Development of Skilled Detection and Extraction of Embedded Prey by Wild Brown Capuchin Monkeys (*Cebus apella apella*)

Noëlle Gunst
University of Georgia

Sue Boinski
University of Florida

Dorothy M. Fragaszy
University of Georgia

Brown capuchin monkeys (*Cebus apella apella*) in Suriname forage on larvae enclosed within healthy bamboo stalks. We applied the searching versus handling dichotomy of optimal foraging models to highlight developmental processes contributing to foraging on embedded prey. Larvae acquisition begins with search; selecting an appropriate stalk and locating the embedded larvae; followed by handling, ripping the stalk open, and extracting the larvae. 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, aged around 6. Selecting appropriate foraging substrates, requiring accurate assessment of the physical properties of bamboo stalks, gradually increased with age and experience. We showed that both components of searching required extended practice beyond that required to master the handling components. We conclude that the developmental sequence of skill acquisition goes counter to the preceding logical sequence of foraging process and suggest that searching components present greater challenges than handling components in extractive foraging. Specifying the searching components of foraging more precisely will enhance understanding of species variation in the developmental schedule of foraging skills.

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

Optimal foraging theory postulates that in diet choices, foraging location, and foraging time, animal decisions are made to maximize the net rate of energy gain (Stephens & Krebs, 1986). The food preferences of foragers are assumed to derive from a cost–benefit ratio of foraging efficiency. According to optimal foraging theory, foragers encounter an array of prey types in a random fashion and rank them along a continuum of energy return rate, defined as a food item's energy content relative to the amount of time spent foraging for this item (Charnov, 1976; Hill & Kaplan, 1999). The prey type that yields the highest energy return rate should always be pursued.

Time spent foraging is usually partitioned into two separate components: searching time and handling time. Searching time is the time devoted to looking for food between encounters of items of the same food type. Handling time is the amount of time required to handle the food item between the time it is encountered and the time it is consumed. Handling encompasses all possible actions between the initial decision to harvest a particular food item and its ingestion, including capture, killing, processing, fighting off competitors, chewing, and swallowing. This process of time allocation involves opportunity costs in the sense that time spent handling any item means that the same unit of time is unavailable for searching for other items. The diet breadth model (or prey choice model), a class of optimal foraging theory, corresponds to a scenario trading off searching time versus handling time (Charnov, 1976; MacArthur & Pianka, 1966).

If searching time is a function of experience and knowledge, and handling time is more dependent on body size and strength, then age should be positively related to foraging efficiency. Indeed, unbalanced foraging time allocation and inadequate foraging skills are thought to be major causes of juvenile mortality (Goss-Custard, Dunbar, & Aldrich-Blake, 1972). Foraging efficiently may be more difficult for a juvenile than for an adult because the juvenile has less experience and is less skilled in locating foods or because its small body size reduces access to particular food items (Janson & van Schaik, 1993). The importance of the juvenile period for the development of skills related to adult competency has long been reported in nonhuman primates (Fairbanks, 1993). Extended juvenility would allow individuals more time to develop and learn effective foraging behaviors (Pereira & Fairbanks, 1993).

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 (King, 1986; Parker & Gibson, 1979). 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 (K. R. Gibson, 1987).

Extractive foraging is common in omnivorous animals that rely on hidden foods. These food-processing techniques are widespread among birds and mammals. Kea birds (*Nestor notabilis*) dig in the ground for roots and turn stones over to get access to insect larvae (Huber & Gajdon, 2006). Sea otters (*Enhydra lutris*) are well known for bashing mollusks against a stone placed on their chests (Ebert, 1968). Among nonhuman primates, yellow baboons (*Papio cynocephalus*) include a wide variety of hidden foods in their diet, such as underground corms and insects from under bark (S. Altmann & Altmann, 1970). Chimpanzees (*Pan troglodytes*) crack open hard nuts using rock hammers (Boesch & Boesch, 1983) and extract termites and ants by "fishing" for them with twigs or grass probes (McGrew, 1992).

Wild brown capuchins in Raleighvallen, Suriname, forage on larvae embedded in healthy (nonrotten) bamboo stalks. First, they have to identify an appropriate stalk of bamboo and the segment of the stalk to open. If they mismanage these components of the task, opening the stalk is futile. Second, they have to locate embedded larvae within a stalk by using auditory, olfactory, tactile, and visual cues. Third, 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.

