

10 The Etho-*Cebus* Project: Stone-tool use by wild capuchin monkeys

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Tool use, according to St Amant and Horton (2008: 1203),¹ is the “exertion of control over a freely manipulable external object (the tool) with the goal of altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism), via a dynamic mechanical interaction.” Among wild great apes, only chimpanzees use tools habitually, in many varied formats across their geographical distribution, and for diverse purposes (see McGrew, 1992; Yamakoshi, 2004 for a review; Boesch *et al.*, 2009; and this volume). Tool use is observed much less often in wild Sumatran orangutans (*Pongo abelii*), and even more rarely in the other wild great apes (Western gorillas, *Gorilla gorilla*, and bonobos, *Pan paniscus*), though in captivity all the great ape species use tools spontaneously in flexible and diverse ways. Among monkeys, very few species use tools in natural settings (*Macaca fascicularis*: Malaivijitmond *et al.*, 2007; Gumert *et al.*, 2009; *Cebus*² *libidinosus* and *C. xanthosternos*: Canale *et al.*, 2009; for a comprehensive review concerning the genus *Cebus*, see Ottoni & Izar, 2008), although many species occasionally use tools in captivity (for reviews, see Anderson, 1996; Panger, 2007; Bentley-Condit & Smith, 2010; Shumaker *et al.*, 2011). Among monkeys, the capuchins (species belonging to the newly identified genus *Sapajus*) excel in all respects (Bentley-Condit & Smith, 2010) and their tool use fully fits St Amant and Horton’s (2008) definition.

Tool-using skills of captive capuchins were reported in Europe in the sixteenth century (see Visalberghi & Fragaszy, 2012), long before the first illustration of a Liberian chimpanzee digging for termites appeared in a stamp issued in 1906 (Whiten & McGrew, 2001)

¹ We cite this definition of tool use, among several available, because it highlights the requirement that the actor must accomplish a mechanical interaction with the target. Use of a stone as a percussor epitomizes this aspect of tool use.

² Recent molecular analysis has revealed that capuchin monkeys, formerly identified as the single genus *Cebus*, are two genera, with the robust forms (including *libidinosus*, *xanthosternos* and several other species) now recognized as the genus *Sapajus*, and the gracile forms retained as the genus *Cebus* (Lynch Alfaro *et al.*, 2011, 2012). To date, tool use has been observed in some species of wild *Sapajus*, but no species of wild *Cebus*. In this chapter we retain *Cebus* when citing published findings using the older nomenclature and *Sapajus* (*Cebus*) to refer to the taxa in general and new findings about species in this newly recognized genus.

or reached the scientific community through the work of Jane Goodall (1964). However, first-hand published reports on tool use by wild capuchins are relatively recent. Fernandes (1991) published the very first account of direct observation of tool use. He observed a wild capuchin (*Cebus apella*) using a broken oyster shell to strike oysters still attached to the substrate and successfully breaking them open. Boinski (1988) observed a wild male white-faced capuchin (*C. capucinus*) hitting a snake with a branch obtained from nearby vegetation. These observations each concerned one individual and one event. Habitual tool use (i.e., by several individuals over a period of time) in wild capuchins has been discovered and investigated only in the present millennium.

Surprising to some, the phenomenon of tool use by capuchin monkeys appears to be geographically widespread in wild populations of bearded capuchins (*Sapajus (Cebus) libidinosus*) and to encompass a range of materials, methods and goals. The reports come from seasonally dry Cerrado and Caatinga habitats in the north and east of Brazil. At Fazenda Boa Vista, State of Piauí (hereafter FBV; Fragaszy *et al.*, 2004a) bearded capuchin monkeys crack open palm nuts and other encased foods with stone hammers and anvils. In the Serra da Capivara National Park, also in the State of Piauí, bearded capuchins use stones to access embedded food by percussion and by scraping, and sticks to probe for honey and to flush vertebrate prey (Moura & Lee, 2004; Mannu & Ottoni, 2009). At the Agua Mineral National Park (Federal District, Brazil) and in the State of Rio Grande do Norte they crack encased foods with stone tools (Waga *et al.*, 2006; Ferreira *et al.*, 2010) (see Figure 10.1). Elsewhere researchers have found indirect evidence of tool use by (presumably) bearded capuchins (i.e., stone tools and palm shells on hard substrates; e.g., Canale *et al.*, 2009). Finally, semi-free-ranging capuchins (that may be mixtures of species and hybrids) have been observed to crack nuts in several sites (for a review see Ottoni & Izar, 2008).

Nut cracking is an integrated dynamic system with biomechanical and morphological components (related to the monkeys' postcranial morphology) and with environmental components (including the mass and material of the hammer stones and of the anvil site, and the material and physical properties of the nut). Using a stone (or log) to pound open or otherwise breach an encased food item placed on a solid surface (an "anvil") is considered the most complex form of tool use by non-human species routinely seen in nature, because it involves producing two spatial relations in sequence (between nut and anvil, and between pounding tool and nut) (Matsuzawa, 2001; Fragaszy *et al.*, 2004b). Furthermore, transporting the food item and sometimes the percussor involves costs (time and energy, among others) and may present cognitive challenges, such as anticipating future needs, recalling elements that are out of sight and planning the course of action. Transporting food resources and repetitive visits to specific places on the landscape to process foods are associated with early *Homo* and are thought to be important innovations of the Oldowan (e.g., Binford, 1981; Isaac, 1984; Potts, 1991).

