

Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments

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Wild bearded capuchins, *Cebus libidinosus*, in Fazenda Boa Vista, Brazil crack tough palm nuts using hammer stones. We analysed the contribution of intrinsic factors (body weight, behaviour), size of the nuts and the anvil surface (flat or pit) to the efficiency of cracking. We provided capuchins with local palm nuts and a single hammer stone at an anvil. From video we scored the capuchins' position and actions with the nut prior to each strike, and outcomes of each strike. The most efficient capuchin opened 15 nuts per 100 strikes (6.6 strikes per nut). The least efficient capuchin that succeeded in opening a nut opened 1.32 nuts per 100 strikes (more than 75 strikes per nut). Body weight and diameter of the nut best predicted whether a capuchin would crack a nut on a given strike. All the capuchins consistently placed nuts into pits. To provide an independent analysis of the effect of placing the nut into a pit, we filmed an adult human cracking nuts on the same anvil using the same stone. The human displaced the nut on proportionally fewer strikes when he placed it into a pit rather than on a flat surface. Thus the capuchins placed the nut in a more effective location on the anvil to crack it. Nut cracking as practised by bearded capuchins is a striking example of a plastic behaviour where costs and benefits vary enormously across individuals, and where efficiency requires years to attain.

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Wild bearded capuchins, *Cebus libidinosus*, crack palm nuts using a hammer stone and anvil (Fragaszy et al. 2004a; Waga et al. 2006). Bearded capuchins in several other areas of the species' range show this behaviour as well (Ottoni & Izar 2008). In addition to using percussive tools, wild bearded capuchins use probing and scraping tools (Ottoni & Izar 2008; Mannu & Ottoni 2009). We now recognize that bearded capuchins, like chimpanzees (e.g. Sugiyama & Koman 1979; Kortlandt 1986; Kortlandt & Holzhaus 1987; Boesch & Achermann-Boesch 2000; Sanz & Morgan 2007) routinely use tools in foraging.

This phenomenon raises interesting questions about the costs and benefits of using tools in foraging by nonhuman animals. It has

been suggested that using tools broadens a population's dietary niche by making available resources otherwise unavailable with anatomical equipment and that it enables more effective harvesting of limited resources, both of which can be especially important during periods of food scarcity (e.g. Beck 1980; Yamakoshi 1998; Boesch & Achermann-Boesch 2000; Moura & Lee 2004). In contrast, little attention has been devoted to the costs to nonhuman animals of using tools, and we lack at present models to predict the variable occurrence of tool use across species, individuals, time and space (Haslam et al. 2009). The broad framework of optimal foraging theory (Stephens & Krebs 1986; Altmann 1998), variations of which conceptualize costs of behaviour in different currencies (e.g. time, risk of predation or injury, energy), can be used to model the occurrence of tool use, as well as other behaviours, from a cost-benefit perspective (S. Boinski & D. Fragaszy, unpublished data).

Here, we approach the topic of the costs of using tools to crack nuts by wild bearded capuchin monkeys (hereafter, capuchins). We adopt 'strike' as the smallest unit of activity that can affect cost of the tool-using event, and assume that factors that affect the number of strikes needed to crack a nut affect the cost of the activity in the short term. We define efficiency in terms of

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the number of strikes used to crack a nut. We were interested in assessing the efficiency with which capuchins crack nuts and the effect of particular behavioural and physical parameters (of the capuchin, the nut, and the anvil) on efficiency.

At the *EthoCebus* research site in Fazenda Boa Vista, Brazil, capuchins use hammer stones that range up to 2.5 kg, and average 1.1 kg in weight (Visalberghi et al. 2007). The weight of larger hammer stones corresponds to a significant proportion of the capuchins' body weight (range 1.9–4.4 kg for adults in our group, as we report below). Anvils are boulders or fallen logs, or occasionally the crotch or bough of a large tree. The capuchins use anvils habitually, forming pits in the anvils' upper surface from repeated striking in the same place (Visalberghi et al. 2007). Liu et al. (2009a) describe the bimanual, bipedal action that capuchins use to crack the nuts. The average striking cycle involves raising the hammer stone vertically 33 cm, and pulling it downward to produce work (4.2 J) upon striking the nut. Multiple strikes are typically required to crack a whole palm nut, and sometimes a capuchin fails to open the nut. Overall, cracking nuts is strenuous, noisy and time-consuming. It generates costs in energy used and in time spent, risk of injury and risk of predation from being on the ground and producing a loud and easily localized sound. In accord with optimal foraging theory (Stephens & Krebs 1986), individuals should strive to minimize these costs. Two effective ways to minimize costs are to minimize the number of strikes used to open the nuts and to minimize the loss of nuts and stones from inaccurate strikes and poor control of the stone (which can result in the nut and/or the stone falling off the anvil).

In the first experiment (experiment 1) reported here, we examine predictions about how specific intrinsic and extrinsic variables affect an individual capuchin's efficiency at cracking nuts. We were particularly interested in the relation between body mass (measured as weight) and efficiency, reasoning that individuals with larger mass can add more energy to the stone in the downward direction than can animals of lesser mass. Liu et al. (2009a) reported that two females, whose body weight was estimated to be 1.5–2 kg less than the two adult males with whom they were compared, produced less work on the stone than the males. Body weight is also likely to correlate with muscle strength and thus the ability of a capuchin to lift a stone and to control it while striking the nut. Second, body weight is closely correlated with body length; individuals with longer bodies can lift a stone higher, increasing its kinetic energy even if they do not add additional energy to the stone on its downward trajectory. For all of these reasons, longer/heavier animals are predicted to be more efficient at cracking nuts than shorter/lighter individuals.

We also expected that the capuchin's behaviour would affect the efficiency of cracking. We made two predictions about the relation between cracking behaviours and the outcome of cracking attempts, based upon our observations of how the capuchins crack nuts at our site. First, we predicted the nut would fall off the anvil less often when capuchins placed the nut in a pit rather than on a flat section because the pit blocks lateral displacement of the nut. Second, we predicted that the consistency of an individual's use of a particular body position relative to the anvil during cracking would correlate with efficiency, reasoning that adopting a consistent position allows refinement of action in a familiar circumstance. We also evaluated whether a particular body position relative to the anvil or the placement of the nut on a flat or pitted surface were associated with greater efficiency.

Physical properties of the nut should also affect the outcome of a cracking attempt. For example, the integrity of the nut shell affects its resistance to cracking. In this study, we presented the capuchins with one species of nut (tentatively identified as *Orbignya* sp.; Visalberghi et al. 2008) locally called *piçava* (or

piçava). The *piçava* nuts cracked by the capuchins at Fazenda Boa Vista contain two to six kernels in separate chambers (Visalberghi et al. 2008). Thus, after the nut is cracked, one or more kernels can be removed and eaten, but there are usually additional chambers left to open, and capuchins often strike these partially opened nuts (hereafter, partial nuts) to open the remaining chambers. We expected that capuchins would crack partial nuts with fewer strikes than whole nuts, and we were interested in documenting the magnitude of the difference in efficiency when cracking whole and partial nuts.

The size and shape of the nut may also be expected to affect the number of strikes needed to crack it. Visalberghi et al. (2008) reported that the *piçava* nuts' resistance to cracking increases with the weight and diameter of the nut. Thus we predicted that larger nuts would require more strikes to open them. Furthermore, we reasoned that the curvature of the nut at the point where the stone strikes it could affect the transfer of force from the stone to the nut because the force is dispersed across a larger area on a flatter surface. Thus, flatter nuts could be harder to crack than rounder nuts of the same diameter.

We obtained an independent measure of how placement of the nut on the anvil affected efficiency and displacement of the nut after striking by having an adult male human participate in a parallel experiment (experiment 2). By limiting the person to many of the same constraints as the capuchins and providing the nuts from the same collection and the same hammer stone and anvil, we were able to use the person's data to interpret the capuchins' data. Measuring a person's performance when he positioned the nut on different surfaces of the same anvil permitted independent evaluation of the effect of using pits and flat surfaces on the outcomes of striking the nuts.

