

## Learning How to Forage: Socially Biased Individual Learning and “Niche Construction” in Wild Capuchin Monkeys

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THIS CHAPTER aims to provide a way to think about how naïve monkeys become proficient foragers. In general, young primates (at the time of weaning and for some period thereafter) are less effective foragers than adults of their species. Primates have complex diets, live highly social lives, and spend months to years as juveniles. These characteristics, taken together, suggest that social partners may influence how young monkeys learn about food and feeding. Much research has addressed psychological processes occurring in the short term and within the learner that allow an individual to match another's behavior (such as imitation, emulation, or social facilitation; for review of these processes in relation to foraging, see Rapaport and Brown 2008, and also this volume). Here, we adopt an ethologically grounded approach to social learning, focusing on how young individuals acquire foraging skills in natural contexts. One of our major tasks is to explain why, in the case of difficult foraging tasks, young animals engage in patently ineffective foraging behaviors over some period of time while they are acquiring the skill. During most of this extended period, their efforts are not reinforced in the usual manner (by obtaining food). Thus, other conditions must support persistent practice. We argue that other monkeys, through their own foraging, construct a niche for young monkeys (*sensu* Odling-Smee, Laland, and Feldman 2003; see also Laland et al. 2000) by providing young monkeys with the opportunity and/or the motivation to practice foraging for those foods that are difficult to find or difficult to obtain.

Niche construction refers to the consequences of individuals' actions that in effect define or partially create their own living environments.

Termites provide a familiar example of niche construction: termites build mounds, which multiple successive generations inhabit. The mound provides a particular environment (temperature, humidity, etc.) that termites require. Through building and maintaining the mound, the behavior of individuals impacts the lives of others at that time and later. Niche construction modifies sources of natural selection and thus, in principle, affects the evolutionary process. For this reason, niche construction theory is one component of an extended theory of evolution (see <http://www.nicheconstruction.com>). Social influences on learning are a form of niche construction, and thus they carry evolutionary as well as developmental importance.

Wild capuchins (New World monkeys in the genus *Cebus*) provide cogent examples of how social learning about foraging can be examined in this ethological way. Capuchins are generalists, meaning they live in a wide variety of habitats and thus eat a wide variety of foods. The diet of capuchin monkeys in one area may have little in common with the diet of monkeys of the same species living in another area, and both populations can exploit hundreds of species of plants and animal foods (Fragaszy et al. 2004, appendix I). They are omnivorous, eating insects, mollusks, vertebrates, fruits, seeds, flowers, roots, leaf buds, fungi, tree gum, underground plant storage organs such as tubers, etc. These foods may contain toxic substances, be hidden from view, be encapsulated in a tough outer covering of some sort, and/or need specific processing techniques (for review see Fragaszy et al. 2004), and these features vary locally. The tufted species of capuchins (*C. apella*, *C. libidinosus*, *C. nigrinus*, species living in the southern and eastern part of the range of the genus) in particular include tough foods in their diet (Wright et al. 2009). Learning about food and feeding from group members is thought to be particularly relevant in generalist species (Galef 1993).

Young monkeys have lesser physical resources for foraging than do adults, with respect to teeth, bite force, and manual strength. During and after weaning, young capuchin monkeys are much smaller than adults, and most of their permanent teeth have not yet erupted. They are also less experienced at foraging. Thus they seem to be ill-equipped to forage on the same foods as adults. The period after weaning is a dangerous one for young capuchins, and they grow slowly, suggesting that acquiring sufficient food is indeed challenging for them (Janson and van Schaik 1993). Thus young monkeys face strong challenges to find and to process many foods common in their diet.

Yet capuchins have certain physical, behavioral, and social resources that allow them to navigate this dangerous period (reviewed in Fragaszy

et al. 2004). Capuchins exhibit well-developed manual dexterity (superior to other New World monkeys) and a strong propensity to explore objects and surfaces in diverse ways, which in some settings is expressed in spontaneous tool use. They have proportionally large brains for their body size, suggesting well-developed perceptual and cognitive processes supporting learning. They are weaned gradually over a period of many months and spend several years as juveniles, providing ample time for learning. Finally, and the feature that is most relevant to the issue of social supports for learning, capuchins live in cohesive social groups, and members of a group exhibit a high degree of tolerance toward each other, especially toward infant and juveniles, both in the wild (Izawa 1980; Janson 1996; Perry and Rose 1994) and in captivity, where food is sometimes transferred from one individual to another (de Waal et al. 1993; Fragaszy et al. 1997; Thierry et al. 1989). Young capuchins are highly motivated to watch others foraging or smell others' food, especially when the food is novel or difficult to acquire (Fragaszy et al. 1997, Ottoni et al. 2005; Perry and Ordoñez-Jiménez 2006; Drapier et al. 2003).

