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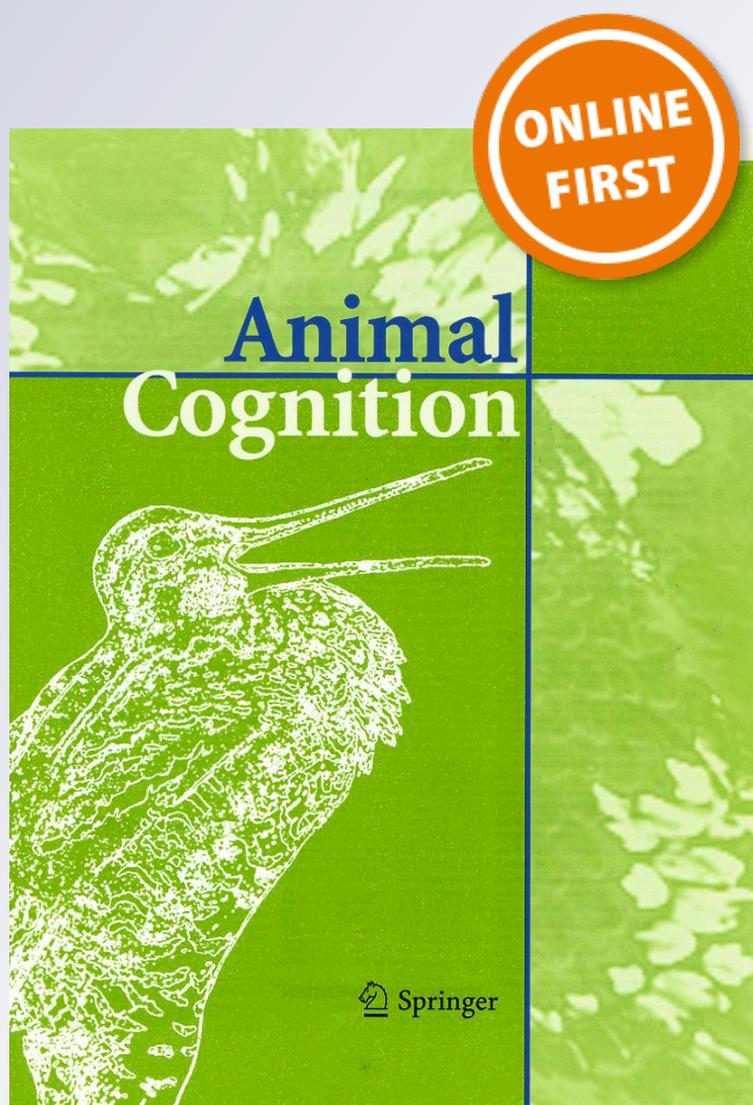
**Luciana Massaro, Qing Liu, Elisabetta Visalberghi & Dorothy Fragaszy**

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# Wild bearded capuchin (*Sapajus libidinosus*) select hammer tools on the basis of both stone mass and distance from the anvil

Luciana Massaro · Qing Liu · Elisabetta Visalberghi · Dorothy Fragaszy

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**Abstract** Contemporary optimization models suggest that animals optimize benefits of foraging and minimize its costs. For wild bearded capuchins (*Sapajus libidinosus*), nut-cracking entails cost related to lifting the heavy stone and striking the nut and additional cost to transport the stone if it is not already on the anvil. To assess the role of stone mass and transport distance in capuchins' tool selection, we carried out three field experiments. In Experiment 1, we investigated whether transport distance affected choice of a tool by positioning two stones of the same mass close and far from the anvil. Capuchins consistently selected the closer stone, effectively reducing transport costs. In Experiment 2, we examined the trade-off between the cost of transport and the effectiveness in cracking by positioning two stones of different mass close and far from the anvil. Most subjects significantly preferred the closer stone, regardless of mass, whereas others preferred the heavier stone regardless of transport distance. In Experiment 3, we changed transport distance of both stones while maintaining the same distance ratios as in Experiment 2. Capuchins maintained the preferences expressed in Experiment 2, with the exception of one

subject. Overall, our findings indicate that (1) individuals vary in their sensitivity to distance of transport, (2) a few meters are perceived as a substantive cost by some monkeys, and (3) monkeys' body mass affects their decisions. We also developed a non-dimensional Preference index (*P*) defined as a function of the stone mass and the transport distance to describe monkey's choice.

**Keywords** Nut cracking · Tool transport · Stone mass · Cost-benefits · Optimization · *Cebus*

## Introduction

The optimal foraging theory (Stephens and Krebs 1986) predicts that animals act to optimize benefits of foraging behavior and minimize costs. Costs and benefits can be calculated in different currencies, such as time, rate, and reliability of return and various forms of risk (e.g., predation, injury, exposure to social threats) as well as energy to be gained (e.g., Altmann 1998). Contemporary optimization models in behavior suggest animals in different foraging situations are attentive to all these currencies (Charnov 1976; Gerber et al. 2004; Verdolin 2006). In the case of nut-cracking by wild bearded capuchins, lifting the heavy stone and striking the nut entail costs in several currencies (e.g., energetic costs, handling time costs, risk of predation from being on the ground and producing noise that is easy to locate, risk of physical injury at each strike). In addition, if the stone is not already at an anvil site, there are additional costs (in terms of time and energy) related to transporting the stone to the anvil where it can be used.

