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ORIGINAL ARTICLE

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Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys

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Abstract Selection and transport of objects to use as tools at a distant site are considered to reflect planning. Ancestral humans transported tools and tool-making materials as well as food items. Wild chimpanzees also transport selected hammer tools and nuts to anvil sites. To date, we had no other examples of selection and transport of stone tools among wild nonhuman primates. Wild bearded capuchins (*Cebus libidinosus*) in Boa Vista (Piauí, Brazil) routinely crack open palm nuts and other physically well-protected foods on level surfaces (anvils) using stones (hammers) as percussive tools. Here we present indirect evidence, obtained by a transect census, that stones suitable for use as hammers are rare (study 1) and behavioral evidence of hammer transport by twelve capuchins (study 2). To crack palm nuts, adults transported heavier and harder stones than to crack other less resistant food items. These findings show that wild capuchin monkeys selectively transport stones of appropriate size and hardness to use as hammers, thus exhibiting, like chimpanzees and humans, planning in tool-use activities.

Keywords Hammer distribution · Anvil distribution · Tool use · Stone transport · Palm nut · Nut-cracking · *Cebus libidinosus*

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Introduction

The tool-using behavior of nonhuman primates provides insights into the origins of tool use in human evolution (Wynn and McGrew 1989; Byrne 2004; Davidson and McGrew 2005). Instances of tool selection are considered particularly informative because they indicate that the animal anticipates using the tool. Nut cracking, which entails bringing together nut, hammer, and anvil (Boesch and Boesch 1983; Sugiyama and Koman 1979; Hannah and McGrew 1987), becomes particularly demanding when nuts, stones suitable for use as hammers, and anvils are not found close to one another, and thus two of the three elements must be transported. Transporting one or more elements is energetically costly and presents physical challenges (i.e., how to carry the items) and cognitive challenges (i.e., anticipating future needs, mentally representing elements that are out of sight, and planning the course of action).

Chimpanzees cracking nuts with hammers manage all the above challenges. Captive (wildborn) chimpanzees released on an island in Liberia studied by Hannah and McGrew (1987) carried nuts to the feeding site that was about 150 m away and the maximum distance of nut transport was 265 m. They also moved hammer stones from one area to another; the heaviest hammer stone transported was 2.6 kg and was carried a distance of at least 175 m. Wild chimpanzees in Bossou, Guinea, bring hammer stones to nuts and nuts to anvil stones when experimenters place stones and nuts apart, but the high availability of stones in Bossou largely obviates the need for tool transport (Sakura and Matsuzawa 1991).

Transport of hammer tools by wild chimpanzees of the Taï National Park (Ivory Coast) has been both (1) directly observed when a hammer just used to crack *Coula edulis* nuts is carried while searching the ground for additional nuts and (2) inferred from changes in the location of the hammers used to crack the nuts of different *Panda oleosa* trees (Boesch and Boesch 1984). The Taï chimpanzees not only transport nuts to sites where anvils and hammers are already present, but also collect a hammer before moving towards a nut tree, or before transporting nuts to an anvil lacking a hammer (Boesch and Boesch 1983), suggesting that they anticipate their need for the hammer. Because the chimpanzees transport hammer stones and nuts to anvils, and hammers from one anvil to another in a smooth sequence and over some time, it appears that they have an organized plan of action from the outset.

Taï chimpanzees use heavier stone hammers for harder species of nuts, such as *Panda oleosa*, and lighter wood hammers for softer species of nuts, such as *Coula edulis* (Boesch and Boesch 1983). Their tool transport is selective and tuned to the type of nut they are about to crack; for example, chimpanzees transport heavier hammers for longer distances when they crack open the hard *Panda* nuts (Boesch and Boesch 1983). Moreover, they apparently remember the location of specific hammers and plan their behavior so as to minimize the distance of transport (Boesch and Boesch 1984).

The issue of tool transport has also been explored in capuchin monkeys. An early study by Jalles-Filho et al. (2001) suggested that captive capuchins did not transport tools: they transported nuts to stones, but not stones to a box containing food. However, other studies have shown that captive capuchins transport tools under appropriate conditions. For example, Fragaszy and Visalberghi (1989) mention that capuchins transported probing tools from one room to another one. Cleveland et al. (2004) found that capuchins rarely transported stones to a nut-cracking apparatus but readily transported probing tools to an apparatus baited with syrup; these authors attributed the different likelihood of transport in the two cases to the higher energetic cost of transporting stones than sticks. Semi-free-ranging capuchin monkeys experienced at cracking nuts transported stone tools for approximately 5 m to an anvil where nuts were provided (Falotico 2006).