A detection technique typically used by capuchins to locate embedded prey 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 (Gunst, Boinski, & Fragaszy, 2008; Izawa, 1978; Janson & Boinski, 1992; Phillips, Grafton, & Haas, 2003; Visalberghi & Neel, 2003). Some authors have mentioned sniffing, as well as manual and visual inspection of bamboo stalks, as potential detection patterns (Gunst et al., 2008; Izawa, 1978; Phillips, Shauver Goodchild, Haas, Ulyan, & Petro, 2004). 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*). Izawa noticed that the internodes containing a frog were physically very different from others because 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 (N. Gunst, personal observation). Detecting embedded larvae may be more difficult for the capuchins than detecting embedded frogs because the former leave fewer physical cues on the bamboo substrate than the latter.

If the handling component constrains proficiency at obtaining larvae, then monkeys with equivalent size and dental equipment would be equally proficient in this task. However, this is not the case. By focusing on the effects of physical maturation on the acquisition of foraging competence in wild brown capuchins, Gunst et al. (2008) reported that although older juveniles and subadults have similar dentitions and body weights, the former were still significantly less proficient than the latter in obtaining 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. These aspects of larvae foraging may be mastered in a different time frame than opening the stalks. In particular, they may be mastered later than the handling components. However, Gunst et al. considered foraging efficiency as a whole, with no distinction between searching and handling components.

This study is a complementary and necessary extension of the latter research. In this article, we address how young monkeys become skilled at selecting appropriate stalks and how they search these stalks to determine whether and where to rip them open and extract the larvae. 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 (E. J. Gibson & Pick, 2003; Lockman, 2000). In accord with this framework, we hypothesize that young capuchins become proficient at locating larvae through 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 capuchins 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). None 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, Ottoni, & Fragaszy, 2008). Therefore, we predict that (a) the behavioral patterns that in adults are associated with effective detection exist in the repertoire of immature capuchins from the outset, (b) frequency of performing these behaviors will increase from infancy to adulthood (i.e., by around age 6), and (c) 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 in infants because 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 capuchins of equal size at opening stalks, but, like younger individuals, they will produce inappropriate behaviors proportionally more frequently than proficient resident adults.

Method

Study Site

Observations took place at the Raleighvallen site within the Central Suriname Nature Preserve, which encompasses 1.6 million ha of primary tropical forest and protects the upper watershed of the Coppename River. Brown capuchins (*Cebus apella apella*) at

Raleighvallen feed on a vast array of food items, including plants, fruits, flowers, invertebrates, and small vertebrates (Boinski, Quatrone, & Swarts, 2000). Among them, we focused 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*). All bamboo patches in the site were impenetrable by human observers because of the homogeneous composition of an average 8,000 bamboo stalks per hectare (Boinski, S., 2008). The study troop allocated the majority of time in bamboo habitats to the largest contiguous patch across which three trails (about 2 m wide and a cumulative length of 475 m) were cut to allow observers to follow the monkeys.

In bamboo patches, capuchins feed on bamboo shoots, stalk pith, and larvae hidden inside internodes of bamboo stalks. The larvae (*Myelobia sp.*, *Pyralidae*; Britton, 1984), which attain a maximum size of 10 cm and 7 g, are prototypical "encased" foods 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 widely distributed throughout bamboo patches, in the same way as surface insects, and can be considered a dispersed food source for capuchins (Gunst, unpublished data).

Study Group

The *Cebus apella apella* study group (Troop A) had been studied intermittently beginning in 1998 and continuously since 2000. During our 8 months of observation, a total of 31 identified individuals were sampled, including all age and sex classes. On the basis of the age classes reported in Gunst et al. (2008), the group contained 10 adults (ages 7 and older), including two immigrant adult males that had lived within the group for fewer than 6 months, six subadults (between 5 and 7 years old), four older juveniles (between 3 and 5 years old), six younger juveniles (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 a.m. and 5:00 p.m. When the study group was ranging within the bamboo patch, Noëlle Gunst collected focal-capuchin samples (J. Altmann, 1974) with continuous video recording using a digital video camera. The duration of focal samples varied from 1 to 15 min, depending on the visibility conditions. 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, to ensure that all individuals had equal sampling opportunities every month. The monkeys could be seen well up to 3 m into the bamboo from the edge of the trail.