Systematic observations of the spontaneous behavior of two wild groups of bearded capuchins living in Fazenda Boa Vista (in Piauí, Brazil; hereafter FBV) indicated that

L. Massaro (✉) · E. Visalberghi  
Istituto di Scienze e Tecnologie della Cognizione,  
Consiglio Nazionale delle Ricerche, Via Aldrovandi 16B,  
00161 Rome, Italy  
e-mail: massaro.luciana@gmail.com

L. Massaro  
Dipartimento di Biologia e Biotecnologie "Charles Darwin",  
Sapienza Università di Roma, P.le Aldo Moro 5, 00185 Rome,  
Italy

Q. Liu · D. Fragaszy  
Psychology Department, University of Georgia,  
Baldwin Street, Athens, GA 30602-3013, USA

they select stone hammers of suitable mass and material to crack encased foods of different resistance (Spagnoletti et al. 2011). Furthermore, given a choice between differently functional hammer stones, capuchins selected the less friable over the more friable and the heavier stone over the lighter stone, even when the lighter stone was smaller than the heavier stone(s) (Visalberghi et al. 2009a). Capuchins were also sensitive to the affordances of the anvil; they preferentially positioned the nuts on one of the pits present in the anvil in which they obtained the higher efficiency in terms of average number of strikes necessary to crack a nut (Liu et al. 2011). They also preferred nuts of lower resistance (easier to crack) to nuts of higher resistance (Fragaszy et al. 2010a). All the above selective strategies increased an individual's efficiency, in accord with the predictions from optimal foraging theory (Stephens and Krebs 1986).

Body mass also affected an individual's efficiency. In fact, an experimental study on wild capuchins demonstrated that body mass was the single best predictor of efficiency (Fragaszy et al. 2010b). A similar result comes from the observational study of Spagnoletti et al. (2011) where heavier individuals were generally more efficient at cracking nuts than lighter individuals and heavier individuals had higher rates of success at cracking high resistance nuts than did lighter individuals.

In the studies cited above, sex per se did not affect efficiency, that is, when a male and a female had the same body mass, efficiency did not differ. However, since adult females weighed on average 2.1 kg and males 3.7 kg (Fragaszy et al. 2010b), adult females were usually less efficient than males. The kinematics of the stone strikes on the nut further explained the difference in efficiency due to body size. Adult female capuchins lifted the stone to a lower maximum height than males (in accord with their shorter body length and lesser strength) and the potential energy they generated was correspondingly lower (Liu et al. 2009). Males were able to apply twice the kinetic energy to the stone in the downward phase as females, increasing the effectiveness of their strikes. Females used heavier stones when cracking high resistance nuts than when cracking low resistance ones (Spagnoletti et al. 2011), indicating that they selectively chose heavier stones when they would produce high kinetic energy to crack the nut. Fragaszy et al. (2010a; see also Spagnoletti et al. 2011) found that females were more sensitive than males to the mass of the stone when cracking nuts.

The distance between the potential tool and the anvil is another likely factor affecting selection of hammer stones. Stones suitable to be used as hammers are rare in the landscape at FBV (Visalberghi et al. 2009b). Capuchins tend to use anvils where a hammer stone is already present (Spagnoletti et al. 2011). However, capuchins do

occasionally transport stones of appropriate size and hardness to be used as hammers. On average, hammer stones found on the anvils in our study area weighed about 1 kg (25–40 % of the body mass of an adult male or female, respectively) (Visalberghi et al. 2007). A recent survey of the anvil sites used by capuchins at FBV showed that a 1.45-kg hammer stone was transported from the anvil where capuchins had initially used it to another anvil located at a linear distance of 94 m (Visalberghi unpublished data). Capuchins transport heavy stones by walking bipedally using a bent-hip, bent-knee gait, which is less efficient than the human gait (Duarte et al. under revision). Indeed, carrying a heavy stone bipedally appears effortful and some smaller monkeys do not carry hammer stones bipedally to an anvil even for short distances.

Given the costs of transport, capuchins choosing between stones to carry to an anvil should balance the benefits of cracking with a heavier stone against the costs of transporting it, rather than a lighter stone. Smaller individuals in particular must balance these costs. When cracking nuts with heavier stones, smaller individuals are more efficient (i.e., they need fewer strikes to crack the nut) than when they use lighter ones, but they likely spend proportionally more effort to lift and carry heavier stones than larger individuals. To explore the role of stone mass and distance of transport in tool selection, we carried out a series of field experiments. The transport distance and the mass of the stones used in these experiments were within the range observed during field observations (Visalberghi et al. 2009b; Spagnoletti et al. 2011). Previous studies demonstrated that capuchins, when choosing between stones of different weight positioned on the anvil or within 1 m to the anvil, significantly preferred the heavier stone to crack a high resistance nut (Fragaszy et al. 2010a). Therefore, 1-m distance was not perceived as costly. Before the experiments, we carried out a pilot study that demonstrated that instead a 3-m transport was perceived as costly by capuchins and some chose the lighter stone to crack a high resistance nut. Consequently, we initially adopted 3 m as the minimum distance in our study.

In the first experiment, we investigated whether distance of transport affected tool choice. Two ovoid quartzite stones of the same mass were positioned close and far from the anvil. Our prediction was that the monkeys would consistently select the stone closer to the anvil in order to reduce the cost of transport. In the second experiment, we examined the tradeoff between the currencies of transport and effectiveness for cracking. Two stones that differed in mass were positioned at different distances from the anvil. If distance of transport drove selection of the stone, then the monkeys should use the closer stone regardless of its mass. If mass of the stone drove selection, then the monkeys should transport the heavier stone, regardless of its

distance. In order to verify whether monkeys would maintain the preferences expressed in Experiment 2 for other distances, we carried out Experiment 3 where all the other variables were as in Experiment 2, except distances from the stone to the anvil.

Finally, we introduced a non-dimensional Preference index ( $P$ ) defined as a function of the mass of hammer stone ( $M$ ) and the distance of transport ( $D$ ) to estimate the value that each monkey gives to both variables in Experiment 2.

