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How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked

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Wild bearded capuchin monkeys, *Cebus libidinosus*, use stone tools to crack palm nuts to obtain the kernel. In five experiments, we gave 10 monkeys from one wild group of bearded capuchins a choice of two nuts differing in resistance and size and/or two manufactured stones of the same shape, volume and composition but different mass. Monkeys consistently selected the nut that was easier to crack and the heavier stone. When choosing between two stones differing in mass by a ratio of 1.3:1, monkeys frequently touched the stones or tapped them with their fingers or with a nut. They showed these behaviours more frequently before making their first selection of a stone than afterward. These results suggest that capuchins discriminate between nuts and between stones, selecting materials that allow them to crack nuts with fewer strikes, and generate exploratory behaviours to discriminate stones of varying mass. In the final experiment, humans effectively discriminated the mass of stones using the same tapping and handling behaviours as capuchins. Capuchins explore objects in ways that allow them to perceive invariant properties (e.g. mass) of objects, enabling selection of objects for specific uses. We predict that species that use tools will generate behaviours that reveal invariant properties of objects such as mass; species that do not use tools are less likely to explore objects in this way. The precision with which individuals can judge invariant properties may differ considerably, and this also should predict prevalence of tool use across species.

From an optimization perspective (Stephens & Krebs 1986; Altmann 1998), using a tool in foraging provides a benefit when using the tool returns more energy gained and/or less time lost or risk incurred than some other foraging activity that could be conducted at the same time. Selecting a suitable tool before use, and determining whether a potential food item could profitably be obtained with a tool before attempting to process it, would maximize the benefits of any given tool-using behaviour.

We know of no evidence that any nonhuman species is selective about potential items to process with a given tool, but there is evidence for selection of tools. We have the most varied evidence of selectivity for tools in birds. New Caledonian crows, *Corvus moneduloides*, select and manufacture sticks of a correct length to obtain food from a hole or tube (Chappell & Kacelnik 2002; Hunt et al. 2006) and select and manufacture tools of an appropriate diameter (Chappell & Kacelnik 2004) for the same purpose. Tebbich & Bshary (2004) showed that woodpecker finches, *Cactospiza pallida*, selected sticks long enough to use as probes. A black-breasted buzzard, *Hamirostra melanosternon* (Aumann 1990) and Egyptian vultures, *Neophron percnopterus*, selected stones within a narrow range of masses when given a choice of stones of varying masses to drop on eggs (Thouless et al. 1989).

Among primates, observations suggest that wild chimpanzees, *Pan troglodytes*, select hammers in accord with the resistance of the nut they have to crack (Boesch & Boesch 1983) and manufacture and use tools with specific properties for honey dipping and termite fishing (Sanz & Morgan 2009; Sanz et al. 2009, 2010), and that longtailed macaques, *Macaca fascicularis*, use differently shaped stones for scraping and hammering (Gumert et al. 2009). Field experiments have shown that wild bearded capuchins, *Cebus*

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libidinosus, preferentially select the heavier stone when given a choice of potential hammer stones, even when the heavier stone has a smaller volume than another, lighter stone (Visalberghi et al. 2009).

We know little about how animals other than humans determine the relevant properties of objects to guide their selection for use as a tool or as targets of tool use, nor how sensitive they are to particular properties. This study addresses specificity of selection of nuts to be cracked and stones to crack them by wild bearded capuchin monkeys at one site, and provides an initial description of how the monkeys may determine the relevant properties of these objects to guide their selection. These monkeys, which have a mass of 2–4.4 kg as adults (Fragazy et al. 2010), use hammer stones with an average mass of 1 kg to crack palm nuts (Fragaszy et al. 2004a; Visalberghi et al. 2007; N. Spagnoletti, E. Visalberghi, E. B. Ottoni, P. Izar & D. M. Fragaszy, unpublished data). The hammer stones are sufficiently large and heavy that the monkeys grasp and lift them with two hands, and when they crack nuts they routinely use postures and movements reminiscent of human weight lifting (Liu et al. 2009). The nuts cracked by these monkeys are as resistant to fracture as the most resistant nuts cracked with hammers by chimpanzees (panda nuts) and as tough as the toughest nuts cracked (in the jaw) by orang-utans (cf. Peters 1987; Lucas et al. 1994; Visalberghi et al. 2008), despite the fact that adult capuchins have far less than 10% of the body mass of these apes. Thus nut cracking in this population of monkeys is probably an energetically costly activity for all individuals, and especially for those of smaller body size and/or lesser skill. Moreover, lifting the heavy stone and striking the nut may entail costs in several other currencies in addition to energy (e.g. risk of predation due to the ease of localizing the sound produced and access to the location of the activity, on the ground; risk of physical injury, handling time). If the monkeys are attentive to any or all of these costs, they should select nuts that are easier to crack and stones that are heavier, both of which should minimize the number of strikes used to open the nut and maximize the reliability that the monkey can crack the nut.

Visalberghi et al.'s (2009) field experiments, using manufactured stones that varied in mass by ratios of 18:1 to 4:1, showed that monkeys preferred heavier stones. The large difference in mass between the two stones in Visalberghi et al.'s study may have made selecting the heavier stone relatively easy. Weber (1978) showed that adult humans can discriminate between two objects held concurrently that differ in mass ('perceived heaviness') by as little as a ratio of 1:1.025, a finding now called Weber's law. For example, a person should be able to discriminate 200 g from 205 g. However, if objects of equal mass differ in volume, the object of larger volume is perceived as lighter than the object of smaller volume, a phenomenon identified from the late 1800s as the 'size-weight illusion' (reviewed in Turvey 1996). Amazeen & Turvey (1996) showed that the so-called size–weight illusion is a function of the inertia tensor of the objects, which a person detects by moving the objects. The inertia tensor quantifies an object's rotational inertia about a fixed point. Thus, the size–weight 'illusion' is actually a simple function of physical quantities, which are perceived by an individual acting on the objects, as Gibson (1960) suggested is the case for perception in general. To detect the mass of an object, an individual should act in a way that reveals the inertia tensor. Handling an object by rolling or moving it gently on a substrate in principle could provide this information.