Our goal here is to provide an overview of the discoveries made by the *Etho-Cebus*³ team since the use of stone hammers and anvils by wild bearded capuchin monkeys at

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Figure 10.1 Sites for which there are published observations of the use of percussive tools by wild capuchins. The stars indicate Fazenda Boa Vista (FBV, PI, Brazil) and Serra da Capivara National Park (SdC, PI, Brazil). The circle indicates the Agua Mineral Park, in the Brasília National Park (DF, Brazil).

Fazenda Boa Vista (Gilbuês, State of Piauí, Brazil) was first reported in 2004. We also briefly compare some of our findings on stone-tool use in bearded capuchins, such as frequency of tool use, sex differences and selection of tools, with those reported for chimpanzees.

Study area and monkeys

Our study area is located at Fazenda Boa Vista ($9^{\circ}39' S$, $45^{\circ}25' W$; see Figure 10.1), privately owned land 21 km northwest of the town of Gilbuês (PI). The physical geography of the field site is a sandy plain at approximately 420 m above sea level, punctuated by

São Paulo, Brazil) started the *Etho-Cebus* Project to investigate the nut-cracking behavior of the FBV capuchins in ecological, developmental, social, physical and historical context. Barth Wright and Kristin Wright, both at Kansas City University of Medicine and Biosciences, have since joined the team. For more information, see <http://www.Ethocebus.org>

sandstone ridges, pinnacles and plateaus surrounded by cliffs composed of sedimentary rock rising steeply to 20–100 m above the plain. The cliff and plateau consist of interbedded sandstone, siltstone and shale. Rock faces often break off these formations and fall to the base of the cliff close to the plain, shattering into boulders with planar surfaces, and forming a talus (for further information about the geology of FBV, see Visalberghi *et al.*, 2007 and video 1 in the electronic supplementary material at www.cambridge.org/9781107011199). The sandstone cliffs and plateaus are heavily eroded and there are ephemeral water courses that have running water briefly after rainfall. The area is lightly populated by humans, and contains cultivated areas, wetlands, grazing land and some less disturbed woodland areas. The flat areas are open woodland, whereas the slopes of the ridges are more heavily wooded. Palms are abundant in the open woodland. The climate is seasonally dry. Over a 20-year period (1971–1990), the average annual rainfall was 1156 mm; 230 mm of that amount fell during the dry season (May–September) (Brazilian Agricultural Research Corporation, Embrapa, www.embrapa.br).

FBV is located in the transition area between the *Cerrado* and the *Caatinga* domains. It presents four types of vegetation physiognomies according to the terrain and the availability of water. The sandy plain is characterized by a high abundance of palms with subterranean stems and medium-height trees like *Eschweilera nana* and *Hymaenaea courbaril*. The vegetation in wetter areas is characterized by a higher diversity of trees forming gallery forests and a high density of the tall palm tree *Mauritia flexuosa*. Shrubs and small trees dominate the cliff and the talus, whereas in the plateau herbaceous vegetation dominates, especially bromeliads and cactus.

We have studied two groups of wild bearded capuchins at FBV: the C group and the Z group. In 2003, when we first visited FBV, the C group was already habituated to human presence and provisioned in support of ecotourism being promoted in that area. During the year in which data on tool use were systematically collected by Spagnoletti for her PhD (June 2006 to May 2007; Spagnoletti, 2009) the C group received a supplement of water and food (on average 3082 ± 908 kcal per day for the whole group consisting of 12–18 individuals). The C group visited the provisioned area to eat in 53 of the 91 days (58%) over which behavioral observations were carried out on that group. Visits to the provisioned area did not occur regularly and sometimes capuchins did not visit for many days in a row (for example, in February 2007 and February 2009 they did not visit for 11 and 12 days consecutively). Our team habituated Z group to human presence in 2005 and this group was not provisioned. The home range (MCP, minimum convex polygon) of Z group was 4.9 km² and that for C group 6.9 km², with an overlap of 3.0 km² during the period of Spagnoletti's study (Spagnoletti, unpublished data).

Between 2004 and 2009 the *Etho-Cebus* team conducted several behavioral studies, some of which are ongoing at the time of writing. Here, we discuss observations on the 28 bearded capuchins belonging to two groups (C and Z) carried out by Spagnoletti *et al.* (2011, 2012) and a series of field experiments conducted with the C group carried out by Visalberghi, Fragaszy and colleagues.

Palm nuts

In the open woodland of FBV palms are abundant and produce fruit at ground level. The four species of palm nuts most commonly eaten by capuchins at Boa Vista are: tucum (*Astrocaryum campestre*), catulè (*Attalea barreirensis*), piassava (*Orbignya* sp.) and catulí (*Attalea* sp.) (see Figures 1–3 in the electronic supplementary material at www.cambridge.org/9781107011199). Behavioral and phenological data collected in Boa Vista show that catulè nuts are more abundant in the dry season, whereas the other species, and especially piassava, are more uniformly available across the year (Spagnoletti *et al.*, 2012).

Typically, the capuchins collect the palm nuts by plucking one nut from the cluster, pulling and turning it until it comes loose. The mesocarp of catulè, catulí and piassava (but not of tucum) is edible, and capuchins usually eat this layer until the woody endocarp of the nut is exposed, as do cattle and other animals in the area. At this point they immediately look for an anvil site to crack the nut, or abandon the nut on the ground. Capuchins will also pick up nuts that have had the mesocarp removed previously and transport them to an anvil site.

