

Capuchin (*Cebus apella*) Tool Use in a Captive Naturalistic Environment

Anthea C. Lavalée¹

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Captive tufted capuchins are proficient at both tool use and manufacture. However, their capacity to comprehend cause-effect relationships as they relate to tool use is a subject of debate. An ability to conceptualize task requirements in assessing the appropriateness of potential tools would be essential to efficient tool use in the wild. Observations of tool use among free-ranging populations of Cebus are extremely limited, and the importance of this behavior to capuchin feeding ecology is unclear. I tested tufted capuchins' ability to conceive solutions to a probing task in a naturalistic captive setting. Three out of 5 participants demonstrated an ability to consistently make and use tools selected from a wide variety of natural materials within a forest exhibit. Over 98% (N = 140) of the tools that they modified enabled them to successfully acquire food rewards. It is likely that wild Cebus apella shares this ability, and that tool use occurs under a highly specific set of natural conditions.

KEY WORDS: Problem solving; tool manufacture; tufted capuchins; extractive foraging.

INTRODUCTION

All animals are equipped with problem-solving skills that enable them to respond to environmental challenges. Solutions may involve anatomic traits or behavioral strategies that are advantageous under a specific set of local conditions (Gomberg *et al.*, 1979). For example, in their native habitats, the disproportionately long fingers of *Daubentonia* and *Leontopithecus* greatly facilitate extractive foraging for concealed insect prey (Hershkovitz, 1977; Petter, 1977; Rylands, 1989). Similarly, all species of free-ranging *Cebus* efficiently excavate hidden insects and

¹Department of Anthropology, 109 Davenport Hall, 607 South Mathews Avenue, University of Illinois, Urbana-Champaign, Urbana, Illinois 61801 (e-mail: yannopls@uiuc.edu).

other embedded food resources (*C. capucinus*: Oppenheimer, 1968; Chapman and Fedigan, 1990; *C. apella*: Izawa and Mizuno, 1977; *C. albifrons*: Terborgh, 1983; *C. olivaceus*: Fragaszy, 1986). They exhibit a diverse repertoire of extractive foraging behaviors including some associated with the use of tools (Visalberghi, 1990; Chevalier-Skolnikoff, 1990; Fragaszy *et al.*, 1990; Fernandes, 1991). In the laboratory, tufted capuchins (*Cebus apella*) frequently use tools as extensions of the body to obtain otherwise inaccessible food rewards (Westergaard and Fragaszy, 1987; Anderson, 1990; Westergaard and Suomi, 1994b; Anderson and Henneman, 1994; Westergaard *et al.*, 1997). Furthermore, occasional object manipulation occurs among wild capuchins (Struhsaker and Leland, 1977; Boinski, 1988; Chevalier-Skolnikoff, 1990; Fernandes, 1991; Phillips, 1998). Complex feeding behavior and extractive foraging in *Cebus* may be associated with a reliance on animal prey (Parker and Gibson, 1977; Izawa, 1978; Fragaszy, 1986; Westergaard and Fragaszy, 1987; Fedigan, 1990; Fernandes, 1991; Janson and Boinski, 1992), large brain size (Bauchot, 1982; Martin, 1984; Gibson, 1990), and enhanced manipulative skill (Struhsaker and Leland, 1977; Fragaszy *et al.*, 1990; Visalberghi, 1990). Unlike other New World monkeys, capuchins are capable of moving their digits independently and have a somewhat opposable thumb allowing for a precision grip (Costello and Fragaszy, 1988). These factors may contribute directly to object manipulation and tool use in capuchins (Visalberghi, 1990; Westergaard, 1995). I accept Beck's definition of tool use:

the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool. (Beck, 1980, pp. 10)

Learning to solve a variety of problems using tools involves an ability (1) to assess accurately cause-effect relationships and (2) to choose an appropriate solution from a set of possible strategies. Solutions to foraging problems in the wild are likely based on a set of behavioral rules determined by past experience (Garber and Dolins, 1996). Naive animals may improvise solutions to ecological problems by performing variations on previously successful patterns of behavior i.e., pre-solutions or learning sets (Harlow, 1949; Adams-Curtis, 1990). The systematic application of pre-solutions allows for nonrandom hypothesis testing in the context of novel problem-solving (Garber and Dolins, 1996). In this way, animal problem solving and learning may be described as rule-based rather than random. The goal of the current project is to examine tufted capuchin tool use in a naturalistic captive setting. I designed an observational study to reveal the monkeys' ability to select, modify, and use natural tool materials available within a forest enclosure. Some of the monkeys had participated in earlier captive studies of capuchin tool use (Westergaard and Fragaszy, 1987; Fragaszy and Adams-Curtis, 1991). They therefore had the opportunity to apply experience obtained under traditional laboratory test conditions to solve tool tasks in a near-to-wild setting.