Overall, this suite of characteristics parallels those of humans in important ways. For example, humans also display extended juvenescence, well-developed learning abilities, curiosity about objects, tolerance toward young individuals, and a diverse, challenging, and locally variable diet. All these parallels make study of capuchin behavior particularly interesting for comparative purposes. Capuchins seem an ideal taxon through which to explore the issue of how youngsters learn to find and process foods, and how social context supports this learning. Our goal is to describe how specific foraging skills are acquired by young wild capuchins living and acting with their group members in natural settings. We focus on examples from three different species of capuchin monkeys: learning to find larvae hidden inside bamboo stalks (*Cebus apella*, the tufted capuchin), learning to use hammer-and-anvil tools to crack palm nuts (*Cebus libidinosus*, the bearded capuchin), and learning to access the encased seeds of *Luehea candida* (*Cebus capucinus*, the white-faced capuchin).

### Socially Biased Individual Learning and the Ecological Approach

In keeping with our ethological perspective on social learning and our interest in linking social propensities to niche construction, Fragaszy and Visalberghi (2001) proposed an inclusive model of socially biased learning in natural circumstances. Socially biased learning is framed within the social and physical setting of behavior, as well as influenced by the characteristics of the individual, and all these elements are interrelated. Individual

characteristics include behavioral repertoire, general attraction to others, salience of specific partners present at that moment, responsiveness to objects, motivation to engage in new activities, prior experience with the setting, and ongoing experience (e.g., current activities, current internal state). Social elements that bear on an individual's likelihood of learning from others include the composition of social partners, tolerance of these individual for the focal learner, the behavior of the other, the value added to an object or a place from another's actions there as well as its emotional expressions while doing so (e.g., vocalizations associated with food), and enduring changes in the environment that remain from the other's activity (e.g., bits of food, altered substrates—hereafter, physical traces). The physical setting includes the abundance of sites to act and the accessibility of these sites. Finally, the physical setting affects risks for action. For example, monkeys are less likely to explore a new opportunity for action in a setting where perceived risk of predation is high compared to a setting where perceived risk of predation is low.

#### Foraging for Larvae Hidden inside Bamboo Stalks

Gunst et al. (2010) describe how young wild brown capuchins (*Cebus apella*) learn to find and retrieve beetle larvae hidden inside tough stalks of bamboo (*Guadua latifolia*) in the Raleighvallen Central Suriname Nature Preserve (Suriname). Gunst et al. (2008) characterize the larvae obtained from the interior of bamboo stalks as difficult foods, in contrast, for example, to the new young leaves of bamboo, which the monkeys find and eat in the same area. Obtaining a larva from its tough, concealing substrate requires selecting an appropriate bamboo stalk, locating the larvae hidden inside (both components of searching), and ripping the stalk open and extracting the larvae (handling components) (Figure 6.1 a, b, c). Locating an appropriate stalk and an appropriate site on the stalk is not easy, because the areas of bamboo that contain larvae do not differ in appearance from areas lacking larvae. Choosing the right spot to open is important because ripping the stalk open requires strength and is time consuming. Monkeys reach adult efficiency at this foraging task—obtaining five to six larvae per hour allocated to searching for larvae—at about five years of age, although they devote considerable time to inspecting and opening bamboo stalks from about one year of age.

Gunst et al.'s studies show how social partners' alteration of the physical environment can aid the young monkeys' development of skill in obtaining larvae. Young monkeys are attracted to canes already opened by

adults, and at these sites they practice behaviors that contribute to finding and obtaining larvae. Specifically, immature monkeys performed significantly more larvae-related foraging behaviors (rapidly tapping the cane with the fingertips—called tap scanning—inspecting the cane with fingers or nose, biting into and ripping bamboo stalks apart) within two minutes after approaching a ripped bamboo stalk left by a skilled forager than they did in the two minutes before (Figure 6.1d). In contrast, experienced foragers inspected ripped bamboo stalks briefly and did not follow inspection with foraging. Thus, the physical traces left by skilled foragers stimulate in youngsters activities likely to contribute to the acquisition of the foraging skill at hand. In short, skillful individuals “leave



*Figure 6.1.* Bamboo ripping by an adult male (the alpha male) while an infant is watching (a and b). After finishing ripping, the adult male is about to extract a larva while a juvenile is watching (c; the infant is hidden behind the adult male, probably watching too, but does not show on the photo). The adult male having left the foraging spot with its larva, the infant is inspecting the already ripped bamboo stalk (d). Photos courtesy of Nöelle Gunst.

the landscape littered with prepared 'practice' sites that appeal to younger monkeys" (Gunst et al. 2008, 21). We can think of physical traces as a form of niche construction and the young monkeys' response to physical traces as delayed, indirect social facilitation.

