

SOCIAL LEARNING, BEHAVIORAL TRADITIONS, AND THE EVOLUTION OF SOCIALITY IN NON-HUMAN ANIMALS: THE CASE OF TUFTED CAPUCHIN MONKEYS

Eduardo B. Ottoni and Tiago Falótico

Social learning, behavioral traditions, and cultural processes in non-human animals

The recognition of social learning as an important adaptation even among non-human animals was already explicit in the works of Darwin and Wallace (and, of course, Romanes), and became hard empirical science more than half a century ago, with the research on bird-song learning (Marler 1970). The notion of ‘animal cultures,’ although floating in our ‘meme pool’ since then, and being the focus of a growing number of conferences and reviews, remains, to say the least, a contentious question, plagued by definition issues.¹

In one extreme view, many cultural anthropologists adhere to variants of Tylor’s definition of culture (1871, apud Hutchins 1995) as “that complex whole which includes knowledge, belief, art, morals, law, custom, and any other capabilities and habits acquired by man as a member of society.” In this sense, *culture* and *civilization* were synonyms – and being something acquired *by man* was part of the definition.

At the other end of the spectrum, many biologists would equate *culture* to social learning or social information transfer in general.

But even anthropologists studying behavioral traditions in non-human primates under a clearly evolutionary framework may disagree on this ‘broader’ use of the term *culture*. Susan Perry (2011) documented a complex repertoire of conventional, group-specific social rituals of white-faced capuchin monkeys (*Cebus capucinus*), apparently designed to test the strength of social bonds, but she refrains from labeling them “cultural,” considering that “culture” involves more than geographically variable traits, or even social learning – including things like “group identity,” symbolically linked to socially learned traits, and “social norms” (though she does not dismiss the possibility of finding evidence of such features in non-human societies; cf. Perry 2009).

The term *traditions*, preferred by Perry and others, besides avoiding the more ‘loaded’ meanings associated with *culture*, allows for a more ‘operational’ definition that can be of practical use by animal behavior researchers.² As defined by Fragaszy and Perry (2003), “a tradition is a behavioral practice that is relatively enduring... that is shared among two or more members of a group, and that depends in part on socially aided learning for its generation in new practitioners.”

¹ A full discussion of these issues would be beyond the scope of this chapter. For a recent overview on ‘culture wars,’ see Laland and Galef 2009a, 2009b.

² But, as McGrew (2003) notes, “tradition” suggests vertical transmission (as well as “relative endurance”), and cultural transmission includes short-lasting, horizontally transmitted “fads.”

We can also think about *culture* as the overall extra-genetic channel of social information transfer (in a counterpoint to *genetics*, as in the *gene-culture coevolution* or *dual inheritance* approaches; cf. Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), and *traditions* as particular behaviors acquired through socially biased learning.

One common understanding is that culture depends on language. Apes in captivity apparently mastered symbolic languages to a certain extent (Gardner et al. 1989; Savage-Rumbaugh et al. 1989), as did African grey parrots (Pepperberg 1994), and functional referentiality was experimentally demonstrated in the alarm calls of wild vervet monkeys (*Chlorocebus pygerythrus*; Cheney and Seyfarth 1990). Hauser et al. (2002), reviewing Chomsky's claims on the unique nature of human language under the light of recent evidence on animal communication, concluded that it is only our capacity for *recursion* (which allows for complex syntax and second- or n-order intentional statements) that sets human language apart from communication in non-humans. We do not know enough, yet, about how complex the communication in other species can be, but, anyway, "communicative language may be a sufficient condition for culture, but not a necessary one" (McGrew 2003) – at least if we are willing to drop the 'symbolic' part of the definition.

Michael Tomasello (1999), a psychologist who studies both children and chimps, believes that social learning in non-humans is a product of simpler cognitive processes, such as stimulus enhancement (i.e., socially biased learning about environmental features), while imitation in humans makes copy fidelity, and, as a consequence, the emergence of cumulative culture, possible.³ Underlying human complex imitation, for him, is the capacity for "joint attention" – which requires the possession of a Theory of Mind (ToM; cf. Premack 1988).

In this view, culture is usually associated with *teaching*. Many animals alter their behavior to facilitate learning by immatures (Terkel 1996), which is usually called *scaffolding*, and, in some cases, they seem sensitive to feedback – as the adult meerkats who apparently adjust their behavior to the changes in the proficiency of pups, while handling scorpions as prey (Thornton and McAuliffe 2006; in this report, the term *functional teaching* was employed; *teaching* in its stricter sense, though, implies a ToM, to allow for the understanding of other individual's ignorance). Moreover, human teaching may constitute a unique adaptation enabling social learning by communication (especially useful for things like conventions, arbitrary referential symbols, or cognitively opaque skills), a "natural pedagogy" (Csibra and Gergely 2011).

