

# Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence

Noëlle Gunst<sup>1,4)</sup>, Sue Boinski<sup>2)</sup> & Dorothy M. Fragaszy<sup>3)</sup>

(<sup>1</sup> Institute of Ecology, University of Georgia, Athens, GA, USA; <sup>2</sup> Department of Anthropology, University of Florida, Gainesville, FL, USA; <sup>3</sup> Department of Psychology, University of Georgia, Athens, GA, USA)

(Accepted: 22 October 2007)

---

## Summary

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 an original 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.

---

<sup>4)</sup> Corresponding author's e-mail address: [nogu@uga.edu](mailto:nogu@uga.edu)

## **Introduction**

Primates are characterized by the longest juvenile period in relation to life span of all mammals (Pereira & Fairbanks, 1993). According to the 'needing-to-learn' hypothesis, prolonged juvenility 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 de-

velopment of mature competence. That is, at least some components of extractive foraging require refinement of technique, and these particular components should reach 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. Compared to other monkeys, capuchins have an extended life span and a long period of postnatal growth of brain and body (Fragaszy et al., 1990), together with reliance on extractive behaviours that epitomize 'complex foraging patterns' (Janson & Boinski, 1992). Capuchin monkeys 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., 2004; 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 (e.g., Izawa & Mizuno, 1977; Boinski et al., 2000). Thus, capuchins 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. They 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. obtaining 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 sabaues*: Harrison, 1983; mountain gorilla, *Gorilla gorilla berengei*: 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, *Saimiri oerstedii*: 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 oerstedii*, 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 1), 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 substantially 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 these 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 s 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 × 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, unpubl. 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 represents the first examination of 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, unpubl. 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 × 150 m (see Figure 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, unpubl. 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 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

**Table 1.** Definition of age classes, number of sampled males, females and total individuals, and minimum, maximum, and mean number of minutes collected 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 year)	Juveniles 1 (1–3 years)	Juveniles 2 (3–5 years)	Subadults (5–7 years)	Adults (from 7 years)
No. of males	6	3	2	4	4
No. of females	1	3	2	2	6
No. of total individuals	7	6	4	6	10
Sample sizes (min)					
Min	26.5	78.5	195.5	426.5	93
Max	409.5	854	744.5	1648.5	1028
Mean	175	503.5	455.5	727	508.5

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 h, between 7:00 am and 5:00 pm. We conducted focal-animal sampling (Altmann, 1974), with continuous observations on the activity of the focal animal taken during consecutive 30-s intervals. 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-s interval was coded once. These data are used to calculate %

**Table 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

intervals in which a specific behaviour occurred. The specific foraging patterns are listed in Table 2. The duration of focal samples varied from 3 to 15 min, 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 possible (because temporarily undersampled) 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-min 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 per age class in bamboo patches is presented in Table 1.

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 1).

#### *Description of variables*

We collected 321 h of focal data (38 520 intervals) in bamboo patches encompassing all age and sex classes over a 2-year period. Frequency data were collated by individual. We tabulated the number of intervals in which specific foraging patterns related to finding larvae occurred. We estimated the time in hours devoted to search for larvae as the number of intervals multiplied by 30 s and divided by 3600. 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



**Figure 1.** Brown capuchin monkey ripping a bamboo stalk apart. This figure is published in colour at <http://www.ingenta.com>

effect of bamboo segments ripped by others was evaluated by comparing the frequency of larvae-related foraging behaviours performed by the focal individuals shortly (2 min) before and shortly (2 min) after inspecting a ripped bamboo segment.

### *Statistics*

Data were screened for normality, independence and homogeneity of variances, using Levene's test (SPSS). When these assumptions were verified, we used parametric tests (ANOVA 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, Chicago, IL, USA) was used for all statistics. Statistical significance level was set at  $\alpha = 0.05$ .