Data Coding

Videotaped data were scored using The Observer (Version 5.0, Noldus Information Technology, Leesburg, VA). The behaviors recorded were divided into nonforaging (e.g., resting, locomoting, grooming, and playing) and foraging behaviors, which in turn were divided into 10 larvae-related foraging behaviors (see Table 1) and foraging behaviors directed to other foods. Behaviors were categorized as events when they were of short duration (i.e., approximated as points in time) and their frequency of occurrence was of interest, whereas they were categorized as states when they lasted longer 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, and 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 in diameter; medium stalk, 2–4 cm; and large stalk, more than 4 cm), condition (rotten vs. healthy stalks), and integrity (intact vs. already-ripped stalks). We investigated which types of bamboo stalk were more likely to contain larvae by cutting open each internode of all stalks found in five 5-m^2 quadrates 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 and two other bamboo patches present in the study area to avoid depleting the supply of larvae.

Data Analysis

We analyzed a total of 45.5 hr of focal data, with a minimum of 0.6 hr and a maximum of 3.1 hr per capuchin ($M \pm SD$: infants, 1.2 ± 0.5; younger juveniles, 1.7 ± 0.5; older juveniles, 1.8 ± 0.3; subadults, 1.6 ± 0.9; and adults, 1.3 ± 0.4). Bearing in mind that our small sample size may have influenced our results, we found medium and large effect sizes, and their confidence intervals did not include zero (see Table 2). We used The Observer to calculate

Table 1

Larvae-Related Foraging States and Events Scored in This Study

Behavior	Definition	Type
Visual inspect	Visual scanning of 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 inserting 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 inhaling	Event
Bite	Quick puncture into a bamboo stalk with canine	Event

the durations and frequencies of the larvae-related foraging behaviors directed to the different types of bamboo substrates. When foraging on larvae, we categorized visual inspect, manual inspect, tap scan, bite, and sniff as detection patterns, whereas we referred to rip apart 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 the number of occurrences of behavior per hour spent foraging. Behavioral durations were expressed as the percentage of time performing a behavior over the total time devoted to foraging. We used data presented in Gunst et al. (2008) to evaluate individual foraging efficiency for larvae, 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. We defined the variable interest in already-ripped bamboo stalks 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.

We used general linear models to test the effect of age on the duration and frequency of different foraging behaviors. We used the least significant differences 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 because these six behaviors represent a large proportion of all the behaviors performed during foraging for larvae. We used SPSS 12.0 (SPSS, Inc., Chicago, IL) for all statistics and set the significance level at an alpha of .05.

Results

Behaviors Contributing to Foraging Efficiency for Larvae

When observed in the bamboo patch, capuchins devoted a total of 40.2 hr to foraging activities, which represents 88.4% of the time spent collecting data in this patch. Table 2 shows a statistically significant effect of age on the percentage of time devoted to foraging on embedded larvae. The percentage of time performing larvae-related foraging behaviors (i.e., detection and extraction patterns) consistently increased with age (infants, 9.5% ± 6.6; younger juveniles, 44.1 ± 21.7; older juveniles, 71.6 ± 6.2; subadults, 75.7 ± 8.1; and adults, 83.0 ± 8.0).

Model 1 shows that among foraging states, visual inspect is a sufficient detection technique, whereas manual inspect and rip

apart are insufficient techniques in the discovery of larvae (see Table 3). Model 2 shows that among foraging events, tap scan is a sufficient detection technique, whereas bite and sniff are insufficient detection techniques (see Table 3).

Age Differences in Detection and Extractive Behaviors When Foraging for Larvae

We found significant effects of age on the percentage of time spent visually and manually inspecting bamboo when foraging in the bamboo patch (see Table 2). Figure 1 shows that the percentage of time devoted to visual inspect by infants was negligible (0.4 ± 1.0%) compared with that of the other age classes (from younger juveniles, 23.1% ± 11.2, to adults, 56.0 ± 13.5). By contrast, manual inspect consistently decreased with age from infants to adults. The frequencies of tap scan and sniff differed significantly with age, whereas bite did not (see Table 2). Tap scan frequencies tended to increase with age (see Figure 1) 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 ($p < .01$). 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).

Regarding extractive behaviors, we found a significant age effect on the percentage of time devoted to ripping apart healthy bamboo stalks (see Table 2). Figure 2 shows a consistent increase in the mean duration of rip apart with age from infants (4.2% ± 3.1) to subadults (30.6 ± 12.3).