Previous studies of tufted capuchin tool use in captivity have been undertaken in relatively small enclosures which, in contrast with a naturally complex environment, afforded limited access to potential tools (Visalberghi, 1987; Anderson and Henneman, 1994). Although, under these experimental circumstances, tools were immediately available to the subjects, there were fewer total tools and less variety from which to choose. I conducted this study in a large forest enclosure and presented the capuchins with a set of conditions that were ecologically similar to those they might encounter in the wild. This setting afforded a diverse selection of natural objects for potential use as tools. In order to assess representational ability, my research objectives were (1) to test if tufted capuchins choose natural tools randomly regardless of their appropriateness and (2) to identify the presence/absence of a pattern of tool selection and manufacture consistent with the functional requirements of a specific foraging problem. Mental representation is the process by which external or perceptual information takes the form of a conceptual substitute (Vauclair, 1990). Some researchers have attributed the rapid mastery of tool-related tasks in captive capuchins to an ability to mentally represent the characteristics of successful tool types (Anderson and Henneman, 1994; Westergaard and Frigaszy, 1987). The results of these laboratory studies imply that capuchins construct mental templates embodying the physical qualities that contribute to the effectiveness of successful tools. Potential tools are then evaluated according to these internal standards and, if sufficiently similar, selected for use. Under the conditions of this study, there were 5 possible outcomes: (1) the capuchins ignore the test apparatus; (2) they are attracted to the apparatus but do not use tools; (3) they only use inappropriate tools and/or techniques; (4) they frequently use tools but are very rarely successful; or (5) they consistently select successful tools and apply effective techniques. Among the 5 possible outcomes, only the fifth is consistent with the properties of representational ability.

METHODS

Subjects and Setting

Monkey Jungle is a privately owned zoological park in South Florida (25.4° N latitude and 80.2° W longitude). The rainforest exhibit is a 1.6-ha subtropical hardwood forest enclosure comprised of both native and neotropical floral species. Dominant broad-leaf genera typical of tropical American wet and deciduous forests include *Ficus*, *Bursera*, *Simarouba*, and *Lysoloma* (DuMond, 1968). The capuchins share their enclosure with a squirrel monkey population (*Saimiri boliviensis peruviansis*) of approximately 90 individuals. The monkeys are free to range throughout their enclosure and, although provisioned twice daily, forage naturally for insects, vertebrate prey, fruit, and plant resources.

I designed a feeding device to elicit probing behaviors. It was the stump of a recently cut tree (23.5 cm in diameter) in which we drilled 6 and 4 holes

(1.2 and 0.8 cm in diameter, respectively, and 6.5 cm deep) into its flat surface. In the rainforest exhibit I filled the holes with honey before each test trial. Previously, the capuchins had been presented with a variety of potential food rewards including yogurt, honey, applesauce, and mealworms. Since more animals were motivated to forage for honey than for any of the other foods, I used it as the reward. No ready-made tools were provided; thus the monkeys were free to select or not to select environmental objects to be used as probes. Suitable tools were necessarily long enough to reach the reward (>6.5 cm), sufficiently rigid, and narrow enough to fit into the holes (<1.2 or 0.8 cm in diameter). Under these circumstances, the experimental design enabled or encouraged the expression of capuchin tool use (*sensu* McGrew and Marchant, 1997).

