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Wild Capuchin Monkeys Spontaneously Adjust Actions When Using Hammer Stones of Different Mass to Crack Nuts of Different Resistance

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ABSTRACT

Objectives: Expert tool users are known to adjust their actions skillfully depending on aspects of tool type and task. We examined if bearded capuchin monkeys cracking nuts with stones of different mass adjusted the downward velocity and the height of the stone when striking palm nuts.

Materials and Methods: During a field experiment carried out in FBV (Piauí, Brazil), eight adult wild capuchin monkeys (five males) cracked *Orbygnia* nuts of varied resistance with hammer stones differing in mass. From recorded videos, we identified the highest strike per nut-cracking episode, and for this strike, we calculated the height to which the monkey lifted the stone, the maximum velocity of the stone during the downward phase, the work done on the stone, and the kinetic energy of the strike.

Results: We found that individual capuchins achieved average maximum kinetic energy of 8.7–16.1 J when using stones between 0.9 and 1.9 kg, and maximum kinetic energy correlated positively with mass of the stone. Monkeys lifted all the stones to an individually consistent maximum height but added more work to the stone when using lighter stones. One male and one female monkey lifted stones higher when they cracked more resistant nuts. The high resistance of the *Orbygnia* nut elicits production of maximum kinetic energy, which the monkeys modulate to some degree by adding work to lighter stones.

Discussion: Capuchin monkeys, like chimpanzees, modulate their actions in nut-cracking, indicating skilled action, although neither species regulates kinetic energy as precisely as skilled human stone knappers. Kinematic analyses promise to yield new insights into the ways and extent to which nonhuman tool users develop expertise. Am J Phys Anthropol 161:53–61, 2016. © 2016 Wiley Periodicals, Inc.

Skill in tool use is evident when the tool user can efficiently and smoothly complete the task in varied circumstances and can adjust actions with different tools to achieve an equally effective outcome for a given task (e.g., Smitsman 1997; Wagman and Carello, 2003; Bril et al., 2009). Both components of skill are clearly evident in human tool use. For example, Bril et al. (2010) showed that expert human stone knappers finely adjusted the velocity of the hammer depending on its mass to maintain the appropriate amount of kinetic energy in a narrow zone when detaching stone flakes from a flint core. Novices adjusted some aspects of their performance in the same situations, but produced more variable kinetic energy with their strikes than the experts.

In nonhuman primates, percussive tool use in the form of nut-cracking has been extensively studied in wild chimpanzees (*Pan troglodytes*) and bearded capuchin monkeys (*Sapajus libidinosus*) (e.g., for reviews see Biro et al., 2010; Visalberghi and Fragaszy, 2013; Visalberghi et al., 2015). In nut-cracking, both species place a nut on an anvil surface and use a hammer (stone or log) to crack open the nut using percussive actions (see Fig. 1).

Across the *cerrado* and *caatinga* of Brazil, bearded capuchins routinely use hammer stones of widely varying mass to crack nuts of several species of palms and other seeds (Fragaszy et al., 2004; Ferreira et al., 2010; Mendes et al., 2015). Spagnoletti et al. (2011) observed capuchins living in Fazenda Boa Vista (hereafter, FBV) using hammer stones ranging from 0.1 to 3 kg (range, median, IQR for males = 0.100–3.00, 1.059, 0.023 kg; for females = 0.100–2.250, 0.991, 0.188 kg), or 2–158% of their body mass (masses obtained from Fragaszy et al. 2010b, smallest adult female = 1.9 kg, largest adult

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Fig. 1. Photo of a capuchin monkey sub-adult male cracking nut in a bipedal stance with a stone held bimanually (photo by Q. Liu). Note this is different from the sitting position and unimanual arm swing technique that wild chimpanzees use to crack nuts.

male = 4.4 kg). Visalberghi et al. (2008) tested mean peak-force-at-failure values of the four species of nuts cracked by the capuchins at FBV. They found that tucum nuts (*Astrocaryum campestre*) have a mean peak-force-at-failure value of 5.57 ± 0.25 kN and piaçava nuts (*Orbygnia* spp) have a mean peak-force-at-failure value of 11.50 ± 0.48 kN, which is very similar to that reported for the panda nuts cracked by wild chimpanzees as reported by these authors. Within the piaçava nuts, mass is strongly correlated with resistance to fracture ($r = +0.62$; Visalberghi et al. 2008); thus heavier nuts are likely to require a higher number of strikes or more forceful strikes to fracture them.

The monkeys at FBV preferred to use stones of larger mass if given a choice (for example, preference for 1.10 kg over 0.82 kg, and preference for 0.82 kg over 0.61 kg in Fragaszy et al., 2010a; see also Visalberghi et al., 2009), and preferred to crack nuts that were less resistant to fracture (for example, preference for the tucum nuts over the piaçava nuts, and preference for partially cracked piaçava nuts over whole piaçava nuts, Fragaszy et al., 2010a). These findings indicate that the monkeys recognize the affordances of stones and nuts for cracking. The wide range of masses of the stones used by the monkeys at FBV, coupled with the range of resistance to fracture of nuts that these monkeys routinely crack (Visalberghi et al. 2008) provides repeated opportunity for the monkeys to learn to adjust their actions to the mass of the stone and the resistance of the nut; i.e., to become skillful.

