $p = 0.002$). Tap Scan frequencies tended to increase with age (Figure 3.4), and were significantly higher in adults than in infants and younger juveniles (50.3±31.0, 0.0±0.0, and 13.2±12.9 events per hour foraging, respectively), and higher in subadults (28.9±24.1) than in infants ($p < 0.01$). Sniff frequencies consistently increased with age from infants to subadults (0.1±0.3, 10.5±12.4, 15.0±5.7, and 22.4±7.7 events per hour foraging, respectively), and decreased in adults (9.2±7.7). Post-hoc analyses showed that these values were significantly lower in infants than in younger, older juveniles, and subadults, and higher in subadults than in younger juveniles and adults ($p < 0.01$). Bite frequencies did not significantly differ with age (infants: 13.0±4.8, younger juveniles: 11.5±6.8, older juveniles: 9.0±3.8, subadults: 10.9±10.1, adults: 4.6±5.3 events per hour foraging; GLM: $F_{4, 26} = 1.87$, $p = 0.146$).

We found a significant age effect on the percentage of time devoted to Rip Apart healthy bamboo stalks during foraging (GLM: $F_{4,26} = 4.03$, $p = 0.011$). Figure 3.5 shows a consistent increase in the mean duration of Rip Apart with age from infants to subadults (4.2% ±3.1 and 30.6±12.3, respectively). Post-hoc analyses showed that subadults and adults (26.2% ±13.3) devoted more time to ripping healthy bamboo stalks than infants ($p < 0.01$).

Age differences in substrate selection when foraging for larvae

Monkeys of different age classes varied in their interest in different types of bamboo stalks according to hardness (soft bamboo pith, versus hard bamboo stalks), thickness (large diameter versus smaller diameter), condition (healthy versus rotten stalks), and integrity (solid versus already-ripped stalks). There was a significant age effect on the percentage of time spent ripping apart bamboo pith (GLM: $F_{4,26} = 4.83$, $p = 0.005$), with higher values found in infants (6.7% ± 6.4) than in all the older age classes (younger juveniles: 1.4±1.4; older juveniles: 0.8±0.7; subadults: 0.5±0.7; adults: 1.0±1.4) ($p < 0.001$).

We found similar results for age differences in the time spent ripping according to the diameter of healthy stalks. There was a significant age effect on the overall duration of Rip Apart large stalks (GLM: $F_{4,26} = 3.60$, $p = 0.018$), with lower values in infants (0.1%±0.3) than in subadults and adults (23.4±12.6 and 18.8±13.7, respectively), and in younger juveniles (6.8±10.1) than in subadults ($p < 0.05$). By contrast, we found no significant differences between age classes in the time spent ripping apart medium stalks (from infants: 2.0% ±1.2 to adults: 6.7±5.8) and thin stalks (from infants: 2.1±2.2 to adults: 0.8±1.3) ($F_{4,26} = 1.28$, $p = 0.303$ and $F_{4,26} = 0.75$, $p = 0.556$, respectively). Figure 3.6 shows the percentage of time devoted to Rip Apart different types of bamboo stalks according to hardness, thickness, condition, and integrity. Rip Apart is present in the behavioral repertoire of infant capuchins, even though infants rarely exhibit this behavior towards tougher substrates (i.e. healthy large stalks).

Interestingly, the diameter of healthy stalks was associated with age differences not only in the time spent extracting larvae by ripping stalks apart, but also in the time (i.e. effort) devoted to detecting larvae hidden inside the stalks. We found a significant age effect on the frequency of Tap Scan and Sniff directed towards large stalks (GLM: $F_{4,26} = 6.21$, $p = 0.001$). The frequency of Tap Scan and Sniff consistently increased with age from infants to adults, and post-hoc analyses revealed infants (2.3±2.3 events per hour foraging) and younger juveniles (10.8±11.6) performed significantly less Tap Scan and Sniff of large stalks than subadults (34.6±17.2) and adults (35.5±23.7) ($p < 0.05$). In contrast, we found no significant differences between age classes in the frequencies of Tap Scan and Sniff directed towards medium stalks (from infants: 1.1±1.6 to adults: 14.3±16.9, $F_{4,26} = 1.68$, $p = 0.185$) or thin stalks (from infants: 4.7±4.4 to adults: 2.4±3.0, $F_{4,26} = 1.86$, $p = 0.147$).

With regards to particular bamboo stalks where no larvae can be found, there were significant age effects on the interest in rotten stalks (GLM on the foraging states Manual Inspect and Rip Apart: $F_{4,26} = 4.75$, $p = 0.005$, and GLM on the foraging events Tap Scan and Sniff: $F_{4,26} = 4.07$, $p = 0.011$) and already-ripped stalks ($F_{4,26} = 18.88$, $p < 0.001$). In the case of foraging states, young individuals spent more time performing foraging behaviors towards rotten stalks, and especially toward already-opened stalks than did subadults and adults, who showed almost no interest in them (rotten stalks, infants: 2.0±2.4%, younger juveniles: 4.6±4.5, older juveniles: 0.9±1.0, subadults: 0.1±0.1, adults: 0.1±0.2; already-ripped stalks, infants: 28.3.±16.2%, younger juveniles: 31.4±11.3, older juveniles: 12.7±3.7, subadults: 2.3±1.9, adults: 1.7±1.7). Post-hoc comparisons on foraging states showed that younger juveniles were significantly more often interested in rotten stalks than older juveniles, subadults, and adults, and infants and younger juveniles showed more interest in already-ripped stalks than older juveniles, subadults, and adults ($p < 0.01$, see Figure 3.7). Post-hoc comparisons on foraging events showed that older juveniles directed Tap Scan and Sniff behaviors towards rotten stalks more often than infants, subadults, and adults ($p < 0.001$). Figure 3.8 shows the percentage of all detection events (Tap

Scan, Sniff, and Bite pooled together) directed toward different types of bamboo stalks according to hardness, thickness, condition, and integrity.