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 vs. hard bamboo stalks), thickness (large diameter vs. smaller diameter), condition (healthy vs. rotten stalks), and integrity (solid vs. already-ripped stalks). There was a significant age effect on the percentage of time spent ripping apart bamboo pith, with higher values found in infants than in all the older age classes (see Table 2).

We found a significant age effect on the overall duration of ripping apart large stalks, with lower values in infants and younger juveniles than in subadults and adults (see Table 2). By contrast, we found no significant differences between age classes in the time spent ripping apart medium stalks and thin stalks. Rip apart was present in the behavioral repertoire of infant capuchins, even though infants rarely exhibited this behavior toward tougher substrates (i.e., healthy large stalks; Figure 3a).

It is interesting that 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 toward large stalks (see Table 2). The frequency of tap scan and sniff consistently increased with age from infants to adults, and post hoc analyses revealed that infants and younger juveniles performed significantly less tap scan and sniff of large stalks than did subadults and adults. In contrast, we found no significant differ-

Table 2
Effect of Age in Different Larvae-Related Foraging Variables

Dependent variable	$F_{(4, 26)}$	p	η_p^2	95% confidence interval for the difference					
				I–J1		I–J2		I–S	
				LB	UB	LB	UB	LB	UB
Time foraging for larvae	39.47	<.001	.859	−49.1	−20.0	−78.2	−46.0	−80.7	−51.6
Visual inspect	22.92	<.001	.779	−22.3	−5.0	−38.7	−19.6	−33.8	−16.6
Manual inspect	5.11	.004	.440	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Tap scan	4.42	.007	.405	−61.7	−11.2	−21.9	−4.7	−76.6	−23.0
Sniff	5.60	.002	.463	−20.4	−0.3	−26.0	−3.7	−32.4	−12.2
Bite	1.87	.146	.224	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Rip apart healthy stalks	4.03	.011	.383	*ns*	*ns*	*ns*	*ns*	−24.9	−6.8
Rip apart pith	4.83	.005	.426	1.2	5.2	1.4	5.8	1.7	5.8
Rip apart large stalks	3.60	.018	.356	*ns*	*ns*	*ns*	*ns*	−22.8	−5.1
Rip apart medium stalks	1.28	.303	.165	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Rip apart thin stalks	0.75	.556	.104	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Tap scan or sniff large stalks	6.21	.001	.489	*ns*	*ns*	*ns*	*ns*	−51.6	−13.7
Tap scan or sniff medium stalks	1.68	.185	.205	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Tap scan or sniff thin stalks	1.86	.147	.223	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Manual inspect or rip apart rotten stalks	4.75	.005	.422	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Manual inspect or rip apart ripped stalks	18.88	.001	.744	*ns*	*ns*	2.6	16.2	9.5	21.8
Tap scan or sniff rotten stalks	4.07	.011	.385	*ns*	*ns*	−1.6	−0.3	*ns*	*ns*

Note. General linear model. $N = 31$; Effect sizes were measured by using partial eta-square and 95% confidence interval. For the differences between age, classes were provided only for statistically significant post hoc comparisons. I = infant; J1 = younger juvenile; J2 = older juvenile; S = subadult; A = adult; LB = lower bound; UB = upper bound.

ences between age classes in the frequencies of tap scan and sniff directed toward medium stalks or thin stalks (see Table 2).

With regard to particular bamboo stalks where no larvae can be found, there were significant age effects on the interest in rotten stalks (see Table 2). Young individuals spent more time performing foraging behaviors toward 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; Figure 3b; see Figure 2 for already-ripped stalks).

Acquisition and Disappearance of Foraging Behaviors During Ontogeny

As predicted, sufficient detection techniques (visual inspect and tap scan) became more prevalent with age (Figures 4a and 4b). 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 1 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%). Bite declined in adults (infants, 12.98 ± 4.85%; younger juveniles, 11.46 ± 6.80%; older juveniles, 9.03 ± 3.77%; subadults, 10.89 ± 10.11%; and adults, 4.65 ± 5.31%). Sniff increased from infants to subadults but decreased in adults (Figure 4b).

