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Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison

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Percussive tool use holds special interest for scientists concerned with human origins. We summarize the findings from two field sites, Taï and Fazenda Boa Vista, where percussive tool use by chimpanzees and bearded capuchins, respectively, has been extensively investigated. We describe the ecological settings in which nut-cracking occurs and focus on four aspects of nut-cracking that have important cognitive implications, namely selection of tools, tool transport, tool modification and modulation of actions to reach the goal of cracking the nut. We comment on similarities and differences in behaviour and consider whether the observed differences reflect ecological, morphological, social and/or cognitive factors. Both species are sensitive to physical properties of tools, adjust their selection of hammers conditionally to the resistance of the nuts and to transport distance, and modulate the energy of their strikes under some conditions. However, chimpanzees transport hammers more frequently and for longer distances, take into account a higher number of combinations of variables and occasionally intentionally modify tools. A parsimonious interpretation of our findings is that morphological, ecological and social factors account for the observed differences. Confirmation of plausible cognitive differences in nut-cracking requires data not yet available.

1. Introduction

The use of tools to forage allows individuals to access embedded food resources that they would not otherwise be able to exploit [1], or that they could exploit only at higher costs (e.g. [2–4]). The selective benefit of tool use is possibly reflected by its independent emergence in three phyla and seven classes of animal species [5]. Birds and mammals can use tools in a non-stereotyped form and learn this behaviour, but only primates use tools for different purposes, in a variety of contexts and display a wide array of behaviours, the acquisition of which is socially influenced [5]. Tool-using skills in primates emerge in a nested set of ecological, morphological, social and cognitive conditions. Several factors promote tool use, namely an extractive foraging style, well-developed manipulative skills, social tolerance, relatively large brain size and sophisticated cognitive skills [6]. Tool use has undoubtedly been important in the evolution of our species, and percussive tool use is the first type of tool use visible in the archaeological record [7].

Percussive tool use occurs in a very limited number of mammals (e.g. otters, capuchins, macaques and chimpanzees [1]) and is extensively studied only in western chimpanzees, bearded capuchin monkeys and, to a lesser extent, long-tailed macaques [8–11]. Otters practise a simple form of percussion: they acquire a hard object and use it as either a hammer or an anvil to crack open invertebrate prey [12]. Nut-cracking is more complex than this form of percussion and other tool-using behaviours, because it involves controlling more movable objects [13–15]. For example, using a probing stick to collect invertebrate larvae from

inside tree trunks or branches, as seen in New Caledonian crows [16], involves managing one moving object (the probe) to produce one spatial relation (inserting the probe into the hole). Nut-cracking involves two or three movable objects (nut, hammer and sometimes the anvil) and the production of two independent spatial relationships (nut to the anvil and hammer to the nut). These spatial relationships should be produced in a specific temporal pattern [13,17,18] and paying attention to the position of the nut on the anvil, the orientation of the stone with respect to the nut, the trajectory of the strike with respect to the nut, the kinetic energy of the strike and the control of the stone at the end of the strike [19,20]. Perhaps this set of requirements explains why cracking nuts with a hammer is rare, despite the high nutritional value of nuts (see §3b).

Stone tool use[1] in chimpanzees, inferred over 150 years ago (cited in [9]), was considered as induced by captivity and proximity with humans until several types of tool use were observed in the wild [21]. In fact, chimpanzees possess extensive tool sets and the tool set of each population reflects adaptation to local ecological conditions and cultural differences [22–24]. Chimpanzees use tools for foraging, as well as in social and symbolic contexts [23]. Tool use in captive capuchins was first mentioned in the sixteenth century in chronicles of the first scientific expeditions in the New World and its variety and flexibility thoroughly studied in the past century (for a review, see [18]). However, only in the present millennium has habitual tool use in wild capuchin populations been reported, indicating that different populations have different tool repertoires and that tool use occurs in foraging and social contexts [25,26]. To date, tool sets in one population [27] and variability among populations in the types of stone tool used to exploit seeds or nuts have been described [28,29]. Hence, capuchins' stone tool use has become a reference point for those studying the evolution of tool use in hominins, as is chimpanzees' stone tool use [30].

The last common ancestors of living stone tool-using non-human primate species and *Homo* lived 7–8 Ma for *Pan* and *Homo* [31], 25 Ma for *Macaca* and *Homo* [32] and 35 Ma for *Cebus/Sapajus* and *Homo* [33]. The phylogenetic distance among these taxa makes the argument that their common ancestor also used tools unlikely; instead, it suggests that stone tool use has emerged independently in capuchins, macaques and hominids.

In this article, we compare stone tool use by chimpanzees (*Pan troglodytes verus*) and by bearded capuchin monkeys (*Sapajus libidinosus*). The findings come from the long-term studies carried out in the Taï National Park (hereafter Taï) on chimpanzees and in Fazenda Boa Vista (hereafter FBV) on capuchins. The Taï chimpanzees project started in 1979. Owing to the long habituation process, individual behavioural data were first published after 5 years. At present, research involves three neighbouring habituated chimpanzee communities [23,34]. Ecological surveys have been regularly conducted in the past *ca* 30 years, and recently field experiments on nut-cracking have started [35]. Capuchins in FBV have been studied during a much shorter period. The Etho*Cebus* project started soon after stone tool use was discovered in 2003. Systematic data collection on two habituated groups began in 2006. Since then, field observations, ecological surveys and controlled experimental studies of nut-cracking have been carried out [10]; moreover, subjects' body masses have been systematically recorded [36].
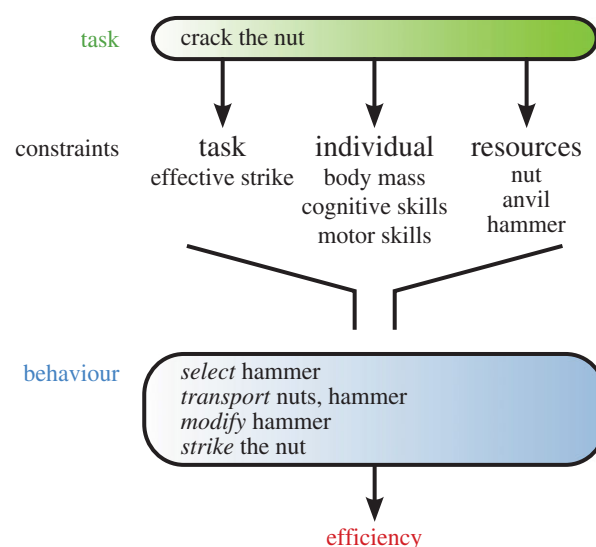

Figure 1. The diagram indicates the main task, ecological and individual constraints influencing percussive tool-use behaviour and ultimately efficiency in cracking nuts. (Online version in colour.)

Taï and FBV are located in very different habitats and thus provide a unique opportunity to explore the influence of ecological variables on the percussive tool use of these species. In §2, we schematically describe the demands that nut-cracking poses to a tool user. Then, we illustrate the ecological setting in which nut-cracking occurs in Taï and in FBV, focusing on the availability and physical properties of nuts, anvils and hammers (§3) and on body mass of individuals of the two species (§4). Having presented this background information, in §5 we summarize our findings on nut-cracking behaviour, focusing on aspects that have important cognitive implications such as selection, transport and modification of hammers, modulation of percussive actions and efficiency. This is the first time in which field researchers jointly compare stone tool use in capuchins and chimpanzees. The closer phylogenetic distance and the stronger cognitive similarities between humans and apes than between humans and capuchins [37] predict greater complexity in the use of hammers in *Pan* than in *Sapajus*. So, in §6, our goal is to examine support for this prediction by commenting on those aspects where the species resemble one another and on aspects where they differ and by discussing the extent to which ecological, morphological and social factors are sufficient to account for species' differences. If these factors can account for observed differences, then predicted cognitive differences must be evaluated via other studies.