In summary, we determined how use of different features of the anvils, shape and size of the nuts and capuchin's body weight affected the number of strikes a capuchin used to open a nut. We also evaluated other outcomes of striking that affect the cost of the activity (whether the stone fell off the anvil; whether the nut was displaced), and we compared a person's efficiency when cracking nuts in the same circumstances. Jointly, these elements of the study allowed a broad evaluation of the factors influencing capuchins' efficiency at cracking nuts and the costs to the capuchins for inefficient actions.

EXPERIMENT 1: CAPUCHINS' EFFICIENCY AT CRACKING NUTS

Methods

Site description

The *EthoCebus* field site is located at Fazenda Boa Vista, privately owned land, in Piauí, Brazil (9°39'S, 45°25'W), at approximately 420 m above sea level. Fazenda Boa Vista is an area of Cerrado/Caatinga (open woodland) ecotone (Oliveira & Marquis 2002). This region has low-nutrient sandy soils and highly seasonal and interannually variable precipitation, 800–1600 mm, the vast majority coming in the summer months of November–April (Oliveira & Marquis 2002). Fragaszy et al. (2004a) and Visalberghi et al. (2007) reported that anvil stones and logs and palms with fronds and fruiting stalks emerging from the ground are abundant in this area. Hard stones suitable for cracking these tough palm nuts are present, although stones large enough and hard enough to crack nuts (300 g or more) are rare (Visalberghi et al. 2008).

This study was conducted from early July to early August 2007. The experiment took place in a forested area that contained multiple stone anvils and a log anvil in close proximity. There were ground palms in and around the local vicinity of the experimental area, as in the region generally. The experimental protocol was approved by the animal research committee (IACUC) at the University of Georgia.

Subjects

Eleven members (seven males and four females) of one group of bearded capuchins, *Cebus libidinosus* ($N = 17$) participated in the experiment. Table 1 presents a list of all members of the group and their body weight; Table 2 lists individual capuchins that participated in the experiment, together with data on their age, sex and body weight. We assigned females of unknown age to adult status on the basis of reproductive status. We assigned males of unknown age to adult status on the basis of behaviour, size and appearance. Smaller males that did not participate in courtship ($N = 2$) were classed as young adults.

Palm nuts

A local resident identified and collected the 210 palm nuts used in this study. Table 3 presents descriptive data on the piaçava nuts (*Orbignya* sp.; previously identified as *Attalea*; e.g. Fragaszy et al. 2004a) used in this study. These nuts were locally abundant, although nuts of other species of palms were available to the capuchins in their home range at this time. We elected to use piaçava nuts as these are, according to our measurements, the most resistant to cracking of the nut species the capuchins commonly crack (Visalberghi et al. 2008). All the collected nuts had hard intact shells and contained fully formed kernels. The mesocarp was removed from the nuts after collection if necessary (most nuts already lacked the mesocarp, which is frequently eaten by other animals such as cows, goats and armadillos). This exposed the tough woody capsule enclosing the endosperms (hereafter, the kernels). Piaçava nuts can have two to six kernels, each fully enclosed by the woody capsule. The nuts were weighed to the nearest gram using an electronic scale (Polder™, Polder Inc., Port Chester, NY, U.S.A.). We measured each nut's length (mm), widest diameter (mm) and second diameter (mm) using calipers; the second diameter measurement was taken 90 degrees from where the widest diameter measurement was taken (as described in Visalberghi et al. 2008). A flatness index was calculated for each nut by dividing the smaller diameter by the widest diameter. Thus a flatness of 1.00 would indicate that the nut was perfectly round. Each nut was assigned a number written along its side in indelible ink so that it could be identified from a distance. Weight data were lacking for 29 of the 210 nuts collected for the study. The Pearson correlation between weight and widest diameter for 181 nuts was +0.87 (see also Visalberghi et al. 2008). As the two properties are highly positively correlated, in all analyses involving nut size, we used widest diameter, for which we had data for all of the collected nuts.

Table 1
Age, sex and weight of all capuchins in the study group

Individual	Age	Sex	Weight (kg)
Chicão	Adult	Male	4.4
Mansinho	Adult	Male	3.5
Dengoso	Adult	Male	3.3
Dita	Adult	Female	2.0
Piaçava	Adult	Female	1.9
ChuChu	Adult	Female	2.2
Dende	Adult	Female	1.9
Teninha	Adult	Female	2.2
Chiquinha	Adult	Female	2.4
Jatobá	Young adult	Male	2.7
Teimoso	Young adult	Male	2.7
Tucum	Juvenile (30 months)	Male	1.8
Caboclo	Juvenile (30 months)	?	1.7
Pico	Juvenile (20 months)	?	1.2
Tomate	Infant (7 months)	?	0.8
Catu	Infant (5 months)	?	0.6

During the course of testing, capuchins attempted to crack 189 whole nuts. We could identify the number label for 89 of these. We could not identify the remaining 100 nuts and hereafter refer to these as unknown nuts. Unknown nuts were visibly indistinguishable from identified nuts (lacking the mesocarp, etc.), except we could not read an identification mark. These nuts were likely to have come from our experimental supply because alternative sources of whole nuts were rare in that place at that time. If the first capuchin to attempt to crack a given nut failed, the nut potentially could be 'reused' by a second or subsequent capuchin. We kept track when this occurred for identified nuts.

Capuchins' weights

Over the same time period in which we collected the nut-cracking data, we measured the capuchins' individual body weights. This was done by mounting an electronic scale on a tree using a metal stand (see Fig. 1 for picture of set-up). The stand consisted of a vertical portion (73 × 18 cm) that was strapped against a tree trunk. The horizontal platform (57 × 45 cm; 92 cm above the ground) on the stand was covered with grey/brown outdoor carpet. The scale (Cardinal Detecto 50 kg model, sensitivity to 1 g; 30 × 35 × 5 cm) was bolted to the stand. A removable metal collar (33 × 29 cm) attached to the distal portion of the platform and a metal bowl (25 cm diameter, 16 cm deep) rested in the collar at a distance of 7 cm from the scale. The rim of the bowl was the same height as the platform. We provisioned the bowl with water and kernels of corn. The weight of an object on the scale was displayed on a digital screen attached to the scale via a 280 cm long cable.

The experimenter sat a few metres from the scale, viewing the digital display, and recording the displayed weight when one animal was stationary and fully supported by the scale as the capuchins freely visited the provisioned bowl. We collected several weights per capuchin and report the average.

Anvil

We collected all behavioural data as the capuchins cracked nuts on one log anvil (1 m long, 12 cm high and 12 cm wide; see Fig. 2). A tree bordering the log anvil on the west side afforded easy arboreal access. This anvil was used frequently by all animals in the study group and it afforded good visibility for direct observation and filming. We designated five surface areas on the anvil on which the capuchins could place a palm nut. Moving from the eastern anvil side along its long axis to the western side (where the anvil abuts the tree), surface A was flat; surface B was a pit 1.9 cm in depth, followed by small flat surface C, a 1.5 cm wide area between the two pits. The closest pit to the tree was surface D. This pit was 1.0 cm in depth and was bordered by the final flat surface E on the farthest west position (closest to the tree). The flat surfaces A, C and E sloped 5–10 degrees towards the southern side of the anvil.

Hammer stone

At the start of each day's testing, we placed one hammer stone (1.465 kg) near the anvil. We weighed the stone using the same scale that we used to weigh the nuts. The stone was a roughly ellipsoid quartzite cobble. This stone was used spontaneously and often by all the capuchins that participated in this experiment prior to the experiment, even when they could choose a lighter stone. The stone was among the several stones, both lighter and heavier, normally found at the cracking site. We removed all other stones prior to testing and returned them each day at the end of testing.