Humans detect properties of objects such as mass, texture and temperature through a relatively small repertoire of haptic exploratory actions (Klatzky & Lederman 1987). Capuchin monkeys displayed the same repertoire of exploratory actions as humans to locate without vision small objects (sunflower seeds) lodged in a clay form (Lacreuse & Fragaszy 1997). The monkeys deployed two actions not seen in humans in the sunflower retrieval task: grasp and pull, in which the whole hand acted to apply force to an object (in this case, to the clay form in which sunflower seeds were lodged). These actions seem suited to discovering the inertia tensor of an object if the object is free to move with respect to the substrate (i.e. to slide or to rock). Visalberghi et al. (2009) found that capuchin monkeys applied force to potential hammer stones resting on the substrate in a manner reminiscent of grasp and pull as described by Lacreuse & Fragaszy (1997). Capuchins may also detect something about relative density by tapping hard surfaces, which they commonly do while foraging for hidden invertebrate prey (e.g. in dead branches: Fragaszy 1986; Phillips et al. 2003; in tree trunks: Ottoni & Mannu 2001; in bamboo stalks: Gunst et al. 2008). Visalberghi et al. (2009) reported that capuchin monkeys tapped stones in the course of selecting the heavier one.

The monkeys may also attend to features of a nut when evaluating costs and benefits of an opportunity to crack the nut. Wild monkeys at our research site have extensive experience cracking several species of palm nuts. Some species contain a single kernel (e.g. tucum; *Astrocaryum* spp.); other species (e.g. piaçava; *Orbignya* spp.) contain multiple kernels, encapsulated separately, and these nuts are more resistant to cracking than those with a single kernel. However, when the monkeys crack nuts with multiple kernels, after they open the whole nut, they continue to crack individual sections to get into each kernel. It takes fewer strikes to open a section of an already-cracked piaçava nut ($\overline{X} = 22$ partial nuts opened per 100 strikes) than to open a whole nut ($\overline{X} =$ less than 5 nuts opened per 100 strikes; Fragaszy et al. 2010). Thus monkeys may choose nuts to crack on the basis of associations of species or size with quantity of endosperm (preferring the species with more endosperm per nut), or on the basis of resistance to cracking (preferring single-kernel nuts to multiple-kernel nuts; or partial nuts to whole nuts).

We conducted a series of field experiments examining bearded capuchin monkeys' preference for potential hammer stones varying in mass, and their preference for various types of nuts varying in resistance (single kernel or multiple kernel; and whole or partial nuts of a multiple-kernel variety). In all these experiments, we tested the prediction that monkeys would select the heavier stone and/or the easier nut to crack (in accord with optimizing rate of return from cracking effort). Like Visalberghi et al. (2009), we presented pairs of manufactured stones of equivalent shape, material and volume but variable mass as potential hammer stones. We gave the monkeys a choice of two nuts differing in resistance to cracking (experiment 1: whole piaçava (*Orbignya*), more resistant; and whole tucum (*Astrocaryum campestre*), less resistant; experiment 2: whole piaçava nuts, more resistant, and partial piaçava nuts, less resistant) and two manufactured stones of equal volume but of different mass (1110 g and 538 g). Experiments 3, 4 and 5 presented a choice of two manufactured stones of differing mass to crack one whole piaçava nut. We predicted that the monkeys would be more motivated to select the heavier stone to crack the whole piaçava nut, because this type of nut is more resistant to cracking than a partial piaçava nut or a tucum nut. In experiments 4 and 5, we made the discrimination between heavier and lighter stones more difficult by reducing the proportional difference in mass between them, from 2:1 in experiments 1–3, to 1.8:1 in experiment 4, and 1.35:1 in experiment 5.

In addition to examining the monkeys' sensitivity to the features of the nuts and of mass when choosing a hammer stone, we were interested in the form and timing of the monkeys' exploratory actions with the stones and the nuts, as indexes of how the monkeys arrived at their choices. Thus, in experiment 5, which presented the most difficult choices, we examined the monkeys' actions directed towards the nuts and the stones preceding and during cracking attempts. We predicted that exploratory actions would precede selection of the stone, and that they would occur more frequently when the stones differed less in mass.

In the final experiment (experiment 6), we examined humans' accuracy while blindfolded at selecting the heavier stone of a pair of equal volume stones, to compare with the monkeys' accuracy at selecting heavier stones. Humans were instructed to detect the heavier stone using the same behaviours used by the monkeys (tap or exert pressure on each stone in sequence, with one hand, without lifting or hefting the stones). As we expected the monkeys might be using tapping or moving actions to evaluate the mass of the stones, we wanted to know how well humans could predict the relative mass of stones using the same actions. Moving the stone could lead to detecting the inertia tensor (and thus, indirectly, the mass) of each stone. Tapping could provide information (from auditory or vibratory consequences) about density and thus, by inference, relative mass.

EXPERIMENTS 1–5

Methods

Subjects and site

This project was conducted at Fazenda Boa Vista (FBV) in the southern Parnaíba Basin (9°39′S, 45°25′W), Piauí, Brazil. FBV is an area of Cerrado/Caatinga (open woodland) ecotone (Oliveira & Marquis 2002). The experimental site contains many sandstone anvils and one log anvil scattered in a flat, wooded area (approximately 200 $m^{2)}$ at the foot of a sandstone ridge.

Bearded capuchin monkeys in one habituated group come reliably to the experimental site and crack nuts there. Composition of the study group, including body mass during the period of this study, is presented in Table 1. Body masses were obtained using a voluntary system as described in Fragaszy et al. (2010). Briefly, the monkeys stood on a balance scale to drink water. Ten monkeys (7 males and 3 females, indicated with an asterisk in Table 1) were filmed opportunistically as they cracked nuts at a prepared site during these experiments. The experiments were conducted over a 5-week period in June and July 2008. Some of these monkeys participated in Visalberghi et al.'s (2009) and Fragaszy et al.'s (2010) studies of nut cracking. This study began 7 months after the previous experimental work with this population.