Visalberghi *et al.* (2008) characterized the four species of nuts cracked by capuchins and assessed their peak-force-at-failure. The resistance of the structure of the nuts differed across species and was correlated positively with weight (and volume). In particular, the mean peak-force-at-failure values were 5.15 kN for catulè, 5.57 kN for tucum, 8.19 kN for catulí and 11.50 kN for piassava. Since catulè and tucum values were significantly lower than those of catulí and piassava, nuts were categorized as low-resistance (catulè and tucum) and high-resistance (piassava and catulí). To put these findings into context, all four species of palm nuts exploited by capuchins are at least 13 times more resistant than walnuts (*Juglans regia*) and between two (catulè, tucum, catulí) and five times (piassava) more resistant than macadamia nuts. Indeed, the piassava nuts are approximately as resistant as panda nuts, the most resistant nuts cracked open by chimpanzees (see Table 10.1).

Stones used as hammers and their availability in FBV

Nut cracking by capuchins leaves physical evidence, such as distinctive shallow depressions (pits) on the surface of both wooden anvils and stone anvils, cracked shells and stone hammer(s) on the anvil (see Figure 4 in the electronic supplementary material at www.cambridge.org/9781107011199). Visalberghi *et al.* (2007) used these diagnostic physical remains to infer the occurrence of nut cracking in the area of FBV. By surveying a sample of these anvil sites they found that: (1) anvils (boulders and logs containing shallow, hemispherical pits) were located predominantly in the transition zone between the flat open woodland and the ridges, in locations that offered some overhead coverage, and with a tree nearby, but not necessarily near palm trees; (2) hammer stones represented a diverse assemblage of ancient rocks that were much harder than the sedimentary rock (sandstone)

Table 10.1 Summary of the main characteristics of stone-tool use in bearded capuchins living at FBV and in chimpanzees in the Taï National Park (TNP, Ivory Coast). The references are in the text unless indicated.

	<i>Cebus libidinosus</i>	<i>Pan troglodytes verus</i>
Customary and habitual	Yes	Yes
Seasonal	No	Yes
<i>Hammers</i>		
Stone	Yes	Yes
Wood	Unsuitable	Yes
Frequency of suitable hammer stones	17.5 stones per hectare (0.3–3 kg)	0.09 hammers (>1 kg) per hectare ¹
Peak-force-at-failure of the hardest species of nuts ²	<i>Orbignya</i> sp., average 11.5 kN	<i>Panda oleosa</i> , range: 9.6, 12.2 kN
Hammer selectivity on the basis of material and weight	Yes*	Yes
<i>Anvils</i>		
Material	Stone and wood	Stone and wood
Reuse of the same anvil site	Yes	Yes
Anvil transport	No impossible	No, but common in Bossou (pers. obs.)
Anvil selection	Yes	Yes ²
Anvil pits selection	Yes ³	In progress ⁴
Frequency of tool use	Males > females	Males < females
Body position when cracking	Bipedal	Seated
Tool use in trees	Yes ⁵	Yes
Age of nut cracking acquisition	2–3 years	3.5–5 years ⁶

Notes

¹ Boesch & Boesch, 1983.

² Carvalho *et al.*, 2009.

³ Liu *et al.*, 2011.

⁴ Carvalho *et al.* in progress.

⁵ Etho-*Cebus* team, unpublished.

⁶ Inoue-Nakamura and Matsuzawa, 1997.

* Experimental confirmation.

prevailing in FBV out of which they eroded; and (3) hammers were mostly cobbles eroded from the few conglomerate layers present in the local stratigraphy.

The stones found on the anvils (or within 3 m of them) were predominantly quartzite (the hardest rock in the area), siltstone, ironstone and sandstone that underwent metamorphism under higher temperature and pressure, becoming harder and less porous than the prevailing sandstone. Overall, the weight of these stones averaged 1096 g ($n=62$, $SD=462.78$; max weight 2530 g, min weight 140 g). Therefore, it appeared that sufficient hardness and weight were requirements for stones to be used as hammers. Since hard stones that make durable, effective hammers were significantly more frequently found on the anvil, or within 30 cm of it, than in the corona (the zone surrounding the base of the anvil, 30–300 cm from the base), Visalberghi *et al.* (2007) suggested that capuchins transport hammer stones to the anvils.

To investigate the latter point, Visalberghi *et al.* (2009a) estimated the occurrence of surfaces suitable as anvils, stones suitable as hammers and palms in the home range of our two study groups of capuchins by counting their frequencies in 40 plots (each measuring 10 m² located along a 3 km line transect crossing four different physiognomies (the marsh, the plain, the talus, i.e., the area of transition between the plain and the cliff, and the cliff-plateau). The transect census showed that palms and anvil-like surfaces were relatively common, whereas stones large enough and hard enough to use as hammers were rare. Overall, in the 40 plots (totaling 400 m² of surface area) there were only seven hammer-like stones which were found in two plots located at the cliff-plateau and in one plot located at the talus. The low number of hammer-like stones (17.5 stones per hectare) contrasts with the abundance of anvil-like surfaces, which in many areas are present as boulder fields at the foot of the cliffs. Both hammer-like stones and anvil-like surfaces were found more frequently in the talus and in the cliff-plateau areas than elsewhere, whereas palms were common everywhere except in the cliff-plateau. In short, the elements indispensable for tool use to crack nuts (i.e., hammer-like stones, anvils and palms, and therefore nuts) co-occur only in the cliff-plateau and in the talus; only the talus is close to the plain where palms are abundant. This picture confirms Visalberghi *et al.*'s (2007) report that active anvil sites are located at the transition zone between the cliff and the flat open woodland. Finally, the overall abundance of ephemeral water courses and direct observation of stones and tree trunks moved by water during heavy rainfalls support the hypothesis that when the conglomerate beds are weathered and eroded, the quartzite pebbles become loosened from the surrounding rock matrix, and are carried from the cliff-plateau to the talus below by water. Thus they become available to the capuchins as loose stones on an unpredictable basis, temporally and spatially.