Acquisition and disappearance of foraging behaviors during ontogeny

To illustrate the gradual acquisition and disappearance of larvae-related foraging patterns over the developmental course of brown capuchins, we plotted, within each of the five age classes, the mean durations and frequencies of behaviors showing significant age differences (Figure 3.9a and 3.9b). As predicted, sufficient detection techniques (Visual Inspect and Tap Scan) tended to become more prevalent with age. Visual Inspect existed at a very low rate in the repertoire of capuchins from the outset (infants: 0.43 ± 0.96 % of foraging time), and Tap Scan appeared from the age of one year. Insufficient detection techniques such as Manual Inspect and Bite tended to disappear according to the same timeline, but remained in the repertoire of adults at a very low rate. Manual Inspect consistently decreased from infants (5.42±4.47%) to adults (0.74±0.74%) (Figure 3.3). Bite declined in adults (infants: 12.98±4.85%, juveniles 1: 11.46±6.80%, juveniles 2: 9.03±3.77%, subadults: 10.89±10.11%, adults: 4.65±5.31%). Sniff increased from infants to subadults, but decreased in adults (Figure 3.7b).

Extractive behavioral patterns (Rip Apart) directed toward appropriate substrates, i.e. large healthy stalks, were virtually absent in infants and tended to become more prevalent with age, at least until the subadult stage. In contrast, interest in already-ripped stalks represented an important part of 0- to 3-year old individuals' foraging activities, but decreased between 3 and 5 years of age, and almost disappeared in individuals aged more than 5 years.

Case study on immigrant adult males

We compared the data obtained from the two adult males recently integrated into the study group, and whose original group(s) was/were not known, with those from all other individuals of the same age class. The former had the lowest foraging efficiency values (mean ± SD = 3.7 ± 0.5 larvae found per hour foraging) of all adults (mean ± SD for the latter = 6.2 ± 1.6). The two immigrant adult males were also less efficient than all subadults (6.3 ± 1.7). However, Figure 3.8 shows that the average foraging efficiency of these two subjects was exactly the same as one of the older juveniles (3.7 ± 1.7). With regards to extractive behavior, the two immigrant males and the other adults or subadults did not notably differ in the time they devoted to ripping bamboo stalks apart (30.2 ± 6.9%, 25.2 ± 14.7%, and 30.6 ± 12.3%, respectively). Interestingly, they spent less time performing larvae detection behaviors than other adults, and were similar to older juveniles in their Tap Scan frequencies (29.8 ± 20.9 and 30.7 ± 20.5 Tap Scan events per hour foraging, respectively) and the percentage of time devoted to Visual Inspect (46.1 ± 13.7% and 49.1 ± 10.5, respectively; Figure 3.10). Our small data set did not allow us to present analyses on the selection of stalks by these two males.

Discussion

We set out to study the development of proficient extraction by young brown capuchin monkeys foraging for larvae living inside healthy stalks of bamboo. To get at these larvae, which are highly prized by the monkeys, they must learn to select appropriate stalks, to search these stalks effectively, and to open them and extract the larvae. We have shown that the final step, which can be considered "handling" in the terminology of optimal foraging models (cf. MacArthur & Pianka, 1966), is mastered by monkeys in a timeline set by physical growth and dental development. The first two steps, which correspond to “searching” in the terminology of optimal foraging models, are mastered more slowly. Effective searching behaviors directed at appropriate stalks are not fully mastered before the age of six years. Moreover, the relatively low proportion of effective detection behaviors by immigrant adult individuals and their low efficiency at obtaining larvae suggest that they were naïve about this particular foraging activity, and highlight the dependence of efficient searching behaviors upon extended practice even for individuals with full physical capabilities.

Below we compare age-related morphological changes with the timeline of acquisition of extractive behaviors (i.e. ripping bamboo stalks apart to get access to encased larvae), and those components of extractive foraging that are not strength-dependent (i.e. the acquisition of detection skills to locate hidden larvae) as they may serve as constraints on the development of mature competence (cf. Ross & Jones 1999; van Schaik et al. 2006).

The importance of specific detection techniques

We found that visually inspecting and tapping bamboo stalks were the most adequate techniques to detect larvae. Performance of these foraging behaviors was significantly associated with the discovery of a larva, as opposed to other detection techniques, such as manually inspecting, biting, and sniffing stalks.

Tap scanning has been described many times in capuchins in diverse settings. The assumed function is identification of locations where potential prey are embedded in woody substrates, and to check ripeness of fruit (Izawa, 1978, 1979; Panger et al., 2002; Phillips et al., 2003; Visalberghi & Neel, 2003; Phillips et al., 2004). For example, Izawa (1978) described wild capuchins listening for sounds while tapping before starting to rip the bamboo stalk and extract a frog hidden inside a bamboo internode. We conclude that the challenge in the foraging task we studied is not to learn to tap – the monkeys do this anyway. The challenges are to learn what to notice while tapping, and to tap in the right places.

We suggest that close visual inspection of the bamboo stalks (and especially the possible presence of the tiny hole made by the insect while laying eggs that develop into larvae) may help the forager select which particular internode would be “worth” ripping apart, while tap scanning could serve to confirm or refine the search (see also Phillips et al., 2004). Sniffing apparently adds little to the process, although young monkeys do sniff stalks both before and after tapping and ripping (Gunst, pers. obs.).

Aye-ayes (*Daubentonia madagascariensis*, nocturnal prosimians) extract embedded foods in a manner superficially similar to capuchins. This species depends heavily on tap scanning to locate the galleries of insect larvae inside woody substrates, and perhaps also to generate audible movements by the prey (Erickson, 1991). However, experimental studies showed that visual and olfactory cues may not be necessary for aye-ayes to detect larvae hidden in woody substrates. It has been suggested that tapping could serve the detection of embedded invertebrates by providing more than auditory cues. Aye-ayes’ third digit may discriminate among surface vibrations, suggesting use of a “cutaneous sense” while performing tapping (Erickson, 1991). The low mass of the middle digit may allow it to resonate with the surface vibration without serious dampening.

Capuchins and aye-ayes differ notably in the ontogenetic timeline of appearance of detection techniques and timeline of efficiency at obtaining larvae. Unlike capuchins in this study, in which tap scanning was observed from the age of one year, this behavior was present in the repertoire of captive aye-ayes from as early as three months (Krakauer, 2005). Tapping is purely exploratory and non-functional when exhibited by infant aye-ayes. High foraging efficiency for larvae is not attained before post-juvenility (i.e. around the age of six years) in capuchins (Gunst et al., 2008, this study), whereas in captive aye-ayes, it is reached considerably earlier than adolescence (immediately after weaning, i.e. around 15-17 months of age) (Krakauer, 2005). When considering the ontogeny of the handling component, i.e. extracting the larva by biting into the protective matrix and ripping it apart, the two species show more similarities. When biting into foraging substrates, infant and young juvenile capuchins tear much thinner bamboo stalk fragments (Gunst, pers. obs.), and infant aye-ayes make less robust gnaw marks in woody materials than older individuals (Krakauer, 2005). This suggests that dental equipment and strength limit successful extraction.