Procedure

This experimental site has been provisioned daily (or periodically less often) by the landowner with bananas, nuts and/or dry

Table 2
Efficiency, rank in efficiency and characteristics of the subject and the sample of nuts cracked by that subject

Individual	Sex/age class*	Efficiency rank	Weight (kg)	Efficiency† with		Number of		
				Whole nuts	Partial nuts	Whole nuts	Partial nuts	Strikes
Mansinho	A/M	1	3.5	15.20	32.78	32	22	225
Chicão	A/M	2	4.4	13.20	30.80	27	9	140
Dengoso	A/M	3	3.3	9.12	29.20	37	27	374
Dita	A/F	4	2.0	7.04	28.57	14	10	106
Tucum	J/M	5	1.8	5.00	15.12	10	15	146
Piaçava	A/F	6	1.9	3.31	25.50	9	16	169
Teimoso	Y/M	7	2.7	3.09	18.90	11	10	150
Chuchu	A/F	8	2.2	1.88	22.20	27	11	282
Jatobá	Y/M	9	2.70	1.32	30.00	22	3	162
Dende	A/F	10	1.94		6.30	0	7	63
Caboclo	J/M	11	1.70		5.00	0	6	40
Human	A/M	NA	78	16.10	42.40	81	28	497

* A = adult; Y = young; J = juvenile; M = male; F = female.

† Efficiency = number of nuts opened per 100 strikes.

corn and water since 2000. The capuchins came to the area on an almost daily basis. The capuchins were thus habituated to close human presence, and we were able to observe them consistently at the provisioning site. We could easily identify every individual in the group. We used a tripod-mounted mini DV camera (Canon™ GL2; Canon USA Inc., Lake Success, NY, U.S.A.) positioned at an oblique angle 8 m from the anvil to film all episodes of cracking. The field of view included the capuchin and anvil, and we could distinguish the designated surface areas of the anvil from the video. To begin a test session, we threw one of the previously measured and marked nuts towards the anvil, and we threw additional single nuts as needed as the session proceeded. We filmed each episode of cracking from the time the capuchin approached the anvil until it left the anvil. An experimenter audibly identified each capuchin and narrated events to aid in future scoring from video. The number of the nut the capuchin was striking was identified with the aid of binoculars. Capuchins cracked on a voluntary basis and all individuals were recorded as often as they participated.

Behavioural coding

We collected behavioural data from video playback. We noted every episode of cracking, identifying the capuchin, the nut number (if possible to identify), and whether the nut was whole or partial. Per strike, we noted the capuchin's position relative to the anvil, the nut position on the surface of the anvil, whether the nut cracked in that strike, and if it did not crack, the outcome of the strike with respect to displacement of the nut.

We used a clock-face rubric, with the western end of the log (by the tree) designated as the 12 position, to record the capuchin's position relative to the anvil when it began each striking motion. We pooled clock positions 2–4 into 'position 3' and clock positions 8–10 into 'position 9', producing eight possible positions. Figure 3 illustrates an adult female in position 9 (Fig. 3a) and an adult male in position 12 (Fig. 3b). No capuchin ever used position 3. The capuchins used the following seven positions: position 1: right foot on anvil, left foot on ground; position 5: left foot on anvil, right foot

on ground, facing west; position 6: both feet on anvil facing west; position 7: right foot on anvil, left foot on ground facing west; position 9: both feet on ground facing north; position 11: left foot on anvil, right foot on ground, facing east; position 12: both feet on anvil, facing east.

If the nut did not crack on a given strike, we coded the outcome of the strike with respect to displacement as follows.



Figure 1. Capuchins' weights were obtained using a mounted scale. The scale was mounted 1 m above the ground with water and food provisioned at the distal end. An experimenter, seated a few metres away, recorded the weight showing on the digital display when one capuchin was fully supported by the scale. Photo: T. Pickering.

Table 3
Nut properties: number measured, weight, length, widest diameter and flatness

	N	Minimum	Maximum	Mean	SD
Weight (g)	181	14	80	45.55	13.52
Length (mm)	210	40	87	60.26	7.43
Widest diameter (mm)	210	27	59	40.97	5.28
Flatness*	210	0.64	1	0.89	0.07

* Flatness = second diameter measure divided by the widest diameter.



Figure 2. A view of the anvil showing two pits (D and B) and the adjacent flat surfaces (A, C, E). Photo: T. Pickering.

(1) Fall: the nut fell within 1 m of the anvil. The capuchin had to pick it up to continue cracking, but did not necessarily have to move from its position.

(2) Fly: the nut flew >1 m from the anvil. The capuchin had to leave its position in order to retrieve and continue cracking the same nut.

(3) Catch: the capuchin caught the nut as it bounced or rolled, before it fell to the ground.

(4) Reposition: the capuchin picked up the nut although it had not been displaced, replacing it immediately on the anvil or inspecting it and then replacing it. The nut could be placed in its previous location or another location on the anvil.

(5) Nothing: no nut displacement occurred and the capuchin did not reposition the nut.

We also noted whether the capuchin let the stone slip to the ground after a strike and therefore whether it had to lift the stone to the surface of the anvil again before the next strike. We called this variable 'stone fall'. Stone fall could happen only when the capuchin stood on the anvil while striking (i.e. positions 6 and 12). Normally

a capuchin standing in positions 6 or 12 let the stone rest on the surface of the anvil between strikes, and in this way it lifted the stone from the surface of the anvil at the next strike. If the stone fell to the ground while the capuchin stood on the anvil, the capuchin had to lift it to the surface of the anvil before lifting it in the next strike, which added to the cost of the strike.

Stone lift height and body length measurements

From independently acquired video samples collected while the monkeys cracked nuts at the same anvil, we calculated body length (lower leg + upper leg + torso) for nine of the 11 capuchins using standard two-dimensional measurement techniques (see Liu et al. 2009a for methodological details). These videos were collected in the same time period as we conducted the experiment. The capuchins were filmed while cracking nuts outside of the experimental sessions using a stone that weighed 1.42 kg (97% of the weight of the stone used during the present study). We selected one to six representative cracking episodes per individual, in accord with their availability in the video corpus. From among these episodes, we determined the single strike at which the stone reached its maximum height. For this strike, we calculated the stone's height above the anvil, and the length of the capuchin's body. We used these data to evaluate the relation between the absolute and proportional height the capuchins lifted the stone and their efficiency rank, reasoning that more efficient capuchins would lift the stone absolutely higher than would less efficient capuchins, and that more efficient capuchins would raise the stone to a proportionally greater height relative to body length than would less efficient capuchins.

Data analysis

Data were collated by individual. Efficiency was calculated per individual as the number of strikes on whole nuts divided by the number of whole nuts cracked, and expressed as the number of whole nuts cracked per 100 strikes. A second efficiency score was calculated per individual in the same manner, using the number of strikes on partial nuts. We used paired *t* tests to compare efficiency between partial and whole nuts and Pearson correlations to



Figure 3. Illustration of (a) an adult female and (b) an adult male bearded capuchin striking a piaçava nut with a hammer stone on the log anvil. The female is standing in position 9 and the male is standing in position 12. A piaçava nut is clearly visible on the anvil in (a). Photos: E. Visalberghi.

evaluate relations among individuals' efficiencies on whole nuts and body weight. For the paired *t* test, we report Hedge's unbiased *d* as a measure of effect size, together with confidence interval (CI) for the Hedge's *d*.

We conducted a logistic regression analysis (with SPSS v. 16) using the final strike per nut as the unit of analysis, and cracked or not cracked as the binary outcome variable. The nine capuchins that cracked whole nuts contributed data to this analysis. We selected cracking episodes with whole nuts, using only the episode from the first capuchin that attempted to crack any particular nut (as some nuts were attempted by more than one capuchin). The data set included strikes on 69 whole nuts, 40 of which were cracked.

This analysis used the likelihood ratio test of significance. The likelihood ratio test compares the goodness of fit of the model including a given predictor to the model omitting that predictor (Cohen et al. 2003). Predictor variables included the body weight of the capuchin striking the nut, the capuchin's position on the anvil at this (last) strike, the location of the nut on the anvil surface, the diameter of the nut, the flatness index of the nut, and the number of the last strike. Body weight, nut diameter, flatness index and number of strikes were centred in the analysis. We report Nagelkerke R^2 as a measure of the null deviance accounted for by the set of predictors, where the maximum value is 1.0. The Nagelkerke R^2 provides a logistic analogy to R^2 (used in ordinary least squares regression). The Nagelkerke measure varies from 0 to 1, as does R^2 in ordinary least squares regression. The Hosmer–Lemeshow goodness-of-fit test was used to confirm that the model's estimates fit the data at an acceptable level; $P > 0.05$ for this test indicates acceptable fit of the model to the data.