Table 1
Age, sex and mass of all monkeys in the study group

Individual	Age	Sex	Mass (kg) (2008)
Chicão*	Adult	Male	4.2
Mansinho*	Adult	Male	3.6
Dengoso*	Adult	Male	3.5
Dita*	Adult	Female	2.1
Piaçava*	Adult	Female	2.0
Chuchu*	Adult	Female	2.1
Teninha	Adult	Female	2.1
Chiquinha	Adult	Female	2.3
Ameralinha	Subadult	Female	1.6
Jatobá*	Subadult	Male	2.9
Teimoso*	Subadult	Male	3.0
Tucum*	Juvenile (42 months)	Male	1.8
Caboclo*	Juvenile (42 months)	Male	1.9
Tomate	Juvenile (19 months)	?	1.4
Catu	Juvenile (17 months)	?	1.3
Pati	Infant	?	?
Doree	Infant	?	?
Congaceiro	Infant	?	?

* Monkeys that participated in the experiments reported here.

Experimental materials

We used whole tucum (*Astrocaryum campestre*) and whole piaçava (*Orbignya* sp.) palm nuts in experiment 1, whole and half piaçava nuts in experiment 2, and whole piaçava nuts in experiments 3, 4 and 5. The monkeys crack nuts of these species routinely (Spagnoletti 2009). Tucum nuts contain a single kernel and are rounder, smaller and less resistant to cracking than piaçava nuts (Visalberghi et al. 2008). Visalberghi et al. (2008) reported a mean mass for tucum nuts of 15.5 g and an average largest diameter of 29.0 cm, compared to 50.6 g and 40.9 cm for piaçava. Tucum nuts, compared to piaçava nuts, contain equivalent protein (9–10%), less fat (38% versus 61%), more fibre (23% versus 9%) and more carbohydrates (27% versus 17%) per unit dry weight (W. Mattos & D. Fragaszy, unpublished data). The nuts were collected locally and used within a few days following collection. For experiment 2, piaçava nuts were halved along the long axis using an axe or machete 12–24 h prior to presentation.

The hammer stones were manufactured by filling silicon molds with unsaturated liquid polyester resin (Silica synthetic Amorphous Colloidal Silicon Dioxide, aereosil), and Organic Peroxides for curing (Butanox M 50) (see Visalberghi et al. 2009 for further description). The stones were ellipsoid in shape and had equal volumes (diameters 11 cm and 7 cm) but different masses (see Table 2 for details of the stones in each experiment). Lead beads were added to make stones of a given mass. Pigment in the resin produced grey or black colour.

Figure 1 shows the experimental set-up. We placed the stones 50 cm from the centre of a commonly used log anvil, about 10 cm apart, in a randomized positional order with respect to the longitudinal axis of the anvil. The nuts were placed 5 cm in front of the stones towards the anvil. The top surface of the log anvil was 10 cm above the ground, on level, sandy soil. We taped all trials using a video camera (Canon GL-2) mounted on a tripod 4 m from the anvil in oblique view.

Procedure

The experimenter prepared each trial by positioning the stones and nut(s). An experimental trial began when a monkey approached the site and moved one of the stones, and ended when the monkey left the anvil site. Monkeys were free to use both stones in sequence and to crack each nut in sequence during a single trial, but usually they selected one nut and one stone, cracked the nut, and left the anvil to eat the nut elsewhere. After the monkey left the anvil site, the experimenter repositioned or replaced each stone and replenished the nut(s) as needed. The experimenter picked up and moved each stone briefly before each trial even if its position did not change from the previous trial, to control for possible influence of the experimenter's actions with the stones on the monkeys' choice.

In experiment 2, the half nut was placed with the open face of the nut in the sand so that the monkey saw two similar shells. In experiment 5, we presented two conditions: in condition 1, the stones had masses of 1110 g and 824 g; in condition 2, the stones had masses of 824 g and 611 g. The proportional masses of the two stones were 1.35:1 in both conditions.

We coded from video the following variables per trial: first choice of nut (experiments 1, 2) and stone (experiments 1–5), number of strikes on the nut, and the outcome (nut cracked or not). We coded the nut as cracked if we saw a visible long fracture in the shell or the nut split open. Partial nuts were coded as cracked by the same criterion: if the original piece of nut taken to the anvil split again, or a new long fracture appeared in the shell, the partial nut was designated as cracked. Carrying the nut or the stone to the anvil constituted a choice. In experiments 1 and 2, we did not code actions directed towards the second nut if the monkey acted on it

Table 2
Features of stones and nuts presented in experiments 1–5

Experiment	Stones mass (g)		Proportional difference (A:B)	Absolute difference (g)	Nuts	
	A	B			A	B
1	1110	538	2.06:1.00	572	Whole piaçava	Whole tucum
2	1110	538	2.06:1.00	572	Whole piaçava	Half piaçava
3	1110	538	2.06:1.00	572	Whole piaçava	NA
4	1110	611	1.82:1.00	499	Whole piaçava	NA
5 (condition 1)	1110	824	1.35:1.00	285	Whole piaçava	NA
5 (condition 2)	824	611	1.35:1.00	213	Whole piaçava	NA

after cracking the first nut it selected. We did, however, code trials in which the monkey brought a tucum nut (in experiment 1), a partial nut (in experiment 2), or a whole piaçava nut (experiments 1, 2) to the experimental area. In these cases, we counted the nut that the monkey brought as its choice of nut. The first two circumstances occurred 11 times, and the latter just once.

To examine exploratory behaviour we coded the behaviours shown in Table 3 for experiment 5. Recall that in experiment 5, compared to experiments 1–4, the monkeys chose stones that were the most similar in mass. For each action, we noted to which stone the behaviour was directed. We also coded successive use of different stones (termed switches) in this experiment, noting if the monkey switched from heavy to light or vice versa. A switch was coded if the monkey struck the nut with one stone, and then struck the nut with the other stone. Multiple switches could occur within a single trial. Note that our definition of 'switch' concerns use of both stones, whereas Visalberghi et al. (2009) denoted successive exploration of both stones, without using the first one contacted, as a switch.