Finding the larvae seems to be the most challenging part of this foraging task. Bamboo grows in dense groves, and the sections containing larvae do not appear visibly different from canes that do not. In direct inspection of all the canes in five five-square-meter quadrats in a large bamboo patch, researchers found no larvae inside rotten stalks with light brown epidermis, internodes (sections of cane between growth nodes, usually about 30 centimeters long) already ripped apart by capuchins, or thin stalks. In contrast, large and medium green stalks contained an average of 0.05 larva per intact internode, and never more than one per internode. These findings indicate the importance of directing ripping activity to where larvae might be present. Accordingly, they suggest that perceiving cues associated with larvae and using them to guide search is important to optimize the time and effort devoted to searching for larvae.

Faced with a vast expanse of bamboo canes in a patch, how do capuchins search for larvae? Before finding a larva, the monkeys commonly tap scan, sniff, and inspect canes visually and manually and bite and rip the stalk apart. Stepwise linear regressions using foraging efficiency as the dependent variable demonstrate that visual inspection and tap scanning predict foraging efficiency, whereas the other behaviors do not. Visual inspection and tap scanning tended to become more frequent with age, whereas manual inspection and biting, which were not predictive of finding a larva, tended to decline with age, although even adults performed these behaviors at low rates.

Whereas younger animals directed extractive behavioral patterns toward small healthy stalks, or already-ripped stalks, the adults focused on large healthy stalks, where larvae are likely to be found. Interestingly, two adult males that had recently immigrated into the study group spent less time than other adults searching for larvae and were no better than older juveniles at finding larvae. These findings suggest that these monkeys were relatively naïve about this particular foraging activity, and highlight the dependence of efficient searching behaviors upon extended practice even for individuals with full physical capabilities.

Social context could help the monkeys learn the perceptual cues that indicate the presence of a larva inside a cane. For example, through their attraction to the sites where others have already opened canes and extracted larvae, youngsters could learn to notice the presence of the tiny

hole made by the insect while laying the eggs that develop into larvae, or the odor associated with the larva. Similarly, from watching adults searching, they could learn that tapping serves as a relatively reliable cue about the presence of the larva inside the stalk. Capuchins in other regions than Gunst et al.'s study area tap scan while foraging for insects embedded in dead branches (weeper capuchins, *C. olivaceus*, Fragaszy 1986; brown capuchins, *C. apella*, Phillips et al. 2003). Thus tapping is a genus-typical behavior, performed by capuchin monkeys in many settings, but the monkeys in each location must learn when to use it effectively and for what purpose.

### Use of Hammers and Anvils to Crack Palm Nuts

All over their geographical distribution, capuchin monkeys pound objects, such as hard fruits or snails, on hard surfaces in order to get access to the inner parts (for review see Fragaszy et al. 2004). Both in captivity and in the wild, some capuchins learn to use hammer stones and anvils to crack open nuts (for review see Visalberghi and Fragaszy 2006). Young capuchins, like young chimpanzees (Inoue-Nakamura and Matsuzawa 1997), learn to crack nuts over several years (Resende et al. 2008). Why does it take so long to master cracking nuts using a hammer stone and anvil? How does social setting support or hinder learning to crack nuts?

Resende et al. (2008) systematically investigated the ontogeny of manipulative behavior and nut cracking in nine young semi-free-ranging capuchins (*Cebus* spp., probably mostly *C. libidinosus* and *C. nigritus* and hybrids of these species) living in Tiête Ecological Park (near the city of São Paulo, Brazil) over 23 months of observation. The monkeys began to pound objects on surfaces at 2–3 months of age, and at the same time as they began to act directly with objects. Between 6 and 12 months they manipulated stones or nuts separately; banging the nut or stone directly on a substrate was the most common action. During the second year, manipulative activities became both very frequent and more vigorous. In particular, pounding became the most common action linking object and surfaces. Placing an object, such as a nut, on a surface and then releasing it was rare and was the last action necessary for nut cracking to appear; this action was first seen when the monkeys were 19–24 months old. The two young monkeys in the study that cracked nuts did so for the first time at 25 and 29 months. Resende et al. (2008) suggested that placing the nut on an anvil and releasing it posed one of the main difficulties for nut cracking for capuchin monkeys. Perhaps releasing an object in which

they are still interested requires overriding a strong proclivity to maintain a secure grip on it. Eventually, the monkeys open nuts by placing them one at a time on an appropriate substrate and striking them forcefully and accurately with a hammer. Young capuchins generally follow the same pattern of acquisition described by Visalberghi (1987) for two captive adult capuchins when they encountered, for the first time in their life, wooden blocks and nuts and learned to use the blocks as hammers to crack the nuts on a concrete floor. One striking difference, however, is that the captive adults first cracked nuts in a few days, rather than a few years.