At the time of the study (January-March 1996), 11 semifree-ranging, captive-born tufted capuchins inhabited the rainforest exhibit of Monkey Jungle. They included 2 infants in the very early stages of independent exploration, which rarely interacted with the feeding device and were not considered potential participants in the experiment. The remainder of the group consisted of 5 adult females (Erna, 19 yrs.; Jill, 19 yrs.; Charlie, 7 yrs.; Lindy and Carol, 4 yrs.), 2 adult males (Willie, 10 yrs.; and Paul, 8 yrs.), and 2 juvenile males (Nicki, 2 yrs.; and Phil, 2 yrs.) (Table I). In an effort to interpret whether individual dominance status was a factor affecting access to the device, I collected data on aggression displayed in dyadic interactions, e.g., threats and displacements. As previous research has shown, participation was influenced by both dominance (Fragaszy and Adams-Curtis, 1991) and interest in the task (Visalberghi, 1988; Parker and Poti, 1990; Fragaszy and Adams-Curtis, 1991). Some tool-using subordinates were frequently chased away by the dominant male, while other tolerated individuals were not motivated to take part in the study. In addition, several subordinates interacted with the device but either failed to use tools or did so inappropriately. Since performance was constrained by social tolerance, interest, and ability, I primarily presented on the tool-using techniques of 3 adult capuchins (1 female and 2 males) which (1) were able to gain routine access to the device, (2) were motivated to participate, and (3) applied successful tool-use solutions to the task. Although successful strategies

Table I. Participation and performance

Subject	Age in yrs.	Sex	Lab experience	Participation	Tool use	Successful tool use
Erna	19	F	+	+	+	+
Jill	19	F	+	-	n/a	n/a
Charlie	7	F	-	-	n/a	n/a
Lindy	4	F	-	-	n/a	n/a
Carol	4	F	-	-	n/a	n/a
Willie	10	M	+	+	+	+
Paul	8	M	+	+	+	+
Nicki	2	M	-	+	+	-
Phil	2	M	-	+	-	n/a

were not demonstrated by human models, each of the 3 monkeys had previous experience in laboratory studies of capuchin tool use (Westergaard and Fragaszy, 1987; Fragaszy and Adams-Curtis, 1991). Before my experiment, however, their abilities had not been tested in a naturalistic environment.

Procedure

In an attempt to quantify the rate of successful tool selection, modification, and use, I timed all occurrences of tool use within 15-minute trial periods using a focal animal sampling strategy (Altmann, 1974). I also noted the material chosen, e.g., plant part, and the state of the tool: manufactured or selected and used without modification (Westergaard and Fragaszy, 1987). The device accommodated a range of potential tools. Appropriate objects were <1.2 cm in diameter and >6.5 cm in length. Tools of inappropriate size or shape never contributed to the solution of the task. Therefore, I judged the success of unmodified or manufactured tools according to their potential use as probes. Similarly, nonprobing tool-use techniques involving either appropriate or inappropriate tools were never successful. For this reason, I considered any technique other than probing, such as slapping the device with the tool, inappropriate. The first capuchin to indicate interest by touching the apparatus was the focal animal for that particular trial. Individual sample periods were followed by a 15-minute intertrial interval during which the device was covered. The intertrial period was intended to prevent dominant animals from monopolizing access to the device and presented an opportunity for new test subjects to arrive after former participants had left the area. Abandonment of the task (no interaction for 90 seconds) marked the conclusion of the trial.

A second experiment examined capuchin ability to select tools at a distance from the device. This was a variant of the original task in which the feeding apparatus was placed on the center of a bridge at a distance of >5 meters from potential tools. Under these circumstances, the monkeys were obliged to select their tools from remote sources, the nearest of which was out of sight of the device i.e., the riverbank below, and to transport them several meters to the apparatus.

Data Analysis

The most infrequent successful tool-user participated in 32 trials. To eliminate the confounding effects of differences in performance due to unequal experience, I restricted analysis to the first 32 trials of each successful tool-using monkey. I calculated the percentages of time engaged in probing behaviors and the use of appropriate and inappropriate tools for each capuchin and compared individual levels of proficiency among these 3 capuchins. I analyzed successful vs. unsuccessful tool-using behaviors via a Wilcoxon Signed-Ranks Test and assessed consistency

in individual performance patterns by calculating coefficients of variation associated with the reliability of successful tool use across trials (trial time engaged in successful tool use). I used the Kruskal-Wallis One-Way Anova to compare the reliability of successful tool use among individuals.