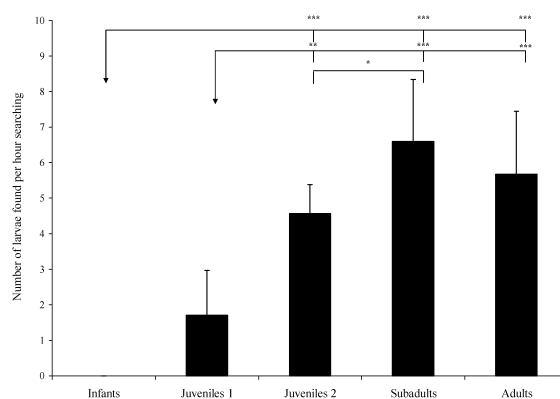
## Results

### *Variation in efficiency of foraging for larvae across ages and sexes*

Capuchins spent 128 h (15 360 interval samples) foraging on larvae, which represents 40% of focal samples 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 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. 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). Coefficients of variation (CV)





**Figure 2.** Foraging efficiency on larvae according to age class. Bars represent the mean number of larvae found per hour spent foraging on larvae  $\pm$  SD. The number of individuals sampled per age class were: No. of infants = 5, No. of juveniles 1 = 6, No. of juveniles 2 = 4, No. of subadults = 5, No. of adults = 10. Asterisks indicate statistically significant paired differences between arrowed and plain lines (\*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ) or between two plain lines (\*  $p < 0.05$ ).

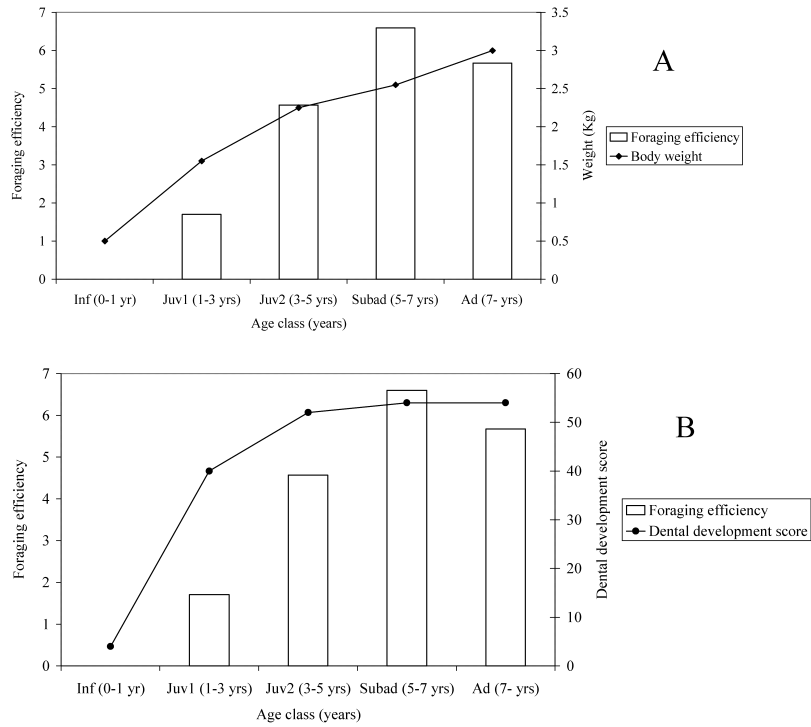
range from 0.18 in older juveniles to 0.74 in younger juveniles. In subadults  $CV = 0.26$  and in adults  $CV = 0.31$ .

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 (Figure 3A and 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).

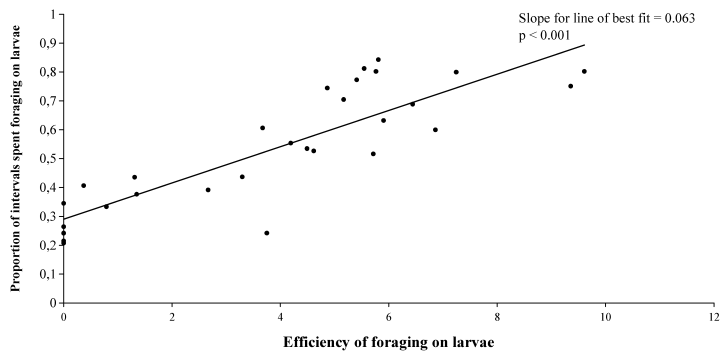
#### *Variation in type of foods foraged according to age and sex*

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 4).