Results

Capuchins' body weight and body length

The weight and body length of each capuchin is shown in Table 1. The largest capuchin, an adult male, weighed 4.4 kg. The adult females were much smaller, ranging from 1.9 to 2.2 kg. Adult males averaged 3.7 kg ($N = 3$) and adult females, 2.1 kg ($N = 6$). The animal with the smallest body weight in the group that cracked nuts was a juvenile, 30 months old (Caboclo, 1.7 kg). Body length for adult animals that cracked nuts ranged from 0.347 to 0.408 m (see Table 4).

Nut sizes and weights

Nuts weighed an average \pm SD of 46 ± 13.5 g and had a mean \pm SD length of 60 ± 7.4 mm, a mean \pm SD widest diameter

Table 4
Rank of the maximum height to which each capuchin lifted the stone, together with the length of its trunk, the ratio of its trunk length to the height to which it lifted the stone, and the rank of its overall efficiency*

Subject	Rank, highest lift	Stone height (cm)	Trunk length (cm)	Stone height/trunk length	Efficiency†
Mansinho	1	65	40	1.64	1
Dengoso	2	52	37	1.42	3
Chicão	3	49	41	1.21	2
Dita	4.5	44	37	1.18	4
Chu Chu	4.5	44	35	1.25	7
Jatobá	6	43	37	1.16	8
Piaçava	7.5	42	35	1.21	6
Tucum	7.5	42	36	1.17	5
Caboclo	9	40	35	1.14	9
Average		46.8	37.0	1.26	

* These data were available for a subset of the capuchins that cracked nuts.

† Rank order of efficiency on whole nuts among this subset of individuals.

of 41.0 ± 5.3 mm and a mean \pm SD flatness index of 0.89 ± 0.07 . Maximum and minimum values for these variables are given in Table 3. Nut weight and nut length were strongly correlated (Pearson correlation: $r_{179} = +0.62$), as were nut weight and widest diameter ($r_{87} = +0.87$).

Nut-cracking efficiency

The data set consisted of 1857 strikes on 189 whole nuts and 136 partial nuts. Individual efficiencies (expressed as the number of nuts cracked per 100 strikes) for whole and partial nuts are presented in Table 2. This table also presents the number of nuts for each category that each capuchin attempted to open. Since there was a high correlation (Pearson correlation: $r_7 = +0.85$, $P < 0.01$) between efficiencies with nuts of known size and unknown nuts, we pooled data for known and unknown nuts in our analyses.

Efficiency scores to crack whole nuts ranged from 1.32 to 15.20 (see Table 2). That is, capuchins cracked 1–15 nuts per hundred strikes, or expressed another way, individual capuchins used on average 6.6 to 75.8 strikes to crack one whole nut. Some capuchins often failed to crack a particular nut and abandoned it to try another. The greatest number of consecutive strikes used to open a single nut was 57 (made by an adult female). Efficiency on partial nuts ranged from 5.0 to 32.8 (5–33 partial nuts cracked per 100 strikes). All nine capuchins that cracked whole nuts used fewer strikes to crack partial nuts than they did to crack whole nuts (paired *t* test: $t_8 = 11.50$, $P < 0.001$; Hedge's $d = 1.38$, 95% CI = 0.26, 2.50). Individuals' efficiency at cracking whole nuts correlated moderately with their efficiency at cracking partial nuts (Pearson correlation: $r_7 = +0.59$, $P < 0.10$). Two capuchins (one juvenile and one older adult female) attempted to crack partial nuts but not whole nuts. These two capuchins held the lowest efficiency scores on partial nuts of all subjects (see Table 2).

Effect of body weight on efficiency

The capuchins' weights were significantly positively correlated (Pearson correlation: $r_7 = +0.75$, $P < 0.05$) with their efficiencies at cracking whole nuts (see Fig. 4). The smallest capuchin to crack a whole nut weighed 1.8 kg. The correlation between body weight and efficiency at cracking partial nuts was also significant ($r_9 = +0.66$, $P < 0.05$).

Relations among maximum height of lift, trunk length and efficiency

Table 4 illustrates each capuchin's trunk length, the maximum height above the anvil to which it lifted the stone, and its rank order for these two variables and for efficiency. All the capuchins lifted the stone a greater height than the length of their trunk. The

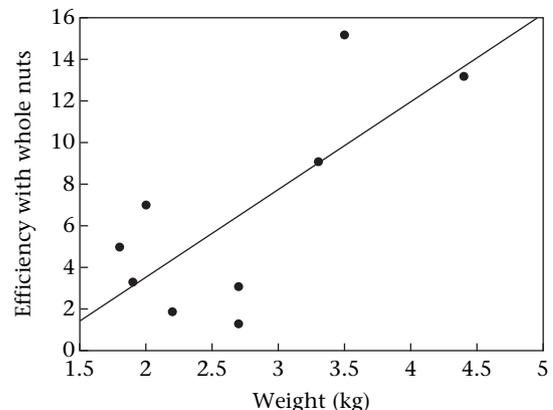


Figure 4. Capuchin's efficiency at cracking nuts, measured as the number of nuts cracked per 100 strikes, plotted by weight. Line of best fit is shown.

maximum absolute height to which the capuchin lifted the stone was significantly positively correlated with efficiency (Pearson correlation: $r_6 = +0.83$, $P < 0.05$) and nearly as strongly correlated with the proportion of the individual's trunk length ($r_6 = +0.68$, $P = 0.06$). That is, more efficient capuchins raised the stone higher and tended to raise the stone a greater proportion of their trunk length. Figure 3b shows the adult male Mansinho, the most efficient capuchin, lifting a stone well above his head.

Outcomes of striking: displacements, catches, repositions and stone falls

Per capuchin, on average, the nut was displaced following 34% of strikes (range 11–68). On 16% of these events, the capuchins caught the nut before it fell off the anvil (range 0–59% of strikes per capuchin). On 67% of those strikes when it was displaced, it fell within 1 m; on the other 33% the nut flew more than 1 m from the anvil. When the capuchins stood at positions 6 or 12, the stone fell off the anvil on 3.5% of strikes on average (range 0–16.4% of strikes per capuchin taken from these positions). The probability that the nut would be displaced after it was struck was modestly negatively correlated with the efficiency of the capuchin striking the nut (Pearson correlation: $r_7 = -0.557$, $P = 0.12$).

Use of different parts of the anvil surface and body position

Table 5 presents the data for the proportion of strikes that each capuchin made with the nut in one of the two pits, its bias to use a particular position on the anvil, and which position it preferred for both whole and partial nuts. The majority of the capuchins (5 of 9) exclusively used one or both of the anvil pit surfaces while cracking whole nuts. The other four individuals struck a whole nut at least once while it was on a flat surface, but these individuals still used pits on at least 79% of their strikes. In contrast, five of 11 capuchins used flat surfaces for the majority of their strikes on partial nuts. All nine capuchins that cracked whole nuts used flat surfaces more often with partial nuts than with whole nuts (binomial test: $k = 0$, $N = 9$, $P = 0.002$; average of 43% of strikes on a flat surface, partial nuts, versus 4% of strikes on a flat surface, whole nuts). Overall, the odds ratio for cracking a partial nut versus a whole nut on a flat surface was 38.2.

Each individual used one of the three positions (6, 9 and 12) on greater than 50% of strikes on whole nuts. In these positions both feet were placed at the same level. The capuchins maintained their preference for a given position and the same magnitude of preference for that position when they cracked partial nuts and whole nuts (average use of one position on partial nuts = 69%, whole

nuts = 73%). Four capuchins were more consistent in the use of one position when cracking whole nuts than when cracking partial nuts, and five capuchins were more consistent when cracking partial nuts than when cracking whole nuts. The magnitude of an individual's preference for one position was not significantly correlated with its efficiency (Pearson correlation: $r_7 = -0.256$, $P = 0.505$).