2. Constraints on percussive tool use

As shown in figure 1, the challenges faced by a stone tool user depend on (i) the task constraints of producing an effective strike; (ii) the resources (spatial distributions and characteristics of nuts, hammers and anvils) and (iii) the individual's characteristics (body mass, motor skills and cognitive skills). At the behavioural level, the individual should find, or travel to, a suitable object to use as percussor (that has adequate resistance and mass to be used effectively to crack the nut; hereafter, 'functional tool'), a suitable nut and a suitable anvil. Bringing these three objects together requires transport of at least one of them. To maximize the energetic benefits of

this activity, the individual could select the 'optimal tool' that minimizes costs of transport and maximizes production of appropriate kinetic force. Moreover, during the striking phase, an individual should hit the nut with sufficient kinetic energy to overcome the resistance of the encased food item, while holding the hammer in an appropriate orientation, and striking at an appropriate angle. The specific parameters to be optimized depend upon the hammer, the anvil and the nut. In addition, the resistance properties of the nut change dynamically as cracking progresses [38].

We now proceed to examine whether and how chimpanzees and capuchins manage these components of nut-cracking. As we shall see, chimpanzees and capuchins crack nuts of equivalent resistance; to accomplish the same task, they use strategies suited to the resources available in their respective habitats and to their body masses.

3. Ecology: habitat, nuts, anvils and hammers

(a) Habitat

The chimpanzee study site is located in the Taï National Park, Côte d'Ivoire. It is a pristine tropical rainforest with an average rainfall of 1800 ml yr^{-1} and average temperature of 24–28°C, characterized by two rainy seasons (May–June and September–October) and two dry seasons (July–August and November–April) [9]. The territory of the North group, from which most of the data presented here come, is predominantly flat, with some hills; the numerous small streams are bordered by specific flora, whereas the rest of the forest is quite homogeneous in terms of type and density of vegetation.

The capuchin study site, FBV, is located in the southern Parnaíba Basin in Piauí (Brazil). It is a transition area between wooded savannah and thorny shrub land (cerrado and caatinga) with the alternation of a dry season (from May to September with mean monthly rainfall of 5.5 mm) and a wet season (from October to April with mean monthly rainfall of 181 mm) [39]. The area is a flat plain punctuated by sandstone ridges, pinnacles and mesas rising steeply to 20–100 m above the plain. The cliff and plateau consist of inter-bedded sandstone, siltstone and shale. According to the terrain, the proximity to water sources and the types of vegetation physiognomies it is possible to distinguish among plain, marsh, cliff, talus and plateau [40].

(b) Nuts: characteristics and distribution

As shown in table 1, both species use tools to crack several species of nuts, the characteristics of which vary within site and may overlap between sites. In both sites, most of the nut species present are cracked with tools, though some are not consumed, possibly because they require a special technique (e.g. Irvingia by chimpanzees), they are too resistant (Palmeira by capuchins), or for ecological/cultural reasons [42,44].

Chimpanzees have nuts available almost all year around (about 8–10 months per year). The most exploited nuts are Coula and Panda whereas Parinari are eaten only at trees producing especially large nuts. Coula trees are among the most abundant trees in the forest (10 ind ha^{-1}), growing clustered (their spatial correlation according to the Moran's index is +0.11) on the slopes and crests of hilly areas [45]. At the beginning of the Coula season (table 1), chimpanzees crack Coula

nuts in the tree, when they are still attached at branches; later in the season they do so on the ground when the nuts are homogeneously distributed below the crowns of the many trees growing in proximity to one another. Each tree can produce 200–500 single kernel nuts per year.

Panda trees are relatively rare (0.5 ind ha^{-1}), typically dispersed along the rivers, not overlapping much with Coula trees, and solitary (Moran I = −0.02; [45]). During the Panda season (table 1), chimpanzees crack Panda nuts fallen to the ground below the tree crown. Panda nuts are very hard and therefore remain edible for many months. Each tree usually produces from 3 to 50 nuts per year (though in mast years they produce several hundred nuts). Each nut contains three to four kernels that must be accessed individually by repeatedly repositioning the nut on the anvil.

Panda are the hardest nuts found in Africa and require a hit about five times stronger than Coula nuts (table 1) [13]. The resistance of Panda is similar throughout the season, whereas that of Coula decreases throughout the season so that at the beginning of the season they are 22% harder than late in the season when they are brittle [13,34,46].

Capuchins use tools more frequently to exploit palm nuts (86% of the episodes) than other food items [25]. Although many palm species producing nuts are present at FBV, capuchins crack mostly those of catulè, piassava, tucum and catulí. Overall, palm nuts are available all year whereas cashew nuts (Anacardium spp.) are available seasonally (table 1). A transect census estimated that palm trees exploited by capuchins are very abundant in the plain and in the marsh (859 ind ha^{-1} and 779 ind ha^{-1}, respectively), and less abundant in the talus and in the cliff-plateau (460 ind ha^{-1} and 130 ind ha^{-1}, respectively [47]). Despite the abundance of palm trees, palm nuts are never very abundant as palms produce them intermittently and in much smaller quantities than, for example, Coula trees. Capuchins find the palm nuts loose on the ground or attached to fruit stalks at ground level. Cashew nuts are collected in the tree or from the ground, where they fall and dry.

The most resistant palm nut cracked by capuchins (the piassava) has a peak-force-at-failure similar to that of the Panda cracked by chimpanzees, whereas tucum and catulé are about five times less resistant (table 1) [41]. Sometimes palm nuts are parasitized (and capuchins eat the grub); resistance to fracture does not differ between parasitized and non-parasitized nuts. The monkeys can open the dry cashew nuts either with their teeth or with tools [4,25]. In this case, tool use serves to open the nut without exposing the hands or mouth to the caustic resin present in the shell [48].

Nutritional analyses performed on nuts from the Taï forest show that they provide 274–539 kilocalories per 100 g dry weight, with Parinari having the highest caloric value and Panda the highest protein content (table 1); this nut can be parasitized and chimpanzees eat the larvae. Nutritional analyses performed on the palm nuts from FBV show that they provide 487–664 kilocalories per 100 g dry weight with piassava having the highest caloric value and protein content (table 1). Cashew nuts are similar to palm nuts in caloric and protein contents.

Summary. Overall, nuts seem more seasonal and abundant in Taï than in FBV. Chimpanzees crack the nuts at all Panda and Coula trees producing them. Capuchins exploit palm nuts more opportunistically. All nut species have high caloric and protein contents. The hardest species cracked by the two species (Panda and piassava) have similar resistance.