In 2003, we discovered a population of wild bearded capuchin monkeys (*Cebus libidinosus*) that, like chimpanzees, use stone hammers to pound palm nuts on stone and log anvils (Fragaszy et al. 2004a; see Fig. 1). Capuchins use hammers weighing on average 1 kg (Visalberghi et al. 2007); they strike the nut by holding the hammer with both hands and raising it above their shoulders in a bipedal stance (Liu et al. 2009). The palm nuts exploited by capuchins are very resistant to cracking and the peak-force-at-failure of the piassava nuts (*Orbignya* sp.) is similar to that of the *Panda* nuts (Visalberghi et al. 2008). Hammers are mostly cobbles eroded from the few conglomerate layers present in the local stratigraphy; these hammers are much harder than the prevailing sedimentary rock out of which they eroded (Visalberghi et al. 2007). Because hard stones suitable for use as hammers appear scarce in the landscape and more abundant on the anvils than in the surrounding area, Visalberghi et al. (2007) suggested that capuchins transport hammers to the anvils.

Here we report the estimated frequency of suitable stone/wood anvils, suitable hammers, and palms (which provide an indirect indication of availability of nuts) in different areas of the capuchins' home range (study 1). We also report direct observations of transports of stones and nuts (study 2). In this way, we test Visalberghi et al.'s (2007) hypothesis that wild capuchins transport hammers to anvil sites, and compare hammer transport and selectivity between capuchins and chimpanzees.

Fig. 1 An adult male capuchin monkey uses a stone tool weighing 1,800 g to crack open a nut (photograph by Elisabetta Visalberghi)

Site

The study area is located at Fazenda Boa Vista in the northeastern Brazilian state of Piauí (9°39′ S, 45°25′ W), 21 km northwest of the town of Gilbués. The physical geography of the field site is a sandy plain at approximately 420 m above sea level punctuated by 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. Boulders often break off of these formations and fall to the base of the cliff close to the plain (for further information about the geology of Boa Vista, see Visalberghi et al. 2007). The sandstone cliffs and plateaus are heavily eroded and there are water courses that have running water only after rainfall (hereafter, ephemeral water courses). The climate is seasonally dry (annual rainfall 1,156 mm, total rainfall during dry season, April to September 230.00 mm, data from 1971–1990, source: Embrapa, Empresa Brasileira de Pesquisa Agropecuária).

Boa Vista presents four types of vegetation physiognomies according to the terrain and the proximity to water sources. The sandy plain is characterized by a high abundance of palms with subterranean stems and medium-height trees (3–20 m) including *Eschweilera nana* and *Hymaenaea courbaril*. The vegetation by the marsh is characterized by a higher diversity of trees forming gallery forests and high density of the tall palm tree *Mauritia flexuosa*. Shrubs and small trees dominate the cliff (face), and in the plateau herbaceous vegetation dominates, especially bromeliads and cactus.

Study 1: distribution of hammer stones

Procedure

The home range of the two groups of capuchin monkeys studied (see section "Study 2," below) includes an area called Morro das Letras in which the different physiognomies are present. In 2005 we established a 3-km line transect that followed a cross-section of vegetation types starting from the seasonally flooded wetland (marsh) at the low point, continuing in a flat dry area (sandy plain), over the ridges and up to the cliff-plateau, and descending to another flat dry area (sandy plain) (Fig. 2). To estimate the occurrence of anvil-like surfaces, hammer-like stones, and palms in the home range of our two study groups of capuchins, we counted their frequencies in 40 100-m^2 plots. The plots were located in the following four areas along the transect: the marsh, the plain, the talus (the area of transition between the plain and the cliff in which Visalberghi et al. 2007 found many anvil sites in use), and the cliff-plateau. We examined 10 plots evenly distributed in each of the four areas. Each plot was located 7 m inward towards the hill, in a direction perpendicular to the transect (if that section of the transect was a straight line), or to its tangent (if that section of the transect was not a straight line). The end point of the 7-m distance line was the starting mid-point of the bottom side of the 100-m^2 plot. If the inward direction led to a plot impossible to measure (for example, a vertical cliff), we located the plot 7 m outward from the hill.