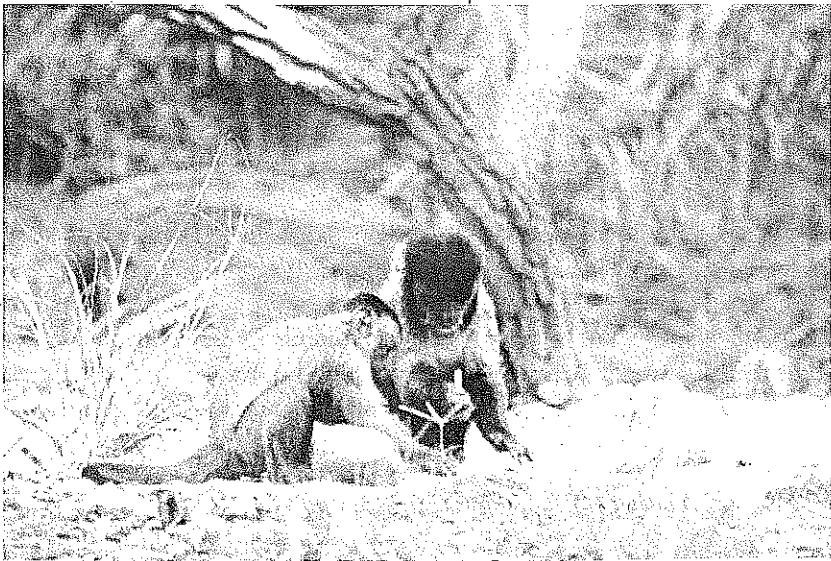
The research team (including the authors) studying the wild bearded capuchins (*C. libidinosus*) in Gilbuès, Piauí, Brazil, at Fazenda Boa Vista (hereafter FBV; see <http://EthoCebus.net>) has written several reports about nut cracking in these monkeys (Visalberghi, Spagnoletti, et al. 2009; Liu et al. 2009; Spagnoletti et al. 2011; Fragaszy, Pickering, et al. 2010; Fragaszy, Greenberg, et al. 2010). This site is in the northeast of Brazil, at approximately 9 degrees south and 45 degrees west. We have as yet few developmental data about nut cracking from FBV. We have noticed, however, that the capuchins seem to acquire nut cracking following the same trajectory as the semi-free-ranging capuchins in Tiête Ecological Park as described by Resende et al. 2008. In FBV, youngsters devote most of their efforts, and achieve their first successes, with partially opened nuts that they recover from the vicinity of the anvil, or with the least resistant species of nuts (unpublished data). Some youngsters at FBV can crack open less-resistant nuts by two years of age.

We suggest that social setting can positively bias learning indirectly, when group members are not presently cracking nuts, and directly, when they currently are involved in nut cracking. Indirect influence arises from the previous actions of others that create a supportive physical environment, as was also the case for monkeys learning to forage for larvae in bamboo canes, as reviewed above. At FBV there are three kinds of physical traces of activity that are helpful to youngsters learning to crack nuts. First, capuchins transport stones to anvil sites and leave them there after having cracked nuts. Later, monkeys arriving at the anvil sites use the hammer stones already present there. Second, because anvils are relatively soft sandstone or wood, as they are used repeatedly, pits develop in the area where the monkeys strike the nuts with the hammer. By producing pits, capuchins improve the affordances of the anvil for themselves as well as for future nut crackers (Fragaszy et al. 2010). By leaving hammer stones on anvils and by creating pits in the anvil surfaces through repeated use, capuchins make it easier for youngsters (or other unskilled individuals)

