Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity

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ABSTRACT

Chimpanzees have been the traditional referential models for investigating human evolution and stone tool use by hominins. We enlarge this comparative scenario by describing normative use of hammer stones and anvils in two wild groups of bearded capuchin monkeys (*Cebus libidinosus*) over one year. We found that most of the individuals habitually use stones and anvils to crack nuts and other encased food items. Further, we found that in adults (1) males use stone tools more frequently than females, (2) males crack high resistance nuts more frequently than females, (3) efficiency at opening a food by percussive tool use varies according to the resistance of the encased food, (4) heavier individuals are more efficient at cracking high resistant nuts than smaller individuals, and (5) to crack open encased foods, both sexes select hammer stones on the basis of material and weight. These findings confirm and extend previous experimental evidence concerning tool selectivity in wild capuchin monkeys (Visalberghi et al., 2009b; Fragaszy et al., 2010b).

Male capuchins use tools more frequently than females and body mass is the best predictor of efficiency, but the sexes do not differ in terms of efficiency. We argue that the contrasting pattern of sex differences in capuchins compared with chimpanzees, in which females use tools more frequently and more skillfully than males, may have arisen from the degree of sexual dimorphism in body size of the two species, which is larger in capuchins than in chimpanzees. Our findings show the importance of taking sex and body mass into account as separate variables to assess their role in tool use.

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Introduction

Stone pounding was a likely precursor of tool making by hominins, since the actions of pounding "can lend themselves to the application of the same bodily motor actions to different raw materials and with novel purposes" (Davidson and McGrew, 2005: 796). Among nonhuman primates living in natural settings, only a few populations of chimpanzees routinely use stone tools to crack nuts (Whiten et al., 1999; Boesch and Boesch-Achermann, 2000). Chimpanzees have been the traditional referential models for those investigating human evolution and the features characterizing hominins' use of stone tools, including the origins of sex differences in tool use and in the division of labor (McGrew, 1979; Tooby and DeVore, 1987).

Our goal here is to expand this comparative scenario to include *Cebus libidinosus*, a South American monkey species that last shared a common ancestor with the Catarrhini about 35 million years ago (Schrago and Russo, 2003). A few populations of this species have been recently discovered to use tools in the wild (Fragaszy et al., 2004a; Moura and Lee, 2004; Waga et al., 2006; Canale et al., 2009; see Ottoni and Izar, 2008 for a review). As argued by Haslam et al. (2009), these findings may (a) challenge the role of continuity in primate tool use, (b) suggest that convergence is plausible (probably owing to similar adaptive pressures, foraging requirements and/or physiological constraints), and (c) open the door to the possibility of repeated gain and loss of tool use among extinct primates in multiple lineages over millions of years. Specifically, on the basis of one year of systematic observations of stone tool activities by adult capuchins, we examine the frequency of tool use, success and stone selectivity in relation to the resistance of food targets. These findings on the spontaneous behavior of wild capuchin monkeys, together with those collected in a series of parallel field experiments (for a review Visalberghi and Fragaszy, in

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press-a), constitute an ample dataset on which to build comparisons with chimpanzees and to interpret the behavior of hominins before the occurrence of flaking technology.

In many chimpanzee populations, several members of a group use tools throughout the year (Whiten et al., 1999), thus earning the label of "habitual" tool users (*sensu* McGrew, 1992). Habitual tool use suggests that technology plays a significant role in the ecology of the population, as opposed to an incidental activity. Here, we provide longitudinal data for a population of wild capuchins, showing that they are also habitual tool users.

In chimpanzees, the use of tools differs markedly between the two sexes. Females use both probing tools and stone tools more frequently than males (see McGrew, 1992 for a review). For example, in Gombe, female chimpanzees engage in termite fishing three times more often than males (McGrew, 1979; see also Pandolfi et al., 2003 for an analysis of the data collected in Gombe over 17 years). Females start to fish for termites at a younger age than males (31 vs. 50 months) and achieve higher levels of proficiency. Moreover, females use a technique similar to their mother's, whereas males do not (Lonsdorf et al., 2004). Females outperform males in the two most difficult forms of stone tool use that chimpanzees practice, namely cracking *Coula* nuts aloft in the tree and cracking *Panda* nuts (which are the most resistant nuts that chimpanzees crack) (Boesch and Boesch, 1984). Finally, females crack *Coula* nuts regardless of whether the nuts are fresh and more difficult to crack, or dry and less difficult to crack, whereas males crack mostly dry, brittle nuts (Boesch and Boesch, 1984). Thus, female chimpanzees, across many regions and foraging tasks, use tools more often and in some circumstances more skillfully than males. This difference has been interpreted as a strategy by which females obtain reliable foods, whereas males devote more time to social activities and to other forms of foraging, such as hunting (Boesch and Boesch, 1984).

Sex differences in tool use in wild capuchins have been little investigated. The few studies on tool use carried out so far with capuchins provide mixed evidence (see Moura and Lee, 2010 on a group of *C. libidinosus* partially composed of reintroduced individuals; Ottoni and Mannu, 2001 on a semi-free ranging group; and Fragaszy et al., 2004b for review of studies with captive capuchins). Similarly, the results from the studies examining precursors of tool use, namely actions combining objects and surfaces (for a review, see Fragaszy et al., 2004b) are contradictory. For example, in Fragaszy and Adams-Curtis (1991) and in Byrne and Suomi (1996), male and female capuchins interact with objects with similar degrees of interest, whereas in Visalberghi's (1988) study males score significantly higher than females for the pooled category of actions, which include pounding, throwing, and rubbing. Boinski et al. (2000) report that wild *Cebus apella* males process husked fruit by pounding them on hard substrates more often than females, although no sex difference in skill and coordination is apparent. In contrast, wild female wedge-capped capuchins (*Cebus olivaceus*) devote absolutely more time than males to foraging and, while foraging, to banging food items (Fragaszy, 1990 and unpublished results). Finally, males are prominent when percussion is used as an aggressive display and as a sexual display (Moura, 2007). Boinski (2004) argues that percussion by males may attract females' attention, and serve as a signal of male fitness.

Although the published findings concerning sex differences in tool use and object manipulation in capuchins are contradictory, energetic and morphological considerations lead to clear predictions about sex differences in frequency and performance of tool use, and stone selectivity by adult wild capuchins.