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Table 1. Species of nuts and other encased food items present at Taï and FBV (question mark indicates uncertainty about the species identity) and cracked with tools by chimpanzees and capuchins. Information about nut resistance, nutritional values and seasonality is also reported.

	capuchins FVB	chimpanzees Taï
nut species present nut cracked with tools (*)	* Catulè (*Attalea barreirensis*) * Tucum (*Astrocaryum campestre*) * Catulì (*Attalea* sp.) * Piassava (*Orbignya* sp.*) * Naja (*Attalea dubia*?) * Tucum (*Astrocaryum aculeatissimum*?) * Pati (*Syagrus cocoides*) * Cashew (*Anacardium occidentale*) * Cashew (*Anacardium othonianum*?) Palmeira (*Palmeira oleifera*?) Burità (*Mauritia flexuosa*) (E. Visalberghi 2004–2015, personal observations; [4,25,41])	* Coula (*Coula edulis*) * Panda (*Panda oleosa*) * Parinari (*Parinari excelsa*) * Detarium (*Detarium senegalense*) * Sacoglottis (*Sacoglottis gabonensis*) Irvingia (*Irvingia gabonensis*) Oil palm (*Elaeis guineensis*) Klainedoxa (*Klainedoxa gabonensis*) ([42]; C. Boesch 1979–1999, personal observations)
other food items cracked with tools	Fruta-danta (fam. Icacinaceae) Caroba (fam. Bignoniaceae) Manioca-brava (fam. Euphorbiaceae) [4,25]	none
peak-force-at-failure of the most commonly cracked nuts	Catulè = 5.1 kN Tucum = 5.6 kN Catulì = 8.2 kN Piassava = 11.5 kN [41]	Coula = 2.7 kN, Panda = 12.2 kN [41]
energy content kcal/100 g	Tucum = 487 Catulì = 651 Piassava = 664 Cashew *Anacardium* spp. = 580 [43]	Coula = 356 Panda = 407 Parinari = 539 Detarium = 274 [42]
protein content g/100 g of dry weight	Tucum = 9 Catulì = 10 Piassava = 10.5 Cashew *Anacardium* spp. = 25 (W. Mattos 2008, unpublished data; [43])	Coula = 5.3 Panda = 17.8 Parinari = 8.7 Detarium = 7.2 [42]
nut seasonality	Catulè = May–September > October–April Tucum = not seasonal Catulì (not assessed) Piassava = not seasonal Cashew = September–November [4,39]	Coula = November–March Panda = January–October Parinari = June–October Detarium = December–January [9,42]

(c) Anvils: characteristics and distribution

At both sites, the anvils used are non-movable; therefore they should not be considered as tools, but as substrates [1]. At Taï, chimpanzees mostly use ground anvils (88% for Coula [49]; 100% for Panda [42]) with an almost horizontal surface. Ground anvils consist mainly of exposed roots (98% for Coula, 94% for Panda) and, less often, of stone outcrops (which are rare in the forest) or dead tree trunks [42]. Root anvils often belong to the tree of which the chimpanzees are processing the nuts, and their abundance reflects the abundance of nut trees. However, since nut-cracking involves many nuts and occurs for many months every year, roots wear steadily. Thus, the search for new anvils forces chimpanzees to move to roots of neighbouring trees and to transport nuts there. Tree anvils, used only for Coula nuts, consist only of branches which are rarely horizontal and can even be almost vertical.
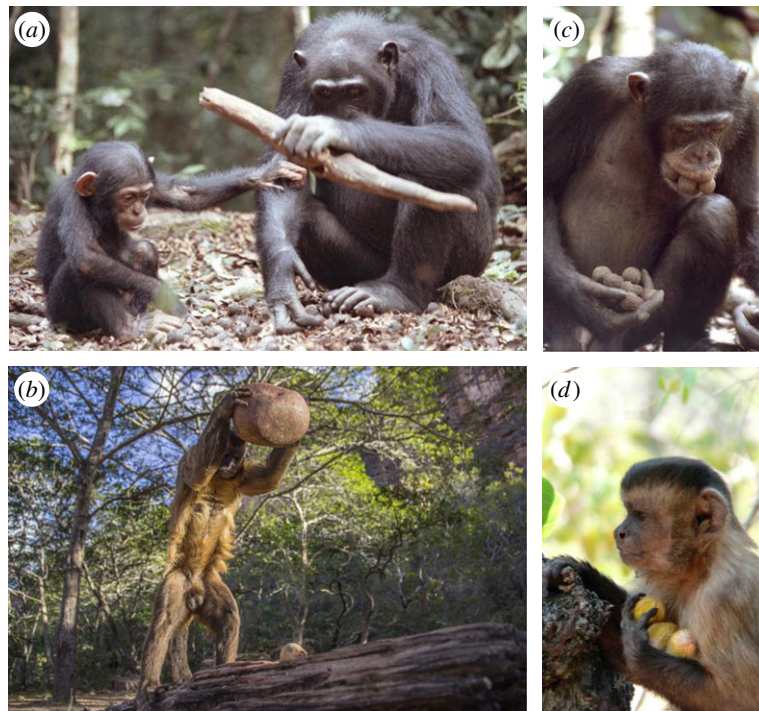
Figure 2. (a) An adult female chimpanzee (weighing ca 42 kg) cracking Coula nuts with a wooden hammer of ca 1.5 kg, adopting a seated posture. (b) A dominant male bearded capuchin (weighing 4.2 kg) cracking a piassava nut with a 3.5 kg stone, adopting a bipedal posture. (c) An adult chimpanzee uses both hands and his mouth to collect Coula nuts. (d) An adult capuchin uses his hand to collect palm nuts. Pictures (a,c) by C. Boesch; picture (b) by L. Marino; picture (d) by G. Sirianni. (Online version in colour.)

At FBV, shear failure of the cliffs leads to boulders at the base of the cliff [40]. The anvils used by capuchins are outcrops of sandstone or siltstone, fallen boulders, fallen tree trunks, or occasionally large horizontal limbs or crotches of living trees. The hardness (estimated in terms of rebound) of wooden anvils does not differ from that of most of the stone anvils [40]. A transect census representing the different physiognomies of FBV indicates that potential anvils (stones and fallen trees) are absent in the marsh, present in the plain (40 ind ha^{-1}), and abundant in the talus and in the cliff-plateau (550 ind ha^{-1} and 900 ind ha^{-1}, respectively). Stone anvils are by far more common than wooden anvils [40,47]. One year of behavioural observations indicate that the vast majority of tool-use episodes occur on anvils located on the ground (boulders or logs), and only 1% of the episodes (seven palm nuts and two other encased food items) on tree branches [39]. Tree branches are used as anvils in 16% of the episodes in which dry cashew nuts are cracked [48].

Summary. Both species usually crack nuts on anvils present in their vicinity. Chimpanzees use both ground and tree anvils while capuchins mostly use ground anvils. Chimpanzees have potential anvils available in most of their habitat whereas capuchins do not.

(d) Hammers: characteristics and distribution

At Taï, functional hammers to crack Coula nuts are wooden hammers and stones weighing at least 0.2 kg, while to crack Panda nuts hammers (mainly stones) must weigh at least 2 kg. Regardless of the methodology used, wooden hammers are more abundant than stones (97% wooden hammers and 3% stones assessed with recce crossing all types of vegetation [13]; 91% wooden hammers, 9% stones assessed with 15 × 6 m

transects around the location where Coula nut episodes occurred [49]). Most available hammers are light, with 50% of the hammers lighter than 0.7 kg [49]. The most abundant stones are laterites (78%) that are also the most friable, followed by granites (16%) and the hardest quartzite (6%) [13]. Hard wooden hammers are rare; 26% fell in the hardest category (out of three hardness categories) [49].