Following joint coding of several trials by D.M.F. and R.G. to consensual agreement, R.G. coded the data. To establish intra-observer reliability, R.G. recoded 10 randomly selected trials from experiments 1–4. Percentage of agreement on the 40 recoded trials was 100% for stone choice, nut choice and number of strikes, and 95% for outcome (whether the nut was cracked or not). R.G. also recoded the first choice of stone, number of switches and exploratory behaviours from experiment 5 (see Table 3) for 20 trials: two trials each for eight individuals and one trial each for two individuals (Teninha and Caboclo). Percentage of agreement ranged from 85 to 100% for exploratory behaviours ($\overline{X} = 95\%$) and 100% for stone choice. R.G. coded one switch in the original coding and in the repeat coding.

Figure 1. Experimental set-up for experiments 3–5. The two stones were placed 20 cm apart and 0.5 m in front of a log anvil commonly used by the monkeys, and one piaçava nut was placed 20 cm in front of the stones toward the anvil. The manufactured stones had equivalent volumes, shapes, and texture.

Analysis

Data from 466 trials were tabulated by subject. We analysed choice of stone and choice of nut in each experiment using chi-square tests individually for each monkey with 10 or more trials per comparison, with 1:1 as the expected proportion of choices for each kind of nut or stone. We calculated the average number of strikes per individual to crack whole piaçava, partial piaçava and tucum nuts, pooling data across experiments. We used the Kruskal–Wallis test with these data to evaluate relative efficiency at cracking the three kinds of nuts. Comparisons of the bias to choose the heavier stone between experiments 3 and 4 and experiment 5 were made using the Wilcoxon signed-ranks test for related samples. We set the two-tailed alpha at 0.05 for statistical significance for these tests.

We tallied the frequency of exploratory behaviours, comparing the frequency of various actions towards the heavier stone and the lighter stone before and after the first choice of stone and comparing the frequency of these actions across time and across conditions using Wilcoxon signed-ranks tests for related samples. As we predicted that exploratory actions would precede selection of the stone, and that they would occur more frequently when the stones differed less in mass, we used one-tailed tests for these comparisons. We compared the frequency of exploratory behaviours before and after switches, the frequency of switches from heavy to light versus light to heavy, and the frequency of exploratory behaviours in trials with switches versus those without switches using two-tailed Wilcoxon signed-ranks tests.

Results

Choice of nut

The monkeys had strong preferences for a particular kind of nut in both experiments 1 and 2. Each of the seven monkeys that participated in experiment 1 selected the tucum nut more often

Table 3
Behavioural variables coded in experiment 5

Behaviour	Description
Tap	Gently and repeatedly hit an object with the tips of the finger nail or (rarely) gently hit an object with a nut
Handle*	Push or roll the object slightly without lifting it off the supporting substrate
Touch	Touch the stone with the hand or foot
Hit stone on stone	Hit one stone against the other stone
Juggle	Lift the stone above head in a playful manner
Push away	A stone already at the anvil is pushed away from or off the anvil

* Equivalent to the term 'move' in Visalberghi et al. (2009).

than the whole piaçava nut. Six monkeys had enough trials in experiment 1 to conduct within-subject chi-square analyses, and each significantly preferred the tucum nut ($\chi^2_1 > 9.31$, $P < 0.01$). In fact, the monkeys selected the whole piaçava nut only five times across 109 trials (5%), an adult female and two adult males once and one adult male twice. In experiment 2, the monkeys' preference for the partial nut was equally clear: the monkeys selected the partial nut 124 times out of 129 trials (96%). Three adult males selected the whole piaçava nut once or twice each. Each of the seven monkeys that completed 10 or more trials selected the partial piaçava nut more frequently than the whole piaçava nut ($\chi^2_1 > 5.40$, $P < 0.05$).

Success and efficiency at cracking

The seven monkeys that participated in experiment 1 cracked the tucum nuts on all but three trials (out of 104; 97% success rate). In experiment 2, 10 monkeys cracked the partial piaçava nuts on 106 trials (out of 124; an 85% success rate). In experiments 3, 4 and 5, nine monkeys attempted to crack 131 whole piaçava nuts with the 1110 g stone. They succeeded at cracking 101 of them (77% success).

We tabulated the number of strikes used by monkeys to crack whole piaçava nuts with the 1110 g stone across all experiments. Monkeys used an unequal number of strikes to crack tucum, whole piaçava and partial piaçava nuts using the 1110 g stone (Kruskal–Wallis test: $H_{21} = 6.17$, $P < 0.05$). A multiple comparisons post-test indicated that whole piaçava nuts (mean rank = 15.4) required more strikes than partial piaçava nuts (mean rank = 7.6). Tucum nuts were intermediate (mean rank 10.1) and the number of strikes used to crack tucum nuts did not differ significantly from either whole or partial piaçava nuts. The median number of strikes to open a nut (+IQR) was 4.1 + 2.4 for a tucum nut ($N = 7$), 3.25 + 2.4 for a partial piaçava nut ($N = 10$) and 5.3 + 5.9 for a whole piaçava nut ($N = 9$).

Choice of stone

The monkeys preferred the heavier stone in all experiments, selecting it on 78% of trials (362 choices out of 466 trials). Pooling the monkeys' choices across all experiments, every monkey chose the heavier stone on 67% or more of all trials. Looking at choice in each experiment, only one monkey (Chicão) in one experiment (experiment 2) did not choose the heavier stone more often than the lighter stone.

Four of six monkeys in experiment 1 and two of seven monkeys in experiment 2 with 10 or more trials showed a significant bias for the heavier stone (Table 4). The monkeys' bias for the heavier stone was stronger in experiments 3 and 4 (86% of choices) compared to experiments 1 and 2 (73% of choices) (Wilcoxon signed-ranks test: $T_7 = 28$, $P < 0.05$; Table 4). Recall that the monkeys nearly always chose to crack a less resistant nut than a whole piaçava in experiments 1 and 2, but that there was only a whole piaçava nut to crack in experiments 3 and 4. The monkeys' bias for the heavier stone was stronger in experiments 3 and 4, when the mass of the stones differed by a ratio of 2:1 or 1.8:1, than in experiment 5, where the mass of the stones differed by a ratio of 1.3:1 ($T_6 = 21$, $P < 0.05$). Notably, Mansinho, Dengoso and Chicão, the three largest males, showed no significant bias for the heavier stone in experiments 1 and 2 but showed significant bias in experiments 3–5 (Chicão only in experiment 3, the other two in all three experiments).