Each of the 40 plots was described with the following nominal variables. We noted the predominant slope of the surface (either mostly flat or mostly sloping); the prominent surface (either mostly sandy or mostly rocky); signs indicative of presence of ephemeral water courses during the rainy season (yes or no) and if yes, estimated their size (width 50 cm or less = small, width 50–100 cm = medium, more than 100 cm = large); and signs of recent fire (yes or no). The presence of ephemeral water courses is important because it indicates the possibility of transport by the flowing water of loose hammer-like stones from the cliff to the talus below (Visalberghi et al. 2007). We also scored the presence (yes or no) of blocks of weathered sandstone of the size of hammer-like stones (see below) and of light hard stones (quartzite, quartz, etc.) categorized by sight as large pebbles (the size of an apricot) and small pebbles (the size of an olive).

In each plot we counted the number of living palms, anvil-like surfaces, and hammer-like stones. Palms provide an indirect indication of nut availability over the years, and they were counted regardless of whether they were bearing fruits. Surfaces larger than 30 × 30 cm (in order to accommodate pounding actions) and nearly horizontal (inclination between 0 and 20°, measured with a level and protractor) were counted as anvil-like. We also noted whether they were wood anvils or stone anvils; the latter were of relatively soft (compared to hammer stones) sedimentary rocks, mostly siltstones and sandstones.

A survey of the anvil sites in Boa Vista showed that the hammers (e.g., quartzites, siltstones, and ironstones) were relatively harder and more dense than the prevailing sandstone and hammers found on the active anvils, or within 30 cm from the anvils ($n = 53$) had a mean weight of 983 g (± 66.8 SEM; range 220–2,530 g) (Visalberghi et al. 2007). In this study, only sufficiently hard stones (see above) weighing between 0.3 and 3 kg were classified as hammer-like. This range reflects the weights of the hammers used by adult capuchins to crack the four most commonly exploited nut species (Spagnoletti, unpublished behavioral observations). Lithology was assessed on the basis of experience and resemblance to the stones available in our collection in Boa Vista. Weight was assessed to the nearest 10 g (stones up to 0.5 kg) and the nearest 20 g

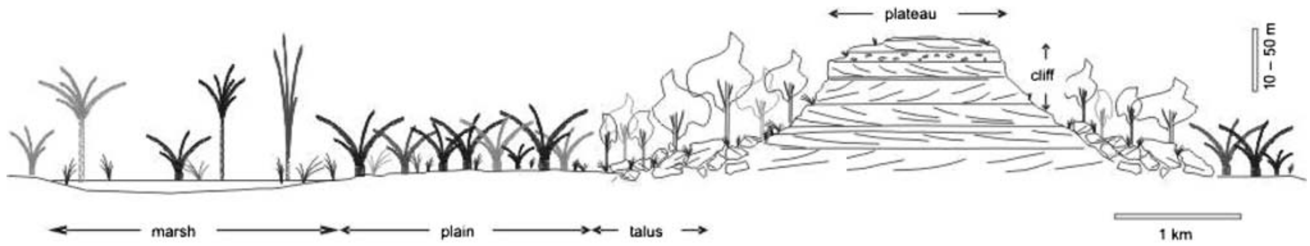

Fig. 2 Schematic cross-section through the analyzed areas, indicating different sampling physiognomies and respective landscapes. *Horizontal* and *vertical* scales are distinct (drawing by Fabio R. D. Andrade)

Table 1 Landscape and other features in four areas at Boa Vista

Areas	Surface				Ephemeral water sources		Fire	Sandstones	Pebbles	
	Sandy	Rocky	Flat	Sloping	Small/medium/large	Total			Small	Large
Marsh	10	0	10	0	8/2/0	8	8	0	0	1
Plain	10	0	10	0	8/3/0	8	9	4	3	1
Talus	3	7	1	9	10/5/0	10	7	10	9	7
Cliff-plateau	0	10	1	9	4/3/5	8	3	10	10	6

Values indicate the number of 10 × 10 m plots in each area sharing the characteristics listed for each variable. For ephemeral water sources we indicated the number of plots with small, medium, and large water courses and the total number of plots with water courses (regardless of size)

(stones up to 2.5 kg) using spring scales (Pesola, Switzerland). For stones heavier than 2.5 kg, weight was assessed with a spring scale with a resolution of 25 g. Data collection occurred in November–December 2006.

Analysis

For all the measures sampled as presence or absence inside the plot, we summed their occurrence across the 10 plots of each area, and compared them across areas with chi-square tests. The Kruskal–Wallis and Dunn's tests were used to determine whether the number of hammer-like stones, anvil-like stones, and palms counted in each plot differed across areas. All tests were two-tailed.