Behavioral traditions and cultural processes in non-human primates

The provisioning of free-ranging Japanese monkeys (*Macaca fuscata*) near beaches triggered a series of unexpected behavioral "innovations:" the most notorious, introduced by a juvenile female, consisted in washing potatoes in a stream to remove the sand (Kawai 1965). This new food washing technique was followed by two other: the washing of provisioned wheat (which floats, while the sand sinks), and the washing of potatoes in salty seawater, "seasoning" them. The enhanced activity by the beach set the conditions for another innovative behavior, the consumption of the smaller fish left over by fishermen. All these

³ Although Tomasello et al. (1993) recognize imitative capacities in chimpanzees.

innovations spread in the monkey groups following patterns predictable from their network of social relationships and became established in these populations, apparently, through socially aided learning (Huffman 1996).

Though Japanese primatologists had long before proposed the existence of cultural processes in non-human primates (Imanishi 1952, apud Huffman 1996; Nishida 1987), it took some decades more until the dichotomous Western view on the relationship between Nature and Culture made room for an evolutionary approach to social information transfer in non-human animals.⁴

But even Imanishi did not use the Japanese word for *culture*, instead he used a neologism based on the English word, and those early studies on Japanese monkeys' socially learned behaviors (Kawamura 1959; Kawai 1965) employed the term *sub-culture*, to avoid equating monkeys' social learning with *human culture*. Afterwards, most researchers studying behaviors that seemed to be perpetuated in an animal population by some form of social transmission referred to them as "sub-," "pre-" or "proto-cultural."

A change in this attitude started, fundamentally, as a consequence of the outcome of long-term field studies such as Goodall's (van Lawick-Goodall 1970), which showed us an unexpected level of complexity in the social life (and social cognition) of great apes in general, and chimpanzees (*Pan troglodytes*) in particular (Wrangham et al. 1994). Besides the social "manipulations" in their "political" life (also described in captivity by de Waal 1982, 1989), we are now well-familiarized with a wide range of objects modified and used as tools by wild chimpanzees. And as happens with some other behavioral patterns (see ahead), many of the variations among populations in their tool use repertoires cannot apparently be explained by ecological or genetic differences alone.

In 1978, McGrew and Tutin reported their first observations about the "grooming hand-clasp," a communicative gesture present in one chimpanzee population but absent in another (variations were later found in other groups), an apparently arbitrary behavior that seemed to satisfy most operational definitions of culture. McGrew (1992) subsequently showed that many behaviors in the wild chimpanzees' repertoire satisfied the "criteria for recognizing cultural acts" proposed by Kroeber (1928, apud McGrew 1992), and initiated a trend of dropping qualifiers such as "sub-" or "proto-," especially when talking about chimpanzees (Laland and Galef 2009b).

The potential role of social information transfer in the diffusion of some complex foraging techniques by wild chimps was brought into evidence by McGrew's "Chimpanzee Material Culture" (1992), where a comparative overview of data from many field studies showed a degree of sophistication and of interpopulation variation so far unexpected in non-humans,

⁴ This "evolutionary view," it must be noted, can assume very distinct forms: if under an extreme sociobiological version (Dawkins 1976) a clear dichotomy between "replicators" (genes or "memes") and their "vehicles" is preserved, in models conceiving the relations between genetic inheritance and behaviorally transmitted information as a "dual inheritance" (or "gene-culture coevolution;" cf. Boyd and Richerson 1985) system or through "niche construction" processes (Odling-Smee 1996; Laland et al. 2000), the distinctions between evolution and ontogeny become much fuzzier, since behavioral traditions, even though being products of a species' evolutionary history, can only be established and transmitted if actively built during individual and group histories (Avital and Jablonka 2000).

suggesting, beyond ecological determinants or “innate,” “species-typical” behavioral patterns, a critical role of socially biased learning in individual ontogenetic development.

These hypotheses gained strength from laboratory evidence showing that the observational learning capabilities of chimps go beyond “stimulus enhancement,” to include, for instance, the ability to reproduce different sequential steps in the opening of a problem box, as demonstrated by different models, conspecifics or not (Whiten et al. 1996), the so-called “program-level imitation” (Byrne and Russon 1998), which amounts to learning about the behavior of another individual (and not only about its final product). More recently, experiments with captive chimpanzee groups (Whiten et al. 2007) on the diffusion of alternative techniques for extracting food from problem boxes demonstrated the effects of social biases (observed techniques exhibited by the models) on the individual learning of the task.