Exploratory actions: frequency and temporal distribution

The frequency and distribution of exploratory actions in experiment 5 are shown in Table 5. These data summarize 86 trials from condition 1 (with stones of 824 g and 611 g) and 83 trials from condition 2 (with stones of 1110 g and 810 g). Recall that in experiment 5 we presented pairs of stones with a mass ratio of 1.35:1, a smaller ratio than in experiments 1–4, and thus we expected discrimination of the heavier stone to require more exploration in experiment 5 than in the other experiments. The monkeys performed exploratory actions in 98 of 169 trials (58%). Exploratory actions tended to occur on a greater percentage of trials in condition 2 than in condition 1 (condition 1:52%; condition 2: 64%; $T_9 = 35$, $P = 0.08$). The monkeys performed exploratory actions more frequently in condition 2 than in condition 1 (median number of actions performed per trial: condition 1: 0.40 + 1.19, $N = 9$; condition 2: 2.29 + 1.83, $N = 9$). All nine monkeys that participated in experiment 5 performed exploratory actions more frequently in condition 2 than in condition 1 ($T_9 = 45$, $P = 0.002$).

The monkeys performed exploratory activities on 50% of trials (243 times) before selecting a stone, and on 17% of trials (89 times) after selecting a stone. The rate of exploratory actions per individual per trial before selecting a stone ranged from 0.13 to 3.92 and 0.0 to 2.6 after choosing a stone (median rate before = 1.28 + 1.32, $N = 9$; median rate after = 0.35 + 1.46, $N = 9$). This difference was significant ($T_9 = 38$, $P = 0.037$).

Monkeys switched stones 19 times, in 17 trials (in two cases, the monkey switched twice) out of 169 trials (10%). The monkeys switched from light to heavy stones 14 times, and from heavy to light stones five times (χ^2_1, $N = 19$, NS). In the 17 trials in which they switched stones, they produced a median of 4.0 + 7.0 ($N = 7$) exploratory acts per trial. In 152 trials in which they did not switch stones, they produced a median of 1.6 + 2.44 ($N = 9$) exploratory acts per trial. A Wilcoxon test revealed that the difference in the rate of exploratory actions per trial was significantly greater in trials in which the monkey made a switch than in trials with no switch ($T_7 = 28$, $P < 0.008$).

Table 6 summarizes the monkeys' exploratory actions with the heavier and lighter stones in experiment 5. Monkeys performed more exploratory actions on the heavier stone (median = 29 + 27, $N = 9$) than on the lighter stone (median = 14 + 16, $N = 9$; $T_8 = 33.5$, $P < 0.02$).

We found that the monkeys performed exploratory actions more often before selecting a stone than after, more often on trials when the choice was between stones closer together in mass, more often on trials in which they made a switch in the stone they used

Table 4

Bias for heavier stone (expressed as number of choices of heavier stone/lighter stone) in experiments 1–5

Individual	Exp. 1 1110 versus 538 g (N)†	Exp. 2 1110 versus 538 g (N)	Exp. 3 1110 versus 538 g (N)	Exp. 4 1110 versus 611 g (N)	Exp. 51110 versus 824 g or 824 versus 611 g (N)	Choice of heavier/lighter stone (N)	Overall proportional choice of heavier stone
Caboclo	—	9/4 (13)	1/0 (1)	—	—	10/4 (14)	0.71
Chicão	9/3 (12)	5/5 (10)	13/3* (16)	4/2 (6)	9/6 (15)	40/19 (59)	0.68
Chuchu	14/1* (15)	18/1* (19)	1/0 (1)	2/0 (2)	8/0 (8)	43/2 (45)	0.96
Dengoso	6/7 (13)	6/3 (9)	12/0* (12)	14/0* (14)	13/5* (18)	51/15 (66)	0.77
Dita	16/2* (18)	8/3 (11)	2/0 (2)	2/0 (2)	11/3* (14)	42/8 (50)	0.84
Mansinho	5/2 (7)	10/5 (15)	13/3* (16)	16/3* (19)	20/5* (25)	64/18 (82)	0.78
Teimoso	15/2* (17)	10/1* (11)	2/0 (2)	4/0 (4)	13/2* (15)	44/5 (49)	0.90
Tucum	18/8* (26)	17/13 (30)	13/5* (18)	12/2* (14)	8/5 (12)	68/33 (101)	0.67

* $P < 0.05$, chi square, $df = 1$. The chi-square test was used if the monkey had at least 10 choices in a given experiment.

† Total number of trials completed is indicated in parentheses.

Table 5
Exploratory actions in experiment 5 before and after first choice of stone, and the number of trials in which no exploratory actions occurred