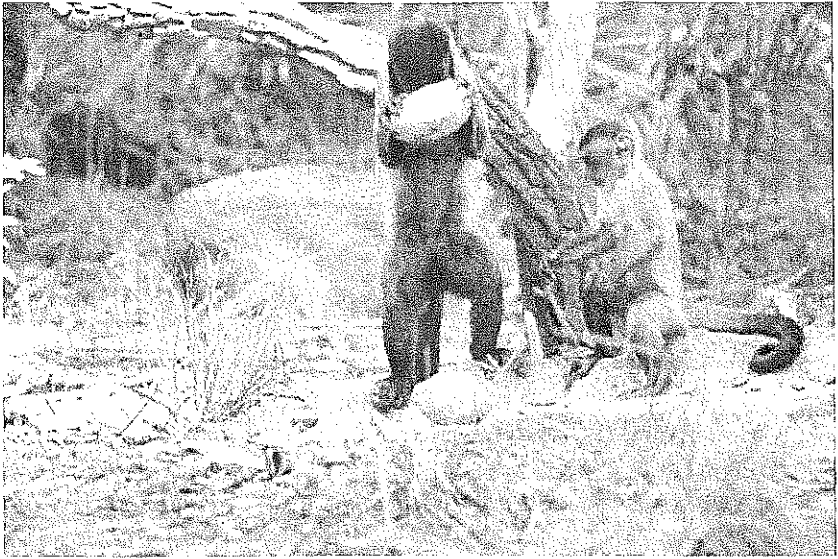


to learn to crack nuts with hammers. The hammers are on the anvils, and the pits provide a ready place to put the nut so that it can be struck securely (Fragaszy et al. 2010). Monkeys only need to show up at the anvil with their nuts; the materials to crack them are ready at hand, prepared by others. Finally, monkeys frequently leave bits of nuts and shells at the anvil when they leave the site, after having cracked one or more nuts. The hammer stones and anvils retain oily (and fragrant) traces of the nut kernels where they have been smashed against these surfaces. These features attract young monkeys' attention when they approach the anvil site, whether or not they are able to crack nuts on their own.

Direct positive social influence occurs when group members are cracking nuts. Nut cracking is a noisy, vigorous activity, and the sound and motion attract youngsters. They may watch from some distance, or they may stay near the anvil while another is cracking, sometimes handling smaller stones and nut shells in the vicinity, and they may take pieces of nuts cracked by others while the others are still at the anvil (Figure 6.2). Over many months they spend a long time in this permissive social setting (Figure 6.3). Eventually, when proficient tool users leave their hammer and/or partially opened nuts on the anvil, youngsters use them to



*Figure 6.2.* The alpha male has extracted a kernel from a piassava nut, and a juvenile is nearby searching for bits of nut remaining on the ground. Photo by Elisabetta Visalberghi.



*Figure 6.3.* A juvenile closely monitors the nut-cracking behavior of the alpha male. Photo by Elisabetta Visalberghi.

“practice,” if they are strong enough to lift the hammer stone (which may weigh more than the young monkey trying to lift it), or when very small, they strike one nut on another. In this way youngsters’ exploratory actions with nuts and stones occur in a place with the appropriate elements for success (that is, pieces of nuts, hard stones, and pitted anvil surfaces). Although adults do displace juveniles from anvils, direct agonism is rare (Verderane 2010).

Ottoni et al. (2005) assessed the proficiency of each tool user in semi-free-ranging capuchins in the Tiête Ecological Park near São Paulo. They also recorded the extent to which other monkeys observed each tool user and/or collected remains of nuts afterward (scrounging), while or just after the other monkey cracked the nut. In 76 percent of dyads, the tool-using monkey was more proficient at cracking nuts than was the observing monkey. Scrounging occurred in 35 percent of the episodes in which the monkey using the tool cracked the nut. Since the most proficient nut crackers would tend to yield, on average, the highest payoff for scrounging, it is likely that the proximate cause of the young monkeys’ selective observation of particular nut crackers is the opportunity for scrounging that these proficient individuals afford the observer. The nonrandom pattern of observing others enhances scrounging payoffs and, coincidentally, maximizes opportunities to associate places, objects, and actions with

obtaining nuts. As Ottoni and co-workers write, "simple associative or reinforcement processes can underlie the tendency of capuchins—youngsters in particular—to watch nutcrackers at work. This simple mechanism could, by itself, optimize the conditions for the social learning of nut cracking techniques and for the diffusion of tool-aided nut cracking as a behavioral tradition" (p. 218).

Ramos da Silva (2008) obtained parallel results in a group of wild bearded capuchins in FBV. He found that one or more monkeys watched 25 percent of the nut-cracking episodes, with the number of observers ranging between one and four. As in Tiête Ecological Park, the more frequently watched capuchins were those that used tools more frequently and with higher rates of success. In 35 percent of the nut-cracking episodes observed by a juvenile, the juvenile manipulated the same hammer or the nut and/or attempted to crack a nut (or part of a nut) with the hammer within a few minutes after watching another cracking with that hammer and anvil. This finding suggests that exploration of anvil sites and hammers is socially biased. Social facilitation of the specific actions associated with nut cracking (e.g., pounding a stone on a surface) is probably part of this package (see also Visalberghi 1987). Experimental studies to determine if pounding an object can be socially facilitated in capuchins would strengthen this interpretation.