Other factors being equal, the nutritional needs of an animal are affected both by reproduction (during the present study seven out of eight of our adult females were either pregnant and/or lactating)

and body mass (Key and Ross, 1999). In primates, the degree of sexual dimorphism in body mass varies greatly among species (Plavcan, 2004) and capuchins are more dimorphic in body mass than chimpanzees (Smith and Jungers, 1997; Key and Ross, 1999; Fragaszy et al., 2010a; see Discussion for details). In particular, the body mass of the adult males observed in the present study was 64% larger than the body mass of the adult females (see Table 1). Key and Ross (1999) examined the relationship between energetic costs for males and females in 19 nonhuman primate species (not including capuchins) and found that when the males' body mass exceeds females' body mass by 60% or more, the major determinant of sex differences in energetic costs is body mass dimorphism, whereas when males are between 30% and 50% larger than females, the costs due to reproduction almost balance those of the males' larger body mass.

Since male capuchins need more energy than females due to the males' larger body mass, our first prediction is that adult male capuchins will use tools to crack nuts as or more frequently than adult females. Second, we predict that heavier (and thus presumably stronger) individuals (i.e., adult males) will be more efficient at cracking nuts (in terms of rate of success, average number of strikes per successful nut cracking episode, and average duration per successful episode) than smaller individuals (i.e., adult females and juveniles of both sexes). However, consideration of the action involved in cracking leads to a more refined set of predictions. Some species of palm nuts are extremely resistant to cracking (Visalberghi et al., 2008), and thus the monkeys must strike each nut several times to crack it (Fragaszy et al., 2010a). Body mass is a strong predictor of efficiency in cracking (measured as the number of strikes needed to crack a piassava nut, the most resistant species of nuts; Fragaszy et al., 2010a) and monkeys of both sexes prefer to use heavier stones to crack nuts (Visalberghi et al., 2009b; Fragaszy et al., 2010b).

Therefore, on the basis of dimorphism in body mass in capuchins and energetic considerations, we make three further predictions. One is that the resistance of the nut (Visalberghi et al., 2008) will affect the rate of success, the average number of strikes per episode, and the duration of successful episodes (third prediction). The others are that females, to maximize reliability of energetic return, will exploit high resistance nuts proportionally less often than males (fourth prediction), but will exploit low resistance nuts and other encased foods at the same frequency as males (fifth prediction).

In wild chimpanzees, deliberate selection of specific materials to use as tools has been inferred by comparing the features of hammers and anvils used to crack open nuts of different resistance. Boesch and Boesch (1984) proceeded in this way at Taï and inferred that high resistance *Panda oleosa* nuts were more often cracked open on stone anvils and stone hammers than with wooden anvils and hammers, compared with the less resistant *Coula edulis* nuts. Furthermore, chimpanzees use heavier stone hammers to crack open *Panda* nuts than *Coula* nuts. Therefore, chimpanzees seem to take into account the resistance of nuts when using percussive tools. Subsequent direct observations confirmed this pattern of tool use in Taï (Boesch and Boesch-Achermann, 2000) as well as in Bossou (Matsuzawa, 1994), indicating that chimpanzees "can recognize the functions of the tools and which stone or combination of stones function best" (Matsuzawa, 1994: 361). Recently, Visalberghi et al. (2009b) experimentally demonstrated that wild capuchins, belonging to the same population investigated in the present study, when presented with a concurrent choice of two or more stones, selectively used stones of particular material and weight to crack low resistance nuts (see also Fragaszy et al., 2010b). Therefore, our sixth and last prediction is that capuchins will select stone tools based on the material and weight that are adequate to overcome the resistance of the food resource at hand.

Table 1
Adult subjects, group to which they belong (CH = Chicão group; ZA = Zangado group), body mass, rank, total number of tool use episodes observed, number of incomplete and complete episodes involving palm nuts and other food items.

| | Group | Subject | Body mass (kg) | Rank | # of episodes of tool use | | | | | | |
| | | | | | Total | Incomplete | | Complete | | Complete and identified | |
						Nuts	Other food items	Nuts	Other food items	Low resistance nuts	High resistance nuts
Males	CH	Chicão	4.4	1	142	130	12	89	12	52	21
	ZA	Zangado	4.4 e	1	296	276	20	77	4	29	28
	ZA–CH	Mansinho	3.5	4	196	193	3	108	2	65	20
	ZA–CH	Dengoso	3.3	3	159	147	12	64	9	21	19
	ZA–CH	Jatoba	2.7	6	103	93	10	40	7	13	5
	ZA–CH	Teimoso	2.7	3	84	72	12	28	7	10	7
	CH	Segundo*	3.6 e	3	14	13	1	7	1	–	
Subtotal					994	924	70	413	41	190	100
Females	CH	Dendé	1.9	5	18	15	3	11	3	19	4
	CH	Teninha	2.2	3	25	24	1	20	1	11	11
	CH	Piassava	1.9	2	55	40	15	24	20	16	1
	CH	Chuchu	2.2	3	60	57	3	39	3	19	11
	ZA	Moça-Br	1.9 e	2	44	27	17	6	8	1	2
	ZA	Moça-Ch	2.2 e	3	141	100	41	29	13	16	6
	ZA	Emilia*	2.4 e	4	20	6	14	0	6	–	–
	CH	Chiquinha*	2.4	3	0	0	0	0	0	–	–
Subtotal					363	269	94	129	54	68	29
Total					1357	1193	164	542	95	258	129

The complete episodes were those recorded from the beginning to the end for which success, latency to solution and number of strikes were scored. The complete and identified episodes were those in which the species of the nut was identified.
ZA–CH indicates individuals that during data collection migrated from ZA group to CH group. The weight of each subject was either assessed with a scale (see Fragaszy et al., 2010a) or estimated (e). (*) individuals excluded from the statistical analyses concerning success and tool selectivity.

Methods

Site

The study area is located at Fazenda Boa Vista (FBV) 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, and surrounded by cliffs composed of sedimentary rock rising steeply from 20 to 100 m above the plain. The cliff and plateau consist of inter-bedded 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 FBV, see Visalberghi et al., 2007). The sandstone cliffs and plateaus are heavily eroded and there are ephemeral watercourses that have running water only after rainfall. The climate is seasonally dry (average annual rainfall 1156 mm, total rainfall during dry season, April to September 230 mm, data from 1971 to 1990, source: Embrapa, Brazilian Agricultural Research Corporation).

FBV 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 trees of medium height such as *Eschweilera nana* and *Hymaenaea courbaril*. The vegetation by the lowest area of the plain, a marsh, is characterized by a higher diversity of trees forming gallery forests and a high density of the tall palm tree, *Mauritia flexuosa*. Shrubs and small trees dominate the cliff and the talus, whereas herbaceous vegetation dominates on the plateau, especially bromeliads and cactus.

Subjects

From June 2006 to May 2007, we observed the behavior of 28 bearded capuchins living in two groups, the Chicão group (CH) and the Zangado group (ZA) (eight adult females, seven adult males,

nine juveniles and four infants). Adult status was conferred on the basis of size and behavior for animals of unknown age. At the beginning of the study, all adult females except one were either pregnant or lactating.