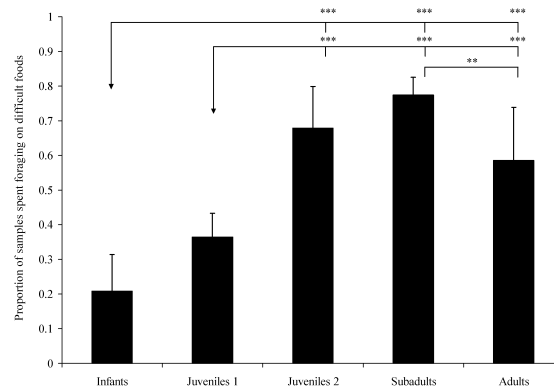
For each sampled individual, we measured the proportion of intervals spent foraging on easy foods (bamboo shoots, bamboo pith, and non-



**Figure 3.** (A) Relationship between foraging efficiency and body weight (after Fragaszy & Bard, 1997) across age classes. (B) Relationship between foraging efficiency and dental development score (after Fleagle & Schaffler, 1982) across age classes.



**Figure 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 5.** Proportion of intervals spent foraging on difficult foods (larvae) according to age class. Bars represent the mean proportion  $\pm$  SD. The number of individuals sampled per age class were: No. of infants = 5, No. of juveniles 1 = 6, No. of juveniles 2 = 4, No. of subadults = 5, No. of adults = 10. Asterisks indicate statistically significant paired differences between arrowed and plain lines (\*\*\*)  $p < 0.001$  or between two plain lines (\*\*)  $p < 0.01$ .

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 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 ( $p = 0.286$ ).

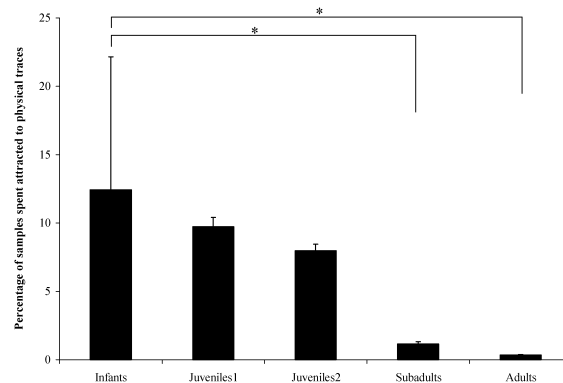
Regarding sex differences in the proportion of intervals spent foraging on difficult foods, we found similar proportions in females and males within younger juveniles ( $t = 0.587$ ,  $df = 4$ ,  $p > 0.05$ ), older juveniles ( $t = -0.053$ ,  $df = 2$ ,  $p > 0.05$ ), and subadults ( $t = -1.370$ ,  $df = 3$ ,  $p > 0.05$ ).

In adults only, females displayed significantly greater proportion of intervals foraging on difficult foods than males (mean  $\pm$  SD =  $0.66 \pm 0.13$  and  $0.47 \pm 0.12$ , 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 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 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



**Figure 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  $\pm$  SD; asterisks indicate statistically significant differences ( $p < 0.05$ ).

foraging behaviours 2 min before and 2 min 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 2 min after than in the 2 min before being attracted to a ripped bamboo stalk left by a skilled forager (mean frequency  $\pm$ SD, before:  $1.1 \pm 1.0$  and after:  $4.8 \pm 5.0$ , 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  $\pm$ SD, before:  $2.1 \pm 1.9$  and after:  $2.5 \pm 1.5$ , 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 7 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/h) to seven years

of age (subadults: 6.6 larvae/h). 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/h; subadults and adults roughly 6 larvae/h. 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 years 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.