At FBV, functional hammers to crack palm nuts are hard stones heavier than 0.3 kg; wooden hammers are not functional. A transect census representing the different physiognomies present in FBV indicates that functional stone hammers are absent in the plain and marsh and very rare in the talus (10 ind ha^{-1}) and in the cliff-plateau (60 ind ha^{-1}). More friable and lighter stones/woods (or big nut shells) are functional as percussors to crack other less-resistant encased foods (e.g. dry cashew nuts, caroba). Light hard stones (less than 0.1–0.2 kg) are present and abundant in all physiognomies [47].

Summary. Functional hammers are a strong limiting factor especially to crack Panda nuts at Taï and all palm nut species at FBV.

4. Subject's body mass

To achieve the goal of fracturing a nut of a given resistance, the necessary kinetic energy should be produced (figure 1). Biomechanically, characteristics such as body mass, strength, body size and arm length affect the kinetic energy with which the individual can strike the nut (figure 2). Body mass has been identified as a key predictor of efficiency of cracking in capuchins [25,50]. Below, we consider body mass in both species and, in §5a, we discuss these data in relation to the mass of the hammers used by each species.

Body mass of wild *P. t. verus* has never been measured, whereas body mass of captive adult individuals averages 48 kg for females and 56 kg for males [51]. The body mass of adult female capuchins at FBV ranges from 1.9 to 2.2 kg, while adult males' body mass ranges from 3.3 kg to 4.4 kg (the latter value corresponds to the alpha male) [50,52]. Therefore, sexual dimorphism in body mass is by far more pronounced in capuchins than in chimpanzees.

Summary. Chimpanzees are 15–20 times larger than capuchins, and less sexually dimorphic in body mass.

5. Behaviour

When Taï chimpanzees arrive at an area in which Coula trees are abundant, each individual typically approaches a nut tree, collects several nuts (the load ability can be about 15–20 nuts, figure 2*c*) and transports them (occasionally up to more than 100 m) to a ground anvil, where a functional hammer is most often (73% of the cases) available within less than 1 m [49], then starts to crack nuts. Most small wooden hammers are held in one hand at the point of balance and struck directly on the nut [2]. Heavier ones are normally held with both hands on both sides, sometimes with the help of one foot, while long wooden hammers can be either held with one hand and one foot or with two hands with one extremity resting on the ground. Youngsters often stand bipedally to hit with more force and, when using a heavy hammer, they may even stand on one foot while holding the hammer with both hands and the other foot (C. Boesch 1982–1999, personal observation). During a feeding session, a chimpanzee collects and transports nuts several times and can either bring the hammer along or leave it on the anvil (where it may be stolen by another individual). At the beginning of the season, when Coula are still attached at the branches, chimpanzees first look for a hammer, then holding it, climb up in the tree, collect the nuts and crack them on a branch. Multiple individuals can be heard cracking Coula at few/several metres from one another, making this a social activity [13]. When Coula nuts are available, chimpanzees spend on average slightly more than 2 h per day feeding on them, cracking up to 270 nuts (700 g) [9]. The net energy gain from Coula can therefore amount to up to 3450 kcal per day, making them a very rich and abundant food resource [9,53]. Panda nuts are cracked only on the ground and the sequence of events is very similar to the one for Coula. However, since Panda trees are usually far from one another, cracking Panda is generally a solitary activity. Chimpanzees' fission–fusion social organization makes solitary cracking possible without individuals being stressed. Occasionally two individuals (usually kin or strongly bonded individuals) crack in alternation at the same site, or a lower ranking individual waits until the first chimpanzee leaves [9].

Capuchins crack palm nuts holding the stone with both hands while standing in a bipedal posture. When cracking other (less-resistant) encased foods capuchins can use a small stone in one hand and a seated posture, as less force is necessary. Typically, they encounter a palm tree bearing nuts or find loose nuts on the ground, collect a few nuts (figure 2*d*) and go straight to an anvil site[2] in the vicinity. The median distance of nut transport (all types of nuts) is 16 m for adult males, 10 m for adult females and juveniles [47]; nevertheless, transports over longer distances have also

been observed (e.g. more than 100 m, D. Fragaszy 2007, personal observation). Capuchins transport on average 1.3 nuts per tool episode (range 1–5); when more than one nut is transported, they may use hands, mouth and/or feet [47]. Typically, an anvil site accommodates one individual at a time, though, in Spagnoletti's study, in 25% of episodes there was more than one individual cracking at the same anvil [54]. In general, while one individual is cracking a nut other individuals with nuts 'wait' nearby for their turn to use the anvil and the stone; in these cases, dominant individuals may try to displace lower ranking individuals from the anvil, who in turn may carry nuts to other anvil sites, including anvil sites out of view [25,55]. Capuchins do not transport loads of nuts as chimpanzees do (figure 2*c,d*). Moreover, nut transport over distances longer than 100 m (as for example, across the plain to reach the base of the cliff) is extremely rare, possibly because of its associated costs. In fact, holding nuts in its hands and mouth during transport would prevent a capuchin from engaging in other foraging activities and would separate the individual from the group. Typically, capuchins travel in rather cohesive groups and for shorter daily distances than chimpanzees [9,56].

How frequently do capuchins crack nuts? Over a one year period Spagnoletti [54] observed monkeys in one group using tools (cracking + eating) in 3% of scan samples, and 2% of samples in another group. This is equivalent to an yearly average of about 22 min and 12 min per day, respectively (estimated from [54] assuming a 12 h day).

Summary. For chimpanzees, nuts are an important food source that they exploit for many hours each day when available. By contrast, capuchins exploit palm nuts opportunistically.

(a) Hammer use and selection

The physical properties of hammers used to crack nuts of different resistance and selection of hammers were evaluated with two methodologies: (i) surveys of artefacts found at anvils in use [13,40,42,57] and (ii) observations of individuals using hammers [25,34,39,49]. The availability of potential tools was measured at different spatial scales (line transects in the whole territory [13,34,40,42,57] or surveys made at the specific location where each episode of tool selection occurred [49]) or, for capuchins, during field experiments (e.g. [41,58]).

Since the Taï project began, even before chimpanzees were habituated to human presence, there was strong indirect evidence that chimpanzees were selecting hammers of specific material and mass. Ninety per cent of hammers found at Panda nut-cracking sites were stones, a rare raw material in the surveyed territory, while only 10% were wood, a much more abundant material (note that the same hammer could have been used once or more times by one or more individuals [42]). Chimpanzees' selection of hammers differed according to the species of nut: the frequencies of stone and wood hammers were practically reversed at Coula cracking sites (8% stone versus 92% wood, versus 90% stone and 10% wood at Panda cracking sites). At Coula cracking sites the relative frequency of use of the two materials was rather similar to the frequency of occurrence of the two materials in the territory [42] (see §3*d*).