Relation between body position with respect to the anvil and outcome of the strike

The position that the capuchin assumed while cracking affected the proportion of strikes resulting in displacement of the nut (see Table 6). Position 9 (facing the anvil, standing on the ground) and position 6 (on one end of the log) were associated with a higher percentage of displacements (totalling 30% and 27% of all strikes for positions 9 and 6, respectively, compared to 19% for position 12; see Table 6).

Although a preference for a specific position affected the rate of displacement, position preference was not associated with efficiency. The mean efficiency rank (out of 11) for capuchins preferring position 6 was 4.7 ($N = 3$); for position 9, 7.4 ($N = 5$), and for position 12, 5.0 ($N = 3$). Dengoso and Mansinho each cracked more than 20 nuts and had equivalent efficiencies for nuts cracked entirely in positions 9 and 6. Dengoso's efficiency scores were 12.5 for position 6 and 11.8 for position 9; Mansinho's scores were 17.2 and 16.7 for the same comparison.

Regression models of the likelihood of cracking a nut

Two factors were identified in the stepwise logistic regression as significantly improving the fit of the model: body weight ($\beta_1 = 1.023$, $P = 0.009$) and the diameter of the nut ($\beta_1 = -0.177$, $P = 0.007$). The odds ratio for diameter of the nut was 0.838, and for weight, 2.782, with Nagelkerke $R^2 = 0.234$. The Hosmer–Lemeshow goodness-of-fit test ($\chi^2 = 10.994$, $P = 0.139$) indicated that the model fit the data at an acceptable level. Increasing body weight improved the likelihood of cracking the nut; increasing diameter of the nut decreased the likelihood. Flatness index, placement of the nut on the anvil (into a pit or on a flat surface), and consistency of the capuchin's position relative to the anvil did not significantly affect the likelihood of cracking the nut.

EXPERIMENT 2: EFFECT OF NUT POSITIONING

Methods

In this experiment we evaluated whether nut positioning (in a pit versus on a flat surface) influenced nut-cracking efficiency and the probability of displacing the nut by striking it. We worked with a human participant so that we could generate a sufficient number of cases where the nut was placed on a flat surface for statistical

Table 5
Capuchins' preferences to use a pitted surface on the anvil and to use one position relative to the anvil, and their preferred body position for whole and for partial nuts

Subject	Whole nuts			Partial nuts		
	% Strikes in pit	% Strikes from one position	Preferred position	% Strikes in pit	% Strikes from one position	Preferred position
Mansinho	100	85	6	61	88	6
Chicão	93	63	9	15	69	9
Dengoso	100	58	6	75	51	6
Dita	79	54	12	43	63	12
Tucum	95	67	12	71	78	12
Piaçava	99	93	12	45	53	12
Teimoso	100	59	9	68	77	9
Chuchu	100	87	9	42	75	9
Jatobá	100	88	9	90	70	9
Dende				52	51	6
Caboclo				12	42	9

Capuchins are ordered by rank in efficiency on whole nuts, as in Table 2.

Table 6
Displacement of whole nuts as a function of the capuchins' position with respect to the anvil, and the capuchins' actions after each strike

	Position 6	Position 12	Position 9
Number of strikes	428	218	606
% Catches	1.7	4.6	6.9
% Falls	21.6	13.4	18.1
% Flies	3.9	1.0	5.0
Sum % Displacements	27.2	19.0	30.0
% Repositions	42.1	38.1	39.3
% Nothing	30.7	42.9	30.7
Sum	100.0	100.0	100.0

In positions 6 and 12 the capuchin was standing on the anvil, and in position 9 the capuchin was standing on the ground perpendicular to the anvil.

analysis. The experiment was conducted at the same site and in the same time frame as experiment 1, and made use of the same hammer stone, anvil and nuts. The experiment proceeded in four phases, each conducted on a different day. In phase 1, the person cracked 20 nuts. He was free to choose the anvil surface (flat or pit). In phase 2, the person cracked 40 nuts, alternating between flat and pit surfaces (one surface type per nut). In phase 3, the person cracked 21 nuts, and as in phase 1, he was free to choose the surface position. In phases 1 and 3, where the person could choose the surface, he usually cracked each nut using a single surface type. In phase 4, the person cracked 28 partial nuts, and he was free to choose the surface position.

Participant

One physically fit adult male (20 years, 185 cm, 78 kg) participated in the experiment. He wore gloves (Ironclad™ utility work gloves, Ironclad Inc., El Segundo, CA, U.S.A.) while cracking. The participant had seen the capuchins cracking nuts and he had previously cracked about five of these palm nuts with a stone before participating in this experiment. Before he began, we explained that we were interested in comparing outcomes of cracking nuts in pits and on flat surfaces, but we did not indicate what those outcomes might be.

Procedure

The person cracked nuts in a seated position using position 9 (facing the long axis of the anvil), at a self-selected distance from the anvil (see Fig. 5). He held the stone bimanually at the long axis, as the capuchins held it. An experimenter held a stick horizontally 45 cm above the anvil, which marked the limit above which the person was not to raise the hammer stone (approximately the

height to which the capuchins lifted the hammer stone). All trials were videotaped in the same manner as in experiment 1. From playback we coded the same behaviours for the person as for the capuchins, except body position relative to the anvil and maximum lift height, because these variables were fixed. The protocol for this experiment was approved by the University of Georgia Institutional Review Board.

Analysis

We calculated efficiency for the person in the same manner as for the capuchins. Using Welch's *t* tests (an adaptation of Student's *t* test intended for use with two samples having possibly unequal variances; Welch 1947), we compared the number of strikes that the person used to open whole nuts placed on a flat surface of the anvil and placed in a pit, and we made the same comparison for partial nuts. To evaluate whether the person's efficiency per nut was affected in the same direction as the capuchins' efficiencies by the size or flatness of the nut, we calculated the Pearson correlation between each of these variables and the number of strikes to crack the nut and the proportion of strikes in which the nuts was displaced. We used two-tailed $\alpha = 0.05$ for determinations of significance.

Results

The person cracked 81 whole nuts and 28 partial nuts in 563 strikes. His efficiency was 16.1 for whole nuts and 42.4 for partial nuts. Across phases 1–3, in which he cracked only whole nuts, his efficiency scores were consistent (range 15.2–17.2). He cracked three whole nuts and six partial nuts on a combination of surfaces, and he cracked all others fully on a flat surface or on a pit surface. For whole nuts, his efficiency was 16.3 on pit surfaces ($N = 57$) and 16.8 on flat surfaces ($N = 22$) ($t_{77} = -0.396$, $P = 0.77$). For partial nuts, his efficiency was 56.3 when the nut was on the flat surface ($N = 9$), and 52.0 when the nut was in a pit ($N = 13$). As for whole nuts, this difference was not significant ($t_{20} = -0.396$, $P = 0.70$).

Table 7 presents the findings for the displacement of whole nuts following a strike by the person when he placed the nut in a pit versus on a flat surface. He displaced whole nuts proportionally more often when he struck them on a flat surface than when he struck them in a pit (27% versus 3%, respectively). This distribution was significantly different than expected ($\chi^2_1 = 61.4$, $N = 497$, $P < 0.001$), and the odds ratio was 10.3. When the person struck a partial nut, he displaced it on just eight strikes out of 66 (12% of strikes). Six cases (75% of displacements) occurred when he struck the partial nut on a flat surface.

The diameter of the nut was positively correlated with the number of strikes that the person required to crack it (Pearson correlation: $r_{78} = +0.263$, $P = 0.018$) and the proportion of displacements that resulted ($r_{78} = +0.230$, $P = 0.04$). The correlations between flatness index and the proportion of strikes on which



Figure 5. A young man cracked piava nuts using the same hammer stone (in his hands) and log anvil as the capuchins. He sat on a small log and cracked open palm nuts in varying anvil surface positions. Photo: E. Visalberghi.