Results

General characteristics of the areas

Plots in the four types of areas differed significantly in terms of surface (rocky vs. sandy, $\chi^2 = 13.3$, $df = 3$, $P < 0.005$) and flatness ($\chi^2 = 14.7$, $df = 3$, $P < 0.02$); in particular, those in the marsh and in the plain were flat and sandy and those in the talus and the cliff-plateau were more rocky and sloping (Table 1). The frequencies of signs of ephemeral water courses (all sizes pooled) did not differ across areas ($\chi^2 = 0.4$, $df = 3$, NS), nor did frequencies of signs of fire ($\chi^2 = 3.1$, $df = 3$, NS).

There were differences among the plots in the number of fragments of sandstone (between 300 g and 3 kg; $\chi^2 = 12$, $df = 3$, $P < 0.01$, Table 1) and of small and large pebbles of harder rocks (small pebbles, $\chi^2 = 12.5$, $df = 3$, $P < 0.01$; large pebbles $\chi^2 = 8.2$, $df = 3$, $P < 0.05$). Sandstones and pebbles were present in most of the plots of the talus and the cliff-plateau, but absent in most of the plots in the marsh and plain.

Frequencies of anvil-like surfaces, palms, and hammer-like stones

Table 2 reports the total number of anvil-like surfaces, hammer-like stones and palms found in the 10 plots in the four types of areas and the corresponding values per hectare. Anvils were unevenly distributed across the areas (Fig. 3; Kruskal–Wallis $\chi^2 = 28.86$; $P < 0.001$). Anvils were more abundant in the talus than in the marsh (Dunn test $P < 0.001$) or in the plain (Dunn test $P < 0.001$); and more abundant in the cliff-plateau than in the marsh (Dunn test $P < 0.001$) or in the plain (Dunn test $P < 0.001$). Ninety-two percent of the anvil-like surfaces were stone and 8% wooden; the only area in which wooden anvil-like surfaces were more frequent than stone ones was the plain.

Palms also were unevenly distributed across the areas (Kruskal–Wallis $\chi^2 = 11.93$; $P < 0.01$). Palms were less abundant in the cliff-plateau than in the marsh (Dunn test $P < 0.01$), in the plain (Dunn test $P < 0.01$), and in the talus (Dunn test $P < 0.05$). In short, the only areas in which anvil-like surfaces and palms were relatively abundant and hammer-like stones present were the talus and the cliff-plateau (Fig. 3). None of the plots examined contained an active anvil, i.e., an anvil with a hammer and broken nut shells on it or nearby.

Table 2 Total number of anvil-like surfaces, hammer-like stones, and palms found in the ten plots in the four areas and the corresponding values per hectare

Areas	Anvil-like surfaces		Hammer-like stones		Palms	
	n	*n*/ha	*n*	*n*/ha	*n*	*n*/ha
Marsh	0	0	0	0	77	770
Plain	4	40	0	0	95	950
Talus	54	540	1	10	46	460
Cliff-plateau	90	900	6	60	13	130
Total	148	370	7	17.5	231	577.5

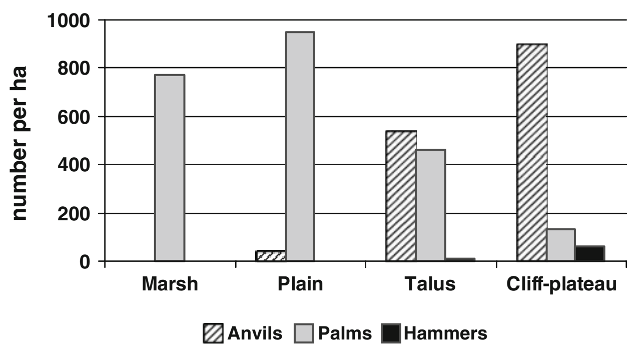

Fig. 3 Number per hectare of anvil-like stone and wooden anvils (*striped*), palm trees (*gray*), and hammer-like stones (*black*) in the different areas analyzed (*marsh*, *plain*, *talus*, and *cliff-plateau*)

Overall, there were only seven hammer-like stones in all of the 40 plots (totaling 4000 m^2 of surface area); therefore, the frequency of hammer-like stones was 17.5 stones/ha. Although no significant difference in occurrence across the areas emerged, hammer-like stones were found in only two plots located in the cliff-plateau and in one plot located in the talus (Fig. 3). The hammer-like stone found in the talus was a quartzite, whereas those found in the cliff-plateau were siltite ($n = 3$), fine sandstone ($n = 2$), and conglomerate ($n = 1$).