The existence of behavioral traditions has, since then, been proposed in many taxa, from apes, cetaceans, and elephants, to birds and fish, and in distinct domains, such as social structure and dynamics (de Waal and Johanowicz 1993; Sapolsky and Share 2004), social knowledge (McComb et al. 2001; Bradshaw et al. 2005), communicative behavior (Whiten et al. 1999; Rendell and Whitehead 2001; van Schaik et al. 2003; Perry et al. 2003), foraging techniques (with and without tool use), dietary preferences (McGrew 1992; van Schaik et al. 1996; Whiten et al. 1999; Panger et al. 2002), and migration routes and schooling sites (Helfman and Schultz 1984). And in most of these studies, the use of the label *culture* became increasingly more commonplace.

Interestingly (and counterintuitively), the current evidence for culture is stronger for “humans plus a handful of species of birds, one or two whales, and two species of fish” (Laland and Hoppitt 2003) than for apes (in part because the critical experimental tests would be more problematic with primates than with fish, for both practical and ethical reasons).

Genetic, ecological, and social determinants of behavioral variability in non-human animals

The permanence of a given behavioral pattern in the repertoire of an animal social group is always the outcome of the interaction of genetic and environmental (social and asocial) factors; it can remain constant for generations as a consequence of (1) predominantly endogenous characters (genetically transmitted), (2) similar histories of interaction with the environment, or (3) by the transmission of these patterns through interactions between individuals. Galef (1976) operationally defined *social transmission* as involving only cases where social interaction is *sufficient* for the acquisition of the behavior (but not *necessary*, as in certain interactions that are fundamental for the normal ontogenetic development of the species), constituting an alternative to the direct interaction between the individual and the environment, and promoting a greater behavioral homogeneity that lasts longer than the receptor–transmitter interaction.

The synthesis of comparative studies on behavioral variability among chimpanzee populations came in Whiten et al.’s (1999) overview on “cultures in chimpanzees,” which mapped the occurrence of 65 behavioral patterns throughout the natural distribution range of *Pan troglodytes*. It was not just about ‘material culture’ anymore since the list of behaviors was not restricted to the use of objects, and was directly inspired by Galef’s model: to uphold expla-

nations centered on the role of social information transfer in order to account for intergroup differences and intragroup similarities, this comparative study tried to sort out differences explainable by genetic differences (when observed in transition areas between subspecies, suggesting possible ‘innate’ differences between them), or by particular environmental pressures or affordances (related, for instance, to availability, or to the absence of the *necessary* environmental elements), which could constitute potentially *sufficient* explanations.

Whiten et al.’s (1999) study allowed us to see behavioral variability among wild chimps’ populations under a new light: behavioral patterns not easily explained away by genetic or ecological determinants were found not only in tool use and other food acquisition and processing techniques, but also in dietary preferences, communicative and affiliative gestures, body care, and, possibly, in the use of medicinal plants.

The notion of cultural traditions among hominoids gained strength after the discovery of the use of tools by a few populations of orangutans (*Pongo pygmaeus*; van Schaik et al. 1996): even though this species is very dexterous in captivity settings, tool use by wild groups was observed only under very particular conditions of gregariousness and social tolerance.

It was pointed out, though (Fragaszy and Perry 2003), that this “comparative” (sometimes called “ethnographic”) approach cannot prove nor falsify claims that any given behavior constitutes a *tradition*, not only because of being prone to “false negatives” or “false positives” (see, for instance, Humle and Matsuzawa 2002), but, first of all, because it does not take into account what should be the critical evidence to label any given behavior as *traditional*: an effective role of social influences in its acquisition by individuals. The “process model” proposed by Fragaszy and Perry (2003) aims to locate traditions in a tridimensional space whose axes correspond to its duration in time, the proportion of the population exhibiting it, and the contribution of social influences in the generation of new practitioners.

These social influences, though, are generally hard to measure in naturalistic research – and here lies the importance of the controlled conditions provided by the laboratory, or the more favorable conditions offered by the observation of semi-free populations.

The general spatial and temporal patterns revealed by comparative studies, the above-mentioned caveat notwithstanding, can be useful in many ways (van Schaik 2003). Firstly, they tell us which behaviors are species-typical, and which are rare or only observed in particular populations: this information can guide our investigation strategies. Secondly, these patterns can help us to identify correlations between behavioral characters and prominent genetic or ecological factors. Sometimes, they can also help in the detection of telltale clues of socially influenced behaviors, such as behavioral discontinuities associated to geographical barriers preventing intergroup diffusion (Whiten et al. 1999; van Schaik et al. 2003). Studies like Biro et al. (2003) highlight the usefulness of combining approaches (comparative, ontogenetic, and experimental) when dealing with cultural innovation and transmission processes by non-human primates in the wild.