The extent to which individuals can accommodate their actions to different tools partly depends on each individual's action capabilities (Liu et al., 2009). Body mass is an important predictor of action capabilities for capuchin monkeys cracking piaçava nuts, the most resistant species of nut cracked by the monkeys at FBV (Visalberghi et al., 2008). In the population of bearded capuchin monkeys at FBV, adult females on average weigh 2.1 kg, subordinate adult males weigh 3.5 kg, and alpha males weigh about 0.7 kg more than subordinate males (Fragaszy et al., 2016). Fragaszy et al. (2010b) studied the relationships among the diameter of the nut, individual body mass, maximum height to which the stone was lifted and the monkeys' efficiency of cracking piaçava nuts (defined as the number of nuts opened per 100 strikes) when using one hammer stone of 1.46 kg. In their study, individual body mass correlated positively ($r = +0.75$, $P < 0.05$, $N = 9$ subjects) with efficiency of nut-cracking. In addition, the maximum absolute height to which an individual capuchin lifted the stone was highly correlated with efficiency ($r = +0.83$, $N = 8$). They also found that the diameter of the piaçava nut predicted efficiency, but that body mass was a stronger predictor of efficiency (Fragaszy et al., 2010b). Liu et al. (2009) found that two adult male monkeys in the population at FBV added force onto the stone in the downward phase when striking piaçava nuts, thus creating more kinetic energy to be transferred to the nut. These heavier males succeeded with fewer strikes than two lighter adult female monkeys. Because adult males in this population are 1.5–2 times heavier than adult females (Fragaszy et al., 2016), the described sex difference in nut-cracking efficiency (Fragaszy et al., 2010b; Spagnoletti et al., 2011) is explained by the difference in body mass between males and females, which is related to the kinetic energy of the strikes they produce (adult males producing strikes with greater kinetic energy than adult females, on average). However, variation in efficiency across individuals of approximately the same body mass suggests that skill plays a role as well (Fragaszy et al., 2010b).

Individuals can increase the kinetic energy of their strikes by raising the stone higher, adding force onto the stone during the downward phase of the strike prior to nut-stone contact, or both. Kinetic energy is increased by raising the stone higher because more potential energy is achieved. If the stone is allowed to fall freely, then work = 0 and kinetic energy/potential energy ratio (i.e., k/p ratio) = 1. In the second strategy, downward force is added onto the stone (thus increasing its velocity prior to contact) so that work > 0 and k/p ratio > 1. In this case, the kinetic energy is >1 because force is added, i.e., work is added. To maximize the velocity of the stone in the downward direction (and consequently kinetic energy of the strike) the monkeys could use either strategy, or both strategies at the same time.

In summary, bearded capuchin monkeys at FBV use a variety of stones differing in mass to crack a variety of nut species differing in resistance (Visalberghi et al., 2015). Our previous research has shown that bearded capuchins prefer stones of larger mass to crack open nuts of lower resistance if given a choice, and that efficiency at cracking piaçava nuts, the most resistant nuts these monkeys crack, is related positively to the height to which the stone is lifted. In this study we examine how capuchins organize their actions with hammer stones of a wide range of masses while cracking piaçava nuts of various masses (and thus, resistances, as these properties are closely correlated). Cracking piaçava nuts calls for maximizing kinetic energy prior to stone-nut contact, making them an excellent case to examine how the aforementioned two strategies might be used by different individuals. In particular, according to the mass of the stone and resistance of the nut, the monkeys might raise the stone higher and/or add more downward force onto the stone. We predicted the monkeys would lift lighter stones higher and/or would add more downward force onto lighter stones than they would do with heavier stones, thus achieving a greater maximum

TABLE 1. Individual information and number of coded trials per stone per individual

Individuals (sex)	Body mass (kg)	Trunk length (m)	Stone masss (kg)					Total trials
			3.47	1.92	1.42	0.93	0.57	$N = 295$
Mansinho (M)	4.28	45.8	10	10	10	10	10	50
Dengoso (M)	3.63	43.5	10	9	10	9	9	47
Teimoso (M)	3.59	43.6	10	10	10	10	10	50
Jatoba (M)	3.44	44.6	10	9	9	9	1	38
Tucum (M)	2.45	40.0	9	10	10	10	0	39
Piassava (F)	2.03	34.3	1	10	8	9	0	28
Dita (F)	2.23	37.0	1	9	8	8	0	26
Chuchu (F)	2.32	37.7	1	6	6	4	0	17

Fig. 2. Photos of five hammer stones used in the study (photo by E. Visalberghi).

velocity prior to contact than would be achieved by the stone during free fall from the zenith point. We also predicted that capuchins would lift stones higher and/or add more downward force to the stones when they cracked more resistant nuts than less resistant nuts.

METHODS

Site and subjects

The study site (9° south, 45° west, altitude ~420 m above sea level) was located on private property (Fazenda Boa Vista, hereafter FBV) in a dry woodland plain in Piauí, Brazil (Visalberghi et al., 2007). A group of wild bearded capuchin monkeys routinely came to an outdoor laboratory area (~30 m diameter) where there were several anvils and stones. This was the area where we carried out the field experiment in June 2009. Details about the site can be found in Visalberghi et al. (2009).