Ontogeny of substrate selection

Extracting a larva from a bamboo stalk is time and energy consuming. Therefore, capuchins should rip a stalk apart only when it is worthwhile to do so, that is, when the stalk is very likely to contain a highly nutritious larva, and not when the energy gain is uncertain, that is when the stalk is small, rotten, or has already been processed by a previous forager. By learning how to select appropriate substrates (mainly large and medium healthy internodes), and by performing adequate detection techniques in appropriate behavioral sequence, growing capuchins gradually optimize their extractive foraging strategies.

How do young monkeys learn what kind of stalk to tap and inspect? Although some detection and extraction techniques, such as sniffing, and ripping apart, appeared in the capuchins' repertoire as early as infancy, whether or not these behaviors were directed toward appropriate foraging substrates (i.e. bamboo stalks likely to contain embedded larvae) largely depended on the age of the forager. The frequency of tap scanning and sniffing directed towards large stalks, where most larvae can be found, consistently increased from infants to adults, with a significant difference between infants and younger juveniles on the one hand, and subadults and adults on the other hand. Infants mainly ripped soft bamboo pith (that cannot contain any larvae) instead of hard bamboo stalks. Older juveniles, subadults, and adults directed significantly less foraging behaviors towards particular foraging substrates where no larvae can be found, due to their health (rotten stalks) or integrity (already-ripped stalks), than younger individuals.

The limited physical capabilities of infants and younger juveniles may explain why they direct more foraging behaviors towards thin or rotten stalks that they can break easily, as well as already-opened stalks, than to large and healthy stalks. Working on thin, rotten, and already-opened stalks allows young individuals to practice opening bamboo, even though it does not result in gaining a larva. Practicing at sites opened by skilled conspecifics may improve their pulling/ripping skills, and may help them develop a preference for appropriate substrates (i.e. large and healthy stalks). To test this hypothesis, future study could document the type of stalks juveniles select following practice at large already-ripped stalks.

Acquisition of detection techniques: "perception-action" perspective and experiential factors

Our results reveal that young capuchins acquire detection techniques to find larvae in bamboo through a gradual increase in the use of effective behaviors and a progressive disappearance of ineffective behaviors. A similar pattern is evident in young capuchins acquiring a different kind of foraging skill, cracking nuts using stone hammers and anvils (Resende et al., 2008). In both cases, young capuchins initially apply the full repertoire of species-typical actions to various types of foraging substrates. In the case studied here, most of them are inefficient for obtaining bamboo larvae, because they are directed to inappropriate substrates (i.e. bamboo stalks unlikely to contain embedded larvae), or because the action does not provide relevant information on the presence of encased food (e.g., Bite and Manual Inspect), or because the sequence of actions is not correctly ordered (for instance, ripping a bamboo stalk apart with teeth before performing the detection patterns). As the individual practices opening bamboo and searching for larvae, such “errors” are gradually reduced and effective species-typical exploratory actions (those that guide detection and extraction) increase (cf. Lockman, 2000; Gibson & Pick, 2003).

We found that ineffective actions and sequences tended to diminish as individuals gain experience at selecting the most appropriate foraging substrates (i.e. large and intact bamboo stalks). Individual practice with different kinds of stalks combined with associative learning through gradual positive reinforcement (finding larvae) may help young monkeys detect the affordances of each action, learn the right foraging sequences, and select appropriate substrates when they become able to open them.

The similarities in efficiency at obtaining embedded larvae between immatures and two immigrant adult males that seemed naïve about this foraging activity provide additional evidence that identifying the right kind of stalk and locating the larva in it are more challenging than opening the stalk, and therefore constrain the appearance of mature efficiency at this kind of foraging. If obtaining larvae were only constrained by the ability to open stalks, which is paced by physical maturation, naïve adults should be more efficient than immatures. Indeed, immigrant adults were similar to other adults with regards to the strength-dependent foraging component (i.e. ripping stalks apart), but their level of detection and their use of various detection techniques was characteristic of older juveniles. The immigrant individuals apparently had less experience in this particular extractive foraging task. Two years after this study was conducted, one of these males, still present in the study troop, had improved considerably his foraging efficiency in obtaining embedded larvae, although without reaching the foraging efficiency performed by subadult males born in the troop (Gunst, unpub. data). Likewise, in captive aye-ayes, regardless of size or age, individuals that were initially inexperienced with tap-foraging (i.e. immatures and naïve adults) demonstrated reduced ability relative to experienced subjects (Krakauer, 2005).

The "needing-to-learn" hypothesis postulates that a relatively slow development with prolonged immaturity can be explained by the need to devote time to acquire complex adult-level skills (Ross & Jones 1999). Our extension of this hypothesis produces the prediction that searching behaviors (detecting larvae) relying on learning may achieve mature form later than handling behaviors (extracting larvae) relying on physical development. Therefore, reaching adult-level proficiency at obtaining embedded larvae may not only be constrained by body size and dental equipment but also by learning how to detect them.

In wild brown capuchins, a several-year period of practice is needed for a young forager to become fully competent in locating encased larvae. This study suggests that the ability to select appropriate substrates and detect hidden larvae hidden is likely to benefit from prolonged individual practice through perceptual learning. In a previous study, we showed that conspecifics' foraging artefacts (i.e. bamboo internodes previously ripped apart by foragers to extract larvae) may have an indirect social influence on the acquisition process (Gunst et al., 2008). Even though an already-ripped stalk cannot lead to success by obtaining a direct reward (i.e. a larva), it prompts young individuals to practice larvae-related foraging behaviors. Persevering practice may turn initially unpolished attempts into a finely controlled and skilled movement (Elliot, 1999).