In sum, the results of the transect census show that palms and anvil-like surfaces are relatively common, whereas stones large enough and hard enough to use as hammers are rare. Study 2 provides direct behavioral evidence of stone and nut transport and suggests selectivity in choice of stones for transport. Since carrying stones is costly (see "Introduction") and nuts are very resistant (Visalberghi et al. 2008), we expect capuchins to transport stones hard enough and heavy enough to crack them.

Study 2: observations of transport

Study groups

From June 2006 to May 2007, Spagnoletti and Ramos da Silva observed the behavior of 28 bearded capuchins living in two groups (eight adult females, five adult males, two sub-adult males, nine juveniles, and four infants). Each group was followed from dawn to dusk 7–10 days per month. Over a total of 1,709 h of direct observation, all the observed instances of tool use were recorded (1,624 episodes). An episode of tool use begins when an individual holding a food item starts to use a percussor to crack it, or when the observer hears the noise of an individual's pounding actions. The episode ends when the individual cracks the food, or abandons it, or leaves the anvil site. If the same individual recommences pounding the same nut, the episode is resumed; on the contrary, if the individual starts pounding another food item (or the observer is not certain that it was the same food item), a new episode begins. During the study period 22 capuchins (all individuals but one adult female, one juvenile female, and four infants) used stones to crack open nuts or other encased fruits.

Focal animal sampling was used opportunistically to record behaviors related to tool use, including transport of stone tools and/or nuts to the anvil. Whenever the observer saw an individual transporting a nut and/or a stone, or using a stone as a tool, or heard the noise of this activity, she/he started the focal observation; the observation lasted as long as the tool use activities continued. Transport was defined as carrying the nut and/or the percussor for distances greater than 1 m. For each episode of percussor transport, we recorded the identity of the subject and whenever possible the weight and the material of the percussor (see Study 1 for details about the procedure), the material of the anvil (stone or wood), and the species of the item processed with hammer and anvil. The distance of transport was estimated by the observer walking the same path (and counting steps) or with a tape measure when possible; measures were approximated to the closest meter. It was not always possible to score all the above variables for each tool-use episode.

The items processed belonged to two categories: (1) palm nuts (tucum, *Astrocaryum campestre*; catulè, *Attalea barreirensis*; piassava, *Orbignya* sp.; and catuli, *Attalea* sp., see Visalberghi et al. 2008) and (b) other encased food items (e.g., seeds of fruta d'anta, fam. Icacinaceae; fruit of caju, fam. Anacardiaceae; seeds of caroba, fam. Bignoniaceae; seeds and fruit of mandioca brava, fam. Euphorbiaceae). Whereas to crack the above palm nuts hammers of specific lithology and weight are required (see above), the other encased food items could be cracked with lighter and more friable stones.

Analysis

As we did not record all the variables of interest for each tool use episode, the sample size (indicated in parentheses) differs according to the variable analyzed. Since the data were not normally distributed, we used nonparametric statistics. Frequencies of observed transport were compared between sex and age classes with the Mann–Whitney *U* test.

Results

Capuchins transported to the anvil nuts/other encased foods ($n = 288$), percussors ($n = 26$), and both food and percussor simultaneously ($n = 33$) (Fig. 4). Fifty-five tool transports involved stones (hereafter called hammers) and four involved intact palm nuts; in the latter episodes, catulè and piassava nuts were used as percussor to crack tucum nuts ($n = 2$) and other food items ($n = 2$).

Transport of nuts/other encased food items

Eighteen capuchins (all except four juveniles) transported nuts/other encased food items that required the use of hammer and anvil to be cracked. The median distance of transport was 16 m [interquartile range (IQR) 30 m, $n = 131$] for adult males, 10 m (IQR 10 m, $n = 45$) for adult females, and 10 m (IQR 5 m; $n = 24$) for juveniles. Monkeys transported on average more than one item per event (1.3 ± 0.04, range 1–5, $n = 262$). Food was transported mostly in one hand, but sometimes using both hands, mouth, or feet.

Transport of hammers

Of the 22 tool-using capuchins, 12 (4 adult males, 4 adult females, and 4 juveniles) were observed transporting a hammer to an anvil. Capuchins transported hammers to stone anvils ($n = 41$) and wooden anvils ($n = 18$). As shown in Table 3, capuchins transported stone hammers to crack (or to try to crack) palm nuts ($n = 47$) and other encased food items ($n = 8$). Frequencies of observed transport did not differ between sex (Mann–Whitney *U* test, $n_1 = 6$, $n_2 = 6$, $U = 12.0$, NS) and age classes (Mann–Whitney *U* test, $n_1 = 8$, $n_2 = 4$, $U = 14.5$, NS).