Eight adult capuchin monkeys (five males and three females) participated voluntarily. We obtained their body mass by provisioning water near a digital scale mounted on a tree (see Fragaszy et al., 2010b, 2016) during the same period in which the field experiment was carried out. Information about individuals' sex and body mass is given in Table 1.

Design

This study utilized a within-subject repeated measures design. A trial was defined as a nut-cracking episode in which one nut was cracked so that at least one kernel became accessible for consumption. All subjects cracked nuts with each of five stones of different masses and cracked nuts of different masses. The number of trials completed with each stone by each monkey is presented in Table 1. The independent variables were stone mass (five levels) and nut mass (a proxy measure for resistance of the nut). The dependent variables were the number of strikes, the maximum vertical height of the stone and the maximum downward velocity of the stone during the highest strike per trial.

Materials

We used an existing log anvil (1-m long, 12-cm high, and 12-cm wide) in the outdoor laboratory. This anvil, frequently used by all monkeys, allowed excellent visibility for filming.

We supplied quartzite stones similar to those that the monkeys routinely use as hammer stones. The five experimental stones were all roughly ellipsoid shaped although differing modestly in volume and smoothness (see Fig. 2). They weighed 0.57, 0.93, 1.42, 1.92, and 3.47 kg. Visalberghi et al. (2007) reported a range of 0.25–2.53 kg for stones found on 42 anvils surveyed in the study area. Spagnoletti et al. (2011) reported a range of 0.1–3.0 kg for stones used by two habituated wild groups observed for a 1-year period in the same area. The lower limit of mass of hammer stones that the monkeys routinely use in the outdoor laboratory is about 0.5 kg (personal observation). The three stones in the middle range of the experimental series are all within the range of the stones the monkey usually use and are ~0.5-kg apart. The heaviest stone (3.47 kg) is outside the upper limit normally used by these monkeys. It was used in this study to reveal how monkeys would use an extremely heavy stone as a hammer, if they would use it at all.

We supplied the piaçava nuts (*Orbignya spp.*), the most resistant species of palm nuts that monkeys routinely crack. They had an oval shape and on average were 4 cm by 6 cm (Fragaszy et al., 2004a; Visalberghi et al., 2008). Mature nuts with the exocarp and mesocarp removed were weighed before the experiment using an electronic scale (Polder^{TM}) to the nearest gram and marked with a number using permanent felt markers for individual identification. The nuts ranged from 14 to 64 g in mass. For our purposes, nuts smaller than 25 g were considered small, 26–40 g were considered medium and nuts above 40 g were considered large. Visalberghi et al. (2008) reported resistance to fracture and nut mass were significantly positively correlated. Hence, the term "resistance" is used hereafter.

A GL2 Canon DV camcorder and a tripod were used to video-record the study. A 2D calibration square was used in the field of view as part of the standard 2D kinematics recording procedure (Liu et al. 2009).

Procedure

Each test day at roughly 7 AM we set up the video camera to record the monkeys' nut-cracking activities and completed calibration recording. We placed one stone on the anvil and when a monkey approached the anvil, we threw one nut (previously weighed and marked) toward the subject. The subject would typically gather the nut, go to the anvil, place the nut on the anvil, and commence cracking the nut with the provided stone by striking the nut repeatedly. The monkey's actions were video-recorded and the stone mass and the nut number (to know its mass) were narrated onto the audio track by the experimenter. Testing continued each day until the monkeys left the outdoor laboratory area (usually by noon). We tried to give each monkey each stone on multiple trials, and with each stone, three small nuts, four medium nuts and three large nuts (10 trials per stone, total). Our goal was for all the subjects to use all five stones to crack a variety of nuts.

Data Capture Setup

Standard two-dimensional motion measurement methodology was used during video-recoding (Robertson et al., 2004). Sixty Hz sampling rate and shutter speed of 1/2,000s were used. The camera was placed ~6 m away from the anvil to capture sagittal plane views (field of view was ~1.5 m) of the monkeys during nut cracking. Before and after the experiments each day, we centered the calibration square on the long axis of the log anvil, leveled it, and recorded it.

Coding

We collected a total of 463 nut-cracking trials (30–95 per monkey). For each stone condition per monkey, if they had more than 10 successful trials, we randomly selected 10 for coding. If they did not have 10 trials, we coded all trials. Table 1 shows the number of coded trials per stone per subject.

For the behavioral coding, number of strikes per trial was recorded. For the biomechanics coding, we first identified the strike in which the monkey lifted the stone the highest from each trial (termed the highest strike). In each highest strike, the metacarpophalangeal joint (MCP point) of the third finger on the monkey's hand and the nut were manually digitized (Peak Motus$^{\text{TM}}$ by Vicon, version 9.0) in each field of video (60 fields per second) throughout the strike. The MCP point of the third finger was used as a proxy for the center of the hammer stone. We assumed that the monkeys' hands covered the stone's center of mass. As the MCP joint of the middle finger is approximately at the center of the hand, we considered it our best estimate of the stone's center of mass.