RESULTS

General Foraging Strategies

Patterns of individual performance and participation were evident (Table I). Willie, the alpha male participated frequently. Jill, a low-ranking individual, never gained access to the device. Erna would approach the test apparatus when dominant animals were at a distance or if permitted to forage in close proximity to Willie. Paul was able to participate only in Willie's absence. The juveniles were well tolerated by the dominant male and frequently interacted with the device. The juveniles observed the successful tool-using techniques of the dominant male and occasionally handled his discarded tools. Although neither juvenile exhibited successful tool use in the context of the present study, both seemed extremely interested in the apparatus and experimented with a variety of tool types and techniques. Carol, Charlie, and Lindy expressed no apparent interest in the task and rarely ventured near the apparatus. Although many group members explored the device to varying degrees and several applied object-related foraging techniques, only the 3 most frequent participants, Willie, Erna, and Paul, exhibited successful tool-using capabilities (Fig. 1). All successful tool-users were adults (Table I). Among these 3 animals, age did not affect interest or ability.

Willie, Erna, and Paul attempted tool use in 69–97% of all problem-solving trials (Table II). Total trial time included time spent searching for and manufacturing tools, non-tool-using attempts, social vigilance at the feeding device, and tool use. Willie, Erna, and Paul spent 38, 27, and 27% of their total trial times engaged in tool use (Table II). Although trials were a maximum of 15 min, they were often of shorter duration due to various interruptions such as displacement or loss of interest (mean = 7.2 min, range = 1–15 min). Willie typically worked

Table II. Use of natural probes

Subject	Trials ^a	Total time ^b	Tool-use time (%) ^c	Tools (N)
Willie	29	232	38	215
Erna	22	219	27	203
Paul	31	235	27	179

^aNumber of trials (out of a possible 32) during which tools were used.

^bTotal interaction time in minutes.

^cThe percentage of trial time devoted to tool use.



Fig. 1. Adult male capuchins, Paul (top) and Willie (bottom), using natural probes of their own choice to obtain honey from the feeding device.

Table III. Successful strategies and their component parts

Subject	Success ^a	Coeff. of variation ^b (%)	Successful technique ^c	Appropriate tools ^d
Willie	96	101.1	99	94
Erna	94	126.4	99.8	85
Paul	93	123.1	95	79

^aPercentage of total tool-use time engaged in successful probing.

^bAnalysis of time engaged in successful probing across trials.

^cPercentage of total tool-use time engaged in appropriate probing techniques.

^dPercentage of tools that were physically appropriate.

slowly and for longer periods of time (average trial time = 8 min). Conversely, Paul and Erna were often displaced and had trials of shorter average duration (7 and 6 min respectively).

The Selection and Use of Tools

Willie, Erna, and Paul used a total of 215, 203, and 179 tools (Table II). I scored tool use as either successful or unsuccessful. Each of these capuchins solved the tool task on the first trial and spent nearly all tool-use time engaged in successful strategies (93–96%) (Table III). For Willie, Erna, and Paul, differences in time spent engaged in successful vs. unsuccessful behaviors were highly significant ($P < .0001$). Although individual differences in the reliability of successful tool use across trials were not statistically significant among them ($P = 0.2$), coefficients of variation indicate that Willie, the alpha male, was the most consistent in his successful tool-using strategies; Paul demonstrated intermediate reliability; and Erna's efficiency varied the most across trials (Table III). Time devoted to inappropriate techniques, such as banging the tool on the surface of the device, ranged from <1–5% of tool-use time (Table III).

Willie, Erna, and Paul rarely probed with unsuitable objects (6–21% of chosen tools) (Table III). Among them, tool choice appeared to be nonrandom. The selection process often involved the careful inspection and handling of potential tools before committing to a single object and using it as a probe. Between 68 and 93% of the chosen unmodified tools were suitable to the task (Table IV). However, in spite of the apparent goal-oriented effort of tool selection, successful tools were frequently abandoned in favor of less suitable substitutes (occurred during 41, 67,

Table IV. Unmodified and manufactured tools (*N*)

Test subject	Unmod. tools	Successful unmod.	Manuf. tools	Successful manuf.
Willie	176	164	39	39
Erna	161	132	42	40
Paul	117	80	62	61

and 38% of tool-use trials for Willie, Erna, and Paul). The capuchins seemed to have little patience with individual tools and, regardless of success, would rarely use one object for more than 60 seconds. The most common inappropriate tools were too thick to fit into the holes in the device.

