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# Capuchin Monkey Tool Use: Overview and Implications

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Nutcracking capuchins are mentioned in reports dating as far back as the sixteenth century,[1,2] as well as in Brazilian folklore.[3] However, it was barely a decade ago that primatologists "discovered" the spontaneous use of stones to crack nuts in a semi-free ranging group of tufted capuchin monkeys. Since then, we have found several more capuchin populations in savanna-like environments which employ this form of tool use.[5–7] The evidence so far only weakly supports genetically based behavioral differences between populations and does not suggest that dietary pressures in poor environments are proximate determinants of the likelihood of tool use. Instead, tool use within these capuchin populations seems to be a behavioral tradition that is socially learned and is primarily associated with more terrestrial habits. However, differences in the diversity of "tool kits" between populations remain to be understood.

Capuchins have long been known for their ability to crack open hard-shelled fruit by pounding it against a hard substrate,[8,9] as well as for their capabilities for complex object manipulation in laboratory settings.[1,10] The complex manipulation of objects, though, was considered to some extent to be an artifact of captive conditions. The use of objects such as hammers to open nuts, for instance, was experimentally induced in captive capuchins, but not expected in the wild because New World monkeys were thought to be entirely arboreal.[11] However, wild capuchins can be quite terrestrial at times; they are able to walk bipedally and carry objects in their hands.[5,12] While there have been no reports of tool use by rainforest-dwelling tufted capuchins, both indirect evidence[13] and anecdotal reports[14] indicate the use of tools to access encapsulated food by tufted capuchins living in other habitats.

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More recently, the regular use of stones for nutcracking, as well as some other forms of tool use, have been found among wild capuchin groups inhabiting savanna-like environments in central and northeastern Brazil.[5–7] The first systematic observations of tool use by noncaptive capuchin monkeys focused on semi-free groups in urban parks.[15,16] For the last decade, we have studied the spontaneous stone-aided cracking of palm nuts by a group that has been living for more than 20 years in the Preservation Area of the Tietê Ecological Park in São Paulo, SP, Brazil. The animals are provisioned daily, but also forage for naturally available resources like fruit, invertebrates, and small vertebrates.[17,18]

## TOOL USE AND SOCIAL INFORMATION TRANSFER BY SEMI-FREE CAPUCHIN MONKEYS

Most mature individuals in the Tietê group crack nuts, although with variable frequency and efficiency. Among the few individuals who did not crack nuts, most were females and, more recently, a pair of immigrant subadult males that transferred into our study group. One of these males, after watching nutcracking episodes for some months, started to exhibit stone-beating behaviors without nuts and to scrounge the leftovers of efficient nutcrackers. Even with the handicap of being less tolerated than other individuals, this newcomer (but so far not the other) started cracking nuts properly after two years, about the same time it takes for juveniles born in nutcracking groups.

Young infants manipulate objects, including stones, by beating them against a substrate. One-year-olds often attempt to crack nuts. However, the proper coordination of movements and positioning of nuts, "hammer" stones, and "anvils" (any hard and level substrate) is not usually reached until the third year of life (Fig. 1).[19] From an early age, though, capuchins are keenly interested in nutcracking by other individ-

Figure 1. Stone-aided nutcracking. A. Boa Vista. B. Tietê Ecological Park (photos by T. Falotico). (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

uals. As in chimpanzees,[20] conspecific observers are typically younger than the observed nutcrackers, but the role of the mothers as models is much less marked, as capuchin infants and juveniles may watch other juveniles or adult males. The food-related activities of the dominant males tend to be quite attractive.[21]

The conspecific observers of nutcracking events, usually younger and less proficient, are well tolerated by the nutcracker. Some scrounging by the young observer is allowed (Fig. 2). Some of our findings imply an active, nonrandom choice of observational targets. Observers preferentially watch the more skilled nutcrackers,[22] probably because such selective attention is likely to enhance scrounging payoffs, which in turn facilitates social learning opportunities. If encapsulated fruit constitutes a seasonal key resource that allows the occupation of drier, savanna-like environments, then tolerance of scrounging by immature individuals that cannot extract fruit by themselves is a necessity. Any changes in social dynamics toward more tolerant societies may thus have had a high adaptive value, even before the advent of tool-aided forms of extractive foraging (Box 1).