For each strike, the fields in which three critical events occurred were marked: "start of lifting," "MCP joint of third digit zenith," and "stone-nut contact." Start of lifting was defined as the instant when the stone began to move upward. The MCP zenith point was defined as the instant when the MCP joint reached the highest vertical height. Because the MCP joint was used as a proxy for the stone's center of mass, this instant was referred to as "stone zenith point." The stone-nut contact occurred in the subsequent downward phase, at the instant when the stone contacted the nut.

After manually digitizing the points, raw coordinates of the points were filtered using a fourth-order Butterworth filter with cut-off frequency of 10 Hz (Jackson, 1979). Filtered coordinates were then scaled to actual measurement units using calibration video. From these datasets, we obtained maximum vertical height of the stone maximum velocity. The height and velocity values were calculated using Peak Motus$^{\text{TM}}$ by Vicon.

From these measures we derived the mechanical energetics (the maximum gravitational potential energy, the maximum kinetic energy, the ratio of maximum kinetic energy to maximum potential energy which shows the work added to the stone in the downward strike) for each trial. From the mechanical energetics (the maximum gravitational potential energy, mgh, and the maximum kinetic energy, $\frac{1}{2}$ mv^2) for each trial, a *k*/*p* ratio (maximum kinetic energy divided by the maximum gravitational potential energy) was calculated to evaluate if the monkey added work onto the stone in the downward phase of the strike. In a free fall the *k*/*p* ratio of the stone at contact with the nut would be equal to 1.0, because the gravitational potential energy possessed by an object becomes kinetic energy as it falls. A *k*/*p* ratio bigger than 1.0 indicated the monkey put work (added downward force) onto the stone.

In addition, from one randomly chosen highest strike per individual from the dataset, we measured each individual's trunk length. We used the methods to measure trunk length described in Fragaszy et al.'s (2010b) study. These values are presented in Table 1. These data allowed us to calculate relative maximum vertical height each monkey lifted the stone as a proportion of its trunk length.

Two research assistants independently identified and confirmed the highest strike for each episode at an agreement rate of 100%. Five episodes were randomly selected and coded by another coder who was blind to the experiment design. We compared the height and velocity values calculated from two datasets and used the ratio of the smaller value to larger value to measure the agreement. The average ratio of values for maximum vertical height was 0.94 and the average ratio of values for maximum downward velocity was 0.91. Therefore we conclude that our error of measurement is acceptable.

Analysis

General analysis. Four stepwise multiple regressions were conducted in SPSS to test if the resistance of the nut, the mass of the stone and the mass of the subjects predicted four variables (two were derived from the 3rd dependent variable, maximum downward velocity). The first regression examined if the three independent variables predicted the number of strikes necessary to crack the nut. Each nut-cracking episode was used as the unit of analysis for this regression analysis.

Four separate stepwise multiple regression analyses were performed using the highest strike per nut as the unit of analysis. These examined if the same three variables (the resistance of the nut, the mass of the stone and the mass of the subjects) predicted the maximum vertical height to which the stone was lifted, relative maximum vertical height (in relation to the monkeys' trunk

TABLE 2. Mean and SD of number of strikes per individual per stone

	0.57	0.93	1.42	1.92	3.47
Mansinho	4.2 ± 2.2	4.4 ± 4.0	2.9 ± 2.1	2.2 ± 1.2	2.2 ± 2.2
Dengoso	6.9 ± 1.8	6.6 ± 8.1	3.3 ± 2.9	4.0 ± 5.7	2.2 ± 1.6
Teimoso	10.3 ± 4.7	5.6 ± 3.6	3.1 ± 2.0	2.7 ± 1.8	2.5 ± 1.4
Jatoba	53 (n = 1)	5.6 ± 4.3	2.8 ± 3.1	3.7 ± 1.7	2.3 ± 1.1
Tucum	–	6.5 ± 3.2	4.4 ± 2.4	4.4 ± 2.0	3.2 ± 2.3
Piacava	–	10.8 ± 6.7	4.3 ± 2.7	4.3 ± 3.0	6 (n = 1)
Dita	–	3.9 ± 1.4	3.3 ± 2.3	5.0 ± 3.6	2 (n = 1)
Chuchu	–	6.0 ± 1.4	5.7 ± 6.7	4.7 ± 2.2	1 (n = 1)

TABLE 3. Mean (in meter) and SD of lifting height per individual per stone

	0.57	0.93	1.42	1.92	3.47
Mansinho	0.54 ± 0.04	0.57 ± 0.02	0.51 ± 0.07	0.52 ± 0.04	0.41 ± 0.04
Dengoso	0.38 ± 0.07	0.41 ± 0.03	0.39 ± 0.05	0.40 ± 0.05	0.38 ± 0.07
Teimoso	0.48 ± 0.02	0.49 ± 0.06	0.45 ± 0.04	0.48 ± 0.03	0.35 ± 0.04
Jatoba	0.47	0.39 ± 0.03	0.37 ± 0.02	0.42 ± 0.05	0.40 ± 0.03
Tucum	–	0.39 ± 0.06	0.40 ± 0.02	0.41 ± 0.02	0.31 ± 0.04
Piacava	–	0.38 ± 0.01	0.37 ± 0.01	0.36 ± 0.02	0.28
Dita	–	0.39 ± 0.04	0.37 ± 0.03	0.37 ± 0.02	0.28
Chuchu	–	0.33 ± 0.03	0.37 ± 0.03	0.36 ± 0.05	0.20