However, direct observations indicate that the use of stones to crack Coula nuts varies across communities and along the season [34,59]. The South community uses stones about 80% of the time during the entire year, whereas the North and

East communities use stones 50% of the time early in the season and 10–20% of the time late in the season [34]. When the availability of raw material at each tool choice site is taken into account, a marked preference for stones over wood to crack Coula nuts emerges for the North community, though these chimpanzees were successful with both materials [49]. When chimpanzees use wood, they prefer harder wood (which is rare) to softer wood (which is abundant) [49]. Finally, chimpanzees select hammers by mass when cracking both Panda and Coula nuts [42,49]. They use heavier percussors for the Panda nuts (min mass 1 kg, max mass 11.9 kg, average mass 5.4 kg, estimated from [13]) than for the Coula nuts (min mass 0.2 kg, max mass 15 kg, average mass 2.1 kg, median mass 1.2 kg [49]). These data show that the average mass of the hammers used for Panda correspond to 11% and 10% of females' and males' body mass, respectively, whereas for Coula they correspond to 4.4% and 3.7% of females' and males' body mass, respectively. Differences between sexes in hammer selection have not been investigated. The small sexual dimorphism in body size of chimpanzees predicts limited to no sex differences in hammer selection.

Systematic surveys of the physical remains of capuchins' nut-cracking activities indicate that they use quartzite and hard sandstones (such as siltstones and ironstones); because stones of these materials are extremely rare in FBV these data provide indirect evidence of selectivity [47]. Systematic behavioural observations confirm that to crack palm nuts capuchins use hard stones, and not friable stones or wood [25]; however, with these latter materials they crack encased food of very low resistance (e.g. cashew nuts). In order to crack palm nuts, adult female capuchins at FBV use stones with a median mass of 1 kg (max 2.3 kg); adult males use stones with a median mass of 1.1 kg (max 3.0 kg). The median values correspond to 48% and 31% of the body mass of adult females and adult non-dominant males, respectively. By contrast, the median mass of the hammers used to crack other much less-resistant food items was 0.1 kg (max 0.4 kg) for males and 0.2 kg (max 0.7 kg) for females; these hammers included friable stones and shells of palm nuts [25]. Females are particularly selective, using significantly heavier hammers for piassava and catulí (hereafter high resistance nuts) than catulé and tucum (hereafter, low resistance nuts; see table 1); by contrast, for males the difference is not significant [25]. Capuchins transport and use hammers of different masses according to the resistance of the nut. When presented with a choice between a heavy stone 2 kg (far from the anvil) and a light stone 0.6 kg (placed on the anvil) and nuts of different resistance, capuchins transported the heavy stone only when given highly resistant nuts [60].

As in 97% of the episodes, the monkeys use a hammer stone already present on the anvil [25], a field experiment was carried out to determine whether capuchins do indeed select stones on the basis of material, size and/or mass [61]. Each capuchin ($N = 8$) was tested in five conditions of 10 trials each. Selecting the functional stone was mandatory for success since the alternative was a non-functional tool(s) and no other functional stone was available in the area. The choice was between novel natural stones, similar to those capuchins usually encounter in their habitat, differing in friability (condition 1), in size and mass (condition 2), or between/among artificial stones made with the purpose of controlling for size and mass (conditions 3–5). In all conditions, all subjects (except one in one condition) selected,

transported and used the functional tool significantly more often than expected by chance; moreover, they did so from the first trials. The monkeys selected the more functional stone even when the volume of the stone of appropriate mass was smaller than the volume of a light stone [61].

Further field experiments investigated selection when two functional tools were presented. Capuchins were offered binary choices of four identical artificial stones ranging in mass between 0.5 and 1.1 kg and given tucum, partially broken piassava and whole piassava [58]. The finding that the capuchins preferred the heavier tool (1.1 kg) and the less-resistant nuts, thus minimizing the number of strikes per nut cracked, further indicates that cracking nuts is a strenuous activity for them. Interestingly, when the mass could not be judged by visual attributes, to guide their selection capuchins moved/lifted the stones and/or tapped them, generating acoustic or haptic information [58,61].

Summary. Both species are sensitive to physical properties of hammers, such as mass, material and hardness. Chimpanzees tend to use hammers weighing up to 11% of their body mass; the corresponding values for capuchins are more than 30% (males) and 48% (females). In addition, both species select/use hammers of different physical properties according to resistance of the nuts, further supporting the idea that they look for the 'optimal tool' among available potential tools.

(b) Hammer conditional selection

As illustrated above, when selecting a hammer chimpanzees and capuchins take into account multiple characteristics of the hammer (e.g. mass, material, hardness). However, when an individual has to crack a nut of a given resistance, he or she may choose among several potential tools, each characterized by a unique combination of relevant and irrelevant physical properties and differently located in space in relation to other relevant elements, such as anvil(s) and nut(s) [49]. Therefore, in each episode of tool selection, optimality depends on the specific set of conditions and on the individual. To optimize cracking efficiency at any given time, the individual must evaluate several properties of the available potential tools and several contextual variables simultaneously.

To study conditional selection, field observations of chimpanzees cracking Coula nuts were carried out [49]. For each episode of hammer selection, the availability of all the potential tools at the spot of hammer selection was recorded and features of potential tools and of the chosen tool compared. Chimpanzees adjusted their preference for hammer mass according to the following variables: material of the hammer (stone versus wood), transport distance of the hammer to the anvil and the location of the anvil (on ground versus on tree). In particular, chimpanzees selected heavy stones, but relatively lighter wooden hammers; mass being equal, the denser stones were of a smaller size than woods, therefore providing the power of a heavy hammer in a compact object, possibly affording better control (table 2). Chimpanzees also selected increasingly heavier hammers the closer they were to the anvil. They selected lighter hammers when they were going to crack nuts in a tree compared to when they were going to crack nuts on the ground. Cracking nuts on a tree branch involves handling multiple objects, never releasing hammer or nut(s), and at the same time is more challenging for maintenance of balance than sitting on the ground. In this situation, smaller hammers present advantages over larger hammers.

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Table 2. Behaviours related to nut-cracking that are present in at least one of the two species. The column 'comparison' reports a synthesis of similarities/differences between chimpanzees (*Pan*) and capuchins (*Sap*). Symbols indicate that the behaviour is: + present in the species; − absent; ≈ performed similarly in both species; > more prominent (more frequent or more complex) in one species than in the other; n.a. data not available. The column 'possible explanations' presents non-mutually exclusive explanations for the observed differences: √ indicates that there is evidence supporting the explanation; (?) indicates lack of data to evaluate the explanation. The column 'notes' provides relevant comments. Details on each behaviour are given in the main text.

behaviour	comparison	possible explanations	support	notes
hammer selection	mass			availability of functional wooden hammers
	material (wood versus stone)	*Pan* + *Sap* n.a.		not assessed for *Sap*
	hardness (within the same material)	*Pan* ≈ *Sap*		
hammer selection according to nut resistance	mass, material, hardness	*Pan* ≈ *Sap*		material not tested in *Sap* (see 'material' above)
conditional selection for hammer mass (same nut resistance)	mass *according to* transport distance	*Pan* > *Sap*	**morphology** (smaller body mass constrains the range of masses and transport distances in *Sap*)	√	
		cognitive (less long-term planning in *Sap*)	?	
		ecology (fewer potential anvils result in more frequent reuse of the same anvil sites in *Sap* than *Pan*)	√	
	mass *according to* hammer material	*Pan* + *Sap* n.a.		not tested in *Sap* because use of wooden hammers is too rare and restricted to soft food items
	mass *according to* anvil location (ground versus tree)	*Pan* + *Sap* n.a.		not tested in *Sap* because use of tree anvils is too rare
hammer transport		*Pan* > *Sap*	**morphology** (smaller body mass constrains the range of masses and transport distances in *Sap*)	√	
		cognition (less long-term planning in *Sap*)	?	
		sociality (fission/fusion in *Pan* allows for solitary activities; *Sap* groups are more cohesive)	√	
	higher frequency, longer distances	**ecology** (fewer potential anvils result in more frequent reuse of the same anvil sites in *Sap* than *Pan*)	√	