We propose that scrounging, as a proximate motivation, optimizes the conditions for social learning of nutcracking techniques. Earlier laboratory studies led to the view that scrounging inhibited or prevented observers from learning the foraging techniques of proficient individuals,[23–25] but the opposite has been found in more recent studies with marmosets[26] and orangutans.[27] These more recent results suggest that correlations between scrounging and learning will vary as a function of many factors, such as the nature of the interaction between producers and scroungers, the relative scrounging or producing payoffs, and the potentially distracting aspects of the setting. Another important point about this hypothesis is that it demon-

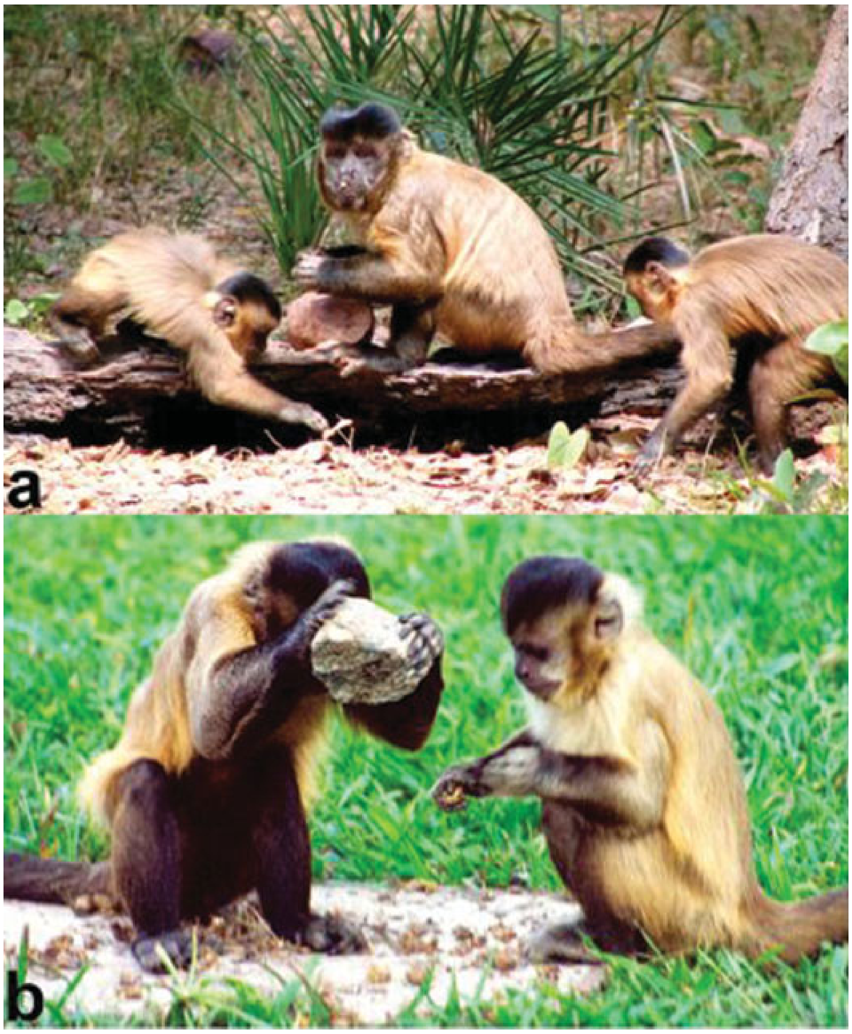

Figure 2. Nutcrackers and scroungers. A. Dominant male and scroungers, Boa Vista, Piauí (photo by T. Falotico). B. Adult male and juvenile male scrounger, Tietê Ecological Park (photo by B. D. Resende). (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

strates how relatively simple individual cognitive processes, such as the association between different observational "targets" and scrounging payoffs, can optimize conditions for the propagation of behavioral traditions.