Extractive behavioral patterns (rip apart) directed toward appropriate substrates, that is, large healthy stalks, were virtually absent in infants and became 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 older 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 or groups were not known with data from all other individuals of the same age class. The average foraging efficiency of these two subjects (3.7 ± 0.5 larvae found per hour foraging) was the lowest of all adults (6.2 ± 1.6) and was also lower than that of all subadults (6.3 ± 1.7) but was exactly the same as that of the older juveniles (3.7 ± 1.7). As for 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). 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). Our small data set did not allow us to present analyses on the selection of stalks by these two males.

Discussion

We studied the development of proficient extraction by young brown capuchins 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 found

95% confidence interval for the difference											
I–A		J1–J2		J1–S		J1–A		J2–S		J2–A	
LB	UB	LB	UB	LB	UB	LB	UB	LB	UB	LB	UB
−86.6	−60.3	−43.1	−12.1	−45.5	−17.7	−51.3	−26.5	ns	ns	ns	ns
−41.1	−25.6	−24.7	−6.4	−19.8	−3.4	−27.1	−12.4	ns	ns	ns	ns
−4.4	−1.2	ns	ns	ns	ns	−4.2	−1.1	ns	ns	−4.0	−0.5
ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
−21.4	−5.0	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
1.6	5.3	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
−19.2	−3.15	ns	ns	−18.4	−1.5	ns	ns	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
−52.2	−17.9	ns	ns	−41.4	−5.3	−41.9	−9.5	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
ns	ns	0.4	3.9	1.2	4.3	1.3	4.1	ns	ns	ns	ns
10.4	21.6	4.7	17.8	11.6	23.4	12.5	23.1	ns	ns	ns	ns
ns	ns	ns	ns	ns	ns	ns	ns	0.4	1.6	0.4	1.5

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, are mastered more slowly. Effective searching behaviors directed to appropriate stalks are not fully mastered before age 6. The few effective detection behaviors by immigrant adults 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 on extended practice even for individuals with full physical capabilities.

Ontogeny of Substrate Selection

Extracting larvae from bamboo stalks is time and energy consuming. 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, is rotten, or has already been processed by a previous forager. By learning how to select appropriate substrates (large and medium healthy internodes) and then by performing adequate detection techniques, growing capuchins gradually optimize their extractive foraging strategies.

Table 3
Behaviors Contributing to Foraging Efficiency for Larvae by Using Two Stepwise Linear Regression Models

Model and predictor variable	R^2	df_1	df_2	F	p	Effect size	95% confidence interval	
							Lower bound	Upper bound
1a								
Visual inspect	.449	1	29	25.43	<.001		0.207	0.691
1b								
Visual inspect								
Rip apart	.624	1	28	14.47	.001	0.465	0.435	0.813
2a								
Tap scan	.275	1	29	12.35	.001		0.025	0.524
2b								
Tap scan								
Bite	.364	1	28	5.06	.033	0.140	0.120	0.607
2c								
Tap scan								
Bite								
Sniff	.542	1	27	11.91	.002	0.389	0.335	0.749

Note. Model 1, on foraging states; Model 2, on foraging events. Effect size attributable to the addition of a new predictor.
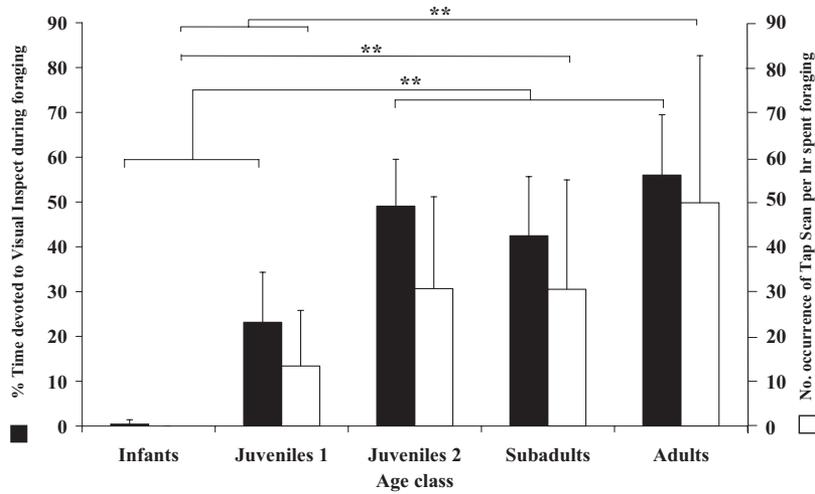
Figure 1.   Percentage of time devoted to visual inspect during foraging and frequency of tap scan (number of occurrences of tap scan per hour spent foraging) for each age class ($M \pm SD$). ** $p < .01$.