Collectively, these experiments open the opportunity to explore individual differences in decisions about tool selection and how these differences relate to body size (and consequently strength).

## Methods

### Study area

The study site (9°39'36"S, 45°25'10"W, altitude approximately 420 m above sea level) is located on private property (FBV) in a dry woodland plain in Piauí, Brazil (Visalberghi et al. 2007). A group of wild capuchin monkeys (*Sapajus libidinosus*)<sup>1</sup> routinely comes to crack palm nuts in an area at the foot of a sandstone ridge containing several sandstone and log anvils. We used this area as our field laboratory (see Visalberghi et al. 2009a).

### Subjects

The subjects were all proficient tool users as they all were observed using tools for several years (Spagnoletti et al. 2011, Fragaszy et al. 2010a, b). Opportunistically, their weight was measured to the nearest 100 g using a digital scale (model 750, Cardinal Scale Mfg. Co, Webb City, Missouri, USA; see Table 1). As described in Fragaszy et al. (2010b), the monkeys voluntarily stood on the scale mounted in a tree while they drank water from a bowl hung at one side of the scale. We obtained 10 or more weights per individual over a 6-week period (corresponding to that in which the experiments were run) and averaged them. The subjects belonged to a group of 19 monkeys.

<sup>1</sup> Recent molecular analysis has revealed that capuchin monkeys, formerly identified as the single genus *Cebus*, are two genera, with the robust forms (including *libidinosus*, *xanthosternos*, and several other species) now recognized as the genus *Sapajus*, and the gracile forms retained as the genus *Cebus* (Lynch Alfaro et al. 2011, 2012). To date, tool use has been observed in some species of wild *Sapajus*, but no species of wild *Cebus*. We retain the genus designation of *Cebus* for published works cited here that used that designation.

### Design and procedure

Each subject was presented with a nut and a choice of two stones to transport to an anvil. Each trial started when the experimenter provided one palm nut (see below). We used high resistance nuts (piassava, *Orbignya* sp.) and low resistance nuts (tucum, *Astrocaryum campestre*); both species are locally abundant and frequently exploited by the monkeys. These nuts have significantly different peak-force-at-failure values (Visalberghi et al. 2008) with piassava being on average twice as resistant as tucum. We used piassava nuts weighing 30–45 g with the esocarp removed. An electronic scale (Polder<sup>TM</sup>) was used to weight the nuts to the nearest g.

All nut-cracking events occurred on a log anvil (1 m long, 12 cm high and 12 cm wide). This anvil was frequently used by the monkeys and it allowed good visibility for filming. Each trial was filmed using either Canon GL2 or Canon XL2 cameras. The experiments took place in July–August 2010 and in June–July 2011.

Each subject was tested opportunistically when present in the experimental area and willing to participate in the experiment. When more dominant individuals approached the testing area and potentially could interfere with the participation by more subordinate subjects, one of the experimenters enticed them away from the testing area by placing a nut and a stone on another anvil. Nevertheless, the experimenter did not have full control of which individual would participate in any given trial. By using this opportunistic procedure, we succeeded in testing each subject individually and all subjects received the four experiments in the same order. Since choices reflect each subjects' locomotion capability, we decided not to exclude any individual that voluntarily participated in the experiments and consequently Mansinho, an adult male who had a physical handicap (lacking one foot, see below) but voluntarily participated in three experiments, was included. As all the other subjects, when he was given a nut, he chose and transported one stone to the anvil where he cracked it.

In the pilot study mentioned in the Introduction, we investigated whether transporting a stone for 3 m was perceived by the monkey as a cost. Five subjects were individually given a choice between a 0.93 kg and a 1.92 kg stone both positioned at 3 m from the anvil (and 0.4 m from one another). Then, a low resistance nut (Condition 1), or a high resistance nut (Condition 2) was placed on the ground behind the stones. Condition 1 was presented before Condition 2 and in each condition, left and right positions of each stone were pseudo-randomized across trials.

In Experiment 1, we investigated whether distance of transport affected tool selection. The subject was given a choice between two quartzite stones of similar shape, color

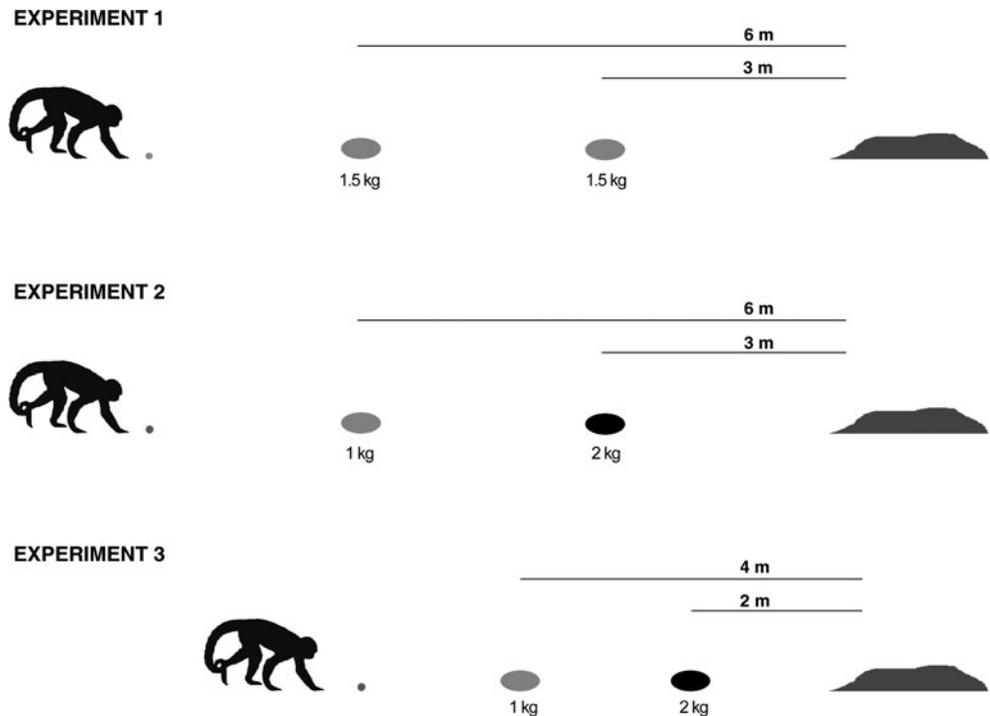
**Table 1** Subjects' sex, body mass, and participation to the three experiments