Tool use and social traditions in non-human animals

On the one hand, communicative behaviors such as chimps’ “handclasp grooming” or white-faced capuchins’ “social rituals” (Perry 2011) have the useful quality of being apparently

free from ecological constraints. On the other hand, behavioral patterns involving the use of objects as tools, though evidently more prone to biases related to environmental constraints and affordances, usually have the nice qualities of being quantifiable in their costs and benefits, and of leaving physical remains which are measurable and comparable and which tend to last longer than the behavior itself (with relevant consequences for both potential conspecific apprentices and human researchers).⁵ Being so, it is not surprising that, as happened in the study of the behavior of extinct hominins and early humans, tool use has played a prominent role in the study of animal traditions.

Tool use was once strictly associated with (human) culture and seen as a defining feature of our species (“Man, the toolmaker;” Oakley 1949). Nevertheless, depending on the breadth of the assumed definition, the scenery on animal tool use changes. Considering spider webs as tools could seem appropriate (even though webs are not ‘detached objects’), while including, say, feces thrown by arboreal animals on potential predators (Chevalier-Skonikoff 1990) might be stretching the concept too much. In our research, we adopted Beck’s classical definition of tool use as “the external employment of an unattached object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.”⁶ For a recent discussion and a proposed definition that includes the mediation of the information flow between organism and environment (and not only changes in physical properties of objects), see St. Amant and Horton (2008).

Tool use does not necessarily require complex cognition or social learning – it can result from quite stereotyped and generalized, species-specific (or “context-specific;” cf. Parker and Gibson 1977) behaviors, such as the quartz-pebble-enhanced traps of *Ariadna* spiders (Henschel 1995) –, which is quite distinct from the creative tool-aided problem-solving strategies exhibited by captive apes (Köhler 1925).

Reports of simple forms of plastic tool use in the literature include, among other species, bottlenose dolphins (Krützen et al. 2005), Asian elephants (Hart et al. 2001), otters (Hall and Schaller 1964), beavers (Thomsen et al. 2007), Egyptian vultures (van Lawick-Goodall and van Lawick 1966), woodpecker finches (Eibl-Eibesfeldt 1961), and even octopuses (Finn et al. 2009) – leaving aside the reports about captives in many taxa. In recent years, the literature highlighted the complex cognitive capacities of corvids, including the use of tools by New Caledonian crows (*Corvus moneduloides*) that produce “hooks” and other kinds of modified objects to probe into tree branches’ holes for larvae (Hunt 1996; Hunt and Gray 2004).⁷

⁵ Including the prospect of a new field of *primate archaeology*, proposed by Haslam et al. 2009.

⁶ Beck (1980, apud its updated and revised edition: Shumaker, Walkrup and Beck 2011) provides an extensive review on tool use by animals. Alcock’s (1972) similar definition, based on Goodall’s (1970), refers to the “manipulation of an inanimate object, *not internally manufactured*, with the effect of improving the animal’s efficiency in altering the position or form of some separate object,” which thus excludes things like spider webs. And all these definitions exclude the quasi-metaphorical sense in which Kummer (1967) and others refer to the use of conspecifics as “social tools.”

⁷ Though there are some suggestions of social influences on learning in the wild, laboratory studies (Weir et al. 2002) have shown a strong “innate” disposition in this species for the use of tools (as we found in our study on

Tool use by non-human primates

In 1995, i.e., by the time we ‘discovered’ the spontaneous use of tools by a semi-captive group of capuchin monkeys, though, widespread and diversified tool use in the wild by non-humans seemed restricted to chimpanzees.

The case of orangutans (*Pongo pygmaeus*) was particularly interesting, considering their performance in lab experiments (Byrne 1995), just like the dexterity of ex-captives in rehab facilities imitating tool use by human caretakers (Russon and Galdikas 1993). In the following year, the first reports on the use of tools by wild populations were published (van Schaik et al. 1996; see above).

Though captive gorillas (*Gorilla gorilla*) are also capable of using objects to solve tasks, the reports about tool use in the wild are extremely rare (Breuer et al. 2005; Wittiger and Sunderland-Groves 2007). Byrne and Russon (1998) observed, notwithstanding, structurally complex behavioral sequences in their manipulation of defended food items.

Intriguingly, the use of tools was never observed in wild bonobos (*Pan paniscus*), which is unexpected, considering their manipulative performance in the lab – including the preparation and use of lithic blades (Toth et al. 1993; Kathy et al. 1999).

Among Old World monkeys, apart from a few anecdotal reports, the only species where spontaneous and customary use of tools in the wild has been observed are long-tailed macaques (*Macaca fascicularis*), who use stones and shells to detach or break oysters, gastropods, crabs, and fruit (Malaivijitnond et al. 2007; Gumert et al. 2009).