Adults were less efficient foragers and less focused on difficult foods than subadults. Because subadults are large-sized but still growing individuals, they may need higher levels of protein in their diet than adults (Richard, 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 and diet choice between age and sex classes may reflect differences in 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 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, unpubl. 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 and 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 oerstedii*: 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 an original 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.

#### **Acknowledgements**

This study would not have been possible without the field expertise of Carson Phillips, Stacey Hodder, Jackson Frechette, Carrie Vath, Megan Bailey, Jon Colburn, Wilson Scherston

and Steven Schet. We are indebted to Jacqueline Molly Sabiran and Mano Ajanki for their kindness and support. We thank STINASU (Suriname Nature Conservation Foundation) and inhabitants of Fongoe island. We are grateful to Jean-Baptiste Leca, Susan Perry, as well as two anonymous reviewers for fruitful comments and suggestions on previous versions of this manuscript. The long-term research program at Raleighvallen is supported by the US National Science Foundation (SRR-9722840, BCS-0078967, BCS-0352316 and BCS-0352035).

### References

- Adams-Curtis, L. & Fragaszy, D.M. (1995). Influence of a skilled model on the behavior of conspecific observers in tufted capuchin monkeys (*Cebus apella*). — *Am. J. Primatol.* 37: 65-71.
- Agostini, I. & Visalberghi, E. (2005). Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*). — *Am. J. Primatol.* 65: 335-351.
- Aisner, R. & Terkel, J. (1992). Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus*. — *Anim. Behav.* 44: 327-336.
- Altmann, J. (1974). Observational study of behaviour: Sampling methods. — *Behaviour* 49: 227-265.
- Altmann, J. & Alberts, S. (1987). Body mass and growth rates in a wild primate population. — *Oecologia* 72: 15-20.
- Anapol, F. & Lee, S. (1994). Morphological adaptation to diet in Platyrrhine primates. — *Am. J. Phys. Anthropol.* 94: 239-261.
- Boesch, C. (1991). Teaching among wild chimpanzees. — *Anim. Behav.* 41: 530-532.
- Boinski, S. (1988). Sex differences in the foraging behavior of squirrel monkeys in a seasonal habitat. — *Behav. Ecol. Sociobiol.* 23: 177-186.
- Boinski, S. & Fragaszy, D.M. (1989). The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedii*. — *Anim. Behav.* 37: 415-428.
- Boinski, S., Quatrone, R. & Swarts, H. (2000). Substrate and tool-use by brown capuchins in Suriname: ecological context and cognitive basis. — *Am. Anthropol.* 102: 741-761.
- Boinski, S., Sughrue, K., Selvaggi, L., Quatrone, R., Henry, M. & Cropp, S. (2002). An expanded test of the ecological model of primate social evolution: Competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). — *Behaviour* 139: 227-261.
- Boinski, S., Quatrone, R.P., Sughrue, K., Selvaggi, L., Henry, M., Stickler, C.M. & Rose, L.M. (2003). Do brown capuchins socially learn foraging skills? — In: *The biology of tradition: models and evidence* (Fragaszy, D.M. & Perry, S., eds). Cambridge University Press, Cambridge, p. 365-390.
- Boinski, S., Ehmke, E., Kauffman, L., Schet, S. & Vreedzaam, A. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*): II. Within-species and local variation. — *Behaviour* 142: 633-677.
- Britton, E.B. (1984). A pointer to a new hallucinogen of insect origin. — *J. Ethnopharmacol.* 12: 331-333.
- Clayton, D.A. (1978). Socially facilitated behavior. — *Q. Rev. Biol.* 53: 373-392.