Characteristics of the hammers transported

Table 4 shows the median weight of the hammers transported to crack palm nuts and the median distance of transport for adult males, adult females, and juveniles. We lack enough data for each subject to run statistical analyses; however, it is worthwhile to point out that adult capuchins transported stones much heavier than those of juveniles. An adult female transported the heaviest hammer, weighing 1,600 g, for 6 m. The median distance of observed transport was similar across age and sex classes.

If capuchins take into account the resistance of nuts when looking for a hammer, they should transport stones suitable to overcome the nuts' resistance, such as quartzites and siltstones, significantly more often than unsuitable

Fig. 4 An adult male transporting two palm nuts (in its left hand) and a hammer stone weighing 1,800 g to a wooden anvil. The pictures document an episode of transport observed after this data collection (photographs by Noemi Spagnoletti)

Table 3 Number of hammer transports in relation to the type of anvil (stone and wooden) and type of food (palm nuts and other encased food items)

Age–sex class	Number of episodes of hammer transport				
	Type of anvil		Type of food		
	Stone	Wooden	Palm nuts	Other item	Total
Adult males ($n = 4$)	23	8	29	2	31
Adult females ($n = 4$)	8	5	7 (1)	4 (1)	11 (2)
Juveniles ($n = 4$)	10	5	11 (1)	2 (1)	13 (2)
Total	41	18	47 (2)	8 (2)	55 (4)

The numbers in parentheses indicate episodes in which a palm nut was transported and used as tool, without attempting to crack it by striking on it

Table 4 Median weight and interquartile range (IQR) of the hammers used to crack palm nuts and median distance of transport and IQR

	Number	Median weight (g)	Median distance of transport (m)
Adult males ($n = 4$)	29	1,025 IQR 510 $n = 19$	3 IQR 3 $n = 23$
Adult females ($n = 4$)	7	870 IQR 615 $n = 6$	4 IQR 4.4 $n = 7$
Juveniles ($n = 4$)	11	250 IQR 60 $n = 9$	4 IQR 2 $n = 7$
Total	47	665 IQR 800 $n = 34$	4 IQR 3 $n = 38$

For median weight and distance, n indicates the number of episodes in which these variables were scored

ones, such as weathered sandstones. When exploiting palm nuts, adult males carried suitably hard stones in 15 cases and unsuitably soft stones in 4 cases; adult females carried suitably hard stones in all 5 cases; juveniles transported suitably hard stones twice and unsuitably soft stones 5 times. 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.

The median weights of the stone hammers used by adult capuchins to crack palm nuts and other encased foods were 930 g (IQR 510 g, $n = 25$; data based on 7 subjects) and 30 g (IQR 90 g, $n = 5$; data based on 3 subjects), respectively. The 30-g stone was unsuccessfully used as hammer to crack open another encased food.

Distance of transport

The stones used to crack nuts and other encased foods were transported by adults for a median distance of 3 m (IQR 3.7, $n = 31$; 8 subjects) and 5.5 m (IQR 18, $n = 6$; 5 subjects), respectively (Table 4). The maximum distances of observed stone transport were 21 m (a stone weighing 480 g) for adult males, 8 m (an 80-g stone) and 6 m (a 1,600-g stone) for adult females, and 12 m (a 220-g stone) for juveniles. These values refer to episodes in which the transport was observed from the beginning; however, since in 13 of 59 transports we first witnessed the event as it was in progress, after the monkey had begun transport, we may underestimate distances of transport here.

Discussion

Study 1 shows that in Boa Vista hammer-like stones are very rare whereas anvil-like surfaces are common, both being more frequent in the talus and in the cliff-plateau areas than elsewhere. Palms are also common, except in the cliff-plateau area. The elements indispensable for tool use (i.e., hammer-like stones, anvils, and palms, and therefore nuts) co-occur only in the cliff-plateau and in the talus; only the latter is close to the plain where palms are very frequent. 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 (i.e., the talus). The overall abundance of ephemeral water courses and direct observation of stones and tree trunks moved by water during heavy rainfalls (Visalberghi and Andrade, personal observation) further support the hypothesis that loose stones are carried from the cliff-plateau to the talus below by water.