Behavioral observations of tool use

Tool use occurred all year round at equivalent rates; monthly frequencies did not differ between groups or seasons (Spagnoletti *et al.*, 2011, 2012). Adult capuchins used tools to exploit palm nuts in 87% of the tool-use episodes and to exploit other encased fruits in the remaining episodes. One-third of the episodes of nut cracking targeted high-resistance nuts. Informal observations by our research team indicate that infants strike nuts on surfaces and strike nuts with other objects during the first year of life, but they do not open a whole nut or any part of a nut for many more months, despite persistent practice. Some individuals have been observed using effective strikes in their second year, but others did not do so until sometime in their third year or even later; Visalberghi and Frigaszy, unpublished data). Of the 23 physically normal capuchins observed by Spagnoletti at FBV that were at least three years old, only one female was never seen to crack nuts using a stone tool. Her health did not seem compromised by this deviation. Indeed, she was the heaviest adult female in her group and she bore several viable infants between 2004 and 2009.

In contrast with the pattern observed in chimpanzees, where females use tools more frequently than males (see McGrew, 1992 for a review; Lonsdorf *et al.*, 2004), adult male

capuchins used tools about three times more often than females did to crack palm nuts (but not other food items) (Spagnoletti *et al.*, 2011). When the weights of the hammer stones are considered in relation to the body mass of the tool users (weighed in the field with a scale by Fragaszy *et al.*, 2010), it emerges that to crack open nuts the two sexes use stones of roughly equal mass. Adult female capuchins used stones weighing on average 978 g (i.e., 44–51% of their body mass, depending on the individual), whereas adult males used stones weighing on average 1072 g (i.e., 24–40% of their body mass, depending on the individual) (see Spagnoletti *et al.*, 2011; Fragaszy *et al.*, 2010 for further details). Overall, females used on average 14 ± 3.2 strikes to open a nut and males 10 ± 1.4 strikes (Figure 10.2).

Why does the frequency of nut cracking vary between male and female capuchins? Females have higher energetic costs of reproduction than males, but if males are sufficiently larger than females they may have higher energetic requirements than females (Key & Ross, 1999). In terms of daily energy expenditure, male and female capuchins appear close to even and should be expected to exploit nuts to similar extents. However, since at our site female capuchins were 36% smaller than males, and use more strikes to open a nut than males, nut cracking is more energy-demanding, more time-consuming and/or a less reliable method of producing food for them than for males. Additionally, females may be more sensitive than males to competitive costs, or costs related to risk of predation, such as spending time on the ground (Fragaszy, 1990; Rose, 1994). However, this does not seem to be the case in FBV, where the daily time spent on the ground by adult males and females is 29% and 31%, respectively (Spagnoletti, 2009). Thus, cracking nuts might entail a different set of costs and potential benefits for males than for females. Any and all of these factors could make tool use more advantageous for male than for female capuchins (Spagnoletti *et al.*, 2011). In contrast, for chimpanzees nut cracking takes little time or effort and is a reliable method of foraging (Boesch & Boesch-Achermann, 2000); physical sexual dimorphism is also less pronounced in chimpanzees than in bearded capuchins (compare Key & Ross, 1999 with Fragaszy *et al.*, 2010).

Spagnoletti *et al.* (2011) report that capuchins were successful in 84% of the episodes with high-resistance palm nuts, 91% of the episodes with low-resistance palm nuts and 99% of the episodes involving other encased foods. The rate of success is similar for females and males, and both sexes cracked low-resistance palm nuts more often than high-resistance nuts. This pattern of food choice may have resulted in equivalent reliability of energy gain for all animals, or may have enhanced reliability of energy gain for females compared to males. Interestingly for the discussion concerning tool selectivity, female capuchins needed significantly more strikes than males to crack low-resistance palm nuts, but not high-resistance palm nuts. Though this might appear contradictory, females used significantly heavier hammers to crack open high-resistance palm nuts than low-resistance palm nuts, whereas males did not.

Efficiency in cracking nuts with tools varies widely among wild capuchins, even when the same hammer stone and the same anvil are used to crack open nuts of the same palm species (Fragaszy *et al.*, 2010). In Fragaszy *et al.*'s sample, the most efficient monkey opened on average 15 nuts per 100 strikes (6.6 strikes per nut). The least efficient monkey