Behaviors and other measures scored

Each group was followed from dawn to dusk for seven to ten days per month by Noemi Spagnoletti (hereafter N.S.) or Eduardo D. Ramos da Silva (hereafter E.D.R.S.), aided by a field assistant (see below). For 1709 hours, we sampled all episodes of tool use (both when in progress or about to begin) until they ended using *ad libitum* sampling. A tool use episode started when the subject (S) approached the anvil site (by definition, an anvil site is a boulder or an exposed stone with a hammer stone on it or within three metres; for details see Visalberghi et al., 2007) with an encased food item and ended when the item was cracked open, or when S left the anvil without the hammer stone. When S began to crack a new food item, a new episode was recorded. If we were observing a tool use episode and another began, we continued to observe the first episode. During concurrent episodes, the field assistant noted the identity of the tool user in the second episode and collected the same data about it. This led to a total of 1565 tool use episodes that were used to analyze tool use frequencies in the two groups. The analyses concerning sex differences in frequency of tool use and the food exploited were based on the 1310 episodes performed by adult capuchins. For the analyses on sex differences in tool use efficiency, we included an additional 47 episodes, which were observed while the subjects cracked nuts provided by the observers for purposes of photography and videography. N.S. collected detailed data on 844 episodes that were used for all of the analyses (frequency, efficiency and selectivity of tool use, see below). E.D.R.S. contributed 513 episodes collected with *ad libitum* sampling, while conducting a concurrent study using the same behavioral definitions (Ramos da Silva, 2008).

As in Resende et al. (2008), N.S. noted per episode whether the (i) food item was cracked (effective nut cracking), (ii) food item was not cracked despite the correctness of both the positioning of the tool in relation to the food item and the strikes (non-effective nut cracking), and (iii) food item was not cracked because the behavior was inadequate (simple pounding, i.e., episodes in which the monkey pounded the nut on the anvil or on the hammer). When possible, N.S. observed the episode from the beginning to the end, noted its duration, counted the number of strikes (i.e., the action of pounding the food item positioned on the anvil with the hammer) performed by the monkey, and the outcome of the episode. Episodes for which all of these variables were recorded are labeled complete episodes. For the complete episodes resulting in a cracked nut and access to the kernel, we scored the number of strikes and the time elapsed (in seconds) between the beginning of the episode and access to the kernel (duration of episode). When possible, N.S. also determined the food exploited and its state at the beginning of the episode (intact or partially cracked) on the basis of direct observation.

Finally, N.S. examined the hammer stone used by the subject and noted its weight and lithology at the end of the episode, when possible. Lithology was assessed on the basis of experience and resemblance to the stones available in our collection in FBV. Weight was assessed to the nearest 10 g (stones up to 0.5 kg) or the nearest 20 g (stones from 0.5 kg up to 2.5 kg) using spring scales (Pesola, Switzerland). N.S. also noted whether the subject had used a stone or an intact palm nut as a "hammer." Hammer stones were categorized as "friable" or "durable." Visalberghi et al. (2007) report that the durable and effective hard stones that capuchins use as hammers to crack open palm nuts are quartzite, siltstone and ironstone (all of these stones are relatively harder and more dense than the prevailing friable sandstone).

The items processed belong to three major categories: (a) nuts with relatively high peak-force-at-failure, namely piassava (*Orbignya* sp.) and catulí (*Attalea* sp.), hereafter labeled "high resistance" nuts; (b) nuts with relatively low peak-force-at-failure, hereafter labeled "low resistance" nuts, namely catulè (*Attalea barreirensis*) and tucum (*Astrocaryum campestre*) (see Visalberghi et al., 2008 for details), and (c) other encased food items whose peak-force-at-failure is much lower than that reported for palm nuts (e.g., fruta-danta, family Icacinaceae; caju, family Anacardiaceae; caroba, family Bignoniaceae; manioca-brava, family Euphorbiaceae). Whereas palm nuts in categories (a) and (b) require hammers of specific lithology and weight, the other encased food items (c) can be cracked open with lighter and more friable stones.

Analyses

Since monthly frequencies of tool use did not differ between groups (Mann–Whitney U-test $= 64$, $n_1 = 12$, $n_2 = 12$, $p = 0.64$, see also Spagnoletti, 2009), we pooled the data from the two groups. To rule out the possibility that the number of observed episodes depended on the different likelihood of observing adult males, adult females, and juveniles, we determined whether these sex and age classes were similarly "in view" to the observer. When the monkeys were not using tools, N.S. sampled their activity every 20 min using group scan sampling (Martin and Bateson, 1993; see also Spagnoletti, 2009). An index of individual visibility is indicated by the number of scans in which each of the 22 tool users was observed/total number of scans recorded. These values were not significantly different among adult males, adult females and juveniles (Kruskal–Wallis ANOVA, $H_{2,22} = 4.48$, $p = 0.11$). Moreover, the number of tool use episodes and visibility were not significantly correlated (Spearman, $r_s = 0.03$, $N = 22$, $p = 0.89$). As there was no bias in the visibility of males versus females in scan sampling, our data can be considered unbiased with respect to the frequencies of tool use.

Analyses concerning frequencies of tool use were run on all the adult subjects (seven males and eight females). Analyses of performance and selectivity were carried out on six adult males and six adult females (see Table 1). We used the Mann–Whitney test to compare sex differences in frequency of tool use and category of food exploited. The analyses on performance were based on mixed model regressions, either linear or logistic, in which the subject identities were inserted as random factors (Rabe-Hesketh and Skrondal, 2008). We used mixed model logistic regressions to test whether efficiency (i.e., the success to crack open the food item) was affected by body mass, sex, individual rank, resistance of the nut and weight of the stone. We used mixed model linear regression to test whether the number of strikes and duration of episodes to crack open nuts was related to body mass, sex, resistance of the nuts and weight of the stone. In order to explore the question of whether adults select hardness and weight of the stone hammer, we used mixed model linear regressions to test separately the effects of individual body mass and sex, and food resistance on the hardness and weight of the hammer stones used. Furthermore, we used mixed model linear regressions to test if individual body mass and food resistance predict the weight of the hammer stones used by males and females separately.

The individuals of the CH group were weighed in July 2007 (Table 1; for details about the weighing procedure see Fragaszy et al., 2010a). The body mass of the members of ZA group was estimated by two independent observers very familiar with both groups. To do so, each observer independently paired each individual of ZA group with the individual(s) most similar in body size belonging to the CH group. The two estimates per subject obtained in this way were averaged.