- Clutton-Brock, T.H. (1977). Some aspects of intraspecific variation in feeding and ranging behavior in primates. — In: Primate ecology (Clutton-Brock, T.H., ed.). Academic Press, London, p. 539-556.
- Cohen, J. (1960). A coefficient of agreement for nominal scales. — *Educ. Psychol. Meas.* 20: 37-46.
- Corp, N. & Byrne, R.W. (2002a). Leaf processing by wild chimpanzees: physically defended leaves reveal complex manual skills. — *Ethology* 108: 673-696.
- Corp, N. & Byrne, R.W. (2002b). The ontogeny of manual skill in wild chimpanzees: evidence from feeding of the fruit *Saba florida*. — *Behaviour* 139: 137-168.
- Coussi-Korbel, S. & Fragaszy, D.M. (1995). On the relation between social dynamics and social learning. — *Anim. Behav.* 50: 1441-1453.
- Di Bitetti, M.S. & Janson, C.H. (2001). Reproductive socioecology of tufted capuchins (*Cebus apella nigrinus*) in Northeastern Argentina. — *Int. J. Primatol.* 22: 127-142.
- Dittus, W.P.J. (1977). The social regulation of population density and age-sex distribution in the toque monkey. — *Behaviour* 63: 281-322.
- Fisher, J. & Hinde, R.A. (1949). The opening of milk bottles by birds. — *Br. Birds* 42: 347-357.
- Fleagle, J.G. & Mittermeier, R.A. (1980). Locomotor behaviour, body size, and comparative ecology of seven Surinam monkeys. — *Am. J. Phys. Anthropol.* 52: 301-314.
- Fleagle, J.G. & Schaffler, M.B. (1982). Development and eruption of the mandibular cheek teeth in *Cebus albifrons*. — *Folia Primatol.* 38: 158-169.
- Forman, E., Minick, N. & Stone, C.A. (1993). Contexts for learning. Sociocultural dynamics in childrens' development. — Oxford University Press, Oxford.
- Fragaszy, D.M. (1986). Time budgets and foraging behavior in wedge-capped capuchins (*Cebus olivaceus*): age and sex differences. — In: Current perspectives in primate social dynamics (Taub, D.M. & King, F.A., eds). Van Nostrand, New York, NY, p. 159-174.
- Fragaszy, D.M. (1990). Early behavioral development in capuchins (*Cebus*). — *Folia Primatol.* 54: 119-128.
- Fragaszy, D.M. & Visalberghi, E. (1989). Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (*Cebus apella*). — *J. Comp. Psychol.* 103: 159-170.
- Fragaszy, D.M. & Adams-Curtis, L.E. (1991). Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). — *J. Comp. Psychol.* 105: 387-397.
- Fragaszy, D.M. & Boinski, S. (1995). Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). — *J. Comp. Psychol.* 109: 339-348.
- Fragaszy, D.M. & Visalberghi, E. (1996). Social learning in monkeys: primate "primacy" reconsidered. — In: Social learning in animals: the roots of culture (Heyes, C.M. & Galef Jr., B.G., eds). Academic Press, Toronto, p. 65-84.
- Fragaszy, D.M. & Adam-Curtis, L.E. (1997). Developmental changes in manipulation in tufted capuchins from birth through two years and their relation to foraging and weaning. — *J. Comp. Psychol.* 111: 201-211.
- Fragaszy, D.M. & Bard, K. (1997). Comparison of development and life history in *Pan* and *Cebus*. — *Int. J. Primatol.* 18: 683-701.
- Fragaszy, D.M. & Adams-Curtis, L.E. (1998). Growth and reproduction in captive tufted capuchins (*Cebus apella*). — *Am. J. Primatol.* 44: 197-203.