TABLE 4. Mean and SD of maximum kinetic E *(J) per individual per stone*

	0.57	0.93	1.42	1.92	3.47
Mansinho	7.43 ± 1.04	9.73 ± 0.89	12.85 ± 1.59	14.94 ± 1.12	19.30 ± 3.50
Dengoso	7.91 ± 3.20	13.01 ± 3.82	16.78 ± 3.48	18.42 ± 2.93	27.14 ± 6.11
Teimoso	6.52 ± 0.81	9.57 ± 1.30	15.35 ± 2.44	18.79 ± 3.45	23.77 ± 4.27
Jatoba	9.25 (n = 1)	9.77 ± 1.89	13.03 ± 3.36	15.67 ± 3.16	26.63 ± 4.90
Tucum	N/A	8.12 ± 2.11	12.51 ± 1.54	14.21 ± 3.20	18.29 ± 3.18
Piacava	N/A	6.22 ± 0.83	10.13 ± 1.26	9.88 ± 1.16	11.90 (n = 1)
Dita	N/A	8.97 ± 1.80	11.47 ± 1.09	12.66 ± 2.06	13.56 (n = 1)
Chuchu	N/A	6.05 ± 0.89	9.79 ± 1.12	10.78 ± 2.60	8.62 (n=1)

TABLE 5. Mean and SD of k/p *ratio per individual per stone*

	0.57	0.93	1.42	1.92	3.47
Mansinho	2.48 ± 0.26	1.89 ± 0.18	1.83 ± 0.21	1.54 ± 0.16	1.37 ± 0.20
Dengoso	3.94 ± 0.65	3.49 ± 0.77	3.09 ± 0.37	2.46 ± 0.30	2.10 ± 0.30
Teimoso	2.41 ± 0.26	2.14 ± 0.22	2.44 ± 0.45	2.05 ± 0.30	1.99 ± 0.34
Jatoba	3.53 (n = 1)	2.73 ± 0.49	2.53 ± 0.58	1.98 ± 0.40	1.95 ± 0.40
Tucum	N/A	2.25 ± 0.43	2.23 ± 0.29	1.86 ± 0.32	1.71 ± 0.22
Piacava	N/A	1.82 ± 0.24	1.96 ± 0.22	1.45 ± 0.20	1.26 (n = 1)
Dita	N/A	2.53 ± 0.30	2.22 ± 0.13	1.83 ± 0.24	1.45 (n = 1)
Chuchu	N/A	2.03 ± 0.20	1.93 ± 0.23	1.56 ± 0.27	1.27 (n = 1)

length, calculated as the ratio between absolute maximum vertical height of the stone and trunk length), the maximum kinetic energy ($k = \frac{1}{2}\ mv^2$) prior to contact, and k/p ratio.

Individual patterns. Similar stepwise multiple regression analysis was performed separately for each individual dataset to examine difference in patterns across individuals (i.e., if nut resistance and stone mass predicted number of strikes, lifting height, maximum kinetic energy and *k/p* ratio). Mean and SD of the four variables were computed for each individual.

In all of the regression analyses described above, trials with the 3.47 kg stone were excluded because the stone mass is an outlier (more than 2 SD above the average of stone mass that monkeys routinely use) that would skew the regression results. However, values for the dependent variables obtained from strikes with the 3.47 kg stone are presented in the tables and mentioned in the results, to illustrate how the monkeys use such a heavy stone. Pairwise comparisons (Holm–Bonferroni method) were conducted among pairs of stones.

RESULTS

General results

On average, the monkeys struck 4.6 (SD = 4.9) times to crack open a nut (see Table 2). Regression analyses showed that the three variables significantly predicted

TABLE 6. Individual regression results—stone mass and nut resistance as predictors for the number of strikes, lifting height, maximum kinetic E *and* k/p *ratio (trials with the 3.47 kg stone were excluded in the regression analyses)*