In each group, we tested if the number of tool use episodes performed by each individual was related to its rank in the group dominance hierarchy. Individual rank in each group was established by Verderane (2010) as a part of her study on social relationships of the two groups, based on all occurrences of contest competition analyzed through the Dominance Directed Tree method (Izar et al., 2006).

Since our data did not follow a normal distribution (Lilliefors test, $p < 0.05$) for the analyses concerning sex differences in frequency of tool use, we used non-parametric statistics (using STATISTICA 7 Statsoft). The mixed model regressions were run using Stata 10.1 (StataCorp, 2007). For all analyses, the significance level was set at $p < 0.05$ and all reported probabilities are two tailed.

Results

Frequency of tool use

During the study period, 22 capuchins (all individuals in both groups with the exception of one adult female, one juvenile female and the four infants) used stones to crack open nuts or other encased foods. We observed 1565 episodes of tool use in the two groups over the course of the study (0.92 episodes per hour/per group). Fourteen adults (seven males, seven females) performed 84% of the episodes ($N = 1310$) and eight juveniles performed the remaining 16% of the episodes ($N = 255$). The seven adult males accounted for 73.5% ($N = 963$) and the seven adult females for 26.5% ($N = 347$) of the tool use episodes performed by adults. Tool use episodes primarily occurred on sandstone anvils (80%) and log anvils (19%); other substrates were rarely used (1%) (Fig. 1). The monkeys used a stone as the percussor in 98.5% of the episodes. A palm nut was used as percussor in 24 episodes; 15 episodes to crack open another palm nut and nine episodes to crack open other food items.

Figure 1. An adult male (Jatoba) using a log anvil (left) and a sandstone anvil (right) (Photos by E. Visalberghi).

Of the nine juveniles, the two oldest (Tucum, an approximately two year-old male and Dita, an approximately three to four year-old female, at the beginning of the study) succeeded in opening intact nuts. The other juveniles often pounded nuts on hard surfaces and had success with tools only when cracking food items other than whole nuts, such as partially opened nuts. Finally, one juvenile female never used a tool (for further information see Spagnoletti, 2009). Since juveniles used tools relatively infrequently, we only compare the data recorded for adult males and females.

Sex differences in tool use by adults and food exploited

As shown in Table 1, 86% of the episodes of tool use performed by adults involved palm nuts and 14% involved other food items. Adult males accounted for a higher number of nut cracking episodes than did adult females (median (interquartile range, IQR): 130 (87.5) and 27 (29), respectively; Mann–Whitney, $U = 8$, $n_m = 7$, $n_f = 8$, $p < 0.05$); whereas the number of episodes aimed at cracking food items other than nuts did not differ between males and females (median (IQR): 12 (5.5) and 14 (13), respectively; Mann–Whitney, $U = 27.5$, $n_m = 7$, $n_f = 8$, $p = 0.95$). For each group, the correlation between an individual's number of episodes of tool use and its social rank was not significant (CH group $r_s = 0.05$, $n = 11$, $p = 0.88$; ZA group $r_s = -0.8$, $n = 4$, $p = 0.2$).

Monkeys used tools more frequently to crack low resistance nuts (66% and 70% of the episodes for males and females, respectively) than high resistance nuts (34% and 30% of the episodes for males and females, respectively). Adult males used tools to crack high resistance nuts significantly more often than did adult females (Mann–Whitney, $U = 5$, $n_m = 6$, $n_f = 6$, $p < 0.04$), whereas there was no sex difference in the frequency of tool use to crack low resistance nuts (Mann–Whitney, $U = 7$, $n_m = 6$, $n_f = 6$, $p = 0.093$).

Efficiency at cracking nuts

Table 2 reports the percentage of episodes resulting in success, number of strikes and duration of episodes for adult males and females to crack low resistance and high resistance nuts. The mixed model regression analyses, reported in Table 3, showed that success in cracking open nuts is predicted by nut resistance ($z = -2.23$, $p < 0.05$, $N = 423$) but not by individual body mass, sex, rank, and weight of the hammer stone. Success at cracking high resistance nuts was predicted by individual body mass ($z = 2.59$, $p < 0.01$, $N = 110$) and hammer weight ($z = 2.68$, $p < 0.01$, $N = 110$).

The number of strikes needed to open nuts varied significantly as a function of the individual body mass and the resistance of the nut, but not to the sex of the individual or the weight of the hammer stone (Table 4; Figs. 2 and 3). The duration of episodes varied significantly as a function of the resistance of the nuts, but not to the individual body mass, sex, and weight of the hammer stone (Table 4). The average duration (±standard deviation) per piassava nut cracking episode, calculated across 37 events for which data are available, is 185 ± 159 s, with the maximum of about 13 minutes.

Selection of hammer stones by the two sexes

In most episodes, the monkeys used a hammer stone already present on the anvil when they arrived. In only 59 cases (3.4% of the episodes), they transported the hammer to the anvil. To crack palm nuts, the monkeys used hammers with a median weight of about one kilogram [males, 100–3000 g (median (IQR) = 1059 (23) g); $N = 373$ nut cracking episodes; females 100–2250 g (median (IQR) = 991 (188) g); $N = 133$ nut cracking episodes]. In contrast, to crack other food items, the monkeys used much lighter stones [males, 20–400 g (median (IQR) = 127 (64) g); $N = 18$ episodes performed by five males; females, 40–650 g (median (IQR) = 148 (154) g); $N = 19$ episodes performed by four females]. The mixed model linear regression showed that the hardness and weight of the hammer stone used to crack open food were predicted by the resistance of the food item, but not by body mass and sex of the individual (Table 5).

The mixed model linear regression split by sex indicated that the resistance of the food predicted the weight of the hammer stones

Table 2
Percentage of success, number of strikes and duration of the episode for adult males and females to crack low resistance and high resistance nuts.

| | Low resistance nuts | | High resistance nuts | |
	Males	Females	Males	Females
Success %	93	87	90	62
Strikes #	8 ± 1.4	13 ± 1.4	12 ± 1.4	15 ± 5.1
Duration (s)	126 ± 19	146 ± 24	182 ± 20	194 ± 62
N	190	68	100	29

N = number of episodes.

Table 3
Success, measured as number of strikes needed to crack a nut, in relation to individual's body mass, sex, and rank, nut resistance, and weight of the hammer stone (nut cracking episodes: $N = 423$).

Independent variable	Coefficient	St. Error	z-value	p-value
Body mass (kg)	0.094	0.595	0.16	0.875
Sex	0.731	0.952	0.77	0.443
Rank	−0.314	0.205	−1.54	0.125
Nut resistance	−0.789	0.354	−2.23	< 0.05
Weight of the hammer stone (kg)	0.478	0.387	1.24	0.216
Intercept	2.96	1.302	2.27	0.023

The overall model was significant (Wald $\chi_5^2 = 16$, $p = 0.0068$).