In summary, nut cracking by wild capuchins appears to be socially biased in several ways that increase the likelihood of naïve individuals learning to crack nuts with stone tools. First, young capuchins up to about two years of age are well tolerated by adults in feeding contexts and are likely to scrounge bits of food from others (see also Fragaszy et al. 1997). Second, the repeated use by group members of the same anvil sites and the same hammers, together with enduring traces of nuts cracked at those sites, provides familiar places with appropriate resources to practice hammering. Third, juveniles are strongly attracted to watch the activities of others, which is linked with the probable social facilitation of pounding, and with the motivation to explore the hammers and anvils. All these socially provided elements increase the likelihood of a juvenile acquiring tool use if it lives in a group that practices this behavior routinely (compared to a group that does not). In other words, through their behavior, adults construct a niche in which youngsters reliably learn to crack nuts. Nut cracking is likely to be a tradition in capuchin groups.

Does this mean that the presence of skillful group members is the *conditio sine qua non* for monkeys to learn to crack nuts? Apparently not, since there is plenty of evidence that the behavior can be acquired by naïve individuals (youngsters as well as adults) without social input (e.g.,

Visalberghi 1987; Fragaszy et al. 2004). When they have access to encased food such as nuts, and in a physical setting promoting nut cracking (with hard substrates and hammers), some capuchins (but not all) discover on their own how to use tools to crack nuts. Interestingly, naïve adults exhibit the same array of explorative behaviors and (spatially correct and incorrect) actions combining the nut and the tool that have been described for young capuchins (Resende et al. 2008). On the other hand, merely living in a group that practices nut cracking does not guarantee that a monkey will acquire this skill. Of the 24 physically normal capuchins observed at FBV that are old enough to use tools, one individual was never seen to crack nuts using a stone tool.

Might young monkeys learn to crack nuts, or improve their technique, from directly copying some aspect of the behavior of others? Field observations cannot answer this question decisively, but we think the answer is no. Pounding because another monkey is pounding is one entry point for skill development, but simply pounding a stone on a nut is not sufficient to crack the nut. Cracking a nut requires skillful placement of the nut followed by skillful handling of a heavy stone, but no specific technique of placing or handling. It is a motor skill more than a matter of special techniques. Novice alpine skiers must practice on their skis to master skiing down a snowy slope under control, and no amount of watching a skilled instructor will substitute for direct practice. It seems that nut cracking is like skiing: the observable components of the action are straightforward, but their competent execution requires extended practice. The trajectory of the stone, the force with which it strikes the nut, the position of the nut in the anvil—all these aspects affect success and need a lot of individual practice to optimize. Even after the young monkey reliably produces all the relevant actions in the correct sequence, it may take years before it succeeds in cracking a nut. Having proficient group members to watch could contribute to skill development over this long period, not because young monkeys learn anything specific from watching others, but because watching others, like encountering physical traces of their activity, increases their motivation to act and channels their choice of elements with which to act toward the right ones to learn to crack nuts.

### Processing Encapsulated Seeds

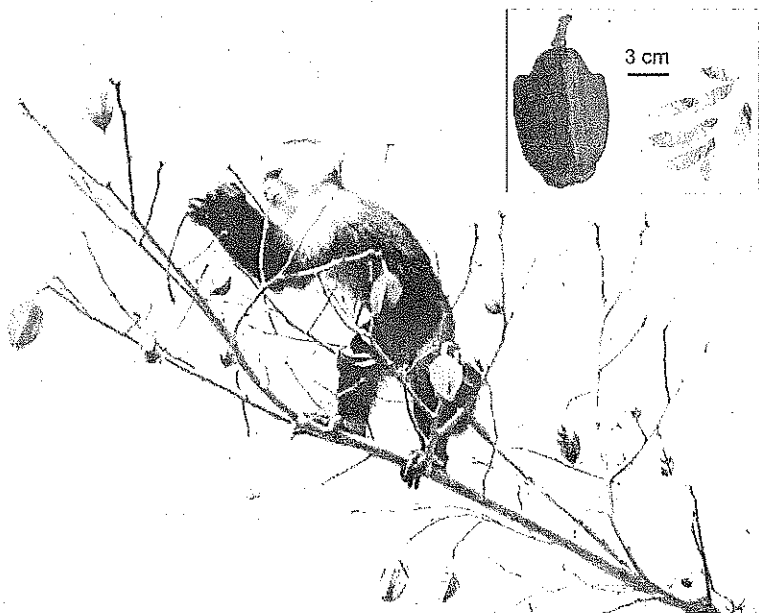
Infant capuchins begin to exhibit most species-typical manipulative actions such as pounding and rubbing objects on substrates in the first months of life (Adams-Curtis and Fragaszy 1994; Spinozzi 1989). At first,

pounding and rubbing are not differentiated, but gradually they become distinctive, with pounding involving brief force applied intermittently in a plane perpendicular to the substrate and rubbing involving sliding a held object in a plane parallel to, and in contact with, the substrate, usually with cyclical back-and-forth motions. In general, during foraging these actions are used for different purposes: pounding is used to break a rigid surface, whereas rubbing is used to remove a pliant layer (for example, to remove the chemical and mechanical defenses of caterpillars). However, in some cases, as the one illustrated below, the two actions are directed at the same object for the same goal.