Table 7

Displacement of whole nuts when struck by a person as a function of their placement in a pit or flat surface

Variable	Flat	Pit
Number of nuts	22	57
Number of strikes	125	372
% Strikes (out of 497)	25.15	74.85
Number of falls	17*	7
% Strikes that were falls	13.60	1.88
Number of flies	17	6
% Strikes that were flies	13.60	1.61

* Includes two catches.

the nut was displaced were much smaller and not significant ($r_{78} = -0.159$ and $r_{78} = +0.048$, respectively).

DISCUSSION

Wild bearded capuchins crack nuts that are extremely resistant to cracking (Visalberghi et al. 2008), striking them repeatedly with a heavy stone from a bipedal posture (Liu et al. 2009a). We consider this a costly foraging activity in terms of energy expenditure, time and risk. Here we show that individual capuchins in the same group, encountering the same conditions, vary in efficiency (expressed as the number of nuts opened per 100 strikes) over more than a 10-fold range, from 1 to 15 nuts opened per 100 strikes. Thus this behaviour provides an opportunity to evaluate costs and benefits of using a tool in foraging across a wide scale of individual variation. We found that features of the nut, the anvil and the capuchin affect efficiency in nut cracking (considered in terms of the number of strikes) and in the probability that the nut will be displaced after it has been struck. Two unique features of our study are that we obtained individual weights of the capuchins, allowing us to investigate the contribution of body mass, and we evaluated a human cracking nuts on the same anvil as the capuchins, providing an independent evaluation of the influence of placement on efficiency and displacement of the nut after striking, and the relationship between the flatness and the diameter of the nut and these variables. Together, these data allow us to begin to understand the factors that make a nut easier or more difficult to crack, and two aspects of cost (the number of strikes and the probability of displacing the nut by striking it) of cracking nuts for individual capuchins.

Body Weights

Before addressing efficiency at cracking nuts and factors affecting it, we comment on our experiences weighing the capuchins and their body weights. To our knowledge, we present the first data for wild capuchins weighed by voluntary participation (rather than following capture). Altmann & Alberts (1987) pioneered voluntary weighing with wild baboons, using a balance scale set on the ground where the baboons would stand on it as they descended from their sleeping trees. Goodall (1986; also see Pusey et al. 2005) had earlier pioneered using a suspension scale with a climbing rope to weigh wild chimpanzees. Battery-powered digital balance scales make this procedure easier, so long as the digital read out is visible from a distance at which the capuchins tolerate a human observer. We used a digital display attached to a tree-mounted scale via a 5 m cable, provided by the manufacturer as standard equipment with the scale, for this purpose. Providing a desirable, nonportable resource (water in the case of our capuchins) proved a sufficient incentive for the capuchins to stand on the scale. The capuchins needed just a few days to habituate to the scale, and all monkeys in the group, even subordinate individuals, used the scale site. Perhaps placement of the scale 1 m above the ground contributed to their quick habituation. We obtained multiple weights per individual over the course of several days. Thus this method proved practical with our group. We hope that others can adapt this method for use at other sites and with other species. Given that body weight and changes in body weight over time are important indexes of health and growth, obtaining these data directly from wild populations is extremely useful. Live-trapping procedures, in which the animals walk into a trap to collect something and are then tagged/weighed and otherwise measured, is effective for some species (e.g. *Callithrix jacchus*; Araújo et al. 2000), and bypasses the need for real-time monitoring, but we did not want to risk the capuchins avoiding the place where an

individual was previously trapped. Furthermore, we did not expect that we could reliably capture all animals in the group with this method, and we wanted a procedure that we could repeat at intervals, to develop a longitudinal record.

The body weights of adults in our group were more sexually dimorphic than we expected on the basis of published literature (reviewed in Fragaszy et al. 2004b). Average weight of adult females in our group (2.1 kg, $N = 6$) was 57% that of adult males (3.7 kg, $N = 3$). The average of male and female average weights (2.9 kg) indicates this population is slightly heavier, by this index, than *C. olivaceus* and *C. apella*, for which Ford & Davis (1992) reported 2.7 kg, and substantially lighter than *C. capucinus* (3.3 kg), with *C. albifrons* much lighter than all these species (2.1 kg). Additional data to increase our sample size will be welcomed.

Variables Impacting the Capuchins' Efficiency

The weight of a capuchin was the single best predictor of its efficiency. Adult males weighed more than adult females and juveniles. Adult males, which weighed 3.5 kg or more, were far more efficient than females and juveniles. However, adult females and 3-year-old juveniles differed in weight by only a few hundred grams, and efficiencies for these capuchins clustered together, at between one and seven nuts opened per 100 strikes. In this group, weight was not a strong predictor of efficiency. For example, two subadult males weighing 2.7 kg each were ranked 7 and 9 in efficiency, out of 11 capuchins, bracketing an adult female that weighed 2.2 kg, and below two other adult females that weighed 1.9 and 2.0 kg. Thus, it is important to identify the contribution of other factors, in addition to weight, to efficiency. Future studies will evaluate how aspects of the capuchins' behaviour, such as control of the stone's downward trajectory or the extent to which the capuchin can add force to the downward trajectory, influence efficiency.

Our predictions that differences in efficiency would correlate with how the capuchins positioned themselves at the anvil and how they positioned the nut on the anvil were partially confirmed. Capuchins consistently placed whole nuts into a pit on the anvil before striking them. Use of a pit reduced the human's probability of displacing a whole nut by striking it. Thus, it can be argued that, by placing a nut into a pit, the capuchins reduce the probability of displacing the nut by striking it. Displacing the nut constitutes a cost, as the capuchin loses time retrieving it, may not find it, and may lose access to the hammer stone and to the anvil by leaving them to search for the lost nut. Minimizing displacement of the nut is one strategy to reduce the cost of nut cracking. All capuchins in this study adopted this strategy. Whether the person struck the nut in the pit or on the flat surface did not affect his efficiency, suggesting that the capuchins' choice of using the pit rather than the flat surface reflects aversion to the higher probability of displacing the nut, rather than expectations about efficiency.

The capuchins' individual preferences for where they stood in relation to the anvil when cracking (facing the long axis of the log while standing on the ground, or standing on either end of the log) did not affect efficiency, as long as they consistently used a position with both feet at the same level (that is, positions 6, 9 and 12, in our clock-face rubric, where 6 and 12 are standing at one of the two ends of the log). There was more variation across and within individuals in this aspect of behaviour than in others that we measured, and position seems a good candidate to examine as an index of skill development. Standing with the two feet at different heights (that is, positions 1, 5, 7 and 11 in our clock-face rubric) requires asymmetric work to maintain postural stability, and may decrease postural stability during lifting and striking, and/or reduce the ability to add force in downswing.

How often the nut was displaced after it was struck, or was caught after it was displaced, and how often the stone fell off the anvil after a strike (this last variable was coded only if the capuchin was standing on the anvil; i.e. in position 6 or 12) did not vary in accord with individual efficiency. Nor did the flatness of the nut affect the number of strikes that a capuchin used to open a given nut. However, the diameter of the nut was identified in regression analyses as affecting the number of strikes used to crack a nut; larger diameters decreased the probability that a nut would crack on a given strike (i.e. increased the number of strikes used to open a nut). This finding is in accord with the finding that *piacava* nuts with greater weight (significantly positively correlated with diameter in this study) are more resistant to cracking under constant load than nuts of the same species with lower weight (Visalberghi et al. 2008). The human's performance cracking the same nuts on the same anvil provides convergent evidence that diameter of the nuts affects resistance to cracking but flatness does not. Diameter of the nut negatively affected the person's efficiency in the same direction as it affected the capuchins', and also positively affected the probability that the nut would be displaced when the person struck it. Flatness of the nut did not affect either of these outcomes. Thus capuchins seeking to reduce the costs of cracking nuts should select smaller nuts, but the shape of the nut is not important.

Capuchins at our site crack several species of nuts, and we know that the species vary in their resistance to cracking (Visalberghi et al. 2008). Of the four species tested by Visalberghi et al. (2008), the nuts we used in this study are the most resistant to cracking (peak force at failure = 11.50 kN, range 7–17), in part because they have an internal woody capsule around each kernel that makes them particularly resistant to failure. To keep this value in perspective, Visalberghi et al. (2008) reported that peak force at failure for walnuts is 0.37 kN, and for macadamia nuts, 2.2 kN, and *Panda oleosa*, the hardest nuts that wild chimpanzees crack, have a peak force at failure of 9.57 to 12.22 kN.