Table 4
Number of strikes and latency to solution to crack open nuts in relation to individual's body mass and sex, nut resistance, and weight of the hammer stone.

Independent variable	Number of strikes[a]				Latency to solution[b]			
	Coefficient	St. Error	z-Value	p-Value	Coefficient	St. Error	z-Value	p-Value
Body mass (kg)	−2.559	1.026	−2.49	<0.05	−34.480	28.913	−1.19	0.233
Sex	0.862	2.132	0.40	0.686	40.635	53.210	0.76	0.445
Nut resistance	6.431	1.199	5.36	<0.001	72.805	15.233	4.78	<0.001
Weight of the hammer stone (kg)	−1.746	1.258	−1.39	0.165	−14.729	15.503	−0.95	0.342
Intercept	3.292	3.378	0.97	0.330	25.705	61.518	0.42	0.676

Nut cracking episodes: $N^a = 314$; $N^b = 338$.
[a] The overall model was significant (Wald $\chi^2_4 = 40.58$, $p = 0.000$).
[b] The overall model was significant (Wald $\chi^2_4 = 24.18$, $p = 0.0001$).

used by both sexes and that body mass predicted the weight of the hammer stones used by females (Table 6). As shown in Fig. 4, females used significantly heavier hammers to crack open high resistance nuts than low resistance nuts [median (IQR): 1250 (180) g and 873 (189) g, respectively; Wilcoxon signed-ranks test, $T = 0$, $n = 5$, $p = 0.043$; this analysis is based on the five females that cracked open high resistance palm nuts]. The weight of the hammers used by males to crack high resistance and low resistance nuts did not significantly differ [median (IQR): 1086 (129) g and 1035 (154) g, respectively; Wilcoxon signed-ranks test, $T = 8$, $n = 6$, $p = 0.6$, see Fig. 4].

Discussion

Despite their wide geographical distribution and their propensity to use tools spontaneously in captivity, capuchin monkeys have rarely been observed to use tools in the wild (Visalberghi and Fragaszy, 2006). Only recently, tool use has been reported for a few wild populations living in the northeast region of Brazil, and most reports refer to C. libidinosus (Fragaszy et al., 2004b; Moura and Lee, 2010; for a review see Ottoni and Izar, 2008). Our study is the first to analyze the frequency of tool use, success in the use of stone tools and stone selectivity on the basis of systematic field observations of wild capuchins. We showed that all of the adult individuals belonging to two wild groups, except for one female, used hammer and anvil tools throughout the year to crack several species of palm nuts, as well as other encased foods. Juveniles were practicing the same activities, although with less success for their efforts. Our findings indicate that the capuchins at our study site fulfill both McGrew's (1992) definition of habitual tool use (a pattern of behavior shown repeatedly by several members of the group), and Whiten et al.'s (1999) definition of customary tool use

(behavior that occurs in all or most able-bodied members of at least one age-sex class).

Frequency of tool use

Our first prediction, that males would use tools to crack nuts more frequently than females, is supported, and further data collected by Sirianni (2010) with focal animal sampling confirmed this pattern. This prediction was based on Key and Ross's (1999) claim that when males' body mass exceeds females' body mass by 60%, males will have greater daily energy expenditure than females, even if females must bear the energetic costs of reproduction. The finding that males cracked nuts (but not other food items) about five times more than females deserves further discussion. In particular, we should consider the effort and utility imposed by using a hammer stone in male and female capuchins.

Though the use of tools to crack palm nuts has utility (the energetic gain deriving from performing an action) for both sexes, the magnitude of utility may differ between males and females. The stone's kinetic energy when the stone contacts the nut is a key determining factor for the effectiveness of the strike (along with the direction of the force). Kinetic energy is determined by the velocity and mass of the stone. When no extra force is added to the stone, then velocity is determined by the height to which the stone is lifted. Biomechanically, body mass or characteristics that co-vary with mass (e.g., body length, strength) affect the kinetic energy with which the monkey can strike the nut. Adult female and juvenile capuchins have a smaller body size than adult males (Fragaszy et al., 2004b, 2010a). Adult males may add kinetic energy to the strike in the downward phase, whereas females are less able to do this (Liu et al., 2009; see Fig. 5); moreover, males with longer limbs and bigger body size can lift the hammer stone higher than
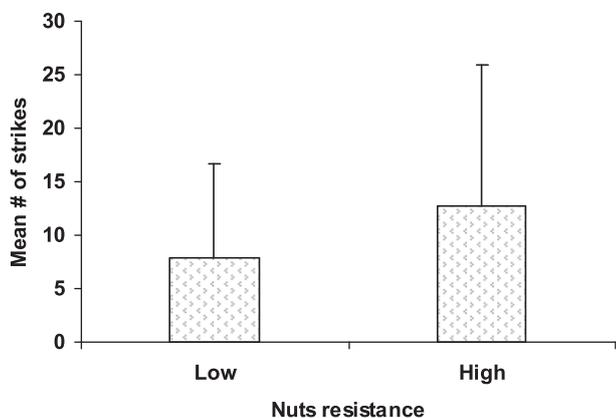
Figure 2. Mean number of strikes performed by adults to crack nuts of low resistance and high resistance. The bar represents the standard deviation.
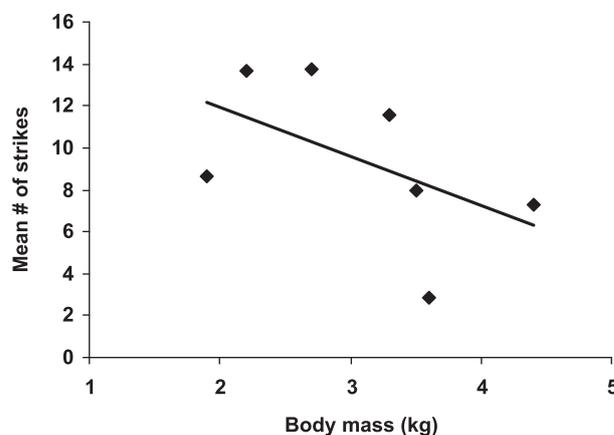
Figure 3. Mean number of strikes to crack open nuts in relation to body mass.

Table 5
Hardness and weight of the hammer stone used by adults to crack open all food items in relation to individual's body mass and sex, and food resistance.