Practice with already-ripped large stalks may also influence choice of subsequent stalks through social enhancement. However, while enhancement narrows immatures' interest to one large already-ripped segment, it cannot lead directly to success. In this case, young individuals have to move away from the opened large segment to adjacent segments that are large too and more likely to contain larvae. Whereas infants and younger juveniles tend to persist in exploring empty already-ripped large segments, older juveniles were more inclined to shift their attention to adjacent segments (Gunst, pers. obs.). By doing so, immatures can learn to associate large diameter stalks with higher probabilities to find larvae. Therefore, practice with particular foraging artefacts (already-ripped large stalks) may affect the selection of appropriate substrates through an expansion of the zone of social enhancement. This is an interesting model that expands or challenges existing notions of social supports for learning (cf. Fragaszy & Visalberghi, 2004).

When solving extractive foraging problems, detection skills may be important for some species (e.g., aye-ayes: Erickson, 1991; Krakauer, 2005), but not for others (e.g., chimpanzees: Inoue-Nakamura & Matsuzawa, 1997). Many studies have addressed different forms of extractive foraging in various primate species (capuchins: Izawa, 1978; Phillips et al., 2004; Gunst et al., 2008; Resende et al., 2008; baboons: King, 1986; aye-ayes: Krakauer, 2005; chimpanzees: Inoue-Nakamura & Matsuzawa, 1997). These species do not present a homogeneous trend towards any particular set of cognitive attributes or behavioral flexibility accompanying encephalization. For example, brown capuchins display not only extractive foraging involving anatomical structures (this study), but also extractive foraging involving the use of tools (Fragaszy et al., 2004). In contrast, aye-ayes use anatomical structures to forage for embedded prey, but are not particularly adept at learning to use objects as rake tools to pull in food (Sterling & Povinelli, 1999), suggesting that extraction per se is not predictive of flexible manual action in other contexts. The large encephalization of aye-ayes (Stephan et al., 1988) is associated with fine motor coordination, olfaction, and auditory capacities. We suggest that embeddedness per se does not predict the challenge of foraging on a given food. Instead, it may be the manner in which individuals find hidden foods.

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Table 3.1: Larvae-related foraging states and events scored in this study.

Behavior	Definition	Type
Visual Inspect	Visually scan bamboo stalks by turning one's head from one stalk to another and tilting one's head to closely watch around each stalk	State
Manual Inspect	Tactile inspection by slipping one's hand on the surface of a bamboo stalk	State
Rip Apart	Repetitive biting actions into a bamboo stalk followed by tearing actions with hands applied on the resulting spray of whitish stalk fragments	State
Explore Hole	Probing with hand or insert fingers into the hole of an already-ripped bamboo stalk	State
Tap Scan	Quick tapping on a bamboo stalk with fingertips	Event
Sniff	Olfactory inspection by putting one's nose to a bamboo stalk and deeply inhale	Event
Bite	Quick puncture into a bamboo stalk with canine	Event

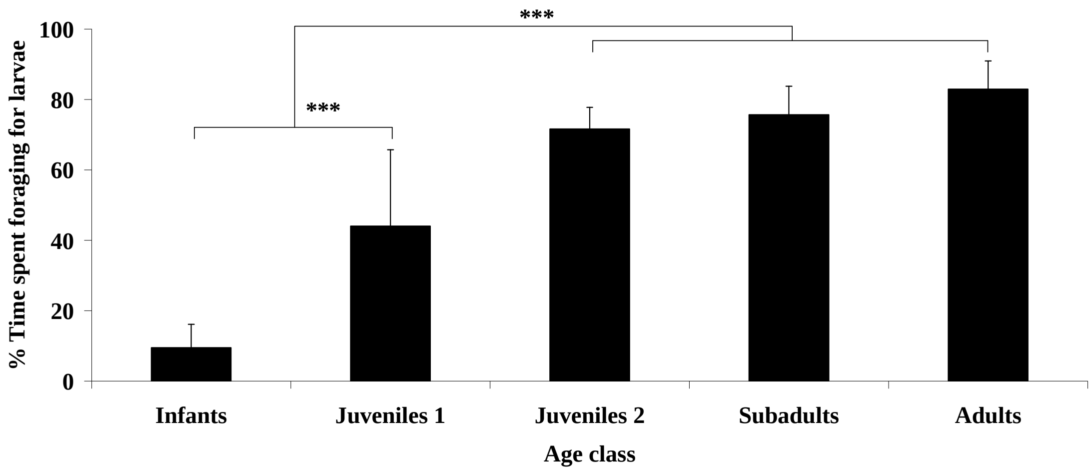

Fig. 3.1. Mean ± SD percentage of time spent performing larvae-related foraging behaviors for each age class. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

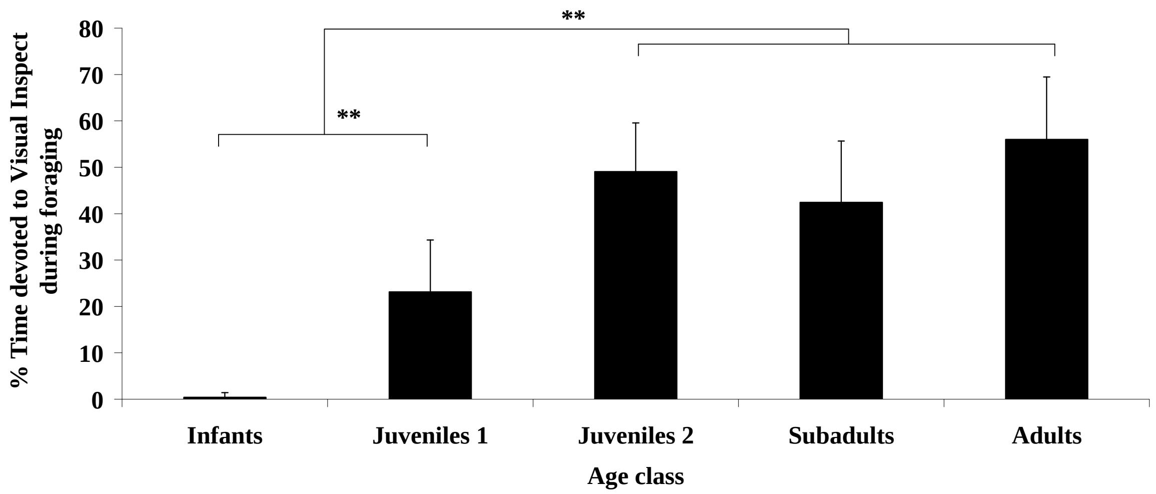

Fig. 3.2. Mean ± SD percentage of time devoted to Visual Inspect during foraging for each age class. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