## MAPPING THE REPORTS OF TOOL USE BY CAPUCHIN MONKEYS

Four species of tufted capuchins are currently recognized[28]: *C. apella, C. nigritus, C. libidinosus*, and *C. xanthosternos*. While some forms of complex manipulation in the extraction of palm pits have been observed among forest-living *C. nigritus,*[29] as well as in palm-nut smashing Amazonian *Cebus apella*,[8,9] there have been no reports of tool use, as defined by Beck,[30] in these populations (Fig. 3). There has been only a single anecdotal observation of tool use in the wild among the Central American *C. capucinus*,[31] for which behavioral traditions have been described in dietary preferences[32] and social conventions.[33] Indirect evidence of tool use (nutcracking sites) by *Cebus xanthostemos* from the Chapada Diamantina (State of Bahia, Brazil) has been reported.[34] There also is one report of the use of bait to catch fish by a captive of this species.[35]

Most accounts of tool use by wild populations involve groups of *C. libidinosus*, which live in the open habitats of the Brazilian *cerrado* and *caatinga*, which are dry thornbush, savanna-like environments. This species is more terrestrial than are other capuchin populations. Indirect evidence of the use of stones in nutcracking by wild *C. libidinosus* was first reported in the primatological literature in 1997 for a population living near Desterro do Malta (State of Paraíba, Brazil).[13] Direct observations of such behavior were later registered by Fragaszy and coworkers[5] for a population in the Fazenda Boa Vista (Gilbués, State of Piauí). Since then, there has been a growing number of reports from other *cerrado* areas in central Brazil.[36,37] Stone-aided cracking of encapsulated food has also been observed, along with other forms of tool use, at another site about 400 km from the Fazenda Boa Vista. Groups of *C. libidinosus* at the Serra da Capivara National Park (São Raimundo Nonato, Piauí) use stones to dig the soil for tubers and cut wood for insects and larvae.[6,7] Individuals in this population have also been observed to use sticks as probes to access food or water in cracks, holes, or insect nests. The use of these stick tools, like that, observed among chimpanzees and captive capuchins,[10] involves some preparation or modification. Stick tools are not only cut from trees and resized when necessary, but some are also trimmed to remove leaves and side branches. In a few cases, the thinning of the distal extremity was registered. This enhanced "tool kit" favors the emergence of more complex behavioral patterns, such as the combined (sequential) use of stones and sticks in the exploration of dead trunks for insects.[7]

## EXPLANATIONS FOR GEOGRAPHIC VARIATION IN TOOL USE

The intensive, plastic, and sometimes complex object manipulation and the use of hard substrates for cracking encapsulated fruit, though not the use of tools (*sensu stricto*)[30] seem to be "taxon-specific" behavioral patterns for tufted capuchin monkeys. In the search for causes of the dissemination of tool use in foraging among some capuchin populations, explanations based on genetic and/or ecological determinants shap-

### Box 1. Encapsulated Food, Scrounging, and the Evolution of Social Tolerance

Searching for general patterns to explain the distribution of the occurrence of tool-use traditions among primates, van Schaik, Deaner, and Merrill,[61] proposed a model based on three major factors: species-specific predispositions such as high encephalization and hand dexterity, the critical reliance on encapsulated food, and a degree of social tolerance that allows less-experienced individuals to watch proficient tool users at work. As Coussi-Korbel and Fragaszy[67] pointed out, the closer an individual is allowed to stay near a conspecific, the more likely it is to be able to observe the other's behavior in detail.

This model seems to fit the available data on tool use by apes quite well and has proved its predictive value in the case of tufted capuchins. Until recently, there was no strong evidence of spontaneous tool use in free-ranging capuchin populations, but van Schaik, Deaner, and Merrill[61] argued that, even lacking the insight and efficient observational learning capabilities of great apes, "*it is theoretically possible ... that a socially tolerant monkey population will be found in which routine use of feeding tools occurs, especially if the skills used are close to naturally occurring operants, and if opportunities for would-be learners are abundant*."

On the other hand, Kummer and Goodall[62] emphasized the greater opportunity for innovative behavior in animals less socially constrained, such as those foraging alone or in small groups. As Boinski and colleagues[63] pointed out, this is the case for the less-tolerated young adult male tufted capuchins, so their society may represent a "propitious balance" between these factors facilitating both innovation and social transmission.