Individual	Condition	Total no. of trials	Before			After			Sum exploratory actions	Mean acts /trial* (grand mean/trial)	No. of trials with no exploratory action
			No. of trials with exploratory action	No. of actions	Mean actions / trial* (grand mean/trial)	No. of trials with exploratory action	No. of actions	Mean actions /trial* (grand mean/trial)			
Chicão	1	12	1	1	0.08	3	3	0.25	4	0.33	8
	2	11	1	2	0.18	2	5	0.45	7	0.63	8
	Sum	23		3	(0.13)		8	(0.35)	11	(0.48)	
Chuchu	1	6	5	14	2.33	2	3	0.5	17	2.83	1
	2	4	3	15	3.75	2	23	5.75	38	9.5	1
	Sum	10		29	(2.9)		26	(2.6)	55	(5.5)	
Dengoso	1	11	3	4	0.36	0	0	0	4	0.36	8
	2	15	11	34	2.27	3	7	0.47	41	2.73	3
	Sum	26		38	(1.46)		7	(0.27)	45	(1.73)	
Dita	1	11	8	17	1.55	1	2	0.18	19	1.73	3
	2	9	8	26	2.89	4	9	1	35	3.89	1
	Sum	20		43	(2.15)		11	(0.55)	54	(2.7)	
Jatobã	1	5	2	2	0.4	0	0	0	2	0.4	3
	2	4	1	1	0.25	2	9	2.25	10	2.50	1
	Sum	9		3	(0.33)		9	(1)	12	(1.33)	
Mansinho	1	20	10	16	0.8	0	0	0	16	0.8	10
	2	9	3	19	2.11	3	12	1.33	31	3.44	6
	Sum	29		35	(1.21)		12	(0.41)	47	(1.62)	
Piaçava	1	1	0	0	0	0	0	0	0	0	1
	2	5	1	2	0.4	0	0	0	2	0.4	4
	Sum	6		2	(0.33)		0	(0)	2	(0.33)	
Teimoso	1	11	6	6	0.55	2	11	1	17	1.55	4
	2	12	10	47	3.92	2	6	0.5	53	4.42	1
	Sum	23		53	(2.3)		17	(0.74)	70	(3.04)	
Tucum	1	9	5	10	1.11	1	1	0.11	11	1.22	3
	2	14	7	30	2.14	2	4	0.29	34	2.43	5
	Sum	23		40	(1.74)		5	(0.22)	45	(1.96)	
Sum condition 1		86	40	70		9	20		90	1.05	41
Sum condition 2		83	45	176		20	75		251	3.02	30
Grand sum		169	85	246	1.46	29	95	0.56	341	2.02	71
% Trials			50			17					42

*Calculated using total trials as the denominator.

to strike a nut, and more often on the heavier stone than on the lighter stone. We turn now to what actions they used, and in what sequence they produced them.

Exploratory actions with the stones: form

The most common exploratory action, handle, made up more than one-third of the actions, occurring 123 times (36% of actions). Figure 2 illustrates a monkey handling one of the two stones. Three other actions occurred frequently: tap the stone with the nut (71 times), tap the stone with the fingers (62 times), and touch the stone (60 times). Together, the percussive actions of tapping the stone with a nut, the other experimental stone, or with the fingers made up 40% of exploratory actions. Actions with sustained contact (handle, touch) made up 54% of exploratory actions. Monkeys touched the stone with the hand on 84% of touches, and with the foot on 26% of touches. When touching with the foot, the monkey was stationary and put the sole of one foot against the stone, in the same manner as it put the hand against the stone.

The youngest individual in our sample, 3.5 years old, produced actions not seen, or seen rarely, in older individuals. He hit one stone with another stone three times (this was seen once in one other individual, adult female Chuchu), and he juggled the stone over his head on three occasions, a behaviour we have seen him perform at other times both with stones and with nuts.

Exploratory actions with the stones: sequence

Seven monkeys occasionally produced relatively long strings of exploratory actions interspersed with strikes on the nut. The greatest number of exploratory actions in one trial per monkey for these seven monkeys ranged from 8 to 23 (median $= 11 + 11$, $N = 7$). For each monkey, the longest string of exploratory actions occurred in condition 2, and in all these cases, the monkey did not crack the nut before leaving the anvil. In these sequences, the monkeys touched, tapped and/or handled both stones before selecting one, and they explored one or both stones again after one or more strikes with the stone they chose first.

Table 7 presents a summary of the first and second exploratory actions prior to selecting a stone at the start of a trial for the six monkeys with 10 or more exploratory actions. The data indicate that the monkeys explored the stones in diverse ways, and performed actions in a variable order, prior to selection. The same outcome was evident for exploratory actions later in the sequence before first choice, and following selection of a stone.

We examined whether the rates of producing exploratory actions were related to age, sex, or size. None of these three dimensions of individual differences corresponded to the rankings of exploratory actions. The two oldest individuals, Piaçava and Chicão, were also among the smallest and the largest, respectively. They were also the alpha male and female of the group (M. Verderane, unpublished data). They had the two lowest rates of exploratory actions. Females ranked lowest (Piaçava) and highest (Chuchu) in rates of exploratory actions per trial. The youngest monkey that participated in our experiments ranked sixth of nine in the frequency of exploratory actions.

EXPERIMENT 6

The objective of experiment 6 was to evaluate humans' accuracy at discriminating the heavier stone of a pair of stones when using

Table 6
Exploratory actions with lighter (L) and heavier (H) stones

Individual	No. of trials	Stone	Handle	Touch	Hit w/stone	Juggle	Push away	Tap stone w/finger	Tap stone w/nut	Total
Chicão	23	H	1	0	0	0	3	0	0	4
		L	1	0	0	0	4	1	1	7
		Sum	2	0	0	0	7	1	1	11
Chuchu	10	H	15	3	1	0	2	0	8	29
		L	8	8	0	0	0	0	10	26
		Sum	23	11	1	0	2	0	18	55
Dengoso	26	H	11	2	0	0	0	14	4	31
		L	6	1	0	0	0	7	0	14
		Sum	17	3	0	0	0	21	4	45
Dita	20	H	8	12	0	0	0	0	15	35
		L	7	5	0	0	1	0	6	19
		Sum	15	17	0	0	1	0	21	54
Jatobá	9	H	4	1	0	0	0	2	1	8
		L	2	1	0	0	0	1	0	4
		Sum	6	2	0	0	0	3	1	12
Mansinho	29	H	10	4	0	0	1	10	10	35
		L	4	2	0	0	2	4	0	12
		Sum	14	6	0	0	3	14	10	47
Piaçava	6	H	0	1	0	0	0	1	0	2
		L	0	0	0	0	0	0	0	0
		Sum	0	1	0	0	0	1	0	2
Teimoso	23	H	20	9	0	0	0	8	1	38
		L	11	6	0	0	0	14	1	32
		Sum	31	15	0	0	0	22	2	70
Tucum	23	H	8	4	1	0	0	0	9	22
		L	8	4	2	1	3	0	5	23
		Sum	16	8	3	1	3	0	14	45
Sum H			77	36	2	0	6	35	48	204
Sum L			47	27	2	1	10	27	23	137
Grand sum	169		124	61	4	1	16	62	71	341

the same behaviours performed by the monkeys when selecting a stone (tapping or handling each stone in sequence). Ten individuals (aged 13 and older; 3 males, 7 females) naïve to the study and with normal manual function were asked to point out the heavier stone in a pair of stones in a series of 60 trials.