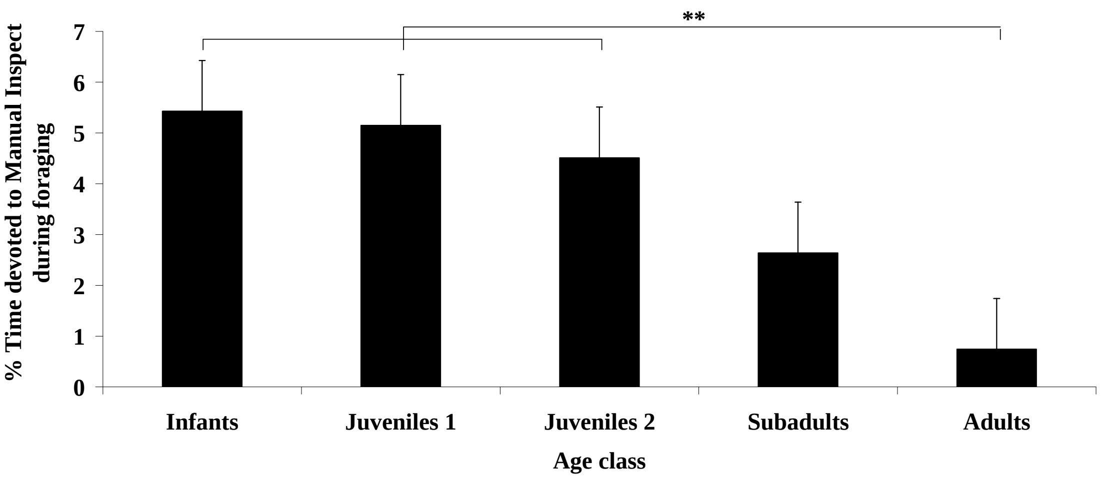

Fig. 3.3. Mean ±SD percentage of time devoted to Manual Inspect during foraging for each age class. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

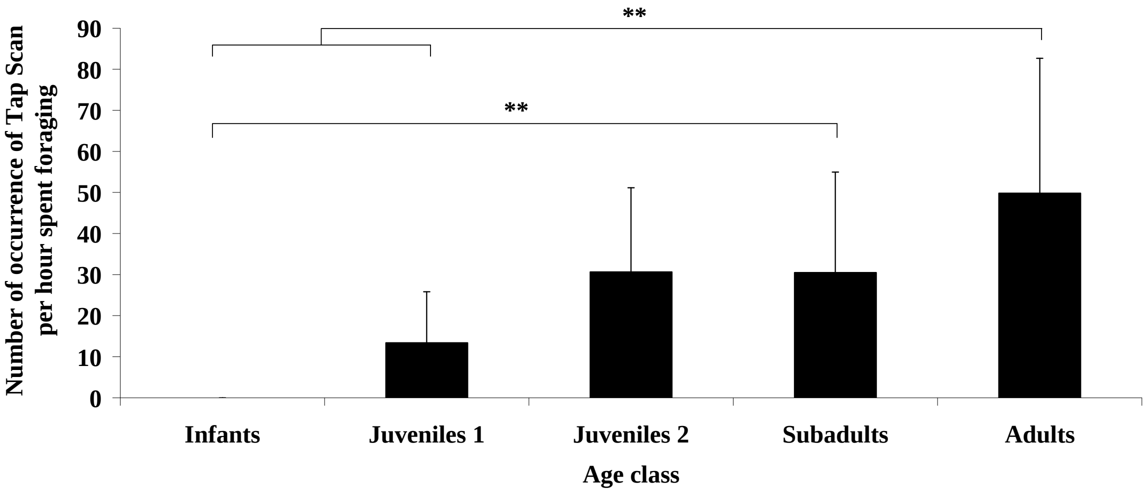

Fig. 3.4. Mean ± SD frequency of Tap Scan (number of occurrence of Tap Scan per hour spent foraging) for each age class. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

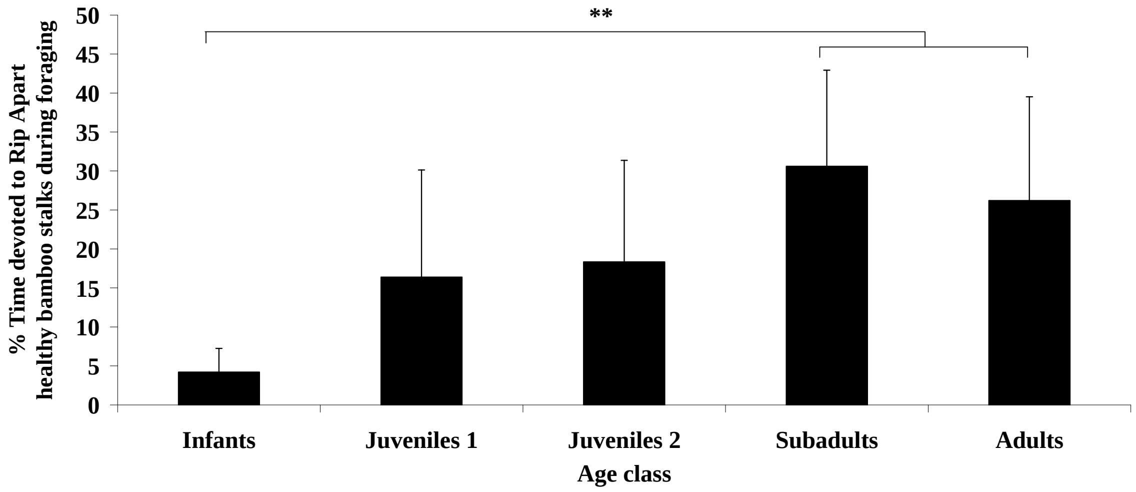

Fig. 3.5. Mean ± SD percentage of time devoted to Rip Apart healthy bamboo stalks during foraging for each age class. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