Individual	Sex	Experiment 1		Experiment 2			Experiment 3		
		Equal stone mass	Body mass (kg)	Condition 2.1 Heavy-close/light-far	Condition 2.2 Light-close/heavy-far	Body mass (kg)	Condition 3.1 Heavy-close/light-far	Condition 3.2 Light-close/heavy-far	Body mass (kg)
Jatoba	Male	10/0 (10)*	4.3	10/0 (10)*	0/10 (10)*	3.8	10/0 (10)*	0/10 (10)*	3.8
Mansinho	Male	9/1 (10)*	3.5	5/5 (10)	9/2 (11)*	3.5	9/1 (10)*	10/0 (10)*	3.5
Teimoso	Male	–	–	10/0 (10)*	0/10 (10)*	3.3	10/0 (10)*	0/10 (10)*	3.3
Tucum	Male	10/0 (10)*	3.0	10/0 (10)*	0/14 (14)*	3.0	–	–	–
Caboclo	Male	9/1 (10)*	2.7	9/1 (10)*	14/0 (14)*	2.7	–	–	–
Chuchu	Female	9/1 (10)*	2.1	10/1 (11)*	13/2 (15)*	1.97	10/0 (10)*	4/16 (20)*	1.97
Dita	Female	10/0 (10)*	2.1	5/0 (5)	10/0 (10)*	2.09	9/1 (10)*	10/0 (10)*	2.09

The number of choices of the closer and the farther stone is presented as “close/far”. The total number of trials for each subject in each condition is in parentheses. The body mass has been measured during the same period in which each experiment was carried out

\* Binomial test:  $p < 0.05$

**Fig. 1** Experimental setup (not in scale) for the three experiments. The experimenter positioned the nut on the ground behind both stones with respect to the anvil. In Experiment 1, the subject was given a choice between two stones of similar mass (1.5 kg). The close stone was at 3 m, the far one at 6 m from the anvil. In Experiment 2, the subject was given a choice between two stones of different mass (1 and 2 kg) at different distances (3 and 6 m), alternatively. In Experiment 3, the same stones of Experiment 2 (1 and 2 kg) were positioned at 2 and 4 m, alternatively. Only one condition per experiment is illustrated (Drawn by Luciana Massaro with Adobe Photoshop CS 4)



and weight (1.38 and 1.42 kg). The difference in weight between the two stones (4 g) was just barely at the 1/40 proportion which humans are able to discriminate (Weber 1978). One stone was at 3 m from the anvil (close stone) and the other 6 m from the anvil (far stone) (see Fig. 1). The experimenter positioned a low resistance nut on the ground about 9 m from the anvil, behind both stones with respect to the anvil.

In Experiment 2, we investigated the relation between cost of transport and cost of cracking. We positioned a high resistance nut at about 9 m from the anvil. The light stone (0.93 kg) was at a distance of 3 m from the anvil and the

heavy stone (1.92 kg) at 6 m from the anvil (Condition 2.1, Heavy-close vs. Light-far), or the heavy stone at a distance of 3 m and the light stone at 6 m from the anvil (Condition 2.2, Light-close vs. Heavy-far) (see Fig. 1).

In Experiment 3, we investigated the relation between cost of transport and cost of cracking with a different set of distances than those used in Experiment 2. We positioned a high resistance nut 6 m from the anvil. Here, we used a set of two stones for each weight class. In Condition 3.1 (Heavy-close vs. Light-far), the heavy stone (2.00 or 1.91 kg) was at 2 m and the light stone (0.93 or 0.97 kg) at 4 m from the anvil. In Condition 3.2 (Light-close vs.

Heavy-far), the light stone was at a distance of 2 m from the anvil and the heavy stone at 4 m from the anvil (see Fig. 1).

In all experiments, conditions were alternated per subject throughout the experiment. In each condition, far and close positions were pseudo-randomized across trials and an equal number of trials per subject with each stone in each position were completed. Table 1 reports the number of trials for each subject in each experiment and condition.

The research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

### Preference index

We developed a non-dimensional Preference index ( $P$ ) that reflects each monkey's preferences for a stone tool in different conditions of mass and distance of transport.

In each experiment, we presented the monkey with two stones that could be light or heavy at a certain distance from the anvil, far or close (i.e., one of four combinations of weight and distance). The combinations presented in our experiments were Heavy-close and Light-far (e.g., Condition 2.1), or Light-close and Heavy-far (e.g., Condition 2.2). We refer to each pairing of weight and distance as a category. Each of these four categories involved a different effort for a monkey. For example, choosing a stone that is light and close costs less for transport than choosing a stone that is heavy and far. Our  $P$  index assigns a value to each category corresponding to different energetic effort. Higher is the effort and higher is the value of the  $P$  index. Thus, it is possible to evaluate how monkeys' choices were distributed in these four categories and determine the relative role played by stone mass and distance of transport on their preferences. Our Preference index ( $P$ ) is defined as a function of the mass of the hammer stone ( $M$ ) and distance of transport ( $D$ ) so that:

$$P = M^i D^k$$

where  $M = \frac{m}{m_0}$ , and  $D = \frac{d}{d_0}$   $m_0$  and  $d_0$  are the minimum stone mass and distance considered in each experiment, whereas  $m$  and  $d$  are the stone mass and distance values used in each experimental condition. For example, in Experiment 2 Condition 2.1 for the category Heavy-close,  $m$  is about 2 kg and the minimum stone mass used in this experiment ( $m_0$ ) is about 1 kg. Thus, the resulting value of  $M$  for this category is 2. The same process is used to calculate the value of  $D$ . In the category Heavy-close, the stone is at 3 m ( $d$ ) and the minimum distance ( $d_0$ ) is also 3 m; thus, the value of  $D$  for this category is 1. Values of  $M$  and  $D$  for each category of Experiment 2 are reported in Table 2.