Perry (2009) studied how young white-faced capuchins (*Cebus capucinus*) developed the processing techniques used to exploit the seeds of *Luehea candida*. At Perry's site, the Lomas Barbudal Biological Reserve in Costa Rica, as well as elsewhere (Fragaszy et al. 2004), white-faced capuchin monkeys eat luehea seeds. The monkeys devote up to 15.4 percent of their foraging time to these seeds during the peak fruiting season (Perry and Ordoñez-Jiménez 2006). Thus luehea seeds constitute an important part of the diet for the monkeys in Lomas Barbudal in the season when they are available. The luehea trees average 10 meters in crown diameter and 15 meters in height, and typically two to three monkeys forage in one tree simultaneously. The fruits are wooden capsules containing many tiny, nutritious seeds, and when ripe, their five seams slowly open to release the wind-dispersed seeds (Figure 6.4). Capuchins feed on the seed pods before they are fully open.

The monkeys adopt two different techniques to loosen the luehea seeds from their point of attachment deep in the cracks so that they fall out or can be more easily plucked from the tip of the fruit. The pounding technique consists of repeatedly striking the fruit against a substrate; the rubbing or scrubbing technique consists of repeatedly moving the fruit back and forth across a rough surface. Fragaszy et al. (2004, 131) describe the action of rubbing as occurring "when an object is drawn backward and then forward against the substrate"; we believe that scrubbing and rubbing refer to the same behavior. Perry (2009) tried herself to extract the seeds by pounding and by scrubbing. Through pounding she obtained 7.8 seeds per 10 seconds and through scrubbing 5.8 seeds per 10 seconds. Thus these methods produce seeds at roughly equivalent rates.

An unusual and very valuable feature of Perry's study is that it was longitudinal, extending five years. Perry observed that juveniles between one and two years old tried a wide variety of techniques, including pounding and scrubbing and a combination of the two, and they were generally not



*Figure 6.4.* A white-faced capuchin extracts winged seeds from luehea pods. In the upper right corner: a close view of the pod and its seeds. Santa Rosa National Park, Costa Rica. Photos courtesy of Katherine C. MacKinnon.

able to get the seeds. When three to five years old, these same youngsters gradually abandoned the inefficient variants they had used earlier. By five, they had generally settled on one technique (pounding or scrubbing). In all four groups studied by Perry (2009), pounding and scrubbing were each used by at least one adult. Young individuals are typically exposed to both pounding and scrubbing, although at different rates (because most adults pound).

Perry (2009) examined the technique used by each youngster during its first five years of life, in relation to that individual's estimated exposure to pounding performed by the mother and by other group members during each luehea season. Her findings show that the youngsters with an early bias for one of the two techniques increased their bias for that technique as they aged. Overall, females were likely to use the same technique as their mothers, whereas males were not. Regression analysis revealed that for both males and females the technique most frequently observed significantly predicted the technique adopted by observers, particularly in the second year of life, although the predictive value of the observed

technique for the practiced technique was lower for male observers than female observers.

According to Perry (2009), her findings suggest that observation of others' foraging techniques influences which techniques youngsters use, as has been found in captive capuchins (Dindo et al. 2009 and Crast et al. 2010). Perry suggests that the intrinsic pleasure individuals obtain from copying the actions of individuals with whom they have special bonds, as proposed by de Waal's (2001; Bonnie and de Waal 2007) "Bonding—and Identification—based Observational Learning Model," may support this process. Alternatively, perhaps the observer prefers to be in proximity with group members performing the same technique as itself. This scenario is suggested by the finding of Paukner, Suomi, et al. (2009) that capuchin monkeys affiliate more with humans that contingently match their behavior than humans that match their behavior, but not contingently. In other words, being imitated promotes affiliation in captive capuchins. When a monkey is scrubbing, another individual doing the same thing provides more contingent matching of its behavior than does an individual that is pounding, and thus the first monkey might prefer to be near another monkey that is scrubbing. This process would on average produce congruent techniques for opening seeds in youngsters and their near neighbors. As another alternative, it is possible that both scrubbing and pounding are socially facilitated, as eating behavior is (Visalberghi and Addessi 2003; Ferrari, Maiolini, et al. 2005), and as we suggest pounding nuts may be. Even weak social facilitation may be sufficient for most young monkeys to match, eventually, the technique used by most members of their group. In any case, Perry's findings illustrate the complexity of the social context in natural settings, where monkeys see individuals acting on the same objects in variable ways. In such situations, the monkeys do not show strong fidelity to the particular method they observe the most, unlike in some experimental studies with captive capuchins, where the monkeys show strong fidelity to the one technique they observe another individual performing (e.g., Fredman and Whiten 2008; Dindo et al. 2009).

