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RESEARCH ARTICLE

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How bearded capuchin monkeys (*Sapajus libidinosus*) prepare to use a stone to crack nuts

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Abstract

Bearded capuchin monkeys crack nuts with naturally varying stone hammers, suggesting they may tune their grips and muscular forces to each stone. If so, they might use discrete actions on a stone before lifting and striking, and they would likely use these actions more frequently when the stone is larger and/or less familiar and/or when first initiating striking. We examined the behavior of (a) four monkeys (all proficient at cracking nuts) with two larger (1 kg) and two smaller (0.5 kg) stones, (b) 12 monkeys with one 1 kg stone, and (c) one monkey during its first 100 strikes with an initially unfamiliar 1 kg stone. Bearded capuchin monkeys used three discrete actions on the stone before striking, all more often with the larger stones than the smaller stones. We infer that the first discrete action (Spin) aided the monkey in determining where to grip the stone, the second (Flip) allowed it to position the stone on the anvil ergonomically before lifting it, and the third (Preparatory Lift) readied the monkey for the strenuous lifting action. The monkey that provided 100 strikes with one initially unfamiliar stone performed fewer Spins in later strikes but performed Flip and Preparatory Lift at consistent rates. The monkeys gripped the stone with both hands along the sides to lift it, but usually moved one or both hands to the top of the stone at the zenith of the lift for the downward strike. The findings highlight two new aspects of the capuchins' nut-cracking: (a) Anticipatory actions with the stone before striking, especially when the stone is larger or unfamiliar, and when initiating striking and (b) shifting grips on the stone during a strike. We invite researchers to investigate if other taxa use anticipatory actions and shift their grips during percussive activity.

HIGHLIGHTS

- While cracking nuts, adult bearded capuchin monkeys used three discrete actions on a stone that we suggest aided them to determine where to grip the stone, to position the stone on the anvil ergonomically before lifting it, and to prepare for the strenuous lifting action.

- Monkeys gripped the stone with both hands along the lateral surfaces to lift it, but usually moved one or both hands to the top of the stone at the zenith of the lift for the downward strike.
- The findings highlight two new aspects of the capuchins' nut-cracking: (a) Anticipatory actions with the stone before striking, especially when the stone is larger or unfamiliar, and when initiating striking and (b) shifting grips on the stone during a strike.

KEYWORDS

exploratory actions, hammer, haptic perception, nut cracking, percussion

1 | INTRODUCTION

Percussion is the most ancient documented form of human tooling (the term coined by Fragaszy and Mangalam (2018) to refer to the actions of using an object to achieve a mechanical outcome on a target). Natural cobbles have been used by hominins as hammers for more than 3 million years (Harmand et al., 2015). The shift from the use of natural materials to the production of tools by knapping stone, and the presumed reliance on tooling to obtain food, has been linked to changes in the anatomy of the hand (Marzke, 2013), obligate bipedality (Harcourt-Smith, 2007) and enlargement of the brain (Almécija & Sherwood, 2017; Schoenemann, 2006), among other physical changes, in the evolution of the genus *Homo*. But percussive tooling does not require these specific features of behavior or anatomy. Some taxa of nonhuman primates (tufted capuchin monkeys, *Sapajus*; chimpanzees, *Pan*; and macaques, *Macaca*) use unmodified stones or wood to break open encased foods such as nuts, molluscs, and crustaceans (Boesch & Boesch-Achermann, 2000; Fragaszy, Izar, Visalberghi, Ottoni, & De Oliveira, 2004; Malaivijitnond et al., 2007; Sugiyama & Koman, 1979) after placing the encased food on an anvil. These actions recall our interpretations of the behavior of extinct hominins, that placed a stone core on an anvil and struck it with another stone to produce flakes (called bipolar stone-flaking), as inferred from artefacts discovered in Kenya (Harmand et al., 2015). Behavioral scientists have an enduring interest in characterizing features of tooling in nonhuman primates that are shared with humans, and thus, by inference, that may indicate how percussive tooling, including bipolar flaking, was practiced by hominin ancestors before the evolution of modern hands, posture, and brains. Percussive tooling is valuable to study in this regard.

We adopt a functional approach considering percussive tooling as a movement problem (Fragaszy & Mangalam, 2018). This approach directs our attention to the actions of the tooler, rather than the object that is used. We seek to characterize how individuals tool skillfully. Following Bernstein (1967,1996), we define skill as efficient fluid production of uniform outcomes in variable circumstances. From the perspective of movement science, to evaluate skill, one must consider the agent, the demands of the task, and the setting (e.g., the objects available to use) as a system (Newell, 1986). Skilled action involves the agent modifying its actions in the course of achieving a desired outcome to take into account its own capabilities, as well as variability in the demands of the task or the setting. For example, a skilled weaver modifies her actions to account for the stiffness and size of the reeds she is using, and the size of her hands and her strength, to make baskets of a uniform size, shape, and tightness of weave. Using a stone percussor skillfully involves lifting and striking with a rigid, dense object, swinging it with accuracy, and to proper effect (i.e., striking the targeted item with the desired force), while avoiding damage to oneself. The stone must be oriented to the target, the force of the strike managed, and so on (Mangalam, Izar, Visalberghi, & Fragaszy, 2016). These are nontrivial challenges. Bril, Nonaka, Rein and their colleagues (Bril et al., 2012; Bril, Parry, & Dietrich, 2015; Bril, Rein, Nonaka, Wenban-Smith, & Dietrich, 2010; Nonaka, Bril, & Rein, 2010; Rein, Bril, & Nonaka, 2013) have studied people knapping stone to produce flakes using the freehand method, the form of skilled percussion most studied by anthropologists and neuroscientists. In the freehand method, the seated actor holds the target core in one hand and strikes it with an object held in the other hand. This body of work shows that knapping stone is a laboriously acquired skill that takes years to master. Its mastery is accompanied by structural remodeling among regions of the forebrain involved in tooling, language, and action planning (Hecht et al., 2015).