Independent variable	Hammer stone hardness[a]				Hammer stone weight[b]			
	Coefficient	St. Error	z-Value	p-Value	Coefficient	St. Error	z-Value	p-Value
Body mass (kg)	−0.026	0.974	−0.27	0.788	14.516	40.005	0.36	0.717
Sex	−0.229	0.171	−1.34	0.181	138.118	78.928	1.75	0.08
Food resistance	−0.218	0.030	−7.08	<0.001	332.434	34.645	9.60	<0.001
Intercept	2.130	0.175	12.18	0.000	−53.631	96.934	−0.55	0.58

Nut cracking episodes: $N^a = 493$; $N^b = 494$.
[a] The overall model was significant (Wald $\chi^2_3 = 62.24$, $p = 0.000$).
[b] The overall model was significant (Wald $\chi^2_3 = 125.89$, $p = 0.000$).

females can. Because males can add extra force to the stone in the downward direction and can lift the stone higher, they can produce more effective strikes. Thus it is likely that the utility of cracking palm nuts with tools differs in the two sexes, being more advantageous for adult males than adult females. Analyses now underway of the relation between the work (in its technical sense as the kinetic energy added) added to the stone by individual males and females and the relative effectiveness of their strikes seems to support this view (Liu et al., unpublished results). Therefore, differential utilities of nut cracking in the two sexes may well be another important factor contributing to the higher frequency with which wild capuchin males use hammer stones to crack nuts.

Capuchins present a different pattern of sex differences in percussive tool use than do chimpanzees, which may well be related to the utility of nut cracking in males and females of the two species. Adult male bearded capuchins in our study groups weigh 64% more than adult females (3.5 kg vs. 2.1 kg; although published data indicate a lesser degree of dimorphism (34.8%) in wild *C. apella*, Ford and Davis, 1992). To crack open nuts, adult female capuchins at FBV used stones with a median weight of 991 g (i.e., 44–52% of their body mass, depending on the individual), whereas adult males used stones with a median weight of 1059 g (i.e., 24–40% of their body mass, depending on the individual). However, when experimentally provided with a 3.5 kg stone, both sexes can use it successfully (Liu, unpublished results). Body mass estimates for wild populations of *Pan troglodytes verus* that use tools to crack nuts are lacking. However, data obtained from wild specimens present in museums indicate that females of this subspecies have a median weight of 41.6 kg ($N = 3$) and the only male specimen has a weight of 46.3 kg (Smith and Jungers, 1997). Wild female *Pan troglodytes schweinfurthii* have somewhat smaller body mass than males (Gombe: median weight of 31.3 kg for female and 39 kg for males, Pusey et al., 2005; Mahale: median weight of 35 kg for females and 40 kg for males, Uehara and Nishida, 1987), but in all populations the sex difference is proportionally much smaller than for our population of capuchins. The heaviest percussor used by adult female chimpanzees to crack *Panda oleosa* nuts weighed 12 kg (Boesch and Boesch, 1984), i.e., less than 29% of the weight reported for wild *Pan troglodytes schweinfurthii* females. Although an accurate comparison between the effort made by

C. libidinosus and by *Pan troglodytes verus* to crack nuts should scale body mass to the 0.75 power (following Kleiber, 1961) and requires a better dataset for the latter species for body mass and the average weight of the hammers used by each sex, it still seems likely that cracking nuts requires more effort for female capuchins at FBV than female chimpanzees from Taï (for an estimate of nut cracking in one male chimpanzee, see Günther and Boesch, 1993).

A further indication that nut cracking at FBV is more effortful for capuchins than for chimpanzees at Taï and Bossou comes from the fact that chimpanzees adopt a seated posture to crack nuts and mostly use one hand (Matsuzawa, 1994; Boesch and Boesch-Achermann, 2000), whereas capuchin monkeys adopt a bipedal posture and use both hands (Liu et al., 2009). To crack seeds softer than palm nuts, capuchins may use a small/light stone and hold it in one hand; this occurs both at our site (Spagnoletti, 2009) and in the Serra da Capivara National Park, a site located at a distance of 460 km from FBV (Falótico, personal communication). Therefore, the differential frequencies of nut cracking in male and female capuchins and chimpanzees can be accounted for by the degree of sexual dimorphism in body mass, as well as by the differential utilities of nut cracking (higher for male capuchins than for female capuchins; lower for male chimpanzees than for female chimpanzees).

Differential utilities of cracking account also for the different pattern with which capuchins of both sexes exploited encased foods. As we predicted, females used tools to crack high resistance nuts significantly less often than males, whereas no sex difference was found for frequencies of cracking low resistance nuts and other encased foods. Females maximize the reliability of energetic return by cracking foods that they were virtually certain to be able to crack.

However, three other factors might also have contributed to sex differences in frequency of tool use: male capuchins might have better access to anvil site due to their rank, and/or females might have a lower propensity to engage in risky activities (nut cracking is noisy, occurs on the ground and is easy to locate by predators) (Fragaszy, 1986; Rose, 1994), and/or males possess a higher propensity to perform pounding behaviors than females (as described by Visalberghi, 1988). Let us examine whether contributions by these three factors are supported.

Table 6
Weight of the hammer stone used by adult females and adult males to crack open all food items in relation to individual's body mass, and food resistance.

Independent variable	Adult females[a]				Adult males[b]			
	Coefficient	St. Error	z-Value	p-Value	Coefficient	St. Error	z-Value	p-Value
Body mass (kg)	681.246	246.332	2.77	<0.05	−1.586	39.806	−0.04	0.968
Food resistance	387.587	59.65	6.48	<0.001	295.912	42.136	7.02	<0.001
Intercept	−1407.314	514.673	−2.73	0.006	362.921	168.887	2.15	0.032

Nut cracking episodes: $N^a = 160$; $N^b = 494$.
[a] The overall model was significant (Wald $\chi^2_2 = 54.02$, $p = 0.000$).
[b] The overall model was significant (Wald $\chi^2_2 = 49.71$, $p = 0.000$).
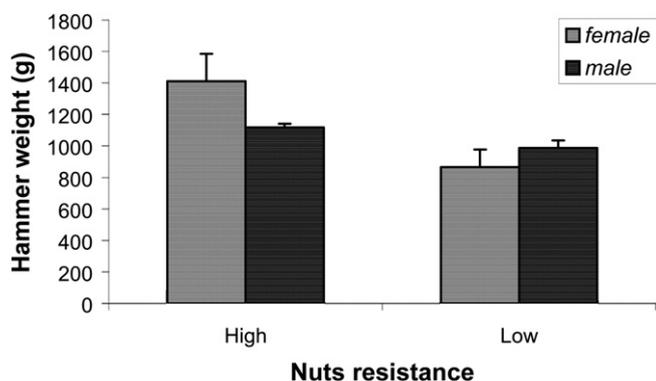
Figure 4. Average weight of the hammer stones used by females and males when cracking nuts of high resistance and low resistance.