Spontaneous and customary use of tools by capuchin monkeys

If the findings about the spontaneous use of tools by wild chimpanzees led us to rethink traditional views on the ‘unique and exclusive’ character of human technological abilities, the discovery of similar behaviors in a few ‘atypical’ monkey species – one Old World monkey species, one genus of New World monkeys – leads us to broader questions, focusing our attention not on phylogenetic proximity, but, rather, on the cognitive, ecological, and social conditions and mechanisms fostering the emergence of tool use and behavioral traditions.

Tufted capuchin monkeys have a broad distribution (*Sapajus spp*, formerly, *Cebus spp*),⁸ from the north of South America to Southern Brazil, Paraguay and the north of Argentina, living in multi-male, multi-female groups ranging from 3 to more than 50 individuals. They have longer and socially more active infancies than similar-sized New World monkeys (Fra-

tool use by hyacinth macaws; cf. Borsari and Ottoni 2005). But see Madden (2008) for evidences on “cultural” features on bower design and decoration by bowerbirds.

⁸ Tufted (or “robust”) capuchin monkeys used to be all included in the *Cebus apella* species, whose subspecies were then raised to species’ level (*Cebus apella* [former *C. a. apella*], *C. libidinosus*, *C. nigrinus*, *C. xanthosternos*, and *C. flavius* being the main species; see Chapter 1 in Fragaszy et al. 2004b for a review). Recently, molecular data (Lynch Alfaro et al. 2012) ratified the proposal of separating “robust” and “gracile” species into two genera, *Sapajus* and *Cebus*. So, under this revised taxonomy – while, for instance, Central American white-faced capuchins remain in the *Cebus* genus (*C. capucinus*) – our study species will all be referred to here as *Sapajus spp* – though in older texts, *S. libidinosus*, for instance, may be named *Cebus libidinosus*, or *C. apella libidinosus*).

gaszy et al. 1991), and they exhibit a relative brain size closer to that of great apes (Rilling and Insel 1999). They are generalist and opportunist foragers, with a much-diversified diet, varying from fruit and other plant parts to animal prey like arthropods, eggs, and small vertebrates such as lizards, snakes, and birds. Many of these food items require complex search and processing techniques, whose acquisition is frequently suggestive of socially aided learning.

The dexterity of capuchin monkeys was already well known in the times of Charles Darwin's grandfather Erasmus, who described the stone-aided nut cracking by an old captive (1794, apud Visalberghi 1990). Anecdotes about captives in zoos abound, but systematic experimental studies started in the 1980s with Westergaard, Fragaszy and Visalberghi (see Fragaszy et al. 2004b for a review).

Behavioral convergences between tufted capuchins and chimpanzees (Visalberghi and McGrew 1997) are not limited to complex object manipulation, but are also reflected in other areas of their social lives (e.g., food sharing and tolerance towards the young), which makes capuchin monkeys a strategically important target in the comparative study of the evolution of primate cognition and sociality.

First studies with a semi-free group

The first reports of direct observation of spontaneous tool use by tufted capuchin monkeys came from semi-free groups in urban parks in Southern Brazil (Mannu and Ottoni 1996; Rocha et al. 1998; Ottoni and Mannu 2001). In our case, while replicating lab experiments on tool-aided problem-solving by Westergaard and Fragaszy (1987) in a semi-captive population on an island in the Tietê Ecological Park (PET) near São Paulo, Brazil, a student (Perondi, pers. comm.) heard percussive sounds coming from the woods in the so-called 'Preservation Area' of the park. When she inquired, a park keeper explained her, quite nonchalantly, that "those were the monkeys cracking nuts with stones..."

Our preliminary investigations showed that, in fact, capuchins from a group formed by animals (poached and retrieved by the authorities) that had escaped from the park islands (where the park management meant them to stay) were doing something very 'chimp-like:' using stones as 'hammers' to crack small *Syagrus* palm nuts to eat their endosperm and the eventual beetle larvae 'bonus.' Since there was no information available on their previous life histories, we could not rule out the possibility that this behavior was an artifact of their interaction with humans, either in the park or before their park-life, but there was already some indirect or anecdotal evidence available from the wild (Langguth and Alonso 1977; Fernandes 1991) suggesting otherwise.

The ontogeny of tool use in tufted capuchins

Our initial, "descriptive" phase in the research with the semi-free PET group was followed by a study on the ontogenetic development of tool use (Resende et al. 2008) – which made clear the importance of both infant curiosity and exploration, on the one hand, and of older individuals' (especially males) tolerance to their proximity and scrounging, on the other.

Most mature individuals in the group crack nuts, although with variable frequency and efficiency,⁹ but it takes about 3 years for a young monkey to start becoming proficient in nut cracking. Young infants frequently manipulate objects, including stones, by beating them against a substrate. 1-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 3rd year of their lives.