Tool Manufacture

Methods of tool manufacture included biting and tearing twigs and branches from nearby bushes, vines, and trees; breaking large, unwieldy branches into shorter, more manageable pieces; stripping away leaves and stems that would prevent sticks from fitting into holes; removing limp or frayed ends from sticks; and splitting branches that were too thick (Beck, 1980; Westergaard and Fragaszy, 1987). Collectively, Willie, Erna, and Paul used 143 manufactured tools (Table IV). Only 3 of them were unsuitable for the task. They include a branch broken from a nearby tree that was too thick to fit into the holes in the device and 2 pieces of wet leaf too limp to be used as probes. The remaining 98% of the manufactured tools were physically appropriate.

Tool Choice and Transport from Distant Sources

I further tested the monkeys' representational capacities by placing the tree stump on a bridge and out of sight of the nearest tool sources. In this situation, capuchin foraging success was related to an ability to gather suitable probes and to transport them from a distance of >5 m to the device for use as tools. Two subjects, Willie and Paul, were successful at this task. Upon discovery of the feeding device in its new location, they typically selected suitable materials from among the bushes and long grasses growing beneath the bridge and carried them to the apparatus, where they further modified them.

DISCUSSION

Given the difficulty inherent in assessing cognitive skill and an animal's behavioral options in the wild, captive studies offer the opportunity to control or to analyze the effectiveness of problem-solving by limiting the number of potential solutions (Gomberg *et al.*, 1979; Tomasello, 1990; Visalberghi and Limongelli, 1996). Traditional research into capuchin tool use has therefore been conducted in the laboratory under carefully controlled test situations. A common conclusion is that tufted capuchins possess the requisite curiosity and physical control to use tools (Westergaard and Fragaszy, 1987; Visalberghi, 1990). What is less certain, however, is the degree to which tufted capuchin tool use is the product of (1) insight, learning, and representational ability, (2) inborn manipulative

propensity, or (3) an ontogenetic trajectory that incorporates elements of both (Gibson, 1990; Parker and Poti, 1990; Anderson and Henneman, 1994; Visalberghi and Limongelli, 1996).

Visalberghi and coworkers argue that tufted capuchins are capable of fortuitous tool use but lack a true understanding of the causal relationship between tool and task (Visalberghi and Trinca, 1989; Visalberghi, 1990; Visalberghi, 1993; Visalberghi and Limongelli, 1994; Visalberghi *et al.*, 1995; Visalberghi and Limongelli, 1996). It has been proposed that, although tufted capuchins use tools to expedite extractive foraging strategies, they fail to recognize the precise properties of a particular tool that make its use effective and context-appropriate. This conclusion is based on the persistence of inappropriate and unsuccessful attempts among experienced test subjects. Tufted capuchins often appear unable to comprehend the limitations of previously useful tools and regard them as magic wands suitable for application in all possible contexts (Visalberghi and Limongelli, 1994; Visalberghi *et al.*, 1995). Overgeneralizations in using tools, i.e., applying the same tool in a range of appropriate and inappropriate settings, may indicate an inability to abstract the true requirements of a task. Similarly, the frequent selection of unsuitable objects may reflect inadequate representational skills (Fragaszy and Visalberghi, 1989; Visalberghi and Trinca, 1989; Visalberghi, 1990, 1993; Visalberghi and Limongelli, 1994). Accordingly, some researchers have concluded that tufted capuchins are unable to learn patterns of success for tasks requiring indirect solutions through systematic trial-and-error experimentation (Visalberghi, 1990). Behaviors leading to success are considered the inadvertent result of manipulative predisposition and incidental to capuchin curiosity.

However, results from other studies indicate that tool-using captive tufted capuchins do in fact understand the causal relationship between tool choices and their consequences. The consistent selection and modification of appropriate tools intended for use in context-appropriate situations imply an understanding of task requirements among captive tufted capuchins (Westergaard and Frigaszy, 1987; Anderson and Henneman, 1994; Westergaard and Suomi, 1995). For example, evidence of conceptualization in captive capuchins has been reported in the appropriate use of stones to cut or to crack nuts (Anderson, 1990), sticks to probe or to dig for an otherwise inaccessible reward (Westergaard and Frigaszy, 1987; Anderson and Henneman, 1994; Westergaard and Suomi, 1995; Westergaard *et al.*, 1997), and paper towels to collect juice (Westergaard and Frigaszy, 1985, 1987). Moreover, a recent study by Westergaard *et al.* (1997) indicates that, in order to obtain food rewards, some tufted capuchins use tools for cutting and probing in logical sequence, i.e., tool sets. The results of this research suggest that experienced capuchins maintain mental catalogs of tools and tool techniques and are capable of matching individual strategies to their appropriate contexts.