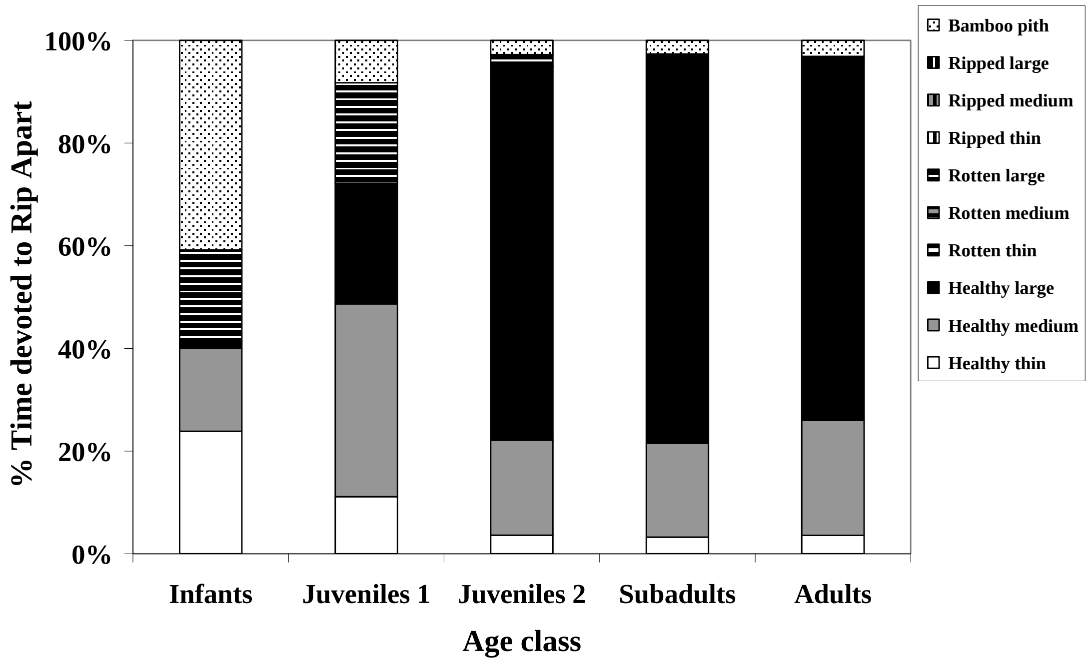

Fig. 3.6. Percentage of time devoted to Rip Apart different types of bamboo stalks according to hardness, thickness, condition, and integrity, for each age class.

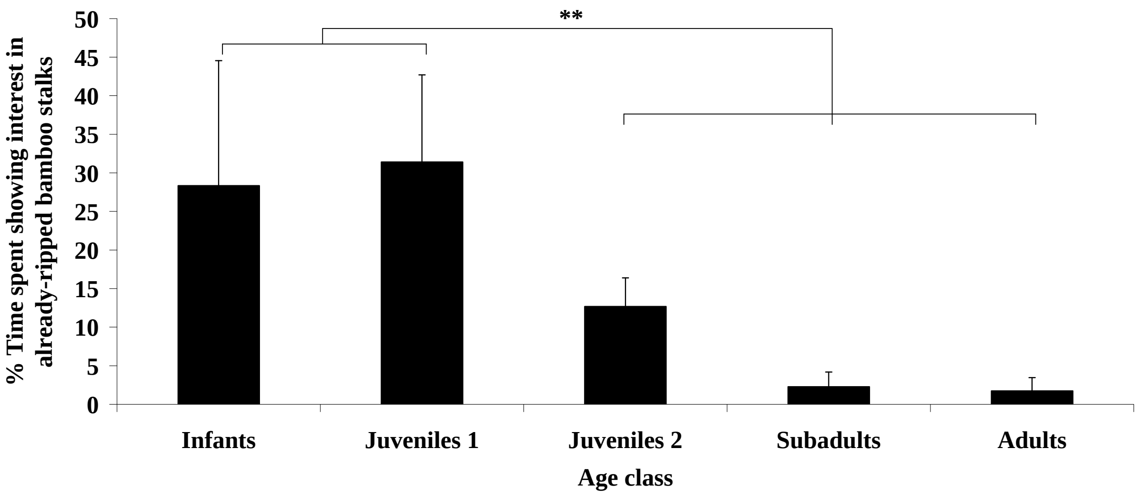

Fig. 3.7. Mean ± SD percentage of time showing interest in already-ripped bamboo stalks during foraging for each age class. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

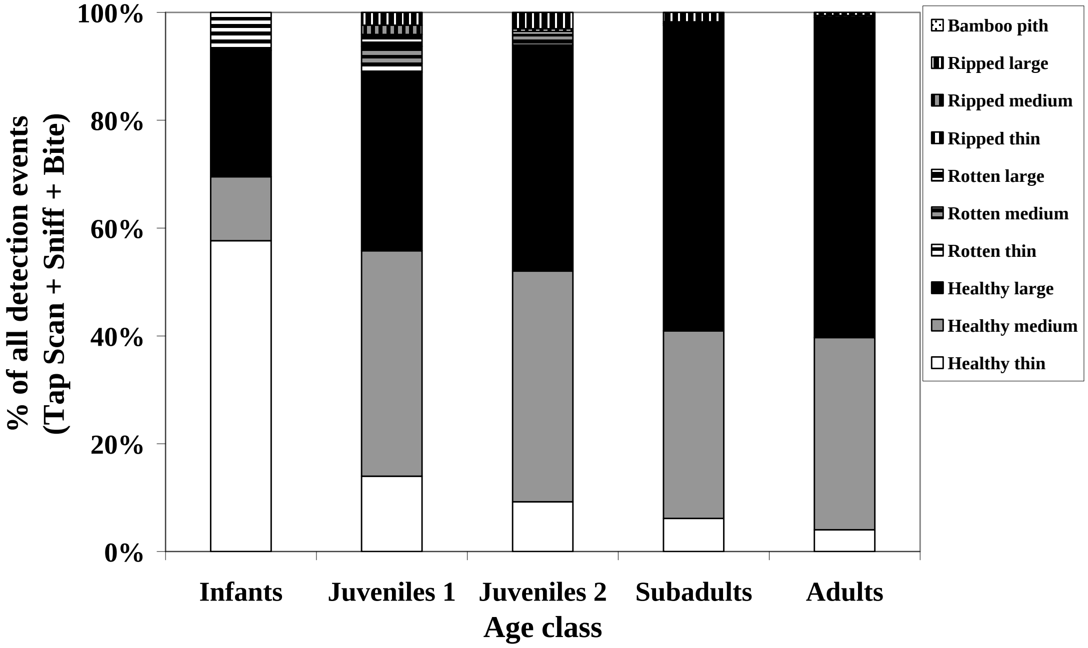

Fig. 3.8. Percentage of all detection events (Tap Scan, Sniff, and Bite pooled together) directed toward different types of bamboo stalks according to hardness, thickness, condition, and integrity, for each age class.