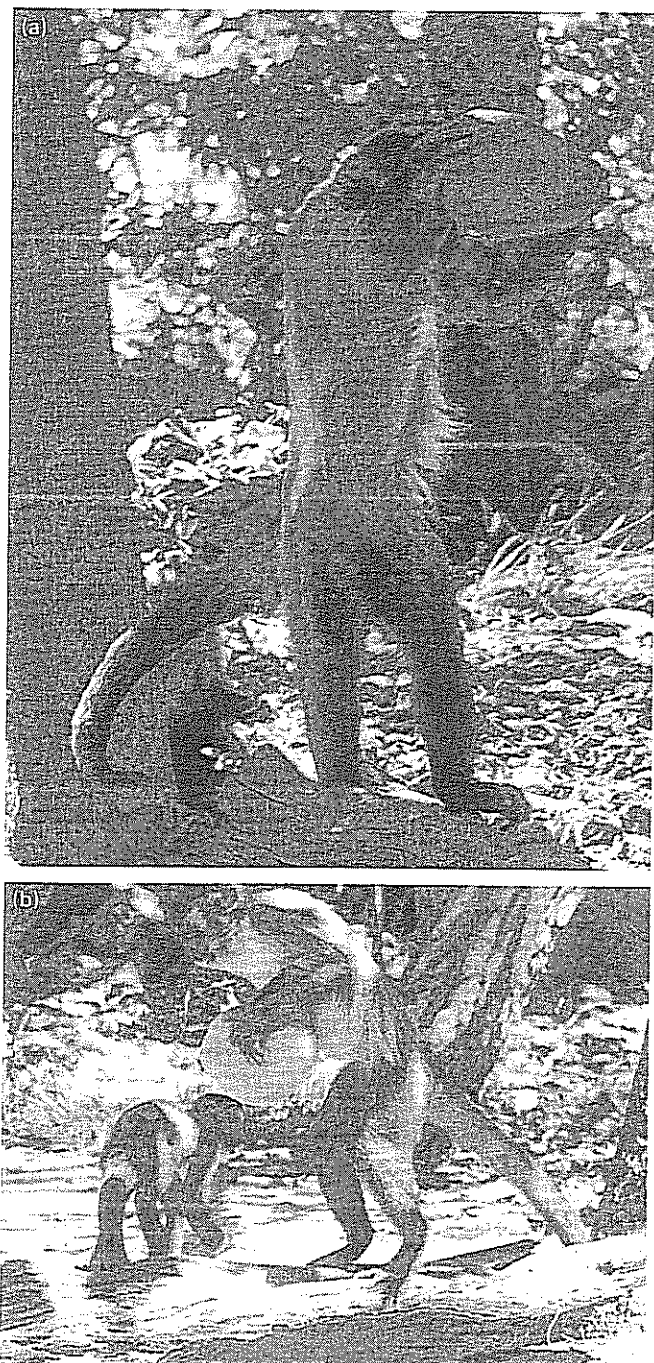


Figure 10.2 An adult male (a) and an adult female (b) bearded capuchin using a 3.5 kg stone to crack a piassava nut. The height of the female's strike is much lower than that of the male. The male weighs 4.2 kg; the female, 2.2 kg. This stone is heavier than those normally used by the monkeys (photos by E. Visalberghi).

opened on average 1.32 nuts per 100 strikes (more than 75 strikes per nut). They also report that the efficiency of one physically fit adult human male (20 years, 185 cm, 78 kg) striking the same species of nuts with the same stone was 16.1 nuts per 100 strikes (6.2 strikes per nut).

Logistic regression revealed that the monkey's body weight and diameter of the nut best predicted whether a monkey would crack a nut on a given strike. Increasing body weight improved the likelihood of cracking the nut; increasing diameter of the nut decreased the likelihood. In fact, smaller monkeys (females and youngsters) often fail to crack whole nuts even after numerous strikes with a stone that weighs proportionally more than 50% of their body weight.

Whereas chimpanzees are seated when cracking nuts, wild capuchins most often adopt a bipedal stance, raising and rapidly lowering the hammer by flexing the lower extremities and the hip. By studying the kinematics and energetics of nut cracking of two adult males and two adult females, Liu *et al.* (2009) demonstrated that the two males achieved greater maximum downward vertical velocities with the stone than the females (mean = 3.81 m s^{-1} vs. 3.16 m s^{-1} ; males and females, respectively). Therefore, the males generated higher maximum kinetic energy than the females. As the males lifted the stones to a higher maximum vertical height (in accord with their longer body length), the potential energy that they generated was also higher than the potential energy generated by females. All the monkeys produced work in the downward phase; that is, they added energy to the stone in the downward direction. Males produced nearly twice the work that females produced (mean = 5.61 J vs. 2.89 J; males and females, respectively). The overall consequence of the above differences is that large monkeys (adult males) crack nuts with fewer strikes than small monkeys. The differential cost of cracking for small and large animals is probably one of the factors accounting for the lower frequency of tool use in females than in males (Spagnoletti *et al.*, 2011).

Table 10.1 summarizes some of the above results and provides a comparison between our findings and those reported for chimpanzees. The findings reported so far provide enough information to draw two conclusions. First, most adult capuchins at FBV use tools throughout the year, fulfilling McGrew's (1992) definition of a habitual behavior (pattern of behavior shown repeatedly by several members of the group) and Whiten *et al.*'s (1999) definition of customary behavior (behavior that occurs in all or most able-bodied members of at least one age and sex class). Second, cracking nuts requires the use of stones of suitable weight and material, which are not very common in FBV. This conclusion prompted us to expect that capuchins select appropriate stones and transport them (as well as nuts or other encased hard fruits) to anvils. We turn now to what we have learned about anvil sites and the transport of nuts and stones to these sites.