In FBV, hammers suitable to crack nuts are rare in the landscape (Visalberghi et al., 2009a) and an anvil site usually has only one hammer stone (Visalberghi et al., 2007). Thus, the anvil sites are a valuable and limited resource, which might elicit both repeated use and competition among tool users. The first point is supported by our observations showing that (a) the episodes of nut cracking ($N = 1565$) occurred in only 122 different anvils (distributed over an area of 9 km^2), and (b) nearly all of the episodes occurred in anvils where the hammer stone was already present (Spagnoletti et al., 2010). Competition also occurred since typically an anvil site accommodates use by one individual at a time. Usually, while the nut cracker is at work, the other individuals "wait" nearby for their turn to use the anvil site. Although infants and juveniles are generally tolerated by tool users and often exploit the bits of nuts that become available on the anvil left from others' cracking (Visalberghi and Fragaszy, in press-b), adults are less tolerated. Only high-ranking individuals may try to displace the nut cracker. The nut cracker seems to signal its "possession" of the hammer (see Kummer and Cords, 1991) by maintaining contact (sometime with a foot) with it during the whole process of extraction. This is particularly evident with piassava nuts that have several kernels inside and need repeated bouts of handling with teeth and hands between strikes. The exploitation of these nuts lasts several minutes.

Do the above results imply that rank affects an individual's likelihood to use tools leading to the observed sex difference in frequency of tool use? Although in both social groups living in FBV the frequency of agonistic interactions during nut cracking is higher than in other feeding contexts (Verderane, 2010), our findings indicate that social rank and number of tool use episodes are not correlated. One dominant male, Zangado, was the most active tool user of his group, whereas the other dominant male, Chicão, was not. Both the third and the fourth ranking males used tools more often than Chicão (see Table 1). Though more difficult to investigate given the small number of subjects, sex did not seem to affect frequency of tool use in similarly ranking individuals. However, to test whether access to the anvil site, and therefore likelihood to use tools, differs according to an individual's rank and sex, we need to examine situations in which several tool users (each carrying a nut) are close to the same anvil site with one hammer. This remains to be done.

Though our study did not assess the propensity to engage in risky activities, studies exploring the degree of vigilance in the two sexes at FBV might be relevant to this issue. If females are less prone than males to engage in risky activities that might attract predators, such as nut cracking (that predators can easily detect by sound and that occurs on the ground from where it is difficult to escape), then they should be particularly vigilant when engaging in this activity. For a small sample of FBV capuchins (two adult males and two adult females), vigilance during nut cracking did not differ between sexes (Cisco, 2006; Liu, unpublished results) and the analysis of activity budget revealed that in both groups males were more attentive to external events (i.e., more likely to give alarm vocalizations) than females (Verderane, 2010). Finally, females are as likely as males to be on the ground (Spagnoletti et al., 2009). Therefore, females do not seem to be less active nutcrackers as a consequence of higher risk avoidance. Future studies should address this issue by investigating vigilance in the two sexes during different activities and when the monkeys are using different substrates.

Finally, it can be argued that the baseline rate of pounding objects predicts individual differences in the rate of using tools. Capuchins bring an object into contact with a surface using percussive actions within the first year of life and these actions are an indispensable element in the development of nut cracking (Resende et al., 2008). If this is so, and if males are more likely than females to pound objects on surfaces, males would also be more likely to use percussive tools. In some studies with captive tufted capuchins (C. apella spp.), males were more inclined to engage in pounding behavior than females (as described by Visalberghi, 1988). Other studies indicate no sex differences in such activities
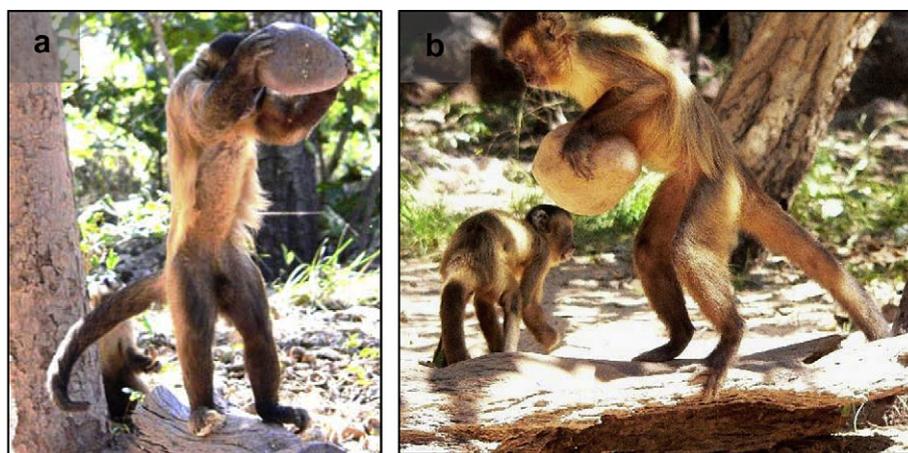
Figure 5. An adult male, 4.2 kg (a) and an adult female, 2.2 kg; (b) crack open a piassava nut using a hammer stone weighing 3.5 kg on a log anvil. This stone is much heavier than the average hammer stone used by capuchins at FBV (1.1 kg). The male lifts the stone higher than the female. (Photo by E. Visalberghi).

in captive capuchins (Fragaszy and Adams-Curtis, 1991; Byrne and Suomi, 1996). In any case, we cannot examine this prediction because we do not yet have data on the rate of pounding food items on substrates by the capuchins in FBV. Future studies should investigate whether an individual's relative frequency of pounding behavior in non-tool-using contexts predicts its relative frequency of tool use.

In sum, since social rank and vigilance can be ruled out, and data are not yet available to examine the hypothesis linking general pounding to use of tools, the differential utility of cracking for the two sexes deriving from the dimorphism in body size, seems the most plausible explanation for the higher frequency of nut cracking episodes by male capuchins. If this explanation is correct, then we should see the same pattern in other populations of bearded capuchins that use percussive tools, assuming equivalent degrees of sexual dimorphism and effort to extract the food. In the Serra da Capivara National Park (Piauí), a few hundred kilometers from our study site, wild capuchins use stones to crack fruit and seeds much less resistant than FBV nuts, and they extract tubers from the ground using stones as scraping or excavation tools, in addition to using sticks as probing tools and to flush prey (Falótico and Ottoni, 2009; Mannu and Ottoni, 2009; Moura and Lee, 2010). Moura and Lee (2010) report that at this site, male bearded capuchins use tools significantly more frequently than females, but due to the limited number of cases where the sex of the individual is reported (tool-using episodes $N = 173$, episodes pounding with stone $N = 26$), strong conclusions require replication of this finding. Apparently the sexes do not differ in the weight of the stone hammers chosen, nor in their efficiency (Falótico and Ottoni, unpublished results).