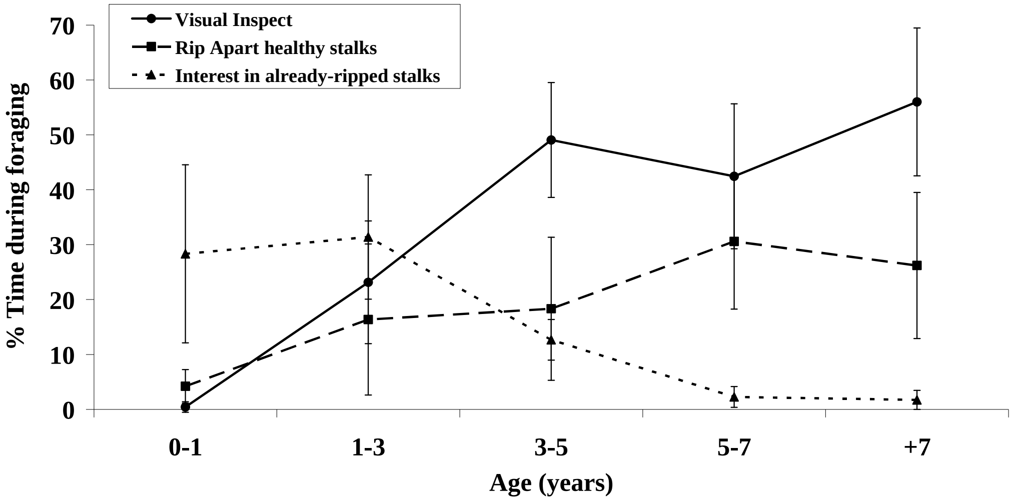

Fig. 3.9a. Timeline of appearance of Visual Inspect and Rip Apart behaviors, and disappearance of interest in already-ripped stalks, expressed as percentage of time during foraging.

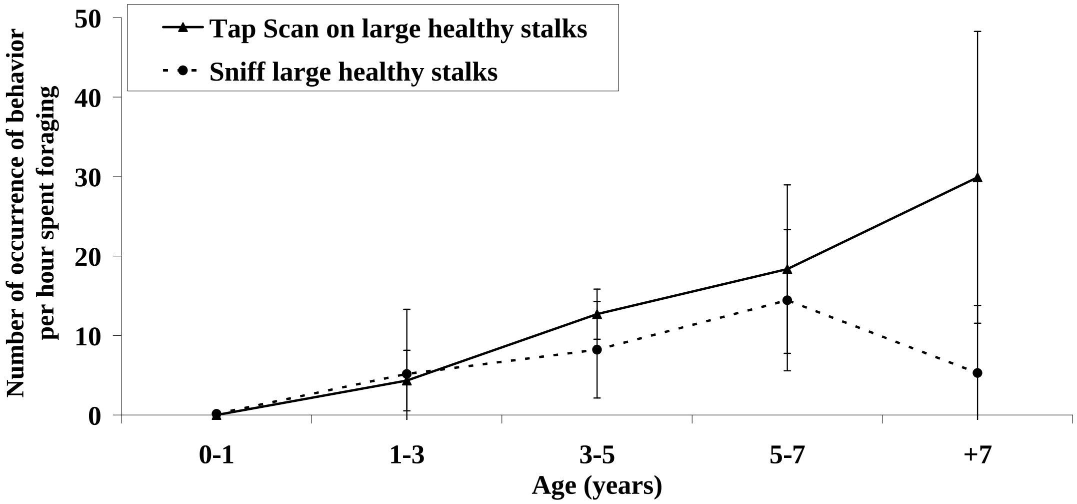

Fig. 3.9b. Timeline of appearance of Tap Scan and Sniff behaviors, expressed as frequency per hour spent foraging.

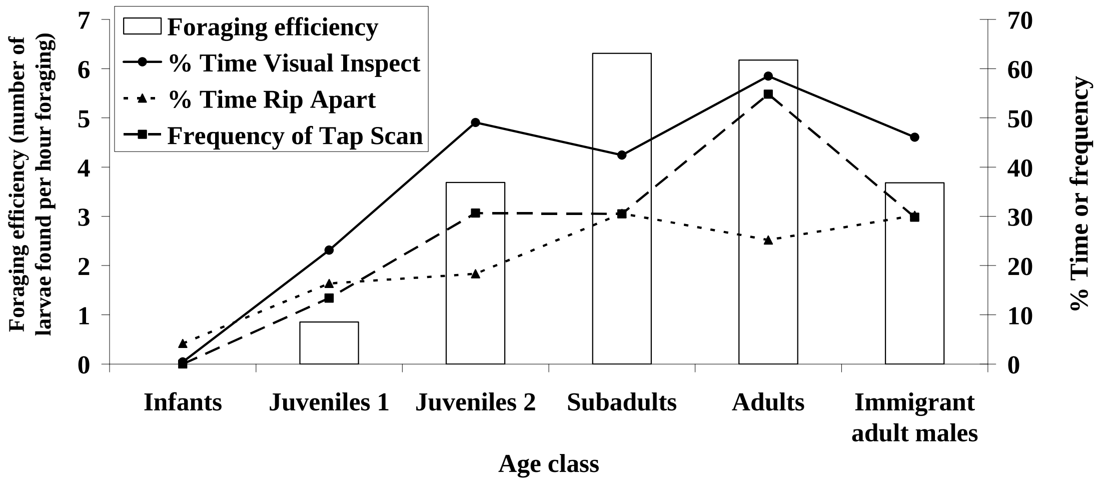

Fig. 3.10. Comparison of efficiency at finding larvae and prevalence of larvae-related foraging behaviors in resident individuals of different age classes and immigrant adult males.