Anvil sites as indirect evidence for tool use

Capuchins use anvil sites habitually. Spagnoletti *et al.* (2011) report that over a 12-month period (1709 hours of observation) capuchins cracked palm nuts on 116 different anvils throughout an area of 9 km^2 , and that these anvils accommodated 607 episodes of tool use

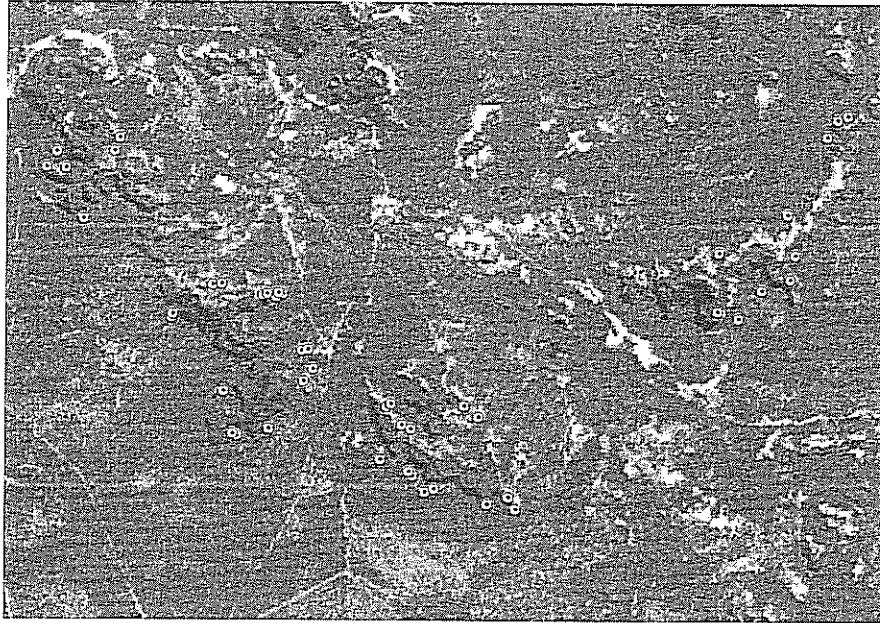


Figure 10.3 Map of the anvil sites surveyed monthly. Note that they are located in the transition area between the plain and the ridges. The two groups of capuchins we observed used the anvil sites located on the center-left.

(5.2 tool episodes per anvil) (Figure 10.3). More comprehensive evidence of repeated use of familiar anvil sites comes from a longitudinal survey conducted monthly by the *Etho-Cebus* team of 40 anvil sites (from February 2005 to January 2006) and 58 anvil sites (which included the previous 40) for two additional years (from February 2006 to January 2008; Visalberghi *et al.*, submitted). As illustrated in Figure 10.4, in each monthly visit we scored (a) displacement of the hammer stone(s), compared to its placement the previous month, and (b) the presence of nut shells on the anvil. The joint occurrence of hammer displacement and presence of shells was considered as strong evidence of tool use, displacement of the hammer stone without shells was taken as weak evidence and the presence of shells without displacement of the hammer position was not considered evidence of tool use. We recorded strong evidence of tool use on an average of 34% of the anvil sites each month, and weak evidence of use on an additional 7% of anvil sites.

During the three years of the study 17 hammer stones went missing from their original anvil sites; two were brought back to the same anvil site by capuchins five months and one month after disappearance. On nine occasions we found a new stone at an anvil site, all of a suitable weight, and seven of these were suitably fracture-resistant to serve as hammers. The other two were weathered sandstone, which breaks when used to strike nuts (Visalberghi *et al.*, 2007). The frequencies with which shells of piassava and catulé nuts were found on the anvils in the survey match the relative frequencies of directly observed tool-use episodes involving these two species of nuts (Spagnoletti, 2009). The similarity between direct and indirect assessments indicates surveying anvil sites is a

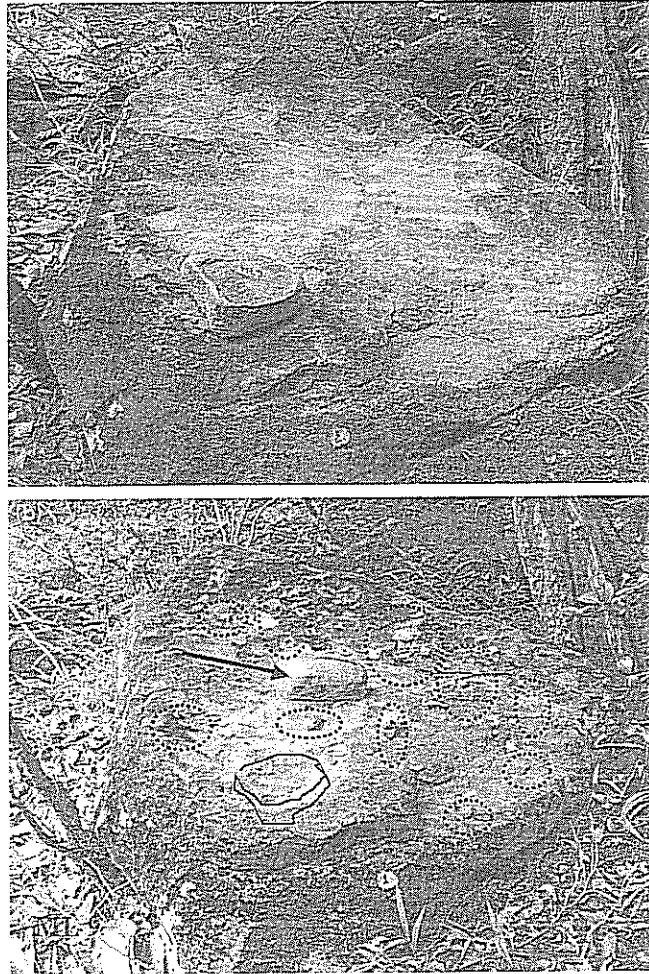


Figure 10.4 Procedure for the survey of the anvil sites. Each month we visited each anvil site to gather indirect evidence of tool use by scoring whether the hammer had been displaced from its initial position (a), and whether shells from nuts or remains from other encased fruits were present on the anvil. The comparison between these pictures shows that the anvil site has been used to crack nuts between when photo a was taken and 30 days later, when photo b was taken. In particular, in the later photo b, the hammer has been moved from its initial position (line in the front) to a new one (indicated by the arrow) and nut shells (circled with dotted lines) are present. Close to the nut shell on the far left there is a new small black pebble, presumably brought by capuchins (photos by E. Visalberghi).

reliable way to assess tool use in capuchins. In short, the evidence shows that (1) capuchins use anvils habitually; (2) capuchins transport new hammer stones to anvils and familiar stones among anvils; and (3) tool use to crack nuts by capuchins can be inferred reliably by surveying anvil sites, lending support to the use of this type of indirect evidence in areas where the monkeys are not habituated to human observers and/or the area is unfamiliar to the researchers, as has been done by Ferreira *et al.* (2010), Canale *et al.* (2009) and Langguth and Alonso (1997).