Methods

Materials

We used three pairs of stones, manufactured in the same manner as described for experiments 1–5. Stones in each pair were of equal volume, shape and composition but varied in mass (pair 1: 824 g and 538 g, ratio 1.5:1; pair 2: 1474 g and 1044 g, ratio 1.4:1; pair 3: 602 g and 465 g, ratio 1.3:1). The stones used in pair 1 were the same as those used in experiment 5, condition 1.

Figure 2. A monkey handling a stone prior to choosing a stone to strike the nut.

Procedure

The experimenter explained the procedures to the participant, asked him/her to sit on a low bench, and then placed a blindfold on the participant. The stones were presented in pairs in front of the participant on sandy soil within easy reach. The person was asked to tap or to handle (but not lift) the stones to determine which was heavier, using one hand at a time and proceeding at his/her own pace. Then he or she indicated his or her choice for the heavier stone. The sets of stones were presented in a predetermined random order, and the left/right location of the heavier stone was randomized. Finally, the requested action (tap or handle) was also randomized. Intertrial intervals were about 10 s. Each participant completed 10 trials of tapping and 10 trials of handling per set of stones (60 trials total) in about 30 min.

Analysis

We tallied the number of correct choices for each action/stone set combination. After confirming that the data met the standards for ANOVA, we conducted a 2 (actions) $\times$ 3 (sets of stones) repeated measures ANOVA on the dependent variable number of correct choices, followed by Tukey tests. A comparison between capuchins' and humans' proportional choice of the heavier stone was accomplished using a t test, after determining the data passed the requirements for normality and equivalence of variance. All analyses used SigmaPlot, version 11.0 (SYSTAT, SPSS Inc., Chicago, IL, U.S.A.).

Results

A summary of participants' choice of the heavier stone across pairs of stones of varying masses is presented in Table 8. Overall,

Table 7
First and second exploratory actions before choosing a stone in experiment 5 by the six monkeys with 10 or more such actions

Individual	Action order	Handle	Touch	Tap stone with nut	Tap stone with fingers	Total
Dita	First	4	7	6	0	17
	Second	0	5	4	0	9
Chuchu	First	3	3	2	0	8
	Second	3	1	2	0	6
Dengoso	First	9	0	1	4	14
	Second	1	1	0	6	8
Mansinho	First	1	4	7	0	12
	Second	4	0	2	1	7
Teimoso	First	12	1	0	2	15
	Second	1	3	0	5	9
Tucum	First	3	2	2	0	12
	Second	2	4	0	0	6
Total	First	34	17	11	6	68
	Second	11	14	8	13	46
Grand total		45	31	19	19	114

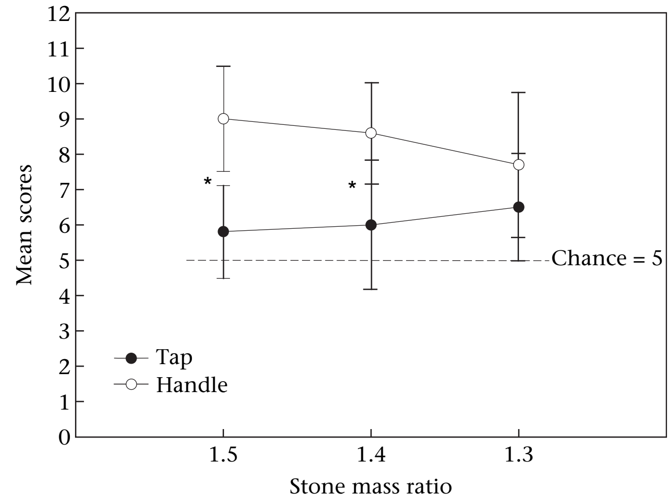

Figure 3. Number of correct choices (out of 10) for humans indicating the heavier of two stones following tapping or handling each stone unimanually in alternation. The dashed line indicates the chance rate of selecting the heavier stone. Bars indicate SD. *Indicates significant difference. Humans chose the heavier stone significantly more often following handling than following tapping when the mass ratio was 1.5:1 and 1.4:1.

humans, like monkeys, chose the heavier stone at above-chance levels (73% of choices), although the strength of their bias for the heavier stone was weaker than the monkeys' in experiments 3–5 (range for humans, 55–88%; mean and range for monkeys, 84%, 70–100%). The difference between the species was significant ($t_{15} = 2.319$, $P = 0.035$; 95% CI = 0.947, 22.424).

We found no main effect for stone pair, but a significant effect for action ($F_{1,9} = 19.009$, $P = 0.002$). People chose the heavier stone more often when handling stones ($\overline{X} = 8.4$) than when tapping ($\overline{X} = 6.1$). We also found an interaction between stone mass ratio and action ($F_{2,9} = 4.486$, $P = 0.026$; see Fig. 3). The action of handling produced significantly more correct choices than tapping for pair 1 (mass ratio 1.5:1) and pair 2 (mass ratio 1.4:1), but not for pair 3 (mass ratio 1.3:1). Thus, people chose the heavier stone less often at closer ratios when handling the stones, but this pattern was not evident for tapping. Instead, when tapping, people chose the heavier stone at equal rates across mass ratios.

DISCUSSION

We found that capuchin monkeys at Fazenda Boa Vista are highly discriminating about the mass of stones they use for cracking nuts, selecting the heavier stone when given a choice of hammer stones, even when the ratio of the mass of the two stones approached 1:1 and even when the stones were of equivalent volume, shape and material. Our findings extend Visalberghi et al.'s (2009) findings that this population of capuchin monkeys attend to a stone's mass when selecting a hammer stone. Visalberghi et al. (2009) presented pairs of manufactured stones of equal volume and similar appearance, as we did. However, the differences in mass, both absolute and proportional, in the pairs of manufactured stones presented by Visalberghi et al. were much greater (difference of 639–1820 g, ratios from 4:1 to 18:1) than in the present study (difference of 213–572 g; ratios from 1.35:1 to 2.06:1).