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 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 toward large stalks, where most larvae can be found, consistently increased from infants to adults, with a significant difference between infants and younger juveniles on 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 fewer foraging behaviors toward particular foraging substrates where no larvae can be found because of their health (rotten stalks) or integrity (already-ripped stalks) than did younger individuals.

The limited physical capabilities of infants and younger juveniles may explain why they direct more foraging behaviors toward thin or rotten stalks that they can break easily and already-opened stalks rather than to large and healthy stalks. Working on thin, rotten, and already-opened stalks allows them to practice opening bamboo, even though it does not result in gaining a larva. Practicing at sites opened by skilled conspecifics may improve their ripping skills and may help them develop a preference for appropriate substrates (large and healthy stalks).

Importance of Specific Detection Techniques in Foraging Efficiency

We found that visually inspecting and tapping bamboo stalks were the most adequate techniques to detect larvae. Tap scanning
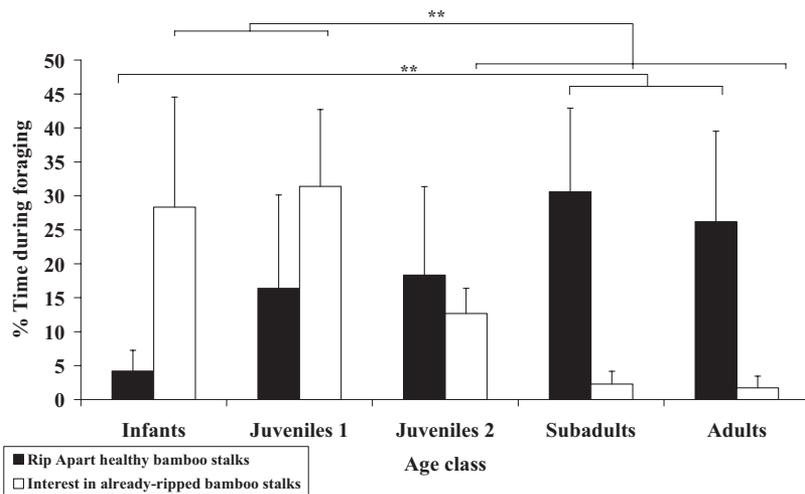

Figure 2. $M \pm SD$ percentage of foraging time devoted to (a) ripping apart healthy bamboo stalks and (b) showing interest in already-ripped bamboo stalks, for each age class. ** $p < .01$.
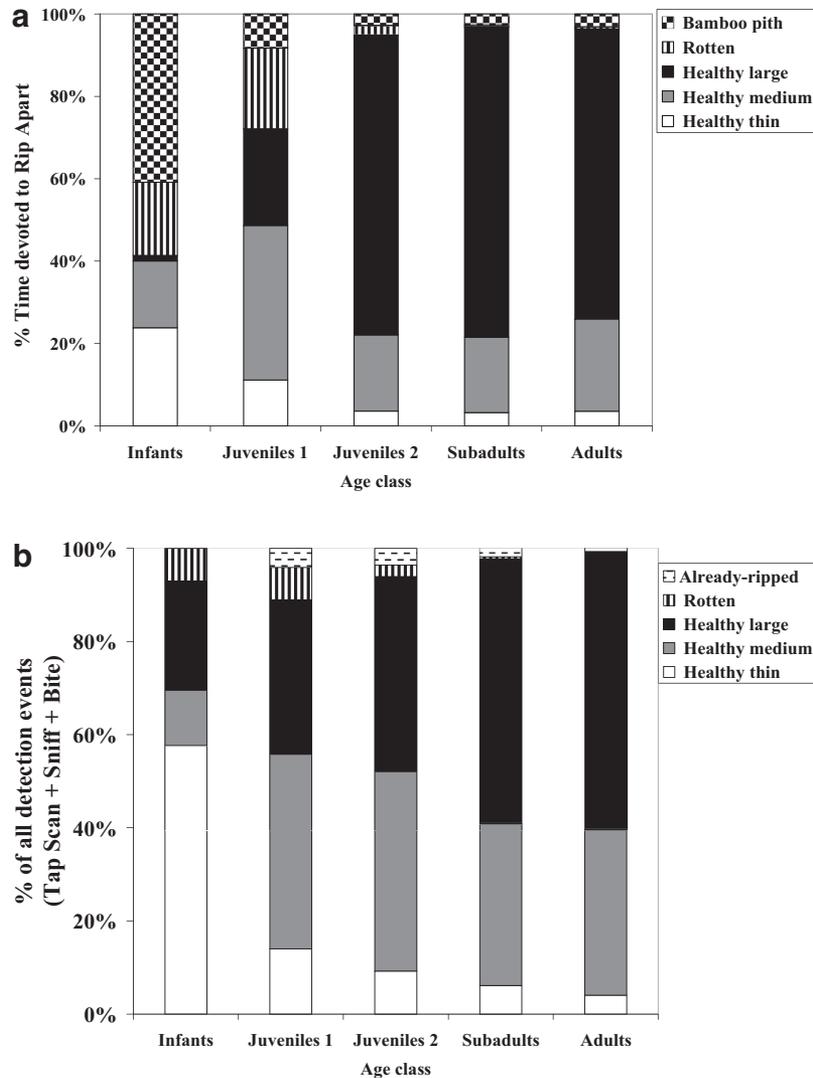
Figure 3. Percentage of time devoted to rip apart (a) and percentage of all detection events, namely tap scan, sniff, and bite pooled together (b), directed toward different types of bamboo stalks according to hardness, thickness, condition, and integrity and for each age class.