Archaeological excavations at abandoned nut-cracking sites of chimpanzees (Mercader *et al.*, 2002, 2007) and combining classical archaeological approaches with direct observation of chimpanzees' nut cracking are promising avenues for archaeologists to infer more accurately the function of pounding tools coming from Plio-Pleistocene assemblages (Mercader *et al.*, 2007; Carvalho *et al.*, 2008, 2009). Studies of this type with capuchin monkeys would allow interesting comparisons among closely and less closely related species that use percussive tools. We expect to begin studies along these lines with capuchins at Boa Vista, such as examining microwear produced by capuchins on percussors of high-quality material (e.g., lava basalt).

Transport and selectivity of hammer stones: behavioral observations and experimental evidence

Although both adult and juvenile capuchins spontaneously transport nuts and other encased foods and hammers to anvil sites (Visalberghi *et al.*, 2009a), only 3.4% of the tool-use episodes observed by Spagnoletti (2009) included stone hammer transport. This low rate of occurrence reflects the rarity of suitable stones in the general habitat, the presence of hammers on anvil in use and, at least for small individuals, the high cost of transport (Visalberghi *et al.*, 2007; Massaro *et al.*, 2012).

Of the 22 tool-using capuchins observed by Spagnoletti (2009), 12 spontaneously transported a hammer to an anvil at least once; frequencies of transport did not differ between sex and age classes. Adult capuchins transported heavier hammer stones than juveniles; an adult female transported the heaviest hammer stone, weighing 1600 g, for 6 m. If capuchins take into account the resistance of nuts when looking for a hammer, then they should transport stones suitable to overcome the nuts' resistance, such as quartzites and siltstones, significantly more often than unsuitable ones, such as weathered sandstones. To exploit nuts adult males carried suitably hard stones in 15 cases and unsuitably soft stones in four cases; adult females carried suitably hard stones in all five cases; and juveniles transported suitably hard stones twice and unsuitably soft stones five times (Visalberghi *et al.*, 2009a). Conversely, when exploiting other encased foods (less resistant than the nuts), adults transported soft stones in four cases out of five, and juveniles transported a soft stone in one out of two cases. Although the sample size is small, our observations suggest that adult capuchins take into account the resistance of the food item to be cracked when transporting and using a stone as a hammer (Spagnoletti, 2009; Visalberghi *et al.*, 2009a).

To confirm that the monkeys selected stones for their weight and friability (resistance to crumbling), we carried out the first experimental study on this topic with wild animals (Visalberghi *et al.*, 2009b)⁴ by repeatedly providing individuals with sets of stones varying in specific properties. We presented to eight capuchins choices between two (or among three) stones differing in functional features. In the first two conditions, when no other

⁴ Video clips can be viewed at <http://www.cell.com/current-biology/supplemental/S0960-9822%2808%2901624-2>

stones were available in the area, subjects chose between novel natural stones, similar to those they usually encounter in their habitat, differing in friability (sandstone vs. siltstone), or in size and weight (small vs. large quartzite stones). One of the stones in each set was deemed "functional"; i.e., it weighed 500 g or more and would not fracture when used to strike a nut. In both the above conditions, all subjects first touched, transported and used the functional stone significantly more often than expected by chance.

In the next three conditions subjects chose between novel manufactured stones (composed of ground stone and resin of the same color and material), the weight (an "invisible" feature) of which did not correlate with size (contrary to the usual case). Capuchins had to choose between stones of the same size and different weight, between a light large stone and a heavy small stone, and among a light large stone, a light small stone and a heavy large stone. Again, each subject demonstrated a significant bias to transport and use the heavier stone in all conditions (except one monkey in one condition). They always used the stone they chose first and never modified their initial choice after the first strike(s).

Interestingly, when visual cues were available and reliable, capuchins always touched the functional stone first, suggesting they discriminated the volume of the stones by sight, and they did not tap either stone. In contrast, when visual cues were not predictive or were conflicting, individuals gained information about the mass of the experimental stones by moving, lifting and/or tapping them. Tapping may have allowed them to infer the density of the stones (see also Schrauf *et al.*, 2008). Fragaszy *et al.* (2010) showed that the monkeys preferentially select the heavier stone when they have a choice of two manufactured stones of equal volume, even when the difference in weight between the two stones is a small fraction of the total weight. Overall, naturalistic observations and field experiments provide compelling evidence that when wild capuchins encounter stones that differ in friability and weight, they choose, transport and use the more effective stones to crack open nuts. Moreover, when weight cannot be judged by visual attributes, capuchins act to gain information to guide their selection. In all these ways, capuchins evidence planning and skill in tool use.