	Number of strikes		Lifting height		Maximum kinetic energy		*k/p* ratio (work added)	
	Stone mass	Nut resistance	Stone mass	Nut resistance	Stone mass	Nut resistance	Stone mass	Nut resistance
Mansinho	Beta = −0.356, $P = 0.005$	Beta = 0.596, $P < 0.001$	NS	Beta = 0.372, $P = 0.018$	Beta = 0.926, $P < 0.001$	NS	Beta = −0.797, $P < 0.001$	NS
Dengoso	Beta = −0.393, $P = 0.012$	Beta = 0.490, $P = 0.002$	NS	NS	Beta = 0.752, $P < 0.001$	NS	Beta = −0.723, $P < 0.001$	NS
Teimoso	Beta = −0.653, $P < 0.001$	Beta = 0.293, $P = 0.018$	NS	NS	Beta = 0.909, $P < 0.001$	NS	NS	NS
Jatoba	NS	Beta = 0.408, $P = 0.034$	NS	NS	Beta = 0.673, $P < 0.001$	NS	Beta = −0.545, $P = 0.003$	NS
Tucum	Beta = −0.343, $P = 0.047$	Beta = 0.407, $P = 0.020$	NS	NS	Beta = 0.789, $P < 0.001$	NS	Beta = −0.416, $P = 0.22$	NS
Piacava	Beta = −0.355, $P = 0.035$	Beta = 0.474, $P = 0.006$	NS	Beta = 0.559, $P = 0.002$	Beta = 0.729, $P < 0.001$	NS	Beta = −0.525, $P = 0.005$	NS
Dita	NS	Beta = 0.551, $P = 0.004$	NS	NS	Beta = 0.676, $P < 0.001$	NS	Beta = −0.793, $P < 0.001$	NS
Chuchu	NS	NS	NS	NS	Beta = 0.699, $P = 0.003$	NS	Beta = −0.646, $P = 0.007$	NS

the number of strikes to crack open the nut ($N = 244$, $R = 0.508$, $P < 0.001$): monkey's body mass (beta = −0.236, $P < 0.001$), stone mass (beta = −0.359, $P < 0.001$), nut resistance (beta = 0.384, $P < 0.001$).

The monkeys lifted the stones (excluding 3.47 kg) between 0.33 and 0.57 m (see Table 3). Body mass (beta = 0.670, $P < 0.001$) significantly predicted the lifting height ($R = 0.670$, $P < 0.001$). Stone mass and nut resistance were not significant predictors of absolute lifting height. A similar regression on relative maximum vertical height showed that again only body mass (beta = 0.174, $P = 0.007$) significantly predicted relative lifting height ($R = 0.174$, $P = 0.007$). Stone mass and nut resistance were not significant predictors of relative lifting height.

The monkeys struck nuts with an average maximum kinetic energy of 8.74 J to 11.03 J (females) and 11.61 to 16.07 J (males) when using stones 0.93, 1.42, and 1.92 kg (see Table 4). Body mass (beta = 0.362, $P < 0.001$), stone mass (beta = 0.716, $P < 0.001$) and nut resistance (beta = 0.116, $P = 0.008$) all significantly predicted the maximum kinetic energy ($R = 0.754$, $P < 0.001$).

The monkeys added work to the stone on their highest strikes: average k/p ratios per stone per monkey ranged from 1.82 to 3.94 (see Table 5). Monkey body mass (beta = 0.159, $P = 0.006$) and stone mass (beta = −0.436, $P < 0.001$) significantly predicted the k/p ratio ($R = 0.494$, $P < 0.001$). Nut resistance was not a significant predictor of k/p ratio.

Individual patterns

Results of individual regression analyses are shown in Table 6. Different individual patterns are described in more details below.

Number of strikes in relation to stone mass and nut resistance. One female and all males except one had fewer strikes when using heavier stones than when using lighter stones. All but one female had more strikes when cracking more resistant nuts than when cracking less resistant nuts. Table 2 shows the mean and SD for the number of strikes per individual per stone. As one can see, the SD's are not small, indicating the variability in number of strikes is sizable. Post-hoc pair-wise comparisons of the number of strikes among pairs of stones per individual are provided in the Supporting Information Table S1.

Absolute lifting height in relation to stone mass and nut resistance. Stone mass did not predict lifting height for any individual. Nut resistance was a significant predictor of lifting height for only one male and one female. These two monkeys lifted the stones higher when they were cracking more resistant nuts than less resistant nuts. As shown in Table 3, lifting height seems to be relatively consistent within each monkey with different stones (except the 3.47 kg stone for most individuals). For all individuals except one male, lifting height for the 3.47 kg stone was the lowest and this is especially true for the females. For all individuals, the ranges of lifting height for the other four stones were surprisingly narrow. Post-hoc pair-wise comparisons among pairs of stones per individual are provided in the Supporting Information Table S2.

Maximum kinetic energy in relation to stone mass and nut resistance. Stone mass was a significant predictor of maximum kinetic energy for all individuals. Nut resistance was not a significant predictor for any individual. As shown in Table 4, maximum kinetic energy generally increased from light stones to heavy stones, for each individual. The monkeys also had higher variations (as shown by SD) with heavier stones compared to lighter stones. For any given stone, males produced higher kinetic energy than females. Post-hoc pairwise comparisons of kinetic energy among pairs of stones per individual (Supporting Information Table S3) show that among 33 possible pairs of comparisons, 27 pairs (with at least one pair contributed by each of eight individuals) were significantly different. The three adult males that routinely used the 0.57 kg stone had very similar patterns among themselves and the five smaller individuals had similar patterns among themselves as well. Overall, monkeys generated significantly different maximum kinetic energy values with different stones, except that the maximum kinetic energy for the 1.42 and the 1.92 kg stones did not differ significantly for 6 individuals.