We believe that this model, in which social dynamics join individual genetically determined cognitive and motor capabilities on one hand and ecologically determined pressures and affordances on the other, is a truly insightful one. However, we propose a "positive feedback loop" in the relationship between extractive foraging and social tolerance. All available evidence suggests that reliance on encapsulated food is a common feature in all tufted capuchin populations and therefore precedes the use of tools, although these may greatly reduce the costs of accessing this kind of food and broaden the range of accessible items. While it is generally accepted that capuchin abilities for extractive foraging enable them to occupy a much wider range of habitats than does the average New World monkey, some developmental constraints are usually overlooked.

If encapsulated fruit constitutes a critical resource for the survival of a given population, and if food selection and processing techniques take some time to be learned, with or without any socially mediated shortcuts to individual trial-and-error learning, there must be a "contingency strategy" whereby weaned infants can survive until they can forage autonomously (assuming that access to these encapsulated foods is critical for immature individuals). Even if extractive techniques were completely innate and not dependent on any kind of learning process, there would be a mechanical issue because infants lack the necessary strength, with or without the aid of tools, to open hard-shelled nuts or similar items. Therefore, adaptations for extractive foraging depend on some associated social features favoring food sharing with youngsters, minimally in the form of tolerated scrounging. Tolerance for scrounging could, therefore, set the stage for the subsequent establishment of tool-use traditions in a sort of "positive feedback."

This hypothetical scenario bears some resemblance to one of the possible causes of cognitive evolution in the human lineage proposed by van Schaik and Pradhan[64]: An increase in sociability during foraging (communal hunting or scavenging) would, *per se*, increase the probability of the social diffusion of the use of tools independently of any immediate changes in cognitive capacities. The subsequent acquisition of more complex skills, however, would raise the selection pressures favoring the evolution of more complex cognitive abilities.

ing individual behavior could, in principle, suffice. However, the available evidence from laboratory experiments and developmental studies in semi-free ranging populations suggests otherwise. Food scarcity in some habitats probably plays an important role in the exploitation of encapusulated food by capuchins, but seems less likely to explain the presence or absence of tool use in any given population. Even though the occurrence of tool use in groups from savanna-like environments, together with its apparent absence in forest populations, has led some authors to propose a food-scarcity explanation,[6] other evidence, such as the absence of tool use in forest areas during periods of food scarcity[38,39] point to other proximal causes. The most intensive use of tools has been observed among semi-free groups living with some degree of provisioning,[4,40] low predation risk, and high levels of terrestriality. A strong association between these factors and both tool use and the frequent use of bipedal postures in the transport of food and tools (Box 2) is suggested by our preliminary surveys. This leads us to favor the degree of terrestriality, instead of food scarcity, as the strongest predictor of tool use, especially nutcracking, by capuchin populations.[41,42]