Final remarks

Capuchins from very early in life pound objects on surfaces (Adams-Curtis & Fragaszy, 1994) and all over their wide geographical distribution they often pound encased foods, such as hard fruits, seeds or shelled invertebrates, on hard surfaces in order to get access to the inner parts (for a review, see Fragaszy *et al.*, 2004b). Although captive capuchins spontaneously learn to use hammer stones to crack open nuts (for a review, see Visalberghi & Fragaszy, 2012), percussive tool use in the wild seems a geographically circumscribed phenomenon reported only in some populations of *Cebus libidinosus* and *C. xanthosternos* living in northeastern Brazil (Ottoni & Izar, 2008; Canale *et al.*, 2009; Ferreira *et al.*, 2010). Why might this be so?

Three hypotheses have been proposed to account for the appearance of percussive tool use in some populations of capuchins and not in others. According to Moura and Lee

(2004), the occurrence of tool use is related to energy bottlenecks. Tool use is thought to allow the monkeys to exploit tough or hidden foods in regions where they experience periods of extreme food scarcity. According to the second hypothesis, terrestriality is the key factor promoting the emergence of tool use (see Chapter 9; Meulman *et al.*, 2012). The reasoning here is that foraging and traveling on the ground increase an individual's chances of discovering and practicing percussive tool use, because nuts, anvils and potential tools are all found on the ground (Visalberghi *et al.*, 2005). These materials can also be combined more readily on the ground. For example, on the ground, but not in trees, nuts can be placed on flat surfaces and they can be recovered if displaced or dropped. Resende *et al.* (2008) suggested that placing the nut on an anvil and releasing it is one of the main challenges facing young capuchins learning to crack nuts; practicing positioning nuts and other objects on flat surfaces on the ground (but not in trees) may help to overcome this reluctance, because the monkey can learn that a released object remains in arm's reach. The third hypothesis is that the abundance of tough foods in the diet can increase the dietary benefits of tool use to access tough foods (independent of food abundance or terrestriality) (Wright *et al.*, 2009).

It appears from estimates of fruit biomass (Verderane *et al.*, unpublished data; see also Spagnoletti *et al.*, 2012) that the monkeys at FBV do not face seasonal food shortages as extreme as those seen in other habitats (e.g., Atlantic coastal forest). Their reproductive performance and general health suggest a consistently good food supply as well. For example, in late 2008, two pairs of twins were born, one pair in each group. Of the four twins, one disappeared at 11 months and the other three are still alive at this writing (at 16–19 months). Twins are not common in capuchins and survival past 30 days is less likely for a twin than for a singleton infant in captivity (Leighty *et al.*, 2004). Time budgets provide another indirect index of food availability. The capuchins at FBV spent 7% of their daylight time in social activities (Spagnoletti, 2009), which is at the upper range for capuchins living in other semi-deciduous dry forest habitats (Fragaszy, 1990; Rose, 1994; Miller, 1997) and substantially higher than for capuchin monkeys living in evergreen forests (Terborgh, 1983), suggesting that the capuchins at FBV manage to find sufficient food quickly enough to have time for "leisure" activities.

However, their diet does comprise a greater proportion of tough items than the diet of monkeys at other sites (Wright *et al.*, 2009). Although most of these items are breached with teeth and hands, the toughest are breached through hammering with a stone. Thus capuchins at FBV are using tools in a relatively food-rich environment.

The monkeys at FBV (similar to other populations of capuchins that use tools – e.g., Mannu & Ottoni, 2009) spend a greater proportion of time on the ground (roughly 26–34.5% of the day; Spagnoletti, 2009) to forage, rest and play than other populations of capuchins for which tool use has not been reported (e.g.: *Cebus olivaceus* 13.4%, Robinson, 1986; *Sapajus (Cebus) nigritus* 1.9%, Brandon Wheeler, pers. comm.; see Spagnoletti, 2009; Spagnoletti *et al.*, 2009). Thus the preponderance of the evidence suggests that seasonal food shortages are not an adequate explanation of the appearance of tool use among capuchins in *Cerrado* environments. Instead, a combination of ecological circumstances including spatial location of resources, scarcity of terrestrial predators (influencing

the risk of descending to the ground) and mechanical properties of available foods would all seem to play influential roles in the appearance of tool use.

Overall, our findings show that at FBV wild bearded capuchin monkeys are habitual tool users (*sensu* McGrew, 1992) and that the sophistication of their behavior with respect to selection and transport of tools matches that reported for wild chimpanzees using percussive tools (see Table 10.1). This is particularly interesting given the phylogenetic distance between the two species. Although extensive and flexible tool use was once considered a defining human characteristic, discovery of habitual tool use among wild chimpanzees (*Pan troglodytes*) in the 1960s led anthropologists to suggest that the last common ancestor of chimpanzees and humans was a tool user. For many archaeologists and anthropologists, chimpanzees have become the referent for modeling early hominins (Sayers & Lovejoy, 2008). However, wild bearded capuchin monkeys, a species that separated from the human lineage about 35 million years ago, also habitually use tools, but great apes other than chimpanzees rarely do. Thus we need to re-think the accepted explanations of continuity and convergence in primate tool use (Wynn & McGrew, 1989; Byrne 2004; Fox *et al.*, 2004; Davidson & McGrew, 2005; but see Panger *et al.*, 2002; Haslam *et al.*, 2009). Percussive tool use in non-humans has particular importance for the understanding of tool use in early hominins that also used percussive tools to access encased food. As an outgroup species, capuchins illuminate convergences in behavior that suggest ecological foundations for the character of interest (in this case, percussive tool use). A rigorous comparison of percussive tool use in capuchins with tool use in chimpanzees and humans, extant and extinct, will contribute to our understanding of the origins and evolution of this key feature of human behavior.

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