The k/p ratio in relation to stone mass and nut resistance. Mean *k/p* ratios were above 1 for all monkeys, indicating that all monkeys added positive work to the stone in their strikes (see Table 5). Stone mass was a significant predictor for *k/p* ratio for all monkeys but one male (Table 5). In the downward striking phase, all monkeys but one male added more work onto lighter stones than onto heavier stones. Post-hoc pair-wise comparisons of *k/p* ratio among pairs of stones per individual show that among 33 possible pairs of comparisons, 18 pairs (with at least one pair contributed by each of eight individuals) were significantly different (see Supporting Information Table S4). Nut resistance was not a significant predictor for work added for any individual.

DISCUSSION

We investigated whether capuchin monkeys adjusted their actions with hammer stones of varying mass, and if so, if the pattern of adjustment accorded with the goal of producing a threshold kinetic energy on impact with a resistant palm nut to crack it. Such a pattern would be in accord with conceptions of expertise in percussive tool use by humans (Bril et al., 2010, 2012). At the same time, we replicated and extended earlier findings relating body size to efficiency in cracking nuts in this population. The nuts we presented (piaçava; *Orbygnia* spp.) have thick woody shells and are highly resistant to fracture, with an average peak-force-at-failure under continuous pressure of >8 kN (for comparison, the equivalent value for macadamia nuts is 2 kN, and for walnuts, 0.4 kN) (Visalberghi et al., 2008). Piaçava nuts have multiple kernels, each encased in a woody capsule. The task for the capuchin monkeys when faced with an intact piaava nut is to produce sufficient kinetic energy to crack the nut and access at least one of the kernels. Less force is needed to crack smaller nuts or for partially cracked piaçava nuts. Given the high resistance of these nuts to fracture, there is little likelihood that a monkey risked smashing the kernel of a piaçava nut, unlike chimpanzees cracking macadamia nuts (Bril et al., 2009) or coula nuts (Boesch and Boesch-Acherman, 2000), or capuchins cracking tucum nuts (Mangalam and Fragaszy, 2015). Thus the single strike per episode in which the monkey lifted the stone to its greatest height was a reasonable index of the monkey's most flexible performance or how best they can modulate their actions when cracking a piaçava nut.

The capuchins' performance when using stones encompassing the range of masses normally used by this population indicates that they acted to maximize the kinetic force of their strikes for all the piaçava nuts. We found that the kinetic energy they produced was positively correlated with their body mass. We also found that heavier monkeys used fewer strikes than lighter monkeys to crack a nut, replicating earlier findings (Fragaszy et al., 2010b). Finally, we found that heavier monkeys lifted the stone higher (both in absolute values and proportionally in relation to trunk length) and added more work onto the stone than did lighter monkeys. Both of these features could contribute to heavier monkeys' greater efficiency at cracking nuts.

Individual monkeys lifted all the stones to a consistent height, rather than raising lighter stones higher. This suggests that rather than modulating kinetic energy by varying lifting height, monkeys modulate kinetic energy by varying downward force. We found strong support for the proposal that the monkeys (seven out of eight in our sample) modulated the kinetic energy of their strikes by putting more work (or in other words, adding more downward force) in the downward striking phase onto lighter stones than they did onto heavier stones. Future studies could examine how more skilled individuals adjust and control their actions differently from less skilled individuals in other dimensions of performance of nut cracking (e.g., coordination of velocity and trajectory, precision of strike location, orientation of the stone, etc.).

We also presented an extremely large stone (3.47 kg) that is outside the range of stones used routinely by these monkeys and that proved to be too heavy for the three females to use regularly. The monkeys' *k/p* ratio for the 3.47 kg stone was the smallest of all five stones, indicating that monkeys add less work or even add negative work onto this stone. Even so, as kinetic energy was strongly positively correlated with the mass of the stone, the monkeys generated the greatest kinetic energy with this stone. Thus, the limit to capuchin monkeys' ability to generate kinetic force is derived from their ability to lift stones rather than from their ability to add work to the stone in the downward strike. When they use a stone light enough that they can add work to it and still control the stone at impact, they do so when cracking piaçava nuts.

Accommodation of action in skilled tool use is usually studied in relation to task constraints in the motor control literature (Newell, 1986; Bril et al., 2010, 2012). Constraints within a given tool use task can include properties of the relevant objects and surfaces. In nut cracking, task constraints include, for example, the mass or shape of the stone, the resistance or shape of the nut, and the angle, uniformity or friction index of the anvil surface. Investigating how skilled individuals use tools in such situations will inform us about both bodily skills and cognitive processes that contribute to expert tool use. For example, Bril et al. (2010) studied how human stone knapping experts finely adjusted the velocity of the hammer to maintain the appropriate amount of kinetic energy when detaching stone flakes from flint core using hammer stones of different weights. In the same study, the authors showed that human tool users adapted their actions appropriately when they were asked to produce flakes of different sizes (a different task constraint) and that they were able to accommodate their actions to two concurrent changes in the task (tool mass and the size of flake desired).