Peak force at failure under constant load increases with weight in *piacava* nuts, which as we have shown here is highly positively correlated with diameter, and other species of nuts follow this pattern (Visalberghi et al. 2008). However, it is possible that resistance of the nuts varies if the shell becomes more brittle as it dries, and force required for failure may also vary as a function of the mechanical properties of the hammer stone and anvil (their stiffness, for example). We do not yet know how mechanical properties of nuts, stones and anvils vary, nor how these variations affect efficiency; we are currently collecting such data. At this time we merely point out that we expect variation in efficiency at cracking nuts even if the capuchin's body weight and the diameter of the nut are unchanged, as a function of variation in the resistance of the nuts to cracking and variation in the mechanical properties of other components in the system (i.e. the stone and the anvil). Efficiency must be regarded as a characteristic of the combination of capuchin's mass and behaviour as well as the nut, anvil and hammer, not the capuchin alone.

Sources of Individual Variation in Efficiency

One factor that accounted for some variability across individuals in efficiency of nut cracking was how high they lifted the stone. To a great degree this variable was affected by the size and strength of the individual capuchins, which was reflected in the strong positive correlation between body weight and efficiency. Efficiency is also likely to be dependent on the capuchin's control of the stone and the angle of its impact on the nut. Kinematic studies are needed to examine individual patterns in these aspects of cracking, as well as on the work performed on the stone (Liu et al. 2009a). Linking these aspects of cracking to efficiency and to choice of actions and

materials under varying conditions (such as when choosing among stones, using stones of different weight or cracking nuts of different hardness) and across individuals offers rich opportunities to examine how the capuchins perceive the problem of cracking nuts, and where acquired skill enters into the picture.

Unfortunately our small sample size does not support statistical analysis of individual differences in efficiency along lines of age, sex or social status. Although we do not think it likely that dominance status determined efficiency in this study, it probably influenced individuals' participation in the study. For example, during the experiment, subordinate individuals usually cracked elsewhere, on the margins of the group, rather than at the experimental anvil. However, outside of experimental sessions, subordinate individuals used the experimental anvil and the experimental stone, indicating that it was the immediate social context that affected their use of these materials during experimental sessions. With respect to age, animals younger than 3 years were not active participants in this experiment. Longitudinal studies suggest that young capuchins do not crack nuts effectively, even smaller nuts using smaller stones than we used in this study, until they are more than 2 years old (Resende et al. 2008; Liu et al. 2009b).

Effect of Flat and Pit Surfaces on a Human's Efficiency at Cracking Nuts

A human cracking the same species of nuts using the same stone and anvil showed similar patterns as did the capuchins with respect to the association between the diameter of the nut and the number of strikes needed to open the nut, and with respect to the large difference in efficiency with whole versus partial nuts. The human used more strikes to crack larger nuts than smaller nuts, and more strikes to crack whole nuts than partial nuts. Thus, we can use the person's data to evaluate the effects of properties of the nut and the anvil surface on the capuchins' efficiency.

The human participant cracked whole nuts equally efficiently using flat and pit surfaces, and he did the same for partial nuts. However, when he struck whole nuts placed on a flat surface, he was significantly more likely to displace them than if he placed them in a pit (there were too few cases in which a partial nut was displaced after it was struck to evaluate this contingency statistically). Thus, the capuchins' strong preference for placing whole nuts into a pit can be interpreted as a reasonable strategy to reduce the probability of displacing the nut. For comparison, capuchins struck whole nuts on flat surfaces just 27 times; the nuts were displaced on 52% of these strikes. When capuchins struck whole nuts placed in a pit, the nuts were displaced on 31% of strikes.

Choice and Variation in Efficiency

In our study the capuchins were constrained to use one hammer stone, one anvil, and the nuts we provided. We know from this study that choice of nut matters for efficiency, and from other data we know that the capuchins prefer nuts that are easy to crack, unlike the whole *piacava* nuts used in this study, with which they have lower efficiency at cracking (Spagnoletti 2009; D. Frigaszy, R. Greenberg, E. Visalberghi & Q. Liu, unpublished data).

We also know from other studies that the capuchins prefer anvils (and their associated pits) associated with higher efficiency (Q. Liu & D. Frigaszy, unpublished data). Finally, we know that capuchins prefer heavy to light hammer stones, even when the difference in weight of the stones is a few hundred grams, and the ratio of the weight difference is 1.3:1 (Visalberghi et al. 2009; D. Frigaszy, R. Greenberg, E. Visalberghi & Q. Liu, unpublished data). Although we have not yet determined the effect of the weight of the stone on efficiency of cracking, it seems safe to assume that using

a heavier stone decreases the number of strikes needed to crack a nut. Thus it seems that the capuchins are attentive to the costs of nut cracking, and their choices of all the elements involved (nut, stone, anvil surface) are directed towards reducing the number of strikes. Our results also indicate that the capuchin's body weight is an important component in efficiency, and of course the individual cannot modify this for the purpose of cracking nuts. But, as Chalk et al. (2008) and Wright et al. (2009) showed, the capuchins at our study site eat foods with a wide range of hardnesses. Thus they need not always crack foods as resistant to cracking as *piçava* nuts. Spagnoletti (2009) notes that adult males crack a larger proportion of palm nuts than other resistant food items, compared to adult females and juveniles. Further work is needed to determine whether sexes and ages differ overall in their propensity to crack foods of different resistance, but we expect that males are more likely to attempt to crack highly resistant foods than are females and juveniles. At other sites, capuchins crack much smaller items than the nuts we presented, using smaller stones (Ottoni & Mannu 2001; Mannu & Ottoni 2009; Canale et al. 2009). No doubt the threshold body weight for effective percussive tool use (cracking) varies in accord with properties of the food item. We consider it likely that capuchins that were not very efficient at cracking whole nuts according to the measures we used in this study are more efficient at using stones as tools with food items that are less resistant than whole *piçava* nuts. Partially cracked *piçava* nuts meet this requirement, as we have seen.

Implications for Acquisition of Nut Cracking

Experiencing low efficiency does not seem to deter young capuchins from attempting to crack whole nuts. But, there are other circumstances in which young/small capuchins do experience better efficiency, namely, when they attempt to crack partial nuts. Because individuals frequently abandon or lose a section of a whole nut that they have cracked, another capuchin may find a partial nut and try to crack it open. We suggest that the presence of partially cracked nuts provided by the activity of others supports the juveniles' abiding interest in practicing nut cracking. Physical traces left at the anvil (shells, stones, remains of nuts) also support juveniles' interest in the cracking site. In this sense, capuchins modify the environment through their behaviour by leaving persistent artefacts that influence the behaviour of conspecifics, an outcome called niche construction (Odling-Smee et al. 2003). Persistent artefacts, coupled with frequent social supports for manipulative activity that are tied more closely in time to the adults' activity (enhancement, facilitation; Fragaszy & Visalberghi 2004; Gunst et al. 2008; da Silva 2008), explains why young capuchins persist at cracking many food items, including nuts, for years before succeeding routinely. In this sense, nut cracking is likely to be a tradition: social context aids its acquisition (Fragaszy & Perry 2003; da Silva 2008).

A similar system of combined immediate and temporally persisting effects of conspecifics' activity appears to influence young brown capuchins' (*C. apella*) attempts to locate beetle larvae inhabiting tough bamboo canes (Gunst et al. 2008). Adults' actions opening bamboo canes to find beetle larvae enhanced infants and juveniles' interest in exploring these places and practising opening bamboo canes for years before the juveniles could locate larvae themselves. Physical traces of the adults' activity in the bamboo attracted infants and juveniles long after the adults left the area. Thus, as in nut cracking, physical traces of adults' activity provide infants and juveniles with opportunities to experience part or all of a difficult foraging sequence in an easier version.