To estimate the value that monkeys assigned to mass and to distance, we need to determine the values of the

**Table 2**  $M$  and  $D$  values for each category presented in Experiment 2

Light-close	Heavy-close	Light-far	Heavy-far
$M = \frac{1kg}{1kg} = 1$	$M = \frac{2kg}{1kg} = 2$	$M = \frac{1kg}{1kg} = 1$	$M = \frac{2kg}{1kg} = 2$
$D = \frac{3m}{3m} = 1$	$D = \frac{3m}{3m} = 1$	$D = \frac{6m}{3m} = 2$	$D = \frac{6m}{3m} = 2$

exponents in the formula that produce the best match of the  $P$  index to the observed data in terms of lowest squared residuals and highest correlation coefficient with respect to the linear relation in the logarithm:

$$\log N = a \cdot \log P(k) + b$$

### Variables scored and data analysis

In each trial, we scored the stone(s) chosen and transported by the subject. To analyze the choices between the two stones made by each individual, we used the nonparametric Binomial test and the nonparametric Grant test for significance of runs (Siegel 1956). One-tailed statistics were used in Experiment 1 in which there was a directional prediction, whereas two-tailed statistics were used in Experiments 2 and 3.

## Results

Monkeys typically picked up the nut and then the stone and transported them both directly to the anvil. Sometimes, they transported the stone in a continuous bipedal bout; at other times, they dropped the stone one or more times on the way to the anvil. These interrupted bouts took longer. Larger individuals were more likely than smaller individuals to transport the stone in one bipedal bout, especially with heavier stones. Although quantitative and kinematics analyses of transport are still in progress, it appeared that the larger stone used in these experiments (2 kg) was at the outer limits of the smaller (2 kg) individuals' ability to carry, although these same monkeys willingly used stones of this size to crack nuts. Evidently, lifting and striking are less effortful than carrying.

### Pilot study

We found that the monkeys preferred the lighter stone for low resistance nuts but did not systematically prefer the heavier stone for the high resistance nut. This indicated that a distance of 3 m was sufficient to cause some subjects to use a lighter stone more than they would if there were no transport involved, as in the experiment carried out by Fragaszy et al. (2010a).

Experiment 1: Transport distance

All six monkeys showed a significant preference for the stone closer to the anvil (Binomial test: all  $p_s < 0.05$ ; Table 1), suggesting that distance (3 vs. 6 m) was a very important factor affecting choice.

Experiment 2: Stone weight  $\times$  transport distance (3 and 6 m)

In Condition 2.1 (Heavy-close vs. Light-far), five individuals preferred the Heavy-close stone at 3 m (Binomial test: all  $p_s < 0.05$ ), whereas two individuals (Dita and Mansinho) did not show any significant preference (Table 1). However, in the five trials that we were able to administer, Dita always chose the Heavy-close stone. In Condition 2.2 (Light-close vs. Heavy-far), four individuals preferred the Light-close stone at 3 m, while three individuals significantly preferred the Heavy-far stone at 6 m (Binomial test: all  $p_s < 0.05$ ; Table 1).

Experiment 3: Stone weight  $\times$  transport distance (2 and 4 m)

In Condition 3.1 (Heavy-close vs. Light-far), all five individuals preferred the Heavy-close stone at 2 m (Binomial test: all  $p_s < 0.05$ ). In Condition 3.2 (Light-close vs. Heavy-far), two individuals preferred the Light-close stone at 2 m, whereas three individuals significantly preferred the Heavy-far stone at 4 m (Binomial test: all  $p_s < 0.05$ ; Table 1). One subject (Chuchu) switched preferences between Experiments 2 and 3, whereas in Condition 2.2, she preferred the light stone at 3 m of distance to the heavy stone at 6 m, in Condition 3.2, she preferred the heavier stone at 4 m to the lighter stone at 2 m. Interestingly, her new pattern of preference evolved gradually (Grant test for significance of runs:  $p < 0.01$ ) as in the first 10 trials, she switched from the light to the heavy stone, and vice versa, almost every trial, while in the last 10 trials, she always chose the heavy stone.

Nut-cracking efficiency and success

Each subject was highly successful (i.e., they cracked the nut with the stone tool) in all experiments. In Experiment 1, when the low resistance nut was given, capuchins were almost always successful (59 out of 60; 98 % success rate). In Experiment 2, when the high resistance nut was given, they cracked the high resistance nut on 114 trials out of 152 (75 % success rate). Only the 4-year-old male Caboclo had a higher number of failures than successes (11 vs. 3) in Experiment 2 Condition 2.2 when he always chose the Light-close stone. In Experiment 3, when the

**Table 3** Nut-cracking efficiency

Subject	Piassava nut						Tucum nut		
	2-kg stone			1-kg stone			1.4-kg stone		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
Jatoba	3.2	1.7	40				4.6	1.2	10
Mansinho	3.3	2.4	15	4	2.4	24	3.6	1.3	10
Teimoso	5.7	4.1	37						
Tucum	4.9	3.3	20				5.3	1.8	10
Caboclo	10.5	5.3	8	17.7	7.2	3	7.4	3.4	9
Chuchu	6	4.5	35	4.7	4.2	7	6.5	2.2	10
Dita	5.2	4.1	13	5.5	4	12	5.1	0.9	10

Number of strikes performed by each subject to open a high resistance nut (i.e., a piassava nut) and a low resistance nut (i.e., a tucum nut). Data are pooled across experiments when stones of the same/similar mass were used

high resistance nut was given, the five subjects that participated cracked it on 102 trials out of 110 (92.7 % success rate).