From an early age on, though, capuchins are keenly interested in nut cracking by other individuals. Conspecific observers are typically younger and less proficient than the observed nutcrackers. Here, the role of mothers as models is much less marked than in chimpanzees since males tend to be more active nutcrackers, but capuchin infants and juveniles can watch older juveniles or adult males, and some scrounging is also allowed. The food-related activities of dominant males tend to be quite attractive.

We propose that scrounging, as a proximate motivation, optimizes the conditions for the social learning of nut cracking techniques.¹⁰ This implies that even simple cognitive processes, such as operant conditioning, can optimize the conditions for socially biased learning that can give rise to traditions.

Some of our findings point to an active, non-random choice of observational targets. In groups where stone-aided nut cracking is already well established (in the so-called “tradition phase;” cf. Huffman and Hirata 2003), young observers can follow a simple rule of thumb, and their curiosity is usually focused in the food-related activity of dominant males. But when there was a range of potential “observational targets” available, differing more in tool use proficiency than in rank, the observers seemed to be able to select the most “profitable” targets, preferentially watching the more skilled nut crackers (Ottoni et al. 2005), probably because such selective attention was likely to enhance scrounging payoffs (which, in turn, enhance social learning opportunities).

Mapping the occurrence of tool use by wild capuchin monkeys

There are virtually no reports of tool use by the Central American white-faced capuchin monkeys (*Cebus capucinus*), among which behavioral traditions on food preferences (Panger et al. 2002) and social conventions (Perry et al. 2003) have been described. And there are no reports at all from free-ranging populations of the South American non-tufted (‘gracile’) capuchin species (*Cebus* spp).

Among the tufted capuchins (*Sapajus* spp), most long-term studies in the wild were done, until recently, with forest-dwelling populations of *S. apella* or *S. nigritus*, and these provided us with apparently robust *negative* evidence of the customary use of tools (whilst there are a few reports of complex food processing), even though these species can show high dexterity in tool-aided problem-solving in the lab (Westergaard and Fragaszy 1987; Visalberghi 1990).

⁹ Especially in the early years of the research, when, we believe, tool use was still an innovation being disseminated in this group (Ottoni et al. 2009).

¹⁰ See Caldwell and Whiten (2002) for a study on the scrounging facilitation of social learning in marmosets.

The first direct observations of tool use by wild groups came from two populations of *S. libidinosus* in the state of Piauí, in Northeastern Brazil – in Fazenda Boa Vista (FBV; cf. Fragaszy et al. 2004a), and in the Serra da Capivara National Park (PNSC; cf. Moura and Lee 2004; Mannu and Ottoni 2009). Since then, our surveys of other areas in Central-Western Brazil have shown that, for savannah-dwelling populations, the use of tools to crack open encapsulated food (Figure 1) is the rule rather than the exception (see Ottoni and Izar 2008 for a review). A comparative exam of the ecology and use of space by tufted capuchins along the genus distribution range led us to consider the degree of terrestriality – rather than food scarcity – as a stronger predictor of the use of tools to crack encapsulated food in present populations (Visalberghi et al. 2005).



Figure 1. Nut cracking and scrounging, FBV

The population in the PNSC, though, exhibits a broader tool kit: stones are used not only as ‘hammers’ and ‘anvils’ to crack hard fruit or seeds, but also as digging tools (to loosen and/or pull the soil; cf. Figure 2a) to access roots, tubers, or invertebrate ground nests, and wooden sticks are used to probe for water, insects, or to dislodge small vertebrate prey in tree trunk holes or rock cracks (Figure 2b). In a similar way to what has been observed among chimpanzees, the use of probes by tufted capuchins usually involves some degree of preparation or modification: the sticks are not only detached from trees and cut to a proper length, but, when necessary, leaves or side branches are trimmed, and the tips are thinned (Mannu and Ottoni 2009; Falótico and Ottoni submitted).

This “enhanced” tool kit favors the emergence of more complex behavioral patterns such as the use of “secondary tools” (i.e., tools used to produce other tools; Sugiyama 1997), as in the case of freeing a quartz pebble (to be used as a hammer) embedded in sandstone with the aid of a smaller stone, or the combined (sequential) use of stone hammers and stick probes to access insect nests in rotten tree trunks or prey in rock cracks. Also, the intensive and diversified use of stones as tools has probably propitiated, in one of our study groups in the PNSC (the Pedra Furada group), the appearance of a peculiar new kind of sexual display

by some females – the throwing of small pebbles at the dominant male they were following as target (Falótico and Ottoni 2013).¹¹



Figure 2. Stone-aided digging and stick probe use, PNSC

Explaining the variation in tool kits among populations

If the degree of terrestriality can explain the differences in the use of percussive tools between tufted capuchins in savannah and forest environments, it does not seem to be a sufficient explanation for the rarity of the use of probe tools. On the other hand, probe tool use does not leave such conspicuous traces as stone-aided digging or nut cracking, and it is most certainly underreported (as so far it has only been observed in one wild group outside the PNSC).¹² It has never, though, been observed in FBV groups, which is the only other wild *S. libidinosus* savannah population with enough direct observation time to make us reasonably sure of its absence.