has been described 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; Phillips et al., 2003; Visalberghi & Neel, 2003). The challenge in the foraging task we studied is not to learn to tap (the monkeys do this anyway) but to learn what to notice while tapping and to tap in the right places. Close visual inspection of bamboo stalks (and 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, whereas tap scanning could serve to confirm or refine the search. Although sniffing by itself adds little to foraging efficiency, immature capuchins may apply this behavior as a complementary technique by sniffing stalks both before and after tapping and ripping.

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 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 this study, most of them are inefficient for obtaining larvae because they are directed to inappropriate substrates (bamboo stalks unlikely to contain larvae), because the action does not provide relevant information on the presence of encased food (bite and
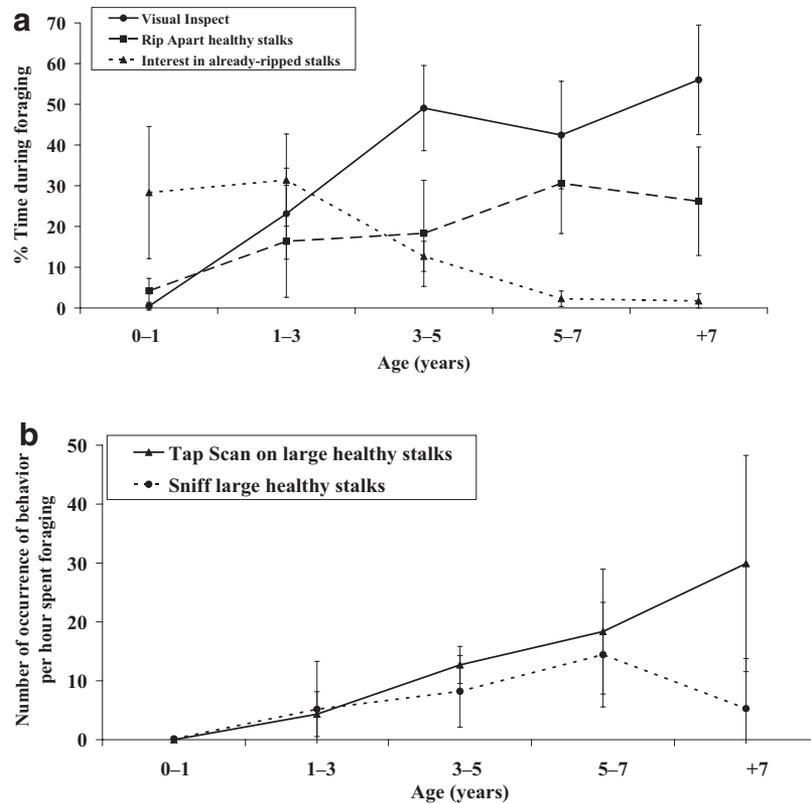
Figure 4. a: Timeline of appearance of visual inspect and rip apart behaviors, and disappearance of interest in already-ripped stalks, expressed as percentage of time during foraging. b: Timeline of appearance of tap scan and sniff behaviors, expressed as frequency (total number of occurrence of behavior per hour spent foraging).

manual inspect), or because the sequence of actions is not correctly ordered (ripping a stalk apart with teeth before performing the detection patterns). As individuals practice searching for larvae, such "errors" are gradually reduced and effective species-typical exploratory actions (those guiding detection and extraction) increase (cf. Gibson & Pick, 2003).