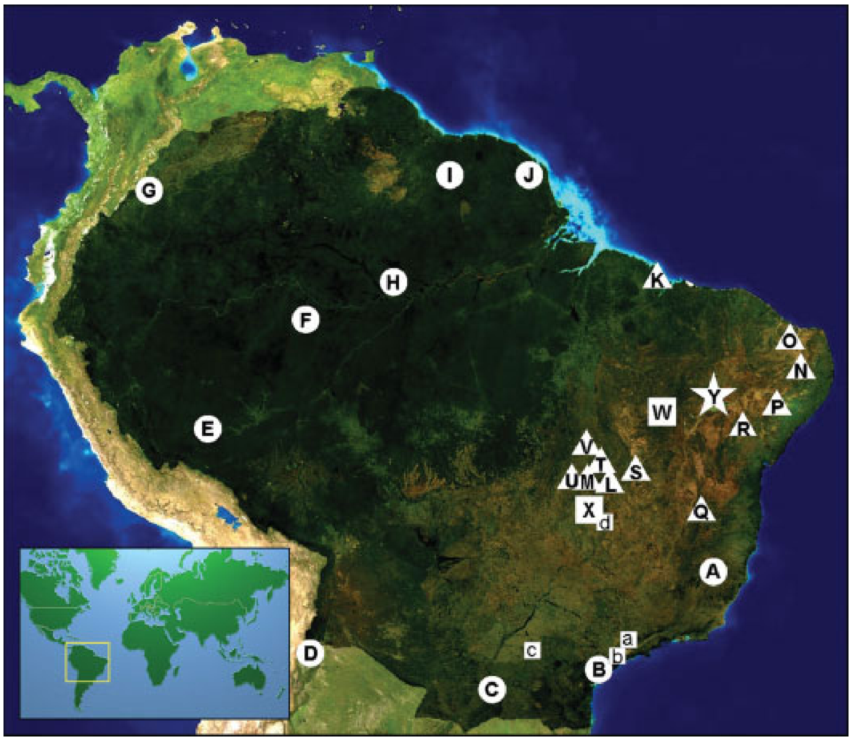

Figure 3. Distribution map of reports on spontaneous tool use by wild and semi-free tufted capuchin monkeys. ●: Negative reports on tool use by wild populations under long-term studies (though with anecdotal evidence of complex object manipulation in foraging contexts). A: Caratinga Biol. Station, MG, Brazil;[68] B: Carlos Botelho State Park, SP, Brazil;[38] C: Iguazú Nat. Park, Argentina;[69] D: El Rey Nat. Park, Argentina;[70] E: Cocha Cashu Biol. Station, Peru;[71] F: Urucu River, AM, Brazil;[72] G: La Macarena, Colombia;[8,9] H: BDFF Project, AM, Brazil;[73] I: Raleighvallen, Suriname;[74] J: Station des Nouragues, French Guiana.[75] ▲: Wild groups with only indirect evidence (cracking sites) or anecdotal observations of tool-aided cracking of encapsulated food. K: Canelatiua, MA, Brazil;[14] L: Alto Paraíso, GO, Brazil;[37] M: Serra da Mesa, GO, Brazil;[76] N: Desterro do Malta, Paraíba, Brazil;[13] O: Martins, Rio Grande do Norte, Brazil;[77] P: Belo Monte, Alagoas, Brazil;[34] Q: Varzelândia/Montes Claros, Minas Gerais, Brazil;[34] R: Itiúba/Ibotirama/Contendas do Sincorá, Bahia, Brazil;[34] S: Terra Ronca Nat. Park, GO, Brazil;[36] T: Minaçu, GO, Brazil;[36] U: Mara Rosa, GO, Brazil;[36] V: Peixe, TO, Brazil.[36] ■: Wild or semifree populations with customary use of stone tools in nutcracking. *Small squares* - semifree groups in urban parks. a: Tietê Ecol. Park, São Paulo, SP, Brazil;[4] b: Jaraguá State Park, São Paulo, SP, Brazil;[40] c: Arthur Thomas Mun. Park, Londrina, PR, Brazil;[16] d: Agua Mineral Park, Brasilia DF, Brazil.[78] *Big squares* - wild groups. W: Bao Vista, PI, Brazil[5] and X: Brasilia Nat. Park, Brazil.[79] ★: Wild groups using stone tools (for cracking fruit, digging and cutting), and stick probes (sometimes combined). Y: Serra da Capivara, PI, Brazil.[6,7] **Dark area:** general distribution of tufted capuchins. A-D: *Cebus nigritus*; E-K: *C. apella*; L-P, S-Y: *C. libidinosus*; Q-R: *C. xanthosternos*; a-d: hybrid or uncertain (urban parks).'' (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

The current data on tool use by wild groups of tufted capuchins clearly documents *C. libidinosus* and, perhaps, *C. xanthostemos* as regular tool users, indicating that genetic differences could account for the observed geographic variation. However, we believe that the associated environmental differences can better account for these differences. The hybridization frequently encountered in the semi-free study groups is apparently not correlated with any noticeable individual differences in the rates or performance of tool use. Furthermore, no behavioral differences have ever been reported from captive or wild groups that could be traced to intrinsic characteristics of the different species of tufted capuchin.

The cracking of encapsulated food with the use of stones is clearly the most widely occurring form of tool use, being present in the "tool kit" of all known tool-using capuchin groups. On the other hand, the customary use of sticks as probes in natural settings has so far been documented only among the Serra da Capivara groups. Of course reports based on indirect evidence could generate a bias toward stone-aided nutcracking, since probing sticks do not usually leave such evidence.