There is so far no clear explanation for the more diversified tool kits of PNSC groups. The abundance of quartz pebbles (as compared to their low availability in FBV) can be a relevant factor. More importantly, perhaps, their atypically large group sizes (some of them around 50 individuals, about twice the size of FBV groups, or three times that of average forest groups) could enhance the opportunities for both innovation and the diffusion of tool-aided foraging techniques and other behavioral traditions.

¹¹ Male nut cracking can perhaps also play a role as a sexual display (Boinski 2004; Moura and Lee 2010).

¹² The use of sticks to probe termite nests was recently reported in a group of the “rediscovered” *S. flavius* (Souto et al. 2011).

Social structure and dynamics, and socially biased learning

Van Schaik et al. (1999) hypothesized that, for species with some degree of motor and cognitive dexterity and relying on extractive foraging, the cultural dissemination of complex food-processing techniques – tool use in particular – would depend on the degree of tolerance among individuals in the group, which determines the extent to which potential “apprentices” have access to the activity of the more experienced “manipulators.” In the same vein, Coussi-Corbel and Fragaszy (1995) proposed that the typical inter-individual distances tolerated in a given species (which vary as functions of age, kin, and rank relationships) determine the level of behavioral detail that can be socially transmitted.

Our studies confirmed van Schaik et al.’s (1999) prediction that, given the above-mentioned genetic, ecological, and social preconditions, the emergence of tool use traditions could be possible even in a New World primate species. Nonetheless, Kummer and Goodall (1985) emphasized the greater opportunity for less socially constrained individuals (such as the ones who forage alone or in smaller groups) to exhibit *innovative* behaviors. Since this is the case of sub-adult or young adult capuchin males, being less tolerated, their society can represent a favorable ‘equilibrium’ between these factors, facilitating both innovation and social transmission.

The evolution of tool use in tufted capuchins

Spagnoletti et al. (2012) analyzed the seasonal variations in food availability and nut cracking activity by FBV capuchins to pit the “necessity hypothesis” (i.e., tool use necessary to access fallback food items during resource scarcity) against the “opportunity hypothesis” (i.e., tool use maintained by repeated exposures to appropriate ecological conditions, such as preferred food resources necessitating the use of tools). The results clearly favored the latter hypothesis: nut cracking was not affected by provisioning, nor correlated with the availability of fruit and invertebrates. Monkeys crack nuts when these are available.

If necessity does not apparently hold as an explanation for the use of tools to access encapsulated food in present savannah populations (or at least in that particular population), it is still a likely candidate as an ultimate explanation for the evolutionary origins of tool use by tufted capuchin monkeys.

The Cenozoic was an era of severe climate fluctuations, with warmer periods alternating with glacial cycles associated with drier weather, which was reflected in cycles of expansion and retraction of the Amazon forest and the wetter types of savannah. These climate changes are thought to have prompted drastic changes in South American fauna: speciation processes affecting populations isolated by forest fragmentation constitute one major theoretical model to explain Amazon biodiversity (i.e., the refuge theory; cf. Simpson and Haffer 1978; Ab’Saber 2000). This may also explain the sudden diversification of New World primate species (Zachos et al. 2001, apud Schrago 2007).

The fossil evidence on the evolution of Platyrrhines is scarce – and virtually lacking for capuchin monkeys (*Cebus/Sapajus*), with no candidate fossils older than 4000 years –, and there are discrepancies among molecular methods. Based on the most recent analyses of genetic data, Lynch Alfaro et al. (2012) concluded that, isolated from their Amazon ancestors,

tufted capuchins originated either in the Atlantic Forest of further inland, in savannah areas (which are now the *cerrado* and the *caatinga*), and in the last 750,000 years expanded out across the *cerrado* and back into the Amazon Forest.

The occupation of drier savannah environments may, at times, have exposed tufted capuchins to more extreme conditions than those currently observed in FBV and other savannah areas,¹³ under which the consumption of encapsulated food can have started – as we hypothesize – out of necessity rather than out of opportunity alone.¹⁴

But even if adults (especially adult males, in the case of harder nuts) have the necessary cognitive and motor skills to use stone tools to crack open palm nuts, that, in itself, is only part of the solution. There is a ‘life history’ catch: since it takes some years until young monkeys acquire the skill and strength necessary to consume these items by themselves, when no other resources of easier consumption are available, youngsters must still be fed. So, tolerated scrounging by infants and younger juveniles would be a key component in this ‘technological’ solution to food scarcity. Incidentally, it also optimizes opportunities for the socially biased learning of tool-aided food processing.