The purpose of our experiments was not to evaluate capuchins' efficiency with stones of different mass, and infrequent use of some stones precludes statistical analysis (see Table 3). Nevertheless, in general terms, we found that two subjects (Mansinho and Caboclo) out of four tended to be more efficient with the heavy stone than with the light stone (Table 3) and that heavier individuals used fewer strikes with each stone than lighter individuals.

Effect of body mass on monkey's preferences

Our results indicate that three monkeys chose a hammer stone primarily on the basis of its mass, whereas four chose primarily on the basis of the distance of transport. All the subjects belonging to the first cluster weighed more than 3 kg, while three of those belonging to the second cluster weighed less than 3 kg. The last individual in the second cluster, Mansinho, weighed more than 3 kg but had a physical handicap (lacking one foot) which hampered his balance in bipedal locomotion. For this monkey, distance of transport was particularly costly, despite his large weight.

Preference index

By assigning different values to the exponents  $j$  and  $k$  in the formula, we can calculate the  $P$  index for each of the four categories. We tested the Preference index using the results of Experiment 2 (for which we have the most subjects and the most data). The choices made by our subjects in this experiment showed that three monkeys preferred a stone on the basis of its mass and regardless of distance, one

**Table 4**  $P$  index for different values of exponents  $j$  and  $k$

	$j = 0$	$j = 1$	$j > 1$
$k = 0$	–	$P = M$	$P = M^j$
$k = 1$	$P = D$	$P = MD$	$P = M^jD$
$k > 1$	$P = D^k$	$P = MD^k$	$P = M^jD^k$

preferred a stone on the basis of the distance of transport, and three showed choices distributed in all the four categories (Table 1). This spread means that they take into account both the distance of transport and the effectiveness of the stone due to its mass. We estimated the value that monkeys assigned to mass and to distance by finding the values of the exponents in the formula that produce the best match of the  $P$  index to the observed data.

As summarized in Table 4, if  $j = 0$ ,  $P$  would be equal to  $D^k$ , which means that stone selection is independent of the stone mass and dependent on the distance of transport. For Dita that showed this pattern of choices, the  $P$  value cannot be quantified. Perhaps if tested with stones of other mass, Dita would take into account both stone mass and distance.

On the other hand, if  $k = 0$ ,  $P$  would be equal to  $M^j$ , which means a preference for a tool on the basis of its mass without considering if it is close or far. This is what happens for three subjects (Jatoba, Teimoso, and Tucum). Because there is a single term, the  $P$  value cannot be quantified. Perhaps at some other distance, monkeys would also choose stones by taking into account both the stone mass and the distance.

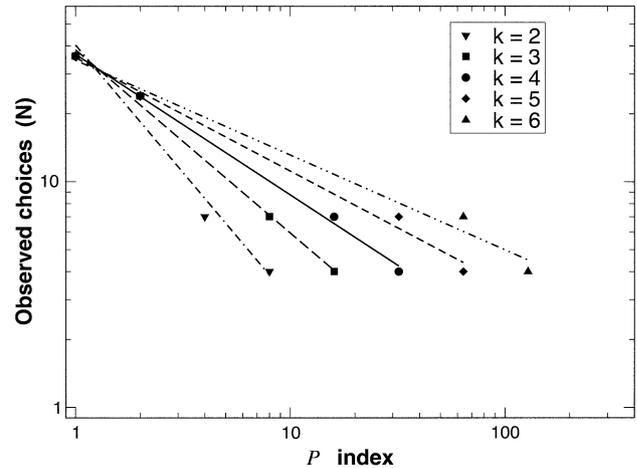
A  $P$  index with both exponents equal to 1 means that both variables (mass and distance) would have the same weight in monkey's choice of a tool. No subject had this pattern of choices.

Our data set from observed choices shows that three subjects (Mansinho, Caboclo, and Chuchu) considered both mass and distance, with distance more important than stone mass. In fact, they have a higher number of choices in the first two categories Light-close and Heavy-close. A  $P$  index formula that reflects this pattern would be with the exponent  $j = 1$  and with the exponent  $k > 1$ .

We performed a numerical test to determine the  $P$  index by assigning the values 2, 3, 4, 5 and 6 to exponent  $k$  when  $j = 1$ . The corresponding  $p$  values are reported in Table 5. The relation between observed data and  $p$  value sequences demonstrated the best agreement for  $k = 4$  (Fig. 2) in terms of lowest squared residuals and highest correlation coefficients (Fig. 3). According to this model, the distance of transport appeared to be fourfold stronger than stone mass in affecting the three monkeys' tool selection.