The successful modification of tool materials provides further evidence of mental representation. The manufactured tool kits of captive tufted capuchins

include stone flake and core tools produced spontaneously by means of anvil, throwing, and hard-hammer percussion techniques (Westergaard and Suomi, 1994a; Westergaard, 1995). Stone tools and modified digging sticks are common among both wild chimpanzees (*Pan troglodytes*) (Boesch and Boesch, 1983; McGrew, 1992) and captive capuchins (Westergaard, 1994; Westergaard and Suomi, 1995). Similarities in the technologies of chimpanzees and captive capuchins include instruments and weapons produced by replication and reduction techniques (Westergaard, 1994). Due to an overall continuity in tool form, function, and manufacture, some researchers have suggested that capuchin cognition has followed an evolutionary pathway parallel to that of the chimpanzees (Parker and Gibson, 1977; Chevalier-Skolnikoff, 1989; McGrew and Marchant, 1997). In this way, studies of tool use in capuchins may offer insights into the evolutionary origins of chimpanzee and human technology (Westergaard, 1995).

Conflicting reports from researchers investigating the cognitive bases of capuchin tool use clearly indicate the need for further study. The rainforest exhibit at Monkey Jungle provided ideal circumstances in which to test questions concerning problem-solving and tool use under near-to-wild conditions. In this setting, the resident capuchins experienced many of the challenges and choices faced by their free-ranging counterparts. Field studies of tufted capuchin socioecology have revealed that a rigid dominance hierarchy dictates individual foraging success at small patches of high quality preferred foods (Janson, 1985, 1990). Under conditions of spatial/temporal resource clustering, the dominant male typically monopolizes the food patch to the exclusion of all or most group members. Since the capuchins at Monkey Jungle were never separated for individual testing, patterns of foraging success and priority of access were determined by dominance status and reflect the natural consequences of tufted capuchin social organization. Compared to Willie, Erna and Paul demonstrated less consistent successful tool use across trials. This may be the result of subordinate rank and social insecurity. Conversely, social tolerance afforded juveniles the opportunity to observe the tool-using strategies of the dominant male at close range. Although previous research has shown that tufted capuchins do not imitate the behavior of successful models (Visalberghi and Fragaszy, 1990), to some degree, the juveniles' tool-use attempts and interest in discarded tools may have been guided by social facilitation or stimulus enhancement or both. Inadequate motor control does not account for unsuccessful tool use among juveniles. Since manipulative maturity is attained during infancy (Fragaszy, 1990; Adams-Curtis and Fragaszy, 1994), practical experience and social learning may be critical to the development of tool use in juvenile tufted capuchins. Adult monkeys with no prior experience as test subjects in laboratory studies of capuchin tool use were not motivated to participate. Failure to participate may be attributed to the absence of opportunities for social learning or environmental conditions that encourage the emergence of tool use during a critical developmental phase (Janson, 1994).

Exploratory probing with tools has occasionally been observed among wild capuchins and is presumably related to insect foraging (Chevalier-Skolnikoff, 1990; Garber and Paciulli, 1997). Although in this study, honey served as the food reward, the test subjects were confronted with a similar foraging problem that required the use of natural probes. The results indicate that 3 out of 5 participants were capable of discriminating among countless objects available in a naturalistic setting and selecting ones suitable to the task. Furthermore, nearly all time that Willie, Erna, and Paul devoted to tool use involved successful probing techniques. An understanding of the physical properties of appropriate materials was also apparent in the reliable manufacture of successful tools. All observed modification strategies increased the effectiveness of tools chosen by Willie, Erna, and Paul and manufactured tools, which often required 10–15 seconds for preparation, almost always proved effective. In addition, two of the test subjects succeeded in locating and transporting tools from more distant sources out of view of the feeding site (>5 m). In keeping with earlier findings (Westergaard and Fragaszy, 1987), they demonstrated complex conceptual abilities in the anticipation of task requirements.