Other potential traditions in tufted capuchins

Other potential behavioral traditions besides tool use, such as anting (as a chemical defense against ticks; cf. Verderane et al. 2007), or some forms of social play, deserve further inspection. The interaction with other species is a promising context for socially aided learning, especially when the costs of solitary, trial-and-error learning are high; snakes, for instance, can be either predators or prey, and the monkeys in PNSC react adequately, harassing from a safe distance or poking with sticks the dangerous ones, such as boas and rattlesnakes, and preying on the harmless *Colubridae* (Falótico and Ottoni submitted). Though the ontogeny of snake-related behaviors has not been examined so far, such encounters (especially threat events, which last longer and are more conspicuous) attract a lot of interest by nearby individuals, suggesting the potential effects of social traditions in snake discrimination learning by capuchin monkeys.

Future field studies with key wild populations will help us to examine the many questions raised by our current knowledge on tufted capuchin monkeys’ tool use, such as the apparent ‘uniqueness’ of the Serra da Capivara population tool kit, the role of social learning on the ontogeny of the different kinds of tool use, and the interactions between group size, social dynamics, foraging strategies, and the emergence of behavioral traditions.

¹³ Wright et al. (2008) suggest that the use of tools to crack palm nuts was the selective agent responsible for “robust” capuchins’ relatively short hind limbs and massive forelimbs – with niche broadening anatomical specializations permitting the exploitation of a range of habitats and food resources.

¹⁴ The use of digging sticks by chimpanzees (to access plants’ underground storage organs [USOs]) was only observed in savannah populations (Lanjouw 2002; Hernandez-Aguilar et al. 2007). Access to USOs has been hypothesized to have played a key role in the initial hominin occupation of savannah environments (Laden and Wrangham 2005).

Cultural processes as selective pressures on the evolution of cognition and sociality

Hypotheses pointing to complex social dynamics as the main selective pressures driving the evolution of primates' big brains and complex cognition have been around for a long time (Chance and Mead 1953; Jolly 1966; Kummer 1967; Humphrey 1976).¹⁵ These were collected under the label of the *Machiavellian intelligence hypothesis* (Byrne and Whiten 1998; Whiten and Byrne 1997), given the authors' emphasis on social manipulation under unequal and competitive conditions, where "tactical deception" is important to avoid unnecessary conflict over resources.

Van Schaik and collaborators, however, focused on the "brighter side" of the "social niche": as socially aided learning of complex (or risky) behaviors became more and more important for survival, social motivations and cognitive capacities that enhanced the conditions for social information transfer have plausibly become the target of intensive selection pressures. The so-called *cultural intelligence hypothesis* (van Schaik and Pradhan 2003; van Schaik and Burkart 2011; see also Whiten and van Schaik 2007) extends to non-human animals the notion of a coevolutionary process (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985) between culture and genetically-based cognitive capacities.

This evolutionary trend can explain sophisticated cognitive features, such as a theory of mind – but socially biased learning and the emergence of social traditions do not necessarily rely on complex individual cognition: they can be established upon 'humbler' cognitive and social features, such as the high motivation of youngsters to observe the behavior of older individuals (that can be driven by simple food reinforcement), and the high tolerance of adults to close proximity and scrounging by youngsters. This parsimonious model places complexity not necessarily into individual brains as such, but into the interaction between individual cognition and social dynamics – evoking concepts like "situated action" and "socially distributed cognition" (Strum et al. 1997; Hutchins 1991).

Bearing in mind that human culture can be a very particular sort of social learning, based on unique cognitive capacities such as a theory of mind, can be a wise approach. It seems equally important, though, to pay attention both to each species' specificities and to more universal aspects of social information transfer in animal societies. Figuring out which underlying features (in individual cognition or social dynamics) are exclusively human may help to understand what has made cultural complexity the defining feature of our species. Gaining a better understanding of similar processes in animals is essential to build a broader picture of an evolutionary science of social learning and culture.

As McGrew (2003) points out, "culture has escaped from anthropology" to other disciplines: anthropology studies culture as phenomenology; psychology asks questions about cognitive and social mechanisms; zoology and evolutionary biology study culture as an adaptation, under a neo-Darwinian paradigm – and cultural primatology can use the insights from all of these approaches.

¹⁵ All reprinted in Byrne and Whiten 1988.



Neurocognitive Development and Impairments

NATURALISTIC APPROACHES TO CULTURE

edited by Csaba Pléh, Gergely Csibra, and
Peter Richerson



AKADÉMIAI KIADÓ, BUDAPEST