In the current study, wild capuchin monkeys adjusted the work added to the stone in response to stone mass in a way that increased the maximum velocity achieved just prior to contact as did the chimpanzees in Bril et al.'s (2009) study. The capuchin monkeys did not, however, adjust work added to the stone in accord with nut resistance (as measured by nut mass). Nut resistance did not predict *k*/*p* ratio for any monkey. Why did the monkeys adjust work added in response to stone mass, but not in response to nut resistance? One possible explanation is that monkeys did not perceive the resistance of the nut as accurately as they perceived the force of the strike. They directly manipulated stones in their hands, but they did not directly manipulate nuts when they lifted the stone and struck the nut. The nut was in indirect contact with the body at the moment of contact and therefore its resistance properties might not have been perceived as accurately as the force of the strike, which is perceptible by the rebound of the stone and the sound of the strike. Alternatively, it can be argued that the resistances of the nuts presented in this study were already too high and varied within too narrow a range for most of the monkeys to perceive the differences. Two monkeys, however, did adjust their actions in accord with the resistance of the nuts, by lifting the stone higher when cracking more resistant (heavier) nuts. Interestingly, these two monkeys are the alpha male and the alpha female in the group. They are probably the most experienced individuals within each sex in our sample if we quantify experience as age. This suggests that experts may notice differences in nuts that less skilled individuals do not, and consequently may be better able to adjust actions in response to quality of nuts. Future studies with larger sample sizes than we have in this study will allow a better test of this hypothesis.

Another line of evidence suggests that capuchin monkeys modulate their strikes while cracking nuts in accord with larger differences in task constraints than presented by piaçava nuts of different sizes. When nuts of tucum and piaçava palms, which differ by 6 kN in average peak force at compressive failure (Visalberghi et al., 2008) were presented to wild capuchins, their preference for heavy vs. light stones shifted in response to the species of nuts presented (Massaro, 2013). This finding indicates that the monkeys approach cracking nuts of the two species differently.

A third way to evaluate how monkeys adjust their strikes to changing task constraints is to examine performance during sequences of strikes on a single tucum nut (as Bril et al., 2010 have done for chimpanzees cracking macadamia nuts). When cracking tucum nuts, the final strike should be below a threshold of kinetic energy so as not to crush the soft kernel, as for chimpanzees cracking *Coula* nuts that are about as resistant to fracture as tucum and macadamia nuts (Peters, 1987). Mangalam and Fragaszy (2015) showed that, in sequences of strikes performed to crack a single tucum nut, adult monkeys from the same group studied here adjusted the force of individual strikes by adjusting the height to which they lifted the stone and the amount of work added to the stone in the downward phase of the strike. They adjusted the force as a function of the condition of the nut (the hull present or absent; the shell intact or fractured) following the previous strike, decreasing force when the hull was partially breached and when the shell was partially cracked.

Finally, a fourth line of evidence concerning modulation of action in accord with task constraints comes from comparison of the temporal organization of percussive movements while cracking tucum and piaçava nuts. Mangalam et al. (2016) report that wild bearded capuchin monkeys modulate successive strikes on tucum nuts in accord with the state of the nut following each strike, but strike piaçava nuts with the maximum force they can generate on each strike. The single stone used with piaçava nuts in this study weighed 1500 g. The kernels of piaçava nuts are not vulnerable to crushing, as are the kernels of tucum nuts, and as piaçava nuts are more resistant to cracking than tucum nuts, consistent high force to crack the former is the most efficient course of action.

Three of five captive chimpanzees accommodated their actions to some extent to crack macadamia nuts using stones of three different masses, producing greater velocity at impact with lighter stones (Bril et al., 2009, 2012), as did the capuchins in this study. The chimpanzees studied by Bril et al. were not experienced nutcrackers. It would be most interesting to have comparable data as those collected here for wild capuchins from experienced wild chimpanzees cracking *Coula* nuts with stones in the range of mass normally used by the apes for these nuts (most often 0.8–3.2 kg; Sirianni et al., 2015), and similarly for Panda nuts, which are more resistant (9.7–12.5 kN) and cracked with heavier stones or wood clubs (Boesch and Boesch-Acherman, 2000). From our studies with capuchins and from Bril et al.'s (2009, 2012) studies with captive chimpanzees, we predict that chimpanzees will add more work to lighter stones, and perhaps also modulate kinetic energy in a sequence of strikes, in accord with the state of the nut after each strike, so as not to smash softer *Coula* nuts, as capuchins did with tucum nuts. Given chimpanzees' body size; they are unlikely to use stones that are at the limit of their ability to lift them, as the much smaller capuchins are challenged to do when cracking the very resistant piaçava nuts.

In conclusion, this study shows that wild capuchin monkeys, when they spontaneously use stone hammers in a wide range of masses to crack open very resistant palm nuts, spontaneously modulate their actions by adding more or less work to the percussor, thus modulating the kinetic energy of their strikes. Chimpanzees cracking nuts and humans knapping stone adjust their actions in this way when using hammer stones of varied masses, suggesting similar accommodative processes are present across species of primates. In addition, we demonstrated the value of using kinematics to study skill in wild animals. Kinematic methods widely used in the study of human behavior allow us to address questions about skilled actions in nonhuman species that have not received due attention (see also Bril et al., 2012). Understanding the motor coordination evident in nut-cracking by living nonhuman primates provides insight into the elaboration of percussive tool use in human ancestors that supported the appearance of stone tool manufacture (Bril et al., 2012).

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