Table 2. (Continued.)

behaviour	comparison	support	possible explanations	notes
wooden hammer intentional modification	Pan + Sap −/?	✓ ?	**morphology/ecology** (body mass and resistance of palm nuts force Sap to use stone tools, which cannot be easily modified) **cognition** (modifying wooden hammers may require complex/persistent modification)	Sap uses wooden hammers rarely and only for soft food items. Modification may not be necessary
modulation of kinetic energy	Pan ≈ Sap			results from Pan are preliminary
careful positioning of nut on anvil	Pan ≈ Sap			results from Pan are descriptive

Observations of naturally occurring episodes of hammer selection in parallel with a detailed assessment of hammer availability at the spot of hammer selection have not yet been carried out in FBV, but a field experiment to investigate conditional selection of hammer mass according to transport distance was performed [62]. Given the high cost capuchins face when bipedally transporting heavy stones [63], the distance between hammer and anvil should affect stone selection in these monkeys. When Massaro et al. [62] placed two stones of the same mass at different distances from the anvil, all capuchins consistently selected the closer stone. However, when capuchins had to choose between a light stone (1 kg) and a heavy stone (2 kg), alternatively placed at 3 m and 6 m from the anvil, individual differences appeared. In this situation, large-bodied capuchins preferred the heavy stone regardless of transport distance, while small-bodied individuals selected the closest hammer regardless of its mass (a physically handicapped large male did not show any preference). Overall, these findings show that (i) individuals vary in their sensitivity to distance of transport, (ii) that a few metres are perceived as a cost by some subjects and (iii) that body mass is a main factor affecting choice.

When the experiment was repeated with the same hammers and smaller transport distances (2 and 4 m) one individual (out of five) reversed her pattern, thus adjusting her preference for hammer mass according to transport distance [62]. This is suggestive evidence of conditional selection that needs replication. To test whether capuchins select hammers conditionally, one should examine choices of several individuals when faced with a broader combination of transport distances and stone masses. If larger capuchins select lighter hammers when the length of the transport of heavier hammers becomes too great, and vice versa, small capuchins select heavier hammers when the length of the transport decreases, this would show that capuchins are capable of conditional selection.

Conditional selection of hammer mass according to hammer material and anvil location has not yet been tested in capuchins. This is because capuchins very rarely use wooden hammers (and never use them for palm nuts) and almost never crack hard encased foods in trees. Therefore, the two species cannot be compared unless ad hoc experimental studies are conducted.

Summary. Chimpanzees adjust their preference for hammer mass in relation to hammer material, distance of transport, and anvil location, taking into account four factors in a single choice. There is a suggestion that capuchins adjust their preference for hammer mass according to transport distance; however, this needs confirmation.

(c) Hammer transport

Chimpanzees pick up a hammer and transport it to the anvil (primary transports), or transport it from one anvil to another anvil within the same nut-cracking session (secondary transports, tertiary transports, etc. [13,46,49,64]). Chimpanzees typically transport hammers and nuts in a tripedal posture, with one hand holding the item(s). Early reports inferred transport distances by tracking movement of raw materials that were previously marked (stones), or recognizable on the basis of shape (woods). Over a 4-year period, transport was recorded in 458 cases for Panda (99% stone and 1% wood) and in 439 cases for Coula (41% stones and 59% wood) [46]. Harder stones (granite), which are rare in the

forest, were transported more frequently than the common softer stones (laterite). Granite stones and heavier hammers were transported proportionally more often for Panda than for Coula [46]. Additionally, hammers were transported over longer distances more for Panda than for Coula, with maximum transport distance being more than 500 m for both nut species [46]. A detailed study with marked stones revealed that chimpanzees select the closest stone at a given goal Panda tree, and lighter hammers for longer transports [46].

The above procedure does not allow distinguishing between primary and multiple transports and between transports performed by one and multiple individuals [46,64], whereas direct observations of hammer transports do. During two consecutive Coula seasons, Sirianni *et al.* [49] observed chimpanzees cracking Coula nuts. In 73% of the hammer selection episodes, the hammer was collected within 1 m from the anvil. Ninety-four per cent of wooden hammers ($N = 114$) were transported for less than 5 m. Primary transports of stone hammers were greater than 1 m in 48% of the episodes and greater than 10 m in 27% of the episodes (maximum primary transport = 166 m [49]).

At FBV, the availability of hammers on the anvil site is much greater than in the 3 m corona around it, suggesting that the monkeys transported stones to the anvils [40]. A monthly survey of 58 anvil sites over a 3-year period revealed that some hammer stones were transported from one anvil to another anvil and used there; the longest transport recorded was 10 m [57]. A 1.5 kg stone was found transported 94 m from its previous location [62]. Informally, D.F. has observed monkeys transporting hammer stones of 1 kg or more over tens of metres every year since 2005.

Capuchins use the same anvil site repeatedly. During one year of observations, 49% of the anvil sites are re-used and each anvil is used on average 4.8 times (N. Spagnoletti 2006–2007, unpublished data). Transports (observed from the beginning to the end and in which the hammer is displaced for more than 1 m) occurred in only 3% of tool-use episodes scored [25]. Overall, it appears that the median distance is similar across age and sex classes. Adults transported the percussors to crack palm nuts and to crack other less-resistant encased foods for a median distance of 3 m and 5.5 m, respectively [47]. The maximum distances of observed stone transport were 21 m (a 0.5 kg stone by an adult male), 12 m (a 0.2 kg stone by a juvenile) and 6 m (a 1.6 kg stone, the heaviest hammer transported, by an adult female). The masses of the percussors transported to crack palm nuts appear higher than those transported to crack other encased food, but since spontaneous transports occur rarely, experimental investigations in which transport is mandatory are needed to gain a better understanding of this phenomenon.

Summary. Chimpanzees transport hammers more frequently and farther than capuchins. Both species take into account the resistance of the food item when they transport the hammer.

(d) Hammer modification

Tool modification can be defined as all the intentional and unintentional alterations accomplished on an object to modify its shape [65]. Over a span of 9 years, Taï chimpanzees modified nut-cracking hammers through breakage while pounding on the nut, apparently unintentionally, in 8% of cases of hammer use, 2% (17 cases) for stone hammers and 6% (44 cases) for wooden hammers. In 17 other cases, the modifications of wooden hammers appeared intentional [65]. Intentional modifications consist of removing protrusions and/or shortening the tool by pounding it on a hard surface or by standing on it and forcefully pulling it upwards until it breaks (see video Tool modification in the electronic supplementary material).

In capuchins, unintentional modifications of stone hammers happen occasionally. Surveys of anvil sites evidenced breakage of hammer stones due to forceful impact almost certainly incurred during its percussive use by a capuchin [40,57]. However, capuchins have never been observed to modify hammers intentionally. Moreover, both species unintentionally produce pits, i.e. shallow depressions due to wear, by repeatedly cracking nuts on the same substrate [40,42,66], as early hominins did [67].

Summary. Both species unintentionally modify tools. Chimpanzees intentionally modify wooden hammers by reduction, although rarely.