## Conclusions

Capuchin monkeys afford an interesting view of how physical, social, and experiential factors contribute to the development of foraging competence in a long-lived primate (Gunst et al. 2008). These monkeys display regionally variable foraging specializations, reflecting local resources. The

three examples of distinctive foraging behaviors acquired by capuchin monkeys in natural settings that we have reviewed here demonstrate how social influences can play out differently in different foraging situations. In the first, young monkeys learning to find larvae embedded in bamboo canes must learn how to find a cane worth opening, as most bamboo canes do not contain larvae. Initially, they preferentially look in canes that adults have already opened. In this example the enduring physical traces of adults' foraging activities strongly influence young monkeys' behavior. From already-opened canes, the youngsters can learn how such canes smell, they can practice ripping bamboo, and perhaps they can learn or practice other features of the task. However, looking in the canes that adults have already opened will not, by itself, ever lead to finding a larvae, because the adults remove the single larva in each cane that they open. We do not yet understand how the monkeys eventually learn to detect the presence of larvae before they open a cane, but it is not from straightforward facilitation of action at the same site.

In the second example, social facilitation of action and activity at a prepared site, together with scrounging opportunities, provides a roundly supportive setting for young monkeys learning to crack nuts. The anvils are improved by use, with the formation of pits that serve to reduce the probability that the nut will be displaced from the anvil as it is struck (Fragaszy et al. 2010). Durable hammer stones, which are rare in the landscape (Visalberghi, Spagnoletti, et al. 2009) are routinely left at anvil sites and thus are available to the next user. Thus, as in the previous example, enduring physical traces of others' activity set the stage for effective practice by young monkeys. Additionally, and unlike the previous example, young monkeys have repeated opportunities to scrounge bits of food at the anvil, while or after others have cracked nuts there, and they have ample opportunities to watch others cracking nuts. All these features of the setting promote persistent exploration of the relevant materials and may directly facilitate pounding actions. Collectively these features contribute to young monkeys becoming proficient nut crackers, but we do not yet know their relative contributions.

In the third example, young monkeys learning to open luehea seeds do not have prepared sites or enduring physical traces to explore, nor do they have extensive opportunities to scrounge food from others foraging on these seeds. But, as in the two previous examples, they do have repeated exposure to others performing a noisy and vigorous activity and obtaining food from doing so, and this seems sufficient to motivate



persistent efforts by young monkeys to open these seeds themselves. In this case, the food item is manipulated directly (as opposed to being hidden inside bamboo or struck with another object, as in the previous examples). Being with others that use a particular technique seems to bias the technique adopted by young monkeys, although the precise mechanism for the congruence between youngsters and their group mates is not yet clear.

These examples illustrate that foraging presents diverse challenges, and that social influences promoting shared foraging skills, a social form of niche construction (Odling-Smee, Laland, and Feldman 2003), can take diverse forms. In recent years, a lot of attention has been paid to some sources of social influence (for example, visible actions), while others (such as physical traces) have received less consideration. We think that broadening our attention to all the components of the social context will improve our understanding of social contributions to learning. Direct visual observation may not be the primary source of social influence on learning, and copying behavior will often not be a sufficient basis for learning a skill. Many of the relevant parameters of foraging actions are not amenable to observation; they could not be learned by copying the behavior of others.

Many of the studies of social learning in monkeys, particularly in foraging (our own included), carried out in the laboratory are necessarily disconnected to a greater or lesser extent from the species' natural ecology. For example, group size and composition, the nature of the food resource, its temporal and spatial distribution and abundance, etc., do not match those known for the species in natural environments. Often the experimental tasks involve problems the animals do not deal with in nature (for example, transparent containers, or fixed panels or levers), and time constraints are imposed, both on our observation and on the animals' exposure to the problem. We believe this state of affairs has contributed to our blindness to the richness of the social biases affecting the behavior of individuals, particularly more naïve individuals, and especially to biases that become manifest over long (developmental) periods. Foraging skills, for example, develop over years. Understanding social contributions to learning important life skills, such as foraging, will be best accomplished if we keep clearly in mind that a wide range of parameters can affect learning over a long period, and the same parameters may have variable impact over this long period, a point of view expressed some years ago by Russon (2003). Social niche construction impacting learning can affect a range of physical dimensions, and individual learners bring diverse

susceptibilities, predispositions, and emerging skills to the setting. Thus it is inappropriate to ask if a given skill is “socially learned” in a natural setting—all skills are acquired, and most slowly, in a social context that, like the learner, changes over time.

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