How do our findings compare with those for the Taï chimpanzees? From the count made by Boesch and Boesch (1983) of the anvils (mostly exposed roots and a few rocks) present along a transect, it is possible to estimate that in Taï there are about 9,000 anvils per hectare. They counted only 40 hammer stones heavier than 1 kg in the 450 ha where chimpanzees usually crack *Panda* nuts; this corresponds to 0.09 hammers per ha, a value about 200 times lower than that estimated for Boa Vista. Therefore, although the rarity of hammer stones can be considered a strong limiting factor for the occurrence of tool use both in Taï and in Boa Vista, the shortage of hammers and therefore the need for transport appears more pronounced in Taï.

Study 2 provides direct evidence that capuchins, both adults and juveniles, spontaneously transport nuts and other encased foods and hammers to the anvil site. Occasionally, transport of food and hammer occurs simultaneously

(Fig. 4). These findings are in contrast with those of Jalles-Filho et al. (2001) and greatly extend those reported for captive and semi-free-ranging capuchins tested in structured experimental situations (Cleveland et al. 2004; Falotico 2006). Although smaller body size and lesser body weight (Fragaszy et al. 2004b) may make transporting heavy stones more demanding for females and juveniles than for males (Cleveland et al. 2004; Liu et al. 2009), frequencies of transport did not differ between sex and age classes.

Assuming that our opportunistic sampling method accurately captures rates of transport, transporting a stone hammer is relatively uncommon at Boa Vista (3.4% of the episodes include stone hammer transport). This low rate of occurrence reflects the rarity of suitable stones in the general habitat, and more importantly, the presence of hammers on active anvils. Transport is not required when the hammer stone is already at the anvil, as is usually the case in Boa Vista (Visalberghi et al. 2007). Here capuchins habitually use anvils where hammers have been left by previous tool users and when one capuchin is using the hammer, others often "wait" for their turn, rather than searching for a new hammer (Spagnoletti, personal communication; see also Hannah and McGrew 1987). In fact, Spagnoletti (unpublished data) found that 116 different anvils accommodated 607 episodes of tool use and that the same anvil was used up to 49 times, distributed over several months. Taï chimpanzees, like capuchins, use the same stone hammer over and over again. For example, when cracking *Panda* nuts they transport the same hammer from an anvil close to a given *Panda* tree, to another anvil close to another *Panda* tree (Boesch and Boesch 1983).

The different methods used in Taï (transport inferred on the basis of the dislocation of marked hammers) and in Boa Vista (observations of transport) do not allow a straightforward comparison of the frequency of transport in the two species; moreover, wooden hammer transport was often not monitored given the far greater abundance of wood than stone in Taï (Boesch and Boesch 1983). However, the relatively few transport episodes observed to crack *Coula* and *Panda* nuts over 2 years (102 for wooden hammers and 344 for stone hammers; Boesch and Boesch 1983) and the high number of nut-cracking episodes per day in chimpanzees (during the *Coula* season an individual cracks on average 270 nuts per day, Boesch and Boesch-Achermann 2000), makes hammer transport not very frequent in chimpanzees. In Taï, as in Boa Vista, hammers are durable and repeatedly used by different individuals (Boesch and Boesch 1984; Biro et al. 2006; Hannah and McGrew 1987). No information concerning sex differences in frequency of transport is available for the Taï chimpanzees.

Very interestingly, there are some indications that adult capuchins take into account the resistance of the food item to be cracked when selecting which stone to transport. Overall, more instances of hammer transport were observed when the hammer served to crack palm nuts than other encased food items, for which the extremely common soft sandstones can be used effectively. In addition, from our observations adults appeared selective in terms of the material and weight of the hammers transported to crack nuts. Field experiments have shown that wild capuchins faced with stones differing in functional features (friability and weight) chose, transported, and used the more effective stone to crack open nuts and, when weight could not be judged by visual attributes, they acted to gain information to guide their selection (Visalberghi et al. 2009). Similarly, Boesch and Boesch (1983, 1984) found that chimpanzees transported (1) harder stone hammers more often than softer wooden hammers to crack the high-resistance *Panda* nuts than to crack the low-resistance *Coula* nuts and (2) harder stones (granites) more often than softer stones (laterites) to crack *Panda* nuts.

Boesch and Boesch (1983, 1984) also reported that *Coula* trees are abundant and each tree is usually within sight of several others, whereas *Panda* trees are widely scattered and much rarer. This makes the decision process of transporting a hammer for *Coula* less complicated than for *Panda*, since the latter requires planning the transport in advance of arrival at the nut tree and when the tree is out of view. Under the assumption that a chimpanzee first selects a nut tree and then the stone that is optimal for transport to that tree, rather than vice versa, and that visibility is about 20 m, Boesch and Boesch (1984) argued that the transports inferred for *Panda* show the use of a least-distance strategy, which minimizes the energy expended for transport. Use of this strategy implies that chimpanzees have some form of mental representation of elements that are out of view, such as the direction and distance from their current location and the kind of nut.