- Fragaszy, D.M. & Perry, S. (eds) (2003). Towards a biology of traditions. — In: The biology of traditions: models and evidence. Cambridge University Press, Cambridge, p. 1-32.
- Fragaszy, D.M., Visalberghi, E. & Robinson, J.G. (1990). Variability and adaptability in the genus *Cebus*. — *Folia Primatol.* 54: 114-118.
- Fragaszy, D.M., Feuerstein, J.M. & Mitra, D. (1997). Transfers of food from adults to infants in tufted capuchins. — *J. Comp. Psychol.* 111: 194-200.
- Fragaszy, D.M., Visalberghi, E. & Fedigan, L.M. (2004). The complete capuchin: the biology of the genus *Cebus*. — Cambridge University Press, Cambridge.
- Galef Jr., B.G. (1988). Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. — In: Social learning psychological and biological perspective (Zentall, T.R. & Galef Jr., B.G., eds). Lawrence-Erlbaum Associates, Hillsdale, NJ, p. 3-28.
- Galliari, C.A. (1985). Dental eruption in captive-born *Cebus apella*: from birth to 30 months old. — *Primates* 26: 506-510.
- Gibson, E.J. (2000). An ecological approach to perceptual learning and development. — Oxford University Press, Oxford.
- Gibson, K.R. (1987). Cognition, brain size and the extraction of embedded food resources. — In: Primate ontogeny, cognition and social behaviour (Else, J.G.F. & Lee, P.C., eds). Cambridge University Press, Cambridge, p. 93-103.
- Giraldeau, L.A. & Caraco, T. (2000). Social foraging theory. — Princeton University Press, Princeton, NJ.
- Giraldeau, L.A., Caraco, T. & Valone, T.J. (1994). Social foraging: individual learning and cultural transmission of innovations. — *Behav. Ecol.* 5: 35-43.
- Guinet, C. & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whales (*Orcinus orca*) calves at Crozet Archipelago. — *Can. J. Zool.* 73: 27-33.
- Gunst, N., Boinski, S. & Fragaszy, D.M. (2006). The ontogeny of foraging skills in wild brown capuchins (*Cebus apella*), Raleighvallen, Suriname. — *Am. J. Primatol.* 68 (Suppl. 1): 32-33 (Abstract).
- Gunst, N., Boinski, S. & Fragaszy, D.M. (2007). Studying how social context aids acquisition of foraging skills in wild brown capuchins (*Cebus apella*) in Suriname. — *Am. J. Primatol.* 69 (Suppl. 1): 76 (Abstract).
- Hanya, G. (2003). Age differences in food intake and dietary selection of wild Japanese macaques. — *Primates* 44: 333-339.
- Harrison, M.J.S. (1983). Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaesus*. — *Anim. Behav.* 31: 969-977.
- Hashimoto, C. (1991). Differences in feeding behavior between adult and juvenile Japanese macaques in Kinkazan Island, Japan. — In: Primatology today: Proceedings of the XIIIth Congress of the International Primatological Society Nagoya and Kyoto, 18-24 July 1990 (Ehara, A., Kimura, T., Takenaka, O. & Iwamoto, M., eds). Elsevier, Kyoto.
- Holekamp, K., Smale, L., Berg, R. & Cooper, S. (1997). Hunting rates and hunting success in the spotted hyenas (*Crocuta crocuta*). — *J. Zool.* 242: 1-15.
- Huffman, M.A. & Hirata, S. (2003). Biological and ecological foundations of primate behavioral tradition. — In: The biology of traditions: models and evidence (Fragaszy, D.M. & Perry, S., eds). Cambridge University Press, Cambridge, p. 267-296.
- Inoue-Nakamura, N. & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). — *J. Comp. Psychol.* 111: 159-173.