**Table 5**  $P$  index for different  $k$  values when  $j = 1$

$k$	Light-close	Heavy-close	Light-far	Heavy-far
0	1	2	1	2
1	1	2	2	4
2	1	2	4	8
3	1	2	8	16
4	1	2	16	32
5	1	2	32	64
6	1	2	64	128



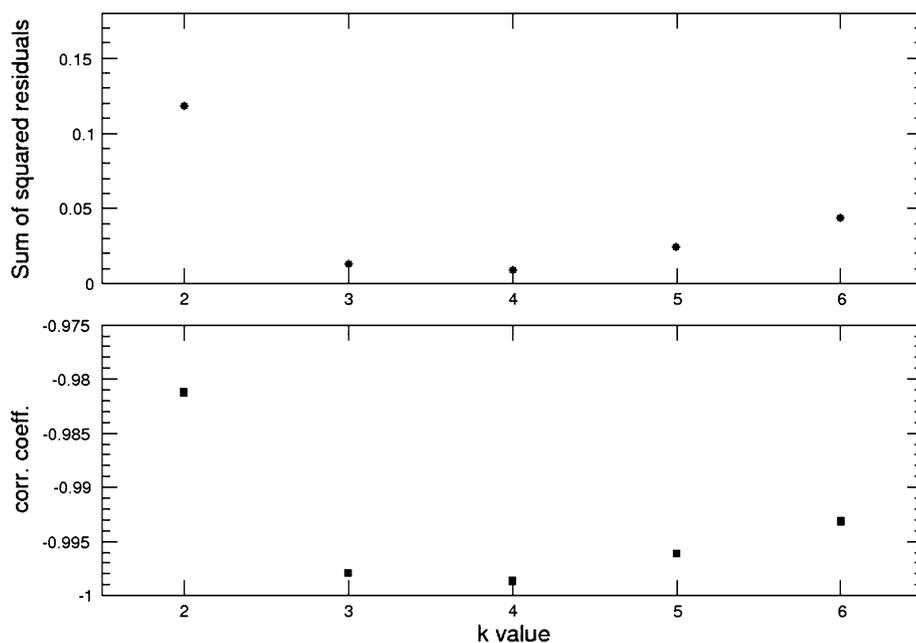
**Fig. 2** Double-log plot of the observed choices ( $N$ ) as a function of the  $P$  index for different  $k$  values. Solid line ( $k = 4$ ) corresponds to the highest correlation between observed choices and  $P$  index. See text for explanation

**Discussion**

Our results clearly demonstrated that individual monkeys were differently sensitive to the two currencies at stake, that is, mass of the stone and distance of transport. In Experiment 1, with two stones of equal mass, all subjects minimized the “transport currency” by choosing the stone that was at 3 m from the anvil rather than the stone at 6 m from the anvil. In Experiment 2, when the monkeys chose between stones of different mass at 3 and 6 m, six subjects out of seven preferred the heavy stone when it was at 3 m and four out of seven subjects preferred the light stone at 3 m when the heavy one was at 6 m.

We presented the monkeys with a choice between stones of equal and different mass (Experiments 1 and 2, respectively). All the stones provided were suitable for cracking both low and high resistance nuts. In fact, the lighter stone used in the experiments (1 kg) is an average weight for hammer stones found on anvil sites in the home range of our population (Visalberghi et al. 2007) and we have experimental observations of capuchins using

**Fig. 3** Sum of the squared residuals and correlation coefficients of the power law best fits for different  $k$  values. The minimum squared residuals (top) and the highest correlation (bottom) are obtained for  $k = 4$



1-kg stones to crack high resistance nuts (Fragaszy et al. 2010a). In fact, in the present study, all subjects used both heavy and light stones to crack both low resistance and high resistance nuts. Thus, capuchins' choices between these stones reflect preferences that relate to relative efficiency and relative cost of transport. Analyses of the velocity and postural adjustment during transport of stone of differing masses by several individuals are in progress and will shed light on the cost of transport. Analyses of efficiency with stones of varying mass are also in progress so we expect to be able to say more on these subjects soon.

Experiment 3 maintained the same ratio between distances as Experiment 2, although absolute values changed from 3 and 6 m to 2 and 4 m. In this experiment, two individuals preferred the heavier stones at 2 and 4 m, two preferred the closer stone in all cases, and one preferred the heavier stone at 2 m and during the experiment developed a preference for the heavier stone at 4 m. These results suggest that a few meters between stones are meaningful to some capuchins and that individuals vary greatly in their sensitivity to transport distance. Sensitivity seems closely related to what the body can afford (i.e., whether a given individual is strong enough to cope with the challenge of carrying a heavy stone for a given distance), and thus monkeys' choices involve more than a comparison of "far" and "close". Absolute values of distance also affected tool selection. The magnitude of the "distance effect" therefore may not depend on the ratio between distances but on their absolute values or, as seems more likely, on some composite of the distance and stone mass in conjunction with locomotor capabilities.

In an effort to create a formal description of choices in this context, we developed a Preference index ( $P$ ), where

$P$  was a joint product of stone mass and distance of transport. The  $P$  index reflects the energetic effort to the extent that these vary as function of stone mass and distance of transport and assigns a "weight" to both variables. Our results showed that for three individuals, the main factor affecting selection was the mass of the stone, while for the others, the main factor was distance of transport. For three individuals of this latter group, since the best  $p$  values to match the observed data were obtained with  $j = 1$  and  $k = 4$ , we found that the distance of transport is four times as important as stone mass.