Ineffective actions and sequences diminish as individuals gain experience at selecting the most appropriate foraging substrates (large and intact bamboo stalks). Practicing 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 immature and two immigrant adult male capuchins 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 immature capuchins. Immigrant adults were similar to other adults with regards to the strength-dependent foraging component (ripping stalks apart), but their level of detection and their use of detection techniques were

characteristic of older juveniles. They seemed to have less experience in this extractive foraging task.

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. Our results showed that infants did not yet visually inspect stalks or tap on them. However, they already performed rudimentary extractive patterns: When biting into bamboo stalks, infant capuchins tear much thinner bamboo stalk fragments than older individuals (Noëlle Gunst, personal observation; see also infant aye-ayes [Krakauer, 2005]). This suggests that dental equipment and strength limit successful extraction. Overall, reaching adult-level proficiency at obtaining embedded larvae may not only be constrained by physical maturation 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 is likely to benefit from prolonged individual practice supporting perceptual learning. In a previous study, we showed that conspecifics' foraging arti-

facts (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 already-ripped stalks cannot lead to success by obtaining direct rewards (larvae), they prompt immature capuchins to practice larvae-related foraging behaviors. Persevering practice may turn initially unpolished attempts into finely tuned and skilled movements (Elliot, 1999).

Practice with already-ripped large stalks may also influence choice of subsequent stalks through social enhancement. However, as long as enhancement narrows immature capuchins' 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 large segments that are 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, Boinski, & Fragaszy, 2007). By doing so, immature capuchins can learn to associate large-diameter stalks with the higher probability of finding larvae. Therefore, practice with particular foraging artifacts (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 existing notions of social supports for learning (cf. Fragaszy & Visalberghi, 1996).

Trade-Offs in Foraging Skill Acquisition

Optimal foraging theory assumes that foragers can assess the quality and availability of their foods and derive their foraging decisions from a cost–benefit calculus of energy return rate. For capuchins foraging on embedded larvae in a bamboo patch, the foraging efforts are compensated by peak energy return rates from high-quality food items rich in animal proteins and fats. This may account for the monkeys' strong preference for such hidden prey over easy-to-access but lower quality plant foods (e.g., bamboo shoots; cf. Gunst et al., 2008).

According to the diet breadth model, there is an immediate trade-off between the searching and handling components of foraging (Charnov, 1976; MacArthur & Pianka, 1966). Longer searching time, greater handling efforts, or both may be costly in terms of foraging time allocation but may also allow more nutrients to be extracted from a captured prey item. Our findings suggest that for capuchins foraging on encased foods, this trade-off should be considered over longer periods of time and particularly through the developmental perspective. In young capuchins, devoting time to searching for hidden prey has a short-term cost resulting from their low level of competence in this task. However, there is a long-term payoff through becoming more experienced and efficient at locating this food. Throughout the juvenile period, time devoted to skill acquisition is a trade-off with time spent on food consumption.

Because of their small size and lack of skills, infant capuchins spend most of their time foraging on easy, low-energy foods such as bamboo shoots, whereas bigger and more experienced individuals tend to focus more and more on learning extractive foraging techniques to obtain higher quality foods (Gunst et al., 2008, and this study). Although searching components can present greater challenges than handling components in this foraging task, large gains are made from investment in learning how to search effi-

ciently for hidden prey. Despite the immediate risks incurred by young individuals allocating time to unsuccessful activities (cf. Clutton-Brock, 1977), the foraging skills acquired during the juvenile period are beneficial in the long term. More generally, the benefits of learning foraging skills continue to influence foraging time allocation over a life course. The timeline of developing adult-level foraging efficiency in relatively long-lived monkeys, such as capuchins, follows that of apes and humans, in that it requires a long investment in hard-to-process foods during a lengthened juvenility and whose payoff may be an increased life span (cf. Kaplan, Hill, Lancaster, & Hurtado, 2000).

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