(e) Motor skills

A key constraint in nut-cracking is that hammer strikes must deliver sufficient kinetic energy (E_k) to crack open the nut. At the same time, however, the E_k should not be so large as to smash the kernel (resulting in wasted effort, loss of a fraction of the kernel and/or increased time needed to collect the kernel fragments). The kinetic energy at impact with the nut is determined by velocity and mass of the hammer ($E_k = 1/2mv^2$). Velocity at the point of impact is a function of the height to which the hammer is lifted and the energy added to the hammer by the individual applying force to the hammer in the downward phase of the strike. Therefore, an individual can modify the kinetic energy of a strike by adjusting the height to which the hammer is lifted and/or the force applied to the hammer in the downward direction. Modulation of kinetic energy is a key indicator of cognitive engagement in nut-cracking [20,68].

To crack Panda and Coula nuts, adult chimpanzees usually adopt a sitting posture (figure 2a). When cracking Panda nuts, chimpanzees lift the hammer at least to chest height [13], while they usually lift the hammers used for the soft Coula nuts to a lower height (C. Boesch 1982–1999, personal observation). This suggests that chimpanzees modulate the energy of their strikes according to the resistance of the nut. Günther & Boesch [53] investigated the kinematics and energetics of pounding in two young male chimpanzees that cracked Coula with two wooden hammers weighing 2.3 and 5 kg (corresponding to 7% and 14% of chimpanzees' estimated body mass, respectively). Both chimpanzees lifted the 2.3 kg hammer higher than the 5 kg hammer, indicating that they might adjust the height of lifting in order to produce a similar amount of kinetic energy when using hammers of different mass. When one chimpanzee performed seven strikes with the 2.3 kg hammer, the higher he raised the hammer, the more force he applied to the hammer in the downward movement, thus adjusting both parameters to modulate the kinetic energy of his strikes. Günther & Boesch [53] reported the energetics of a single strike on a Coula nut. Liu *et al.* [69], using data for the single strike described in [53], calculated that the kinetic energy of the chimpanzee's hammer at the moment of the impact with the Coula was 14.5 J, with the chimpanzee adding 8.2 J during the downward movement (note that to calculate kinetic energy the mass of the arm was considered

together with the mass of the hammer). An ongoing study [35] will provide data for the kinematics of nut cracking in wild chimpanzees with a much larger sample of nut-cracking sessions recorded by remote camera traps.

Liu *et al.* [69] investigated the kinematics and energetics of nut-cracking in two male and two female adult capuchins. To crack palm nuts, they adopt a bipedal posture (figure 2*b*). Adult male capuchins have larger body mass than adult females and also longer trunk and limb [70], and therefore males lift the hammerstone higher than females [50]. Moreover, adult males are more likely than females to apply force to the hammer in the downward direction, thus reaching higher kinetic energy [69,71]. Males added nearly twice the work than did females (mean = 5.6 J versus 2.9 J; males and females, respectively [69]). When provided with piassava nuts and five stones differing in mass (0.6–3.5 kg; 28% to 174% of an average adult female's body mass) wild capuchins lifted stones of varying masses to the same height, but applied more force to lighter stones [71]. When using stones across a range of masses heavy enough to crack piassava nuts (0.9–1.9 kg), capuchins achieved average maximum kinetic energy of 8.7–16.1 J (note that the contribution of the mass of the arm to the kinetic energy of the strike was not considered). Two monkeys also adjusted the height to which they lifted stones as a function of the size (and therefore resistance [41]) of the nut they were cracking at the time. Capuchins cracking tucum nuts, that are less resistant than piassava, modulated the kinetic energy of their strikes by modulating the height of their strike and the force applied to the hammer per strike in accord with the condition of the nut following each strike [38]. When cracking the highly resistant piassava nuts, the chief constraint for capuchin monkeys is to generate sufficient kinetic energy. When cracking the less-resistant tucum nuts, capuchins modulate strikes to keep kinetic energy within an acceptable zone.

Summary. Chimpanzees usually adopt a sitting posture while cracking nuts, whereas capuchins adopt a bipedal posture, one of many indications that nut-cracking is a more strenuous action for capuchins than for chimpanzees. Both species, under some conditions, adjust the height to which they lift the hammer and the force applied to the hammer in the downward direction. Studies of modulation of kinetic energy are just beginning. To date, we know that capuchins modulate the kinetic energy of their strikes in relation to the current state of the tucum nut they are cracking.

(f) Success and efficiency

Success rate is the percentage of cracking episodes in which the nut was opened. Adult chimpanzees are almost always successful when cracking Coula and Panda nuts. Adult capuchins are almost always successful with low-resistance nuts (e.g. 97% with tucum) and moderately successful with higher resistance nuts (e.g. 77% with piassava [58]). Females crack significantly fewer high resistance nuts than males [25] and in an experimental context, all capuchins preferred less-resistant nuts (i.e. tucum versus piassava [58]).

Efficiency can be increased in part by (i) selecting a hammer that can be used with good control to deliver sufficient kinetic energy, (ii) controlling the strikes in various ways, (iii) positioning the nut on the anvil so that it is stable and maximizes the force of the strike transmitted to the nut, (iv) minimizing transport distance and so on (figure 1). Efficiency can be measured in terms of number of strikes and time needed to crack open a nut. It may (or may not) include the time needed to collect materials, and/or to process and to eat the nut. Below we report efficiency data on chimpanzees' and capuchins' nut-cracking.

Early studies showed that adult chimpanzees perform, on average, 6.7 strikes to crack Coula and 19 strikes to crack Panda (i.e. access the first kernel). The number of nuts opened per min is 2.1 for Coula and 0.5 for Panda [13]; note that these measures include time spent collecting nuts and to extract and eat the kernel(s). Chimpanzees use fewer strikes to crack Panda nuts when using heavier hammers [13]. On the ground, females are more efficient at cracking Coula nuts (in terms of number of strikes and number of nuts cracked per min) than males [13,46]. Data on the efficiency of individuals cracking Coula nuts in relation to hammer properties are currently under analysis (L. Luncz & G. Sirianni 2008–2013 unpublished data). Chimpanzees gain an enormous energetic benefit from cracking Coula nuts using tools. The estimated ratio of energy output to energy gained is about 1 : 9 [53].

At FBV, capuchins use fewer strikes for low-resistance nuts (8–13 strikes, on average, males and females, respectively) than for high resistance nuts (12–15 strikes, on average, males and females, respectively) [25]. To crack a piassava nut with a 1.5 kg stone, capuchins used on average 6.6 strikes (the alpha male) to 75.8 strikes (a 30-month-old male). An adult male human, constrained to lift the stone to the same height as the monkeys (about 40 cm), used 6.2 strikes on average to crack piassava nuts [50], giving an indication of how much force is required to crack these nuts.

Body mass is the single best predictor of capuchins' efficiency (number of strikes per nut); sex *per se* does not predict efficiency. Nut diameter (which within the same nut species is a good proxy for resistance [41]) affects efficiency and success [39,50]. More efficient monkeys raised the stone higher and tended to raise it a greater proportion of their trunk length (see §4; [50]).