Among chimpanzees, representational skill is evinced by an ability to collect food-processing tools from remote sources. Under conditions of limited local availability, wild chimpanzees transport rare stone tool materials for use in hard nut-cracking activities from distances >500 m (Boesch and Boesch, 1983).

As reported by Westergaard and Fragaszy (1987), Anderson and Henneman (1994), and Boesch and Boesch (1983), out of sight does not necessarily imply out of mind. In accord with the original hypothesis, the ability to consistently select, modify, transport, and use tools appropriately supports the conclusion that some tufted capuchins mentally represent solutions to tool-related foraging problems.

Robinson (1986), Janson (1985), and Phillips (1995) provide information on the complex temporal and spatial foraging problems capuchins encounter in the wild; however, little is known regarding the degree to which solutions to these problems involve tool use (Parker and Gibson, 1977). Additional research is needed in order to identify the ecological contexts in which technical solutions to foraging problems are most commonly applied (Adams-Curtis, 1990; Fragaszy *et al.*, 1990). Since the earliest field studies of capuchin behavioral ecology, anecdotal reports have been made of their various extractive foraging techniques (Oppenheimer, 1968; Izawa and Mizuno, 1977; Struhsaker and Leland, 1977; Terborgh, 1983; Fragaszy, 1986; Fernandes, 1991). As destructive foragers, capuchins maximize the availability of embedded resources by exposing hidden food items manually, orally, and occasionally with tools. Typical methods of food procurement and preparation include biting and breaking open pieces of dead wood, stripping away tree bark, displacing stones and leaf litter, unrolling dry leaves to expose concealed insects and their larvae, and cracking open nuts and oysters by striking them against hard surfaces (Oppenheimer, 1968; Izawa and Mizuno, 1977; Terborgh, 1983). Parker and Gibson (1977) and Westergaard (1995) suggested that the

extractive foraging strategies of free-ranging capuchins are related to an ability to make and use tools in the natural habitat. In addition, accounts of tool use among wild capuchin populations are consistent with analogous behaviors observed under laboratory conditions. Reports include the use of sticks as weapons against potential predators (Chapman, 1986; Boinski, 1988; Chevalier-Skolnikoff, 1990) and as probes (Chevalier-Skolnikoff, 1990; Garber and Paciulli, 1997); shells to crack open oysters (Fernandes, 1991); nuts to crack open other nuts (Struhsaker and Leland, 1977); and leaves as sponges (Phillips, 1998). Relatively low frequencies of observed tool use among free-ranging populations of *Cebus*, however, raise doubt as to the natural expression of this behavior (McGrew, 1993). It has been suggested that habitual tool use among capuchins is strictly dependent upon captive manipulation and is therefore a contrivance of unnatural laboratory conditions (McGrew, 1993). However, poor visibility in the field may hinder observations of the rapid and intricate behaviors associated with capuchin tool use. Furthermore, due to the difficulties involved in using objects to crack hard-shelled food items while perched on a flexible arboreal support (Boesch and Boesch, 1994), wooden or stone hammers are unlikely to be found within the home ranges of wild capuchin populations.

The results of this study indicate that some tufted capuchins are capable of using tools to solve extractive foraging problems and that successful variations of these solutions can be invoked in a naturalistic environment. Since it is clear that captive tufted capuchins possess the manipulative skill and cognitive capacity to solve tool-related foraging problems, it is possible that tool use among wild capuchins is constrained by limited ecological relevance (Janson, 1994). Perhaps, in nature, the expression of this ability is restricted to environmental conditions that place a selective premium on tool-related foraging solutions. Experimental field studies designed to encourage the use of tools are needed in order to understand the natural expression of this potential. In addition, research conducted among captive populations of *Cebus albifrons*, *C. capucinus*, and *C. olivaceus* would allow for cross-specific comparisons of tool use and task-oriented problem-solving. Kinzey (1974) and Janson (1986) report specific differences in social structure, dietary specialization, and morphology, which may give rise to the expression of species-typical patterns of tool use. In this way, research conducted across species and under varying experimental conditions will contribute to a comprehensive understanding of capuchin tool use.

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