The apparent differences in the "tool kits" and techniques of the two wild populations of *C. libidinosus* currently under study (Fazenda Boa Vista and Serra da Capivara) are a major point to be investigated. There are many environmental dissimilarities, especially concerning the availability of potential "hammers," but they can hardly account for all the observed variation, there are preliminary reports of possibly relevant differences in techniques between groups in the Serra da Capivara.[7]

## BEHAVIORAL VARIATION AND TRADITIONS IN NONHUMAN ANIMALS

The existence of behavioral traditions in animals has been proposed in domains like social dynamics and structure,[43,44] communicative behaviors,[33,45–47] foraging techniques, and dietary preferences.[32,45,48,49] But the permanence of a particular behavioral pattern in the repertoire of an animal group is always the product of interplay between genetic and environmental (social and nonsocial) factors. To uphold explanations focusing on the role of social information transfer in behavioral intergroup differences and intragroup similarities, comparative studies have tried to rule out obvious genetic factors ("innate" differences between subspecies or populations) as well as particular environmental pressures and affordances[50] as potentially sufficient causes.

The reviews by Whiten and coworkers[45] and van Schaik and colleagues[46] on behavioral variation among wild chimpanzees and orangutans, respectively, made it possible to look at capuchin tool use with a new perspective. Behavioral patterns

## Box 2: Bipedalism and the Transport of Tools

Jalles-Filho and collaborators[65] questioned the usefulness of capuchins as models for early human tool use based on experiments in which captive subjects failed to transport stone tools. However, more recent studies have shown that under some experimental circumstances captive capuchins will transport tools.[66] Caged animals can use cement floors as "anvils," so cracking sites can be found anywhere. The wide availability of cracking sites in captivity makes it easier and safer to carry the nuts to the "hammers." In natural settings, hard, flat anvils are usually immovable and less abundant, so the hammers have to be transported at least once. In our own experimental interventions in spontaneous nut-cracking by the semi-free Tietê group,[12] the monkeys readily searched for hammer stones and bipedally carried them (Fig. B1) to the anvils when needed, frequently carrying the nuts simultaneously. The pattern seems to be the same in the wild. In Serra da Capivara, potential hammer stones such as quartz pebbles are abundant, but in Boa Vista,[5,42] they have to be transported for some distance when new cracking sites are established. Stick probes in Serra da Capivara[7] are always carried to their places of use.