In current ecological theory, the costs and benefits of activities are measured at the level of the individual consumer (Stephens & Krebs 1986). Yet, this study and others suggest that the niche

construction outcomes that result from the physical traces of activity, including loss of nuts through displacements, impact the ecology of capuchin groups in important ways. Similar processes may be at work in other highly social genera in which socially biased learning contributes substantively to the acquisition of locally important behaviours, and in which enduring physical traces are common outcomes of activity (e.g. New Caledonian crows using forked trees to launch candle nuts onto a suitable stone surface to crack them; Hunt et al. 2002).

In closing, we suggest that nut cracking as practised by bearded capuchins is a striking example of behavioural plasticity; a behavioural example of the 'two-legged goat effect', in West-Eberhard's (2003) phrase alluding to a well-known case of a goat born with no front legs that walked bipedally. In populations where nut cracking is a tradition, as is likely at our study site, we may look for accommodation to this behaviour in many aspects of morphology (associated with lifting and striking with heavy stones) and behaviour (e.g. bipedal stance and locomotion; exploratory actions; attraction to physical traces) to understand the epigenetic process that leads to its reliable appearance.

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References

- Altmann, J. & Alberts, S. 1987. Body mass and growth rates in a wild primate population. *Oecologia*, **72**, 15–20.
- Altmann, S. A. 1998. *Foraging for Survival: Yearling Baboons in Africa*. Chicago: University of Chicago Press.
- Araújo, A., Arruda, M., Alencar, A., Albuquerque, F., Nascimento, M. & Yamamoto, M. 2000. Body weight of wild and captive common marmosets (*Callithrix jacchus*). *International Journal of Primatology*, **21**, 317–324.
- Beck, B. 1980. *Animal Tool Behavior: the Use and Manufacture of Tools by Animals*. New York: Garland STPM Press.
- Boesch, C. & Achermann-Boesch, H. 2000. *The Chimpanzees of the Tai Forest*. Oxford: Oxford University Press.
- Canale, G. R., Guidorizzi, C. E., Kierulff, M. C. M. & Gatto, C. A. F. R. 2009. First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). *American Journal of Primatology*, **71**, 366–372.
- Chalk, J., Wright, B., Lucas, P., Verderane, M., Fragaszy, D., Visalberghi, E., Izar, P. & Ottoni, E. 2008. The mechanical properties of foods processed by *Cebus libidinosus* at Boa Vista, Brazil. *American Journal of Physical Anthropology, Supplement*, **46**, 77.
- Cohen, P., Cohen, J., West, S. & Aiken, L. 2003. *Applied Multiple Regression/Correlation for the Behavioral Sciences*, 3rd edn. Mahwah, New Jersey: L. Erlbaum.
- Ford, S. & Davis, L. 1992. Systematics and body size: implications for feeding adaptations in New World capuchins. *American Journal of Physical Anthropology*, **88**, 415–468.
- Fragaszy, D. M. & Perry, S. 2003. Towards a biology of traditions. In: *Traditions in Nonhuman Animals: Models and Evidence* (Ed. by D. M. Fragaszy & S. Perry), pp. 1–32. Cambridge: Cambridge University Press.
- Fragaszy, D. M. & Visalberghi, E. 2004. Socially biased learning in capuchins. *Learning & Behaviour*, **32**, 24–35.

- Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E. B. & de Oliveira, M. G. 2004a. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, **64**, 359–366.
- Fragaszy, D. M., Visalberghi, E. & Fedigan, L. M. 2004b. *The Complete Capuchin: the Biology of the Genus Cebus*. New York: Cambridge University Press.
- Goodall, J. 1986. *In the Shadow of Man*. Cambridge, Massachusetts: Harvard University Press.
- Gunst, N., Boinski, S. & Frigaszy, D. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, **45**, 195–229.
- Haslam, M., Hernandez-Aguilar, A., Ling, V., Calvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E. & Warren, R. 2009. Primate archaeology. *Nature*, **460**, 339–344.
- Hunt, G. R., Sakuma, F. & Shibata, Y. 2002. New Caledonian crows drop candle-nuts onto rock from communally-used forks on branches. *Emu*, **102**, 283–290.
- Kortlandt, A. 1986. The use of tools by wild-living chimpanzees and earliest hominids. *Journal of Human Evolution*, **15**, 77–132.
- Kortlandt, A. & Holzhaus, E. 1987. New data on the use of stone tools by chimpanzees in Guinea and Liberia. *Primates*, **28**, 473–496.
- Liu, Q., Simpson, K., Izar, P., Ottoni, E., Visalberghi, E. & Frigaszy, D. 2009a. Kinematics and energetics of nut-cracking in wild capuchin monkeys (*Cebus libidinosus*) in Piauí, Brazil. *American Journal of Physical Anthropology*, **138**, 210–220.
- Liu, Q., Salvatori, A. M., Frigaszy, D., Izar, P., Ottoni, E. & Visalberghi, E. 2009b. Longitudinal case study of nut-cracking in a juvenile bearded capuchin monkey (*Cebus libidinosus*): stand for success. *American Journal of Primatology, Supplement*, **71**, 100.
- Mannu, M. & Ottoni, E. 2009. The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools. *American Journal of Physical Anthropology*, **71**, 242–251.
- Moura, A. C. A. & Lee, P. C. 2004. Capuchin stone tool use in Caatinga dry forest. *Science*, **306**, 1909.
- Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. 2003. *Niche Construction: the Neglected Process in Evolution. Monographs in Population Biology* 37. Princeton, New Jersey: Princeton University Press.
- Oliveira, P. S. & Marquis, R. J. 2002. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. New York: Columbia University Press.
- Ottoni, E. & Izar, P. 2008. Capuchin monkey tool use: overview and implications. *Evolutionary Anthropology*, **17**, 171–178.
- Ottoni, E. & Mannu, M. 2001. Semi-free ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *International Journal of Primatology*, **22**, 347–358.
- Pusey, A., Oehlert, G., Williams, J. & Goodall, J. 2005. Influence of ecological and social factors on body mass of wild chimpanzees. *International Journal of Primatology*, **26**, 3–31.
- Resende, B., Ottoni, E. B. & Frigaszy, D. 2008. Ontogeny of manipulative behavior and nut-cracking in young capuchin monkeys (*Cebus apella*): a perception-action perspective. *Developmental Science*, **11**, 828–840.
- Sanz, C. & Morgan, D. 2007. Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *Journal of Human Evolution*, **52**, 420–433.
- da Silva, E. D. R. 2008. Escolha de alvos coespecíficos na observação do uso de ferramentas por macacos-prego (*Cebus libidinosus*) selvagens. M.Sc. thesis, University of São Paulo.
- Spagnoletti, N. 2009. Tool use in a wild population of *Cebus libidinosus* in Piauí, Brazil. Ph.D. thesis, University of Rome.
- Stephens, J. & Krebs, D. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Sugiyama, Y. & Koman, J. 1979. Tool-using and -making behaviour in wild chimpanzees at Bossou, Guinea. *Primates*, **20**, 513–524.
- Visalberghi, E., Frigaszy, D., Ottoni, E. B., Izar, P., Oliveira, P. S. & Andrade, F. R. D. 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology*, **132**, 426–444.
- Visalberghi, E., Sabbatini, G., Spagnoletti, N., Andrade, F., Ottoni, E., Izar, P. & Frigaszy, D. 2008. Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *American Journal of Primatology*, **70**, 884–891.
- Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Frigaszy, D. 2009. Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*, **19**, 213–217.
- Waga, I. C., Dacier, A. K., Pinha, P. S. & Tavares, M. C. H. 2006. Spontaneous tool use by wild capuchin monkeys (*Cebus libidinosus*) in the cerrado. *Folia Primatologica*, **77**, 337–344.
- Welch, B. L. 1947. The generalization of 'student's' problem when several different population variances are involved. *Biometrika*, **34**, 28–35.
- West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. New York: Oxford University Press.
- Wright, B., Wright, K., Chalk, J., Verderane, M., Frigaszy, D., Visalberghi, E., Izar, P., Ottoni, E., Constantino, P. & Vinyard, C. 2009. Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among capuchins and implications for interpreting morphological variation. *American Journal of Physical Anthropology*, **140**, 687–699.
- Yamakoshi, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, **106**, 283–295.