In addition to presenting stones much close together in mass in this study, a second important procedural difference with Visalberghi et al. (2009) concerns the distance of the stones to the anvil. Visalberghi et al. (2009) placed the two stones 4 m from the anvil, and in this study we placed the stones 0.5 m from the anvil. Thus our set-up diminished the cost to the monkey of switching from using one stone to another, because the transport distance was much less. This difference, together with the smaller ratio between the mass of the two stones that we presented, probably contributed to monkeys occasionally using one stone and then switching to use the other stone in the course of trying to crack a single nut. This happened 19 times in this study (over 169 trials), whereas in Visalberghi et al.'s study (2009), no monkey returned to carry the second stone to the anvil.

We also show that capuchin monkeys overwhelmingly prefer nuts that are easier to crack (i.e. requiring fewer strikes) over nuts that are harder to crack. The monkeys more consistently opened the nuts they chose in experiments 1 and 2 (tucum and partially cracked piaçava nuts) than they did whole piaçava nuts (when no other choice was available) in experiments 3, 4 and 5. They also opened the tucum and partial piaçava nuts with fewer strikes. Thus their preference for the tucum nut or partial piaçava nut maximized the reliability of payoff, and reduced the effort and the time (via reducing the number of strikes) required to crack the nut. Further work is needed to determine the importance of these different metrics to the monkeys' decision making.

The monkeys apparently recognize different kinds of nuts by sight, smell and other perceptual characteristics available at a close distance. However, discriminating heavier and lighter stones, when the stones are visually equivalent, requires contact with each stone. It appears that capuchin monkeys, like humans, are sensitive to the

Table 8
Selection of the heavier stone by humans following handling or tapping with one hand

Participants	Handle (correct choices out of 10) Proportional difference in mass of stones			Tap (correct choices out of 10) Proportional difference in mass of stones		
	1.5	1.4	1.3	1.5	1.4	1.3
1	10	9	10	4	4	5
2	10	9	9	4	5	7
3	10	9	5	6	4	6
4	7	5	4	6	5	6
5	10	10	8	6	7	7
6	9	8	6	8	7	6
7	6	8	8	5	4	5
8	8	9	8	5	7	9
9	10	10	10	7	8	5
10	10	9	9	7	9	9
Mean	9.0	8.6	7.7	5.8	6.0	6.5

consequences on the body of actions that produce force to move an object. Humans are especially sensitive to the inertia tensors of objects that they expect to use to apply force to another object (such as a hammer; Amazeen & Turvey 1996). They use a relatively small set of routine actions to produce movement in objects so that they can evaluate invariant properties (such as inertia tensors), hefting and wielding being the most commonly noted actions (Klatzky & Lederman 1987; Turvey 1996). The monkeys did not heft or wield the stones in this study. Instead, they tapped and handled (moved without lifting) them. Interestingly, they commonly tapped a stone with another object, as well as with the fingers. Using an object to explore another object is characteristic of humans (Burton 1993), but to our knowledge has rarely been described for nonhuman animals. Capuchins occasionally produce combinatorial actions with two objects or an object and a substrate in exploratory contexts (Fragaszy & Adams-Curtis 1991), and this behaviour has been linked theoretically to the spontaneous appearance of using tools in these monkeys (Fragaszy & Cummins-Sebree 2005; Fragaszy et al. 2004b).

We find it interesting that capuchins were more consistent about their choice of nuts than about their choice of stones. Perhaps they can recognize differences between nuts using several sensory modalities, but in these experiments the monkeys were restricted to haptics to detect differences in stones, because the stones appeared the same. When humans were faced with same task, they could also select the heavier stone using manual exploratory actions, and they were better at doing so when they handled the stones than when they tapped them. The monkeys handled and tapped the stones equivalently often (124 episodes of handling and 137 episodes of tapping; 62 with fingers, 71 with the nut, and 4 with the other experimental stone). They directed more actions to the heavier stone, suggesting that they devoted effort to confirming their perception that it was the heavier one. Further work is needed to determine how well the monkeys can detect mass of an object by tapping and by handling. If their perceptual sensitivities parallel those of humans, then tapping is less effective than handling at detecting mass. If that is the case, perhaps the monkeys tap frequently because tapping is a familiar behaviour used to explore surfaces that takes little time or energy, or because it provides some other useful information (such as about the friability of the stone).

Using objects effectively usually involves making use of their invariant properties. Recognizing this opens a new line of comparative inquiry about psychological characteristics that predict tool use in nonhuman species, complementing inquiries into the familiar themes of spatial reasoning, causal reasoning, planning, and so forth that predominate in this area (e.g. Tomasello & Call 1997; Visalberghi & Fragaszy 2006). The predilection to discover invariant properties may be shared among species that spontaneously use objects as tools. It would be useful to explore the relation between perception–action routines and sensitivity to invariant properties across a spectrum of related species (that do and do not spontaneously use objects as tools). We predict that those species that use tools will generate behaviours that reveal invariant properties of objects such as inertia tensors relevant to the ways in which they use tools, and that those that do not use tools will not explore objects in this way. The precision with which various species can judge invariant properties may differ considerably, and this is another dimension that should predict prevalence of tool use across related species. There is wide scope for comparative studies of exploratory behaviour with attention to the perceptual properties revealed by these behaviours.

There is also wide scope for considering selectivity within an optimizing framework. Optimal foraging theory (Stephens & Krebs 1986) predicts that animals will trade-off the time or other costs required to explore alternative choices and the benefits in efficiency or reliability of foraging that derive from making an informed choice. We have not yet examined the costs or benefits to individuals of being selective about their choice of tools but this should be a fruitful line of inquiry linking ecological theory to tool use. For example, we predict that individuals will vary in the effort they devote to selecting tools as a function of their susceptibilty to kleptoparasitism, which has been shown to affect foraging behaviour in many species (Brockmann & Barnard 1979; Carbone et al. 1997; Broom & Ruxton 2003). If tools can be taken from another, and if selecting an appropriate tool takes time, a dominant individual gains more from taking a tool selected by another than from displacing another from a site where tools can be chosen. The subordinate faces loss of time devoted to selection as well as loss of the tool. A range of predictions about who will use tools, when, and their selectivity in doing so, can be developed in this way.

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