- Izawa, K. & Mizuno, A. (1977). Palm fruit cracking behavior of wild black-capped capuchins (*Cebus apella*). — *Primates* 18: 773-792.
- Janson, C.H. (1990). Ecological consequences of individual spatial choice in foraging groups of brown capuchins monkeys, *Cebus apella*. — *Anim. Behav.* 40: 922-934.
- Janson, C.H. & Boinski, S. (1992). Morphological and behavioral adaptations for foraging in generalist primates: the case of the Cebines. — *Am. J. Phys. Anthropol.* 88: 483-398.
- Janson, C.H. & van Schaik, C.P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. — In: *Juvenile primates: life history, development, and behavior* (Pereira, M.E. & Fairbanks, L.A., eds). Oxford University Press, Oxford, p. 57-74.
- Johnson, S.E. & Bock, J. (2004). Trade-offs in skill acquisition and time allocation among juvenile chacma baboons. — *Hum. Nat.* 15: 45-62.
- Jungers, W.L. & Fleagle, J.G. (1980). Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: a longitudinal and comparative study. — *Am. J. Phys. Anthropol.* 53: 471-478.
- Kaplan, H., Hill, K., Lancaster, J. & Hurtado, M. (2000). A theory of life history evolution: diet, intelligence, and longevity. — *Evol. Anthropol.* 9: 156-184.
- King, B.J. (1994). Primate infants as skilled information gatherers. — *Pre-Perinat. Psychol. J.* 8: 287-307.
- Krakauer, E.B. (2005). Development of aye-aye (*Daubentonia madagascariensis*) foraging skills: independent exploration and social learning. — PhD thesis in Biological Anthropology and Anatomy, Duke University, Durham, NC.
- Laland, K., Odling-Smee, J. & Feldman, M. (2000). Niche construction, biological evolution, and cultural change. — *Behav. Brain Sci.* 23: 131-146.
- Lonsdorf, E.V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii* of Gombe National Park, Tanzania. — *Anim. Behav.* 70: 673-683.
- Lonsdorf, E., Eberly, L. & Pusey, A. (2004). Sex differences in learning in chimpanzees. — *Nature* 428: 715.
- Mann, J. & Sargeant, B. (2003). Like mother, like calf: the ontogeny of foraging traditions in wild Indian ocean bottlenose dolphins (*Tursiops* sp.). — In: *The biology of traditions: models and evidence* (Fragaszy, D.M. & Perry, S., eds). Cambridge University Press, Cambridge, p. 236-266.
- Marchetti, K. & Price, T. (1989). Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. — *Biol. Rev.* 64: 51-70.
- Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. — In: *Chimpanzee culture* (Wrangham, R.W., McGrew, W., de Waal, F.B.M. & Heltne, P., eds). Harvard University Press, Cambridge, MA, p. 351-370.
- McGrew, W.C. (1979). Evolutionary implications of sex differences in chimpanzee predation and tool use. — In: *The great apes* (Hamburg, D.A. & McCown, E.R., eds). B. Cummings, London, p. 441-463.
- Mittermeier, R.A. & van Roosmalen, M.G.M. (1981). Preliminary observations on habitat utilization and diet in eight Surinam monkeys. — *Folia Primatol.* 36: 1-39.
- van Noordwijk, M.A. & van Schaik, C.P. (2005). Development of ecological competence in Sumatran orangutans. — *Am. J. Phys. Anthropol.* 127: 79-94.
- Odling-Smee, F.J. (1996). Niche construction, genetic evolution and cultural change. — *Behav. Proc.* 35: 195-205.