Efficiency at cracking nuts

In an experiment carried out in FBV in which 11 capuchins cracked whole and partially opened piassava (hard resistance nuts) with one stone, body mass was the single best predictor of efficiency (Fragaszy et al., 2010a). The present study, evaluating efficiency at cracking several species of nuts with a variety of stones, provides additional insights. Our second prediction, that heavier individuals would be more efficient, is supported. As in Fragaszy et al. (2010a), larger individuals were more efficient (with all nuts, regardless of resistance), and they also enjoyed a higher rate of success in cracking high resistant nuts. However, body mass did not affect the duration of cracking episodes leading to cracking a nut. Apparently the duration of the episodes reflects parameters other than efficiency.

Capuchins were successful in 84% of the episodes with high resistance palm nuts (piassava), 91% of the episodes with low resistance palm nuts (catulè and *tucum*), and 99% of the episodes involving other encased foods of very low resistance (e.g., caju). The piassava nuts have a peak-force-at-failure similar to that reported for *Panda* nuts, the more resistant nuts exploited by the Taï chimpanzees (Boesch and Boesch, 1983). High resistance nuts have a peak-force-at-failure, which is on average 50% higher than low resistance nuts. Our third prediction, that nut resistance would affect efficiency, was supported. Nut resistance significantly affected the proportion of nuts attempted that were cracked, as well as the number of strikes to crack palm nuts, and duration of the episodes. We also found that monkeys were more successful when they used heavier hammers.

Overall, we found that sex did not significantly affect efficiency. This contrasts with what has been described for chimpanzees where females not only perform stone tool use more, but also outperform males in the two most difficult forms of stone tool use that chimpanzees practice (Boesch and Boesch, 1984). This is certainly due to the different demands of nut cracking for the two

species; cracking nuts is proportionally more strenuous for capuchins than for chimpanzees (see above) and therefore body size and sometimes hammer weight are crucial factors whereas sex *per se* is not.

Tool selectivity

Our sixth prediction was that capuchins would select stone tools of suitable material and weight to obtain the food resource at hand. Two aspects of our findings support this prediction. First, monkeys of both sexes used heavier stones to crack nuts than to crack other encased food items. Second, females (but not males) used heavier stones when cracking high resistance nuts than when cracking low resistance nuts. The latter finding may indicate that females crack high resistance nuts only when the stone is heavy enough to allow success, and/or that only females with heavy body mass try to crack high resistance nuts, since in our sample only larger females (of about 2 kg) cracked high resistance nuts. In any case, female capuchins seem to take into account both the resistance of the nut and the weight of the stone when they decide whether or not to try to crack a nut. Occasionally, we saw a female arriving with a highly resistant nut to an anvil site with a light stone and leaving soon afterwards after making only a few strikes.

Because capuchins tend to repeatedly use anvil sites containing stone tools, use of appropriate stones could simply be the byproduct of using the anvil sites where an appropriate hammer is already present. However, this hypothesis can be rejected. Visalberghi et al. (2009b) experimentally demonstrated that capuchins reliably choose hammer stones that are heavier and less friable when given a choice between two or more stones, and Fragaszy et al. (2010b) showed that the monkeys selected heavier stones to crack piassava nuts even when the difference in weight between the two stones varied in a ratio of 1.35:1. The present study shows differential use of heavier stones to crack nuts versus other encased food and that females use heavier stones to crack more resistant nuts.

Conclusions

Our findings demonstrate that bearded capuchins at FBV are habitual tool users and that they select a stone by weight to use as a precursor on the basis of the resistance of the encased food. These findings complement other findings from our team at this site. Capuchins use anvil sites repeatedly, they bring stones to anvils, they discriminate among nuts, anvil sites and stones, selecting specific combinations that suit current needs, and they position nuts systematically (Visalberghi et al., 2007, 2009a; Fragaszy et al., 2010b,c). This set of skills is unmatched by other monkey species that have occasionally been reported to use tools (although crab-eating macaques are also promising in this respect, Gumert et al., 2009), and fully comparable with what has been reported for chimpanzees concerning nut cracking. Phylogeny does not predict this pattern and therefore, nut cracking in capuchins likely arose independently of similar behaviors in Hominoidea.

Nut cracking in capuchins offers a valuable opportunity to consider the behavioral and ecological correlates of stone tool use (Haslam et al., 2009). Further studies on the ecology of chimpanzee and capuchin populations that use stones as tools with those that do not, though living in habitats in which encased foods and percussors are available, might clarify the ecological factors and behavioral factors that contributed to the discovery of percussive tool use in these species, and possibly in the human lineage. In the case of bearded capuchins, percussive tool use is not restricted to populations in marginal habitats or to periods of low food availability, as the behavior is present among bearded capuchins across

their range (Ottoni and Izar, 2008) and occurs throughout the year at consistent rates in the capuchins at FBV (Spagnoletti et al., 2008; Spagnoletti, 2009; Verderane, 2010; this study). Thus, the data call for alternative models incorporating, for example, dietary diversity and morphological characteristics (Wright et al., 2009).

Because hominins likely used stone hammers to crack open encased foods before they used stones to flake (even with the simple techniques evident in the Oldowan material), living nonhuman primates have been used as models for early hominins. In particular, female supremacy in tool use in chimpanzees has inspired numerous scenarios of human evolution and of division of labor between the sexes (e.g., Isaac, 1978; Kuhn and Stiner, 2006). Our study suggests a more nuanced situation in capuchins rather than a simple sex difference. Adult male capuchins use stone tools to crack nuts more frequently than adult female capuchins, but body size is a better predictor of efficiency of tool use than sex. Therefore, we suggest that the physical requirement of lifting heavy stones to crack nuts favors heavier individuals, who are for the most part, males.

Sexual dimorphism is most probably the primitive condition retained by humans from the common ancestors of living African apes and humans (Lockwood et al., 1996). In *Australopithecus afarensis* and *Australopithecus africanus*, males seem to be almost double the size of females (McHenry, 1992; McHenry and Berger, 1998; though Reno et al., 2003 consider skeletal size dimorphism in *A. afarensis* similar to that of contemporary *Homo sapiens*). Dimorphism in body size, and consequently muscular mass and strength, is more marked in our wild capuchin population than in humans and in chimpanzees (Fleagle, 1999; Aiello and Wells, 2002). Capuchins illustrate how tool use practices can be impacted by sexual dimorphism in body size, thus contributing to a comprehensive scenario for the evolution of tool-using skills in the human lineage.

Acknowledgements

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