CHAPTER 4

GENERAL CONCLUSIONS

The overarching goal of this research was to address both underlying mechanisms and functional consequences of the ontogeny of a major ecological competence: locating and extracting embedded food items. Capuchins at Raleighvallen, Suriname are faced with complex foraging challenges, including searching for a hidden, protein and lipid-rich food source requiring extraction from a tough, concealing substrate: larvae living inside bamboo stalks.

As a way to evaluate the complementary contributions of morphological constraints (e.g., body size and dental development) versus experiential process supporting learning on the development of complex foraging competence, I divided the task consisting of foraging on embedded larvae into two types of behavioral components, namely searching and handling. From the perspective of optimal foraging theory, foraging for embedded larvae can be regarded as a tradeoff, where the costs of the handling components (namely, the time and energy spent extracting the food items by ripping apart their tough protective matrix) are balanced with the benefits derived from the consumption of protein and lipid-rich food sources, which in turn, are directly determined by the effectiveness of the searching components.

My findings on the possible role of acoustic information to capuchins in locating embedded invertebrates is consistent with previous field and experimental reports. Capuchin monkeys

(*Cebus* spp.) may pound palm nuts against branches and use tapping as a foraging technique to generate acoustic cues about fruit hardness and ripeness, the presence and content of cavities inside foraging substrates, and embedded invertebrates (Terborgh, 1983; Panger et al., 2002; Phillips et al., 2003, 2004; Visalberghi & Neel, 2003). In addition to auditory information, these foraging techniques may also provide discriminatable cutaneous information about vibrations from cavities underneath the surface (Erickson, 1991).

The results presented in Chapter 3 also indicate that visual cues are an important source of information used by capuchins foraging for hidden food. In a study of the use of the prehensile tail while foraging, Garber & Rehg (1999) reported that white-faced capuchins (*Cebus capucinus*) first visually scanned an area for signs of prey activity, then either further examined the area or searched for another. Bolen & Green (1997) suggested that, as diurnal primates, capuchins may use visual rather than olfactory information to locate hidden foods. Experiments on brown capuchins showed that (a) foraging for invertebrates embedded in a woody substrate was guided by at least three sensory cues (namely, visual, olfactory, and acoustic cues) associated with the presence of the prey; (b) one sensory cue alone was generally not sufficient to successfully locate an encased invertebrate; (c) not one cue appeared to be more salient, and (d) the combination of visual and acoustic cues led most subjects to successfully locate an embedded prey (Phillips et al., 2003). Effective detection of hidden invertebrates demands finely controlled movements and sensorimotor coordination. The acquisition of detection skills is a long-enduring process relying on sensory capabilities, skilled exploratory actions, and individual experience. Just how capuchins acquire the skills necessary to locate embedded preys can be an important indicator of development.

Despite their daily attempts and strenuous efforts in searching for encased invertebrates, immature capuchins do not rely on larvae as a staple food source or a substantial energetic intake before reaching post-juvenility. High foraging success is more explainable by a set of reliable detection techniques applied on appropriate foraging substrates (Chapter 3) than a high frequency of ripping bouts (Chapter 2). Mastering detection skills and selecting stalks likely to contain larvae are key features to minimize the cost of opening hard stalks with no reward, in case they are empty. Thus, learning how to locate hidden preys can be viewed as a long-term investment, whose payoffs are not collected before subadult level. Species characterized by a prolonged juvenescence, like brown capuchins, can benefit from an extended period of learning the repertoire of extractive foraging behaviors. For young capuchins, learning foraging skills may require solitary practice (i.e. individual learning), as well as seeking out situations in which skilled conspecifics aid learning (i.e. socially-mediated learning).

For immature individuals that are unskilled foragers and potential learners, habitat modifications through the usage, choices, and practices of conspecifics increase learning opportunities. Young capuchin monkeys have opportunities to observe skilled foragers and to encounter their foraging artefacts (indirect social influence), followed by individual practice. In chimpanzees, the achievement of adult-level proficiency at using tools to forage on embedded foods requires extensive observation of skilled conspecifics, prolonged exposure to foraging tools and substrates, and solitary repetition of extractive behavioral patterns (e.g., Boesch, 1991; Lonsdorf et al., 2004). Via the physical traces of their activities left in the environment, older individuals indirectly facilitate effective information transmission among group members and across generations, resulting in relatively low costs of learning (Odling-Smee et al., 2003; Laland, 2004). Therefore, community-generated influence on the acquisition of foraging expertise is a form of “niche construction” (cf. Odling-Smee et al., 2003; Russon, 2003), and skilled capuchin foragers can be regarded as “ecosystem engineers” (cf. Fragaszy et al., 2004). Understanding the role of socially-mediated learning from the niche construction perspective is an important task for behavioral biologists.

In accord with the hypothesis that learning contributes substantively to the development of skills needed to locate larvae hidden inside bamboo stalks, we demonstrated that the timeline of physical changes in capuchins does not fully account for differences in foraging efficiency across age classes (Gunst et al., 2008). The appearance over time of sufficient larvae-related detection techniques suggest that such sensory capabilities and finely controlled actions need several years to develop before reaching adult-level proficiency and rely more on experience than physical strength. In sum, the ontogeny of sensorimotor coordination and perceptual learning constrain the effective detection of hidden invertebrates (Fragaszy & Boinski, 1995; Gunst et al., 2008). Sensorimotor immaturity and physical constraints may altogether prevent infants and younger juveniles from applying detection techniques to appropriate foraging substrates and directing extractive behaviors towards tough protective matrices.

The present research 1) improves our understanding of the developmental processes involved in the acquisition of complex foraging skills in wild brown capuchins, 2) offers a view on how the gradual acquisition of extractive foraging competence in capuchins is aided jointly by physical maturation and social influences that provide unskilled immature individuals with opportunities to practice appropriate foraging actions, and 3) provides quantitative evidence that encountering physical traces of previous foraging activity stimulates the performance of subsequent food-searching behaviors by young capuchins.

Through a comparative approach within the Primate order, this dissertation contributes to better understanding 1) the implications of extractive foraging in the evolution of primates, 2) the various ontogenetic correlates of developing adult-level foraging proficiency (such as an increase in body size, body mass, and physical strength, dental development, and improvement of specific perceptual skills), 3) the relations between life history traits and foraging patterns across species (e.g., juvenility duration and diet diversity), and 4) comparative cognition in prosimians, monkeys, apes, and humans (including sensorimotor coordination, perceptual learning, and memorial skills).

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