We lack a similar rule to identify capuchins' transports involving elements out of sight. Furthermore, in Boa Vista, visibility changes dramatically according to season and location, and whether the individual moves on the ground or in the trees. However, during our observations, in many episodes a capuchin carried nuts and/or stones towards anvil sites that were out of the transporter's view. Janson (1998, 2007) demonstrated that capuchins can integrate information on spatial location and resource abundance in planning travel routes, and it is now thought that this kind of navigational ability, integrating spatial and resource information, is widespread in the animal kingdom (Janson 2007). Thus the interesting issue now is not whether capuchins know where familiar anvils are (we can assume that they do) but rather if they minimize transport distance when they carry nuts or stones to anvils. Because familiar anvils usually already have a hammer stone, to minimize transport effort capuchins should probably bring the food to the nearest anvil, and search for a stone (or another anvil with a hammer) only if the nearest anvil lacks a hammer. Field experiments are probably the best strategy to investigate what rules guide capuchins' behavior when, for example, they must choose to transport food or stones to anvils in different circumstances. Their actions might be governed strongly by the time needed for search versus the time needed to transport to a known location. We could also test whether they optimize their travel distances to known anvils while carrying nuts or stones and/or choose anvils on the basis of hammer quality and availability.

Transport of food resources and repetitive visits to specific places in the landscape are associated with the origin and early evolution of *Homo* and are important innovations of the Oldowan (Binford 1981; Isaac 1984; Potts 1991). It is possible that transport of food resources and repetitive use of anvil sites affect the behavior of capuchins as well. Transporting food and hammers to anvils and leaving the hammer by the anvil after use constructs a "niche" (*sensu* Laland et al. 2000) that increases the opportunities for the same individual and for other group members to use the hammer and the anvil in the future; this has consequences in terms of facilitating the acquisition of the behavior by youngsters (promoting traditions) (Fragaszy and Visalberghi 2001). Another example of "niche construction" in this sense in capuchin monkeys is described by Gunst et al. (2008). Wild young capuchin monkeys inspect and manipulate the ripped bamboo stalks from which their group members have previously extracted a larva. These activities are beneficial for learning how to search for the larvae and to extract them (Gunst et al. 2008).

Planning transport that occurs over long distances and encompasses goals that are out of view generates major returns. In human evolution transport has been a "key development of the Oldowan" because "once the transport of resources was engaged, essentially all movable resources were opened up for processing by stone tools" (Potts 1991, p. 171). The typical transport distance covered by our capuchins is much smaller than those reported for some of the Taï chimpanzees and for early humans (Wynn and McGrew 1989). In Taï the average indirectly estimated transport distance was 120 m, with a few cases of transport over 500 m (Boesch and Boesch-Achermann 2000). In Liberia a hammer stone was transported at least 175 m; given the relative abundance of stones suitable for hammers and anvils, in Bossou transports were less frequent and much shorter (no more than 5 m, Sakura and Matsuzawa 1991). The transport distances of Boa Vista capuchins are apparently like those of Bossou chimpanzees; these short transport distances might reflect infrequent need to transport stones over longer distances to arrive at the closest anvil-like surface.

Transport distances might also reflect the high energetic or temporal cost to capuchins of transporting stones, reducing the profitability of foraging in this way compared to the profitability of other foraging actions in which they might engage. After all, chimpanzees transport stones weighing proportionally far less in terms of their body weight than capuchins (Visalberghi et al. 2007; Liu et al. 2009). The cost of transport is therefore substantially greater for capuchins than for chimpanzees. On this basis alone we should predict a lower rate and shorter distance of transport in capuchins than in chimpanzees. Finally, shorter transport distances in capuchins may reflect their greater vulnerability to predation than chimpanzees, and therefore greater aversion to terrestrial travel under conditions of compromised balance and speed. Taken together, this line of argument brings us to the recognition that transport of stone tools should appear under very limited conditions in wild capuchins, but that it should appear under a wider range of conditions in wild chimpanzees (and early humans, also large-bodied). Cognitive explanations for characteristics of transport (or any other behavior) in any species cannot be evaluated meaningfully outside of an ecologically sound framework encompassing the costs and benefits of alternative courses of action.

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