- Otoni, E.B., de Resende, B.D. & Izar, P. (2005). Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. — *Anim. Cogn.* 24: 215-219.
- Pandolfi, S.S., van Schaik, C.P. & Pusey, A.E. (2003). Sex differences in termite fishing among Gombe chimpanzees. — In: *Animal social complexity: intelligence, culture and individualized societies* (de Waal, F.B.M. & Tyack, P.L., eds). Harvard University Press, Cambridge, MA, p. 414-418.
- Parker, S. & Gibson, K. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in *Cebus* monkeys and great apes. — *J. Hum. Evol.* 6: 623-641.
- Pereira, M.E. & Fairbanks, L.A. (1993). *Juvenile primates: life history, development, and behavior*. — Oxford University Press, Oxford.
- Perry, S. & Ordoñez-Jiménez, J.C. (2006). The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics. — In: *Feeding ecology in apes and other primates* (Hohmann, G., Robbins, M. & Boesch, C., eds). Cambridge University Press, Cambridge, p. 203-234.
- Phillips, K.A., Grafton, B.W. & Haas, M.E. (2003). Tap-scanning for invertebrates by capuchins (*Cebus apella*). — *Folia Primatol.* 74: 162-164.
- Phillips, K.A., Shauver Goodchild, L.M., Haas, M.E., Ulyan, M.J. & Petro, S. (2004). Use of visual, acoustic, and olfactory information during embedded invertebrate foraging in brown capuchins (*Cebus apella*). — *J. Comp. Psychol.* 118: 200-205.
- Post, D.G., Hausfater, G. & McCuskey, S.A. (1980). Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. — *Folia Primatol.* 34: 170-195.
- Reichart, H. (1993). *Management plan for Raleighvallen Nature Preserve, 1993–1998*. — Suriname Nature Conservation Foundation, Paramaribo, Suriname.
- Rhine, R.J. & Westlund, B.J. (1978). The nature of a primary feeding habit in different age-sex classes on yellow baboons (*Papio cynocephalus*). — *Folia Primatol.* 30: 64-79.
- Richard, A. (1985). *Primates in nature*. — Freeman, New York, NY.
- Rose, L.M. (1994). Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). — *Int. J. Primatol.* 15: 95-114.
- Ross, C. & Jones, K. (1999). Socioecology and the evolution of primate reproductive rates. — In: *Comparative primate socioecology* (Lee, P., ed.). Cambridge University Press, Cambridge, p. 73-110.
- de Ruiter, J.R. (1986). The influence of group size on predator scanning and foraging behaviour of wedged-capped capuchin monkeys (*Cebus olivaceus*). — *Behaviour* 98: 240-258.
- Russon, A.E. (2003). Developmental perspectives on great ape traditions. — In: *The biology of tradition: models and evidence* (Fragaszy, D.M. & Perry, S., eds). Cambridge University Press, Cambridge, p. 329-364.
- Russon, A.E. (2006). Acquisition of complex foraging skills in juvenile and adolescent orangutans (*Pongo pygmaeus*): developmental influences. — *Aquat. Mamm.* 32: 500-510.
- van Schaik, C.P., Barrickman, N., Bastian, M.L., Krakauer, E.B. & van Noordwijk, M.A. (2006). Primate life histories and the role of brains. — In: *The evolution of human life history* (Hawkes, K. & Paine, R.R., eds). School of American Research Press, Santa Fe, NM, p. 127-154.
- Sherry, D. & Galef, B.G. (1984). Cultural transmission without imitation: milk bottle opening by birds. — *Anim. Behav.* 32: 937-938.

- Sherry, D. & Galef, B.G. (1990). Social learning without imitation: more about milk bottle opening by birds. — *Anim. Behav.* 40: 987-989.
- Strum, S.C. (1991). Weight and age in wild olive baboons. — *Am. J. Primatol.* 25: 219-237.
- Swindler, D.R. (2002). Primate dentition: an introduction to the teeth of non-human primates. — Cambridge University Press, Cambridge.
- Tarnaud, L. (2004). Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte. — *Int. J. Primatol.* 25: 803-824.
- Terkel, J. (1996). Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). — In: Social learning in animals: the roots of culture (Heyes, C.M. & Galef Jr., B.G., eds). Academic Press, San Diego, CA, p. 267-286.
- Visalberghi, E. & Neel, C. (2003). Tufted capuchins (*Cebus apella*) use weight and sound to choose between full and empty nuts. — *Ecol. Psychol.* 15: 215-228.
- Wunderle Jr., J. (1991). Age-specific foraging proficiency in birds. — In: Current ornithology (Power, D., ed.). Plenum Press, New York, NY, p. 273-324.
- Watts, D. (1985). Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla beringei*). — *Am. J. Primatol.* 8: 1-10.
- Whitehead, J.M. (1986). Development of feeding selectivity in mantled howling monkeys, *Alouatta palliata*. — In: Primate ontogeny, cognition, and social behaviour (Else, J.G. & Lee, P.C., eds). Cambridge University Press, Cambridge, p. 105-117.
- Wright, B.W. (2005). Craniodental biomechanics and dietary toughness in the genus *Cebus*. — *J. Hum. Evol.* 48: 473-492.
-

Copyright of Behaviour is the property of VSP International Science Publishers and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.