Both chimpanzees and capuchins have a strong preference for placing whole nuts into the pit(s) of the anvil, rather than on its flat surface [19,42,72]. This behaviour has been investigated in detail in capuchins, showing that placing the nuts in the pit decreases the likelihood that they will bounce off the anvil after the strike from 52 to 31% [50]. Capuchins position piassava nuts in the pit with the most symmetric sides of the nut facing the wall of the hemispheric pit. This position stabilizes the nut, reducing movement following a strike, and possibly increases the transfer of force to the nut, thereby increasing efficiency, compared to other positions of the nut [19,73].

Summary. Chimpanzees easily succeed in cracking Coula and Panda nuts when using a functional tool, and similarly capuchins easily succeed at cracking less resistant nuts. Both species are more efficient when cracking less resistant nuts. Capuchins' efficiency is strongly affected by body mass. Adult capuchins crack piassava nuts with a similar number of strikes than chimpanzees crack the Panda nuts of similar resistance.

6. Discussion

We described the percussive behaviour of Taï chimpanzees and FBV bearded capuchins, devoting particular attention

to frequency and efficiency of nut-cracking, and to similarities and differences across aspects of behaviour that might serve as indicators of skilled performance, such as selection, transport and modification of tools and modulation of strikes. Table 2 summarizes similarities and differences between the species and provides possible explanations for the observed behavioural patterns.

(a) Similarities

Despite enormously different body mass, the two species crack equally resistant nuts [41], necessarily generating a similar kinetic energy to do so, and they do so in roughly the same number of strikes, on average. Adults of both species effectively adjust their behaviour to the variable circumstances they encounter. First, when alternative potential hammers are available, both species select the most functional hammer in relation to the hardness of the food item (e.g. [13,25,60]). Second, individuals modulate their strikes in response to the demands of the task, integrating the resistance of the nut, the properties of the hammer, the individual's strength and mass, and in capuchins, the state of the nut following the previous strike [20,38,53,71]. Third, both species transport tools and/or food items to sites where they use tools to process the food items (e.g. [47,49,61,62]).

(b) Differences

Bearded capuchins crack nuts less frequently than chimpanzees. Given that capuchins are much smaller than chimpanzees, and that the nuts consumed at FBV are at least as nutrient-rich as those consumed in Taï, capuchins should consume many fewer nuts than chimpanzees. Additionally, plausible ecological explanations for this difference are that (i) nuts, hammers and/or anvils are less abundant in FBV than in Taï; (ii) these resources are very often far apart from one another in FBV, making transport costly; (iii) capuchins might have better or more abundant alternative food resources than do chimpanzees. Calculations of each species' metabolic needs together with measures of the nutrient value of nuts consumed are necessary to properly understand the contribution of nuts to the diet of the two species. Nuts are undoubtedly an important food source for Taï chimpanzees (for Coula [53]). The contribution of nuts to the diet of capuchins at FBV is under investigation (L. Peternelli dos Santos 2012–2014, unpublished data).

The two species differ with respect to hammer transport. Chimpanzees transport hammers more frequently and for longer distances than capuchins. Capuchins' small body mass clearly constrains the extent to which they can transport heavy hammers, and the scarcity of potential anvils and hammers in FBV leads to frequent re-use of them. Though at present evidence is lacking, cognitive processes, such as long-term planning, might also contribute to differences between the species in this domain, in addition to the effect of body size.

The two species differ also with respect to hammer modification. Taï chimpanzees occasionally modify wood hammers intentionally, adjusting their length and/or removing some protrusions, whereas FBV capuchins have never been observed to modify stone hammers intentionally. Because of their small body mass, capuchins must use stone hammers to crack palm nuts, and stone is a raw material that is very difficult to modify. However, other wild populations of the *Sapajus* genus modify branches to use them as probes [27,74], as do captive capuchins

manufacturing probing tools [75]. Though morphological and ecological factors seem to be sufficient to explain this difference between FBV capuchins and Taï chimpanzees, future studies should investigate whether cognitive differences might also play a role (table 2). To compare the aptitude of the two species to modify tools, future studies could provide individuals of each species with modifiable objects of uncomfortable shapes (but suitable as tools in terms of material and mass), and that are modifiable by detachment, to use as hammers.

Another possible difference between the two species may be found in conditional selection of hammers (table 2). Chimpanzees have been shown to take into account four different factors simultaneously, adjusting their preference for hammer mass to hammer material, distance of transport and anvil location [49]. In FBV, because of ecological and morphological constraints, capuchins do not face such a varied array of factors at the same time when selecting a hammer. However, they take some of these factors into account when they encounter them (see §5a). So far, suggestion that capuchins select hammers conditionally is available from a field experiment that assessed capuchins' choice of hammerstone when the mass of two hammers and their distance from the anvil varied independently [62].

In order to support straightforward comparisons between capuchins and chimpanzees with regard to conditional selection of hammers, we suggest replicating Sirianni *et al.*'s study [49] with wild capuchins, concurrently varying the type of anvils available as well as the hammer options. However, given the competitive nature of access to nuts and anvils in capuchins [55], this must be done carefully, since capuchins' decisions about whether and what object to transport, and where to take it, are influenced by the immediate social context as well as by the properties of potential tools and anvils.

Individual chimpanzees selected hammers of a particular mass according to transport distance when no anvil is in view and this has been argued to be strong evidence for planning [46,49]. The sophisticated spatial skills revealed in Taï chimpanzees when travelling to individual food trees, out of many thousands in their home range, suggests long-term memory and botanical knowledge [44,76] that are important prerequisites facilitating the long transport of hammers seen for cracking Panda nut. This type of planning has not yet been studied in capuchins. Capuchins commonly transport a nut to an anvil out of view, which may reveal planning ability with respect to travel. They travel directly to preferred feeding locations from distant points out of view [77,78] and to do so they do not use habitual routes in continuous forest [79], thus suggesting spatial planning skills in capuchins. Additional studies with both species on the topic of planning actions at a distance are needed for a more complete understanding of each species' spatial cognition.

(c) Conclusion

Our comparison of percussive tool use in Taï chimpanzees and FBV capuchins indicates that both species modulate motor actions, transport materials to seen and unseen anvils, and concurrently evaluate affordances of various nuts, hammers and anvils. Their similar performances could be an example of convergent evolution of species that are particularly apt to learn from action, a convergence evident also in the neuroanatomy of their motor systems [80]. For example, both capuchins and

chimpanzees possess well-developed cortical areas associated with motor planning, visually guided reaching, grasping and manipulation [81].

However, the species differ in distance of tool transport, modification of tools and conditional selection. These differences likely depend on differences in ecology, morphology and sociality, though cognitive differences between species might also play a role. However, the data collected so far are insufficient to evaluate the contribution of cognition to the observed differences and therefore further studies are necessary to assess the extent to which cognitive differences play a role (table 2). Varying performance ascribed to different cognitive abilities between these species has been documented in some other tool-using tasks (e.g. [82,83]) and in spatial problem solving tasks (e.g. [73] although not in others e.g. [84,85]), making it plausible that cognition has a role in the observed species differences in behaviour. A second important line of research concerns the role of social influence on the acquisition of nut cracking, because social influence on acquisition is a feature central to the status of nut-cracking as a traditional/cultural behaviour [23,86–88].

Endnotes

[1]Note that the expression 'stone tool use' does not necessarily imply that either hammer and/or anvil are made of stone. The expression refers also to wooden hammers and anvils.
[2]The term anvil site indicates anvils in current use and corresponds to the term atelier used by Boesch & Boesch-Acherman [42].

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