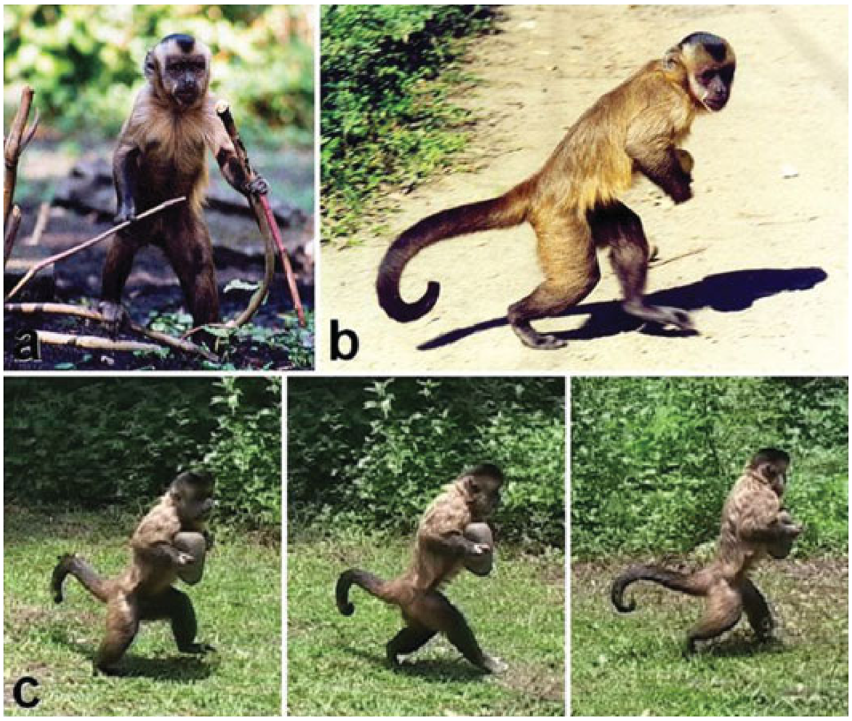

Figure B1. Bipedalism and transport of stone tools (Tietê Ecological Park). A,B. Juvenile males; C. Adult male (A, photo by B. D. Resende; B, C, photos by T. Falotico). (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

Whether or not capuchins can be useful models for the early stages of human technological development depends on the particular questions being examined. Nevertheless, the apparent relationships among the occupation of open, savanna-like environments by a socially tolerant, highly encephalized monkey, the evolution of anatomical adaptations for bipedalism, and the advent of tool use should certainly catch the attention of anthropologists concerned with early hominin tool use and cognitive capacities.

not easily reduced to genetic or ecological determinants were found in tool use, food preferences, communicative gestures, bodily care techniques, and the possible use of medicinal plants. It has been pointed out[51,52] that this "ethnographic" approach cannot prove or disprove that any given behavior constitutes a tradition, not only for being prone to false negatives and false positives,[53] but mainly because it does not take into account the role of social influences on individual acquisition of the behavior in question. These social influences, though, are usually difficult to measure in the field. Here lies the importance of the controlled conditions provided by the laboratory or the near-optimal observational conditions in studies of semi-free ranging groups.

The overall spatio-temporal patterns revealed by comparative studies can be useful in many ways.[54] First, they show us which behaviors are species-typical and which are rare or unique to particular populations. This information can guide investigative strategies. Second, these patterns can help to identify correlations between behavioral traits and prominent genetic or ecological factors such as subspecies' distributions or very different environments. Sometimes they can also help in the detection of tell-tale clues of socially influenced behaviors, such as behavioral discontinuites associated with geographical barriers to intergroup diffusion.[45,46] Moreover, when there is already evidence from developmental studies of social influences on learning, as is the case with tool-aided nutcracking by capuchin monkeys, mapping the occurrence of such behaviors across populations can help us to formulate and test hypotheses about the origins and diffusion histories of particular behavioral patterns.

## IMPLICATIONS FOR UNDERSTANDING THE EVOLUTION OF HOMININ TOOL USE

Although fascinating in and of itself, the research on tool use by tufted capuchins can also provide useful insights to researchers concerned with human evolution. Paleoanthropologists attempt to model early hominin behavior by means of a phylogenetic approach, using the great apes, especially chimpanzees, as a paradigm, or by using the principles of primate socioecology that relate diet, food distribution, and features of social systems.[55] Paleoclimatic and paleobiological data help to reconstruct the features of hominin habitat, including the likely distribution of plant and animal species that could have been part of their diet.[56] Diet can be inferred by comparing certain anatomical features, particularly teeth, with those of extant primates with known diets.

These lines of evidence have indicated that early australopith diets included soft fruit as a preferred food, complemented with nuts, seeds, and underground storage organs.[57] There is also evidence that these food items could have been extracted with the use of stone tools.[58] Recently, Laden and Wrangham[59] suggested that *"the patterning in the early hominid fossil record, such as the existence of gracile and robust australopiths, may be understood in reference to an adaptive shift in the use of underground storage organs."*[59] However, the social consequences associated with such a shift are unknown. The strong reliance on roots and tubers extracted with digging stones by the tufted capuchin monkeys of Serra da Capivara offers a unique opportunity to address this issue. Moreover, studies comparing tool-use and the absence of tool use in populations of tufted capuchin monkeys may provide insight into the impact of the use of foraging-associated tools on primate sociality.[60] Indeed, the emergence of stone tool use by these highly encephalized monkeys in the occupation of savanna-like environments, as well as the associated bipedal transport of tools and food, suggest that capuchins may offer a new perspective on the roles of phylogeny, ecology, foraging strategies, terrestriality, and tolerance in the evolution of technology, cognition, and sociality in the human lineage.

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