Our results indicate that body mass greatly affects hammer tool selection. The three individuals that in Experiment 2 preferred a 2-kg stone at 6 m from the anvil (the most challenging condition we presented) were the bigger individuals (from 3 to 4.3 kg), whereas those that chose the 1-kg stone at 3 m were smaller (from 2.1 to 2.7 kg), or had a physical handicap (see below). However, the same smaller individuals preferred the 2-kg stone at 3-m distance, indicating they could carry it this shorter distance. This scenario suggests that there is a body mass threshold below which monkeys are far more sensitive to distance than mass. The same individual will preferentially use a heavier stone, but not transport it more than 2 or 3 m. Fragaszy et al. (2010b) reported that the efficiency (with a stone weighing 1.25 kg) was positively correlated with body mass and that when using this same stone individual capuchins that weighed more than 3.5 kg required fewer strikes to open a nut than monkeys weighing less than 3.5 kg. Although our data set is not suited for detailed analyses on efficiency, the suggestion in our results that monkeys are more efficient with heavier stones (2 kg) than



**Fig. 4** Mansinho, an adult male that lost his left foot. *Left panel* resting on a branch. *Right panel* cracking a piassava nut on an anvil. Photographs taken in July 2011 by Luciana Massaro

lighter ones (1 kg) when cracking a high resistance nut paralleled previous findings reported by Fragaszy et al. (2010b) that heavier individuals (weighing more than 3 kg) are more efficient at cracking nuts than are lighter individuals (see also Spagnoletti et al. 2011 and Liu 2012).

Ability to transport a heavy stone may be compromised for reasons other than body mass. Mansinho, an adult male that weighed 3.5 kg (at the time of these experiments), chose stones in a pattern similar to those of much smaller individuals. In 2010, Mansinho lost his left foot (Fig. 4) from injuries sustained in a fight with other males in his group. In 2011, when he carried a stone, he dropped it at each step using the stump of his left leg. His physical handicap obviously compromised bipedal locomotion.

Boesch and Boesch (1984) investigated chimpanzees' hammer selection in relation to distance of transport and weight of the hammer. The pattern of chimpanzees' choices suggests that they selected a hammer by taking both currencies into consideration. The chimpanzees took the heavier stone (from 3 to more than 9 kg) in situations where two stones were less than 20 m from the source of *Panda* nuts. When the distance of transport increased over 40 m, the chimpanzees preferred lighter stones (from 1 to 3 kg). However, because in this study transport was

inferred a posteriori, the pattern could reflect choices of individuals of different body mass and carrying capacities.

The present study opens new directions in investigating tool selection in wild bearded capuchins by showing the importance of transport distance and mass of the stone on monkeys' tool selection and providing a model for experimental study of the phenomenon. It also illustrates the important role, especially for lighter individuals, of using anvil sites previously used by other capuchins (Visalberghi et al. 2007). Lighter individuals can use hammer stones left at an anvil by others even when they could not transport those hammers themselves. We plan to continue to study transport style by each individual and its relationship with body mass through experiments and to develop formal descriptions incorporating body mass, stone mass, transport distance, and other factors naturally varying such as resistance of the nut. Our goal is to understand monkeys' decision making in nut cracking in naturally varying circumstances.

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## References

- Alfaro JW, Matthews L, Boyette AH, Macfarlan SJ, Phillips KA, Falótico T, Ottoni E, Verderane M, Izar P, Schulte M, Melin A, Fedigan L, Janson C, Alfaro ME (2011) Anointing variation across wild capuchin populations: a review of material preferences, bout frequency and anointing sociality in *Cebus* and *Sapajus*. *Am J Primatol* 73:1–16
- Alfaro JW, Silva JDSE, Rylands AB (2012) How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *Am J Primatol* 74:273–286
- Altmann SA (1998) Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago
- Boesch C, Boesch H (1984) Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates* 25:160–170
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Pop Biol* 9:129–136
- Duarte M, Hanna J, Sanches E, Liu Q, Fragaszy D (accepted) Kinematics of bipedal locomotion while carrying a load in the arms in bearded capuchin monkeys (*Cebus libidinosus*) and humans (*Homo sapiens*). *J Hum Evol*
- Fragaszy DM, Greenberg R, Visalberghi E, Ottoni EB, Izar P, Liu Q (2010a) How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Anim Behav* 80:205–214
- Fragaszy D, Pickering T, Liu Q, Izar P, Ottoni E, Visalberghi E (2010b) Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Anim Behav* 79:321–332
- Gerber L, Reichman O, Roughgarden J (2004) Food hoarding: future value in optimal foraging decisions. *Ecol Model* 175:77–85
- Liu Q (2012) The selection and adaptive use of materials in nut-cracking by wild bearded capuchins (*Cebus libidinosus*): a perception-action perspective. Dissertation, University of Georgia
- Liu Q, Simpson K, Izar P, Ottoni E, Visalberghi E, Fragaszy D (2009) Kinematics and energetics of nut-cracking in wild capuchin monkeys (*Cebus libidinosus*) in Piauí, Brazil. *Am J Phys Anthropol* 138:210–220
- Liu Q, Fragaszy D, Wright B, Wright K, Izar P, Visalberghi E (2011) Wild bearded capuchin monkeys (*Cebus libidinosus*) place nuts in anvils selectively. *Anim Behav* 81:297–305
- Siegel S (1956) Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company Inc., New York
- Spagnoletti N, Visalberghi E, Ottoni E, Izar P, Fragaszy D (2011) Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *J Hum Evol* 61:97–107
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton
- Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav Ecol Sociobiol* 60:457–464
- Visalberghi E, Fragaszy D, Ottoni E, Izar P, De Oliveira M, Andrade FRD (2007) Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *Am J Phys Anthropol* 132:426–444
- Visalberghi E, Sabbatini G, Spagnoletti N, Andrade FRD, Ottoni E, Izar P, Fragaszy D (2008) Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *Am J Primatol* 70:884–891
- Visalberghi E, Adessi E, Truppa V, Spagnoletti N, Ottoni E, Izar P, Fragaszy D (2009a) Selection of effective stone tools by wild bearded capuchin monkeys. *Curr Biol* 19:213–217
- Visalberghi E, Spagnoletti N, Ramos da Silva ED, Andrade FRD, Ottoni E, Izar P, Fragaszy D (2009b) Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys. *Primates* 50:95–104
- Weber E (1978) The sense of touch (Ed and trans: Ross HE). Academic Press (Original work published 1834), London