Nonhuman primates do not knap stone as humans do (by first producing a platform in a core, then deliberately orienting the percussor with respect to the platform to produce conchoidal fractures; Muller, Clarkson, & Shipton, 2017), but they do crack open encased foods using stone and wood percussors. We refer hereafter to the foods opened by cracking as nuts, but the same analysis applies to other encased food that nonhuman primates crack with percussors (molluscs, crabs, seeds, etc.). Cracking a nut involves controlling fewer functional parameters than knapping stone freehand but even so, for each strike the agent must control the kinetic energy, angle of impact, and orientation of the percussor to the target to be struck. There are substantive costs for not doing so. If the agent does not control these functional parameters, it risks (a) not cracking the nut, if the strike is not forceful enough, or smashing the kernel, if the strike is too forceful, (b) losing control of the stone and/or the nut, so that time must be spent retrieving them, or they may be lost, or (c) injuring itself through rebound forces from the stone to the body or through accidental strikes on its own body. After several years of regular practice, bearded capuchin monkeys become proficient at using natural (variable) materials as hammers and anvils to crack nuts that vary in size, shape, and resistance to fracture (Coelho et al., 2015; Fragaszy et al., 2017; Resende, Nagy-Reis, Lacerda, Pagnotta, & Savalli, 2014).

Perception-action theory provides a complementary approach to that outlined above to understanding skilled action. According to Gibson (1979), individuals generate perceptual information through their actions that they use to organize their subsequent actions to reach specific goals. Exploratory actions are selective and intended to provide information; performatory actions are intended to achieve a specific goal (Gibson,). Lederman and Klatzky (1987, 1990, 2009) describe a repertoire of exploratory manual actions including pushing, lifting, tapping, and enclosure, among others, that humans use to identify objects and properties of objects, and to prepare to use objects for some purpose. Captive tufted capuchins (*Sapajus* spp.) use a repertoire of exploratory manual actions similar to humans' to locate small objects they cannot see (Lacreuse & Fragaszy, 1997) and to determine whether a shell contains a nut kernel or is empty (Visalberghi & Neel, 2003). These studies show that capuchins, like humans, use their hands to explore objects in ways that contribute to effective action with these objects.

Both theoretical approaches have informed our understanding of nut-cracking in wild bearded capuchin monkeys studied at Fazenda Boa Vista, Piauí, Brazil. Bearded capuchin monkeys place palm nuts into hemispheric pits (formed by previous nut-cracking with a stone hammer) in anvil surfaces in specific orientations before striking them. They discover the desired orientation of piaçava nuts by knocking the nut on the anvil surface several times before releasing it (Fragaszy et al., 2013). To crack highly resistant palm nuts, they stand bipedally, lifting the hammer stone to shoulder height or higher. They can use stones across a range of weights, to the boundary of their ability to lift them (up to 3.5 kg for large adults; Liu, Fragaszy, & Visalberghi, 2016). When presented with a nut and two or more potential hammer stones some distance from an anvil that lacks a hammer, they lightly tap and gently move stones on the ground, or fully pick up stones in sequence before selecting one to carry to the anvil, and they choose stones of suitable mass and material to serve as effective hammers (Visalberghi et al., 2009). They modulate the force of each strike on a nut as a function of the outcome of the previous strike when cracking a tucum nut (*Astrocaryum* spp.), that has a relatively thin husk, a relatively brittle shell, and a single, relatively soft kernel (Mangalam & Fragaszy, 2015). In contrast they generate the maximum force possible throughout the series of strikes on a piaçava nut (*Orbygnia* spp.). Piaçava nuts have a thicker and more resistant shell than tucum and the kernels are not vulnerable to smashing, in part because each kernel is encased in a separate locule so that when the outer shell cracks a given kernel is only partially explosed (Mangalam et al., 2016). They coordinate movements of the whole body during lifting and striking, producing highly consistent movement trajectories of the stone (Mangalam, Pacheco, Izar, Visalberghi, & Fragaszy, 2018). In all these ways, capuchins act, before and during striking, to use stones effectively to crack nuts.

Here we investigate how capuchins handle a stone before a strike, how they grip it to lift it, and how they move their hands on the stone during strikes to crack piaçava palm nuts. The prediction drawn from action-perception theory is that the capuchins will behave with the stone in discrete ways in advance of striking to aid gripping and moving the stone (e.g., to explore different locations to grip the stone). They should do so more often when using a larger than a smaller stone, as a larger stone poses a greater challenge to grip securely and to aim accurately during a strike. We also predicted they would use these actions more often before initiating a bout of striking (i.e., when they first grip and lift the stone) rather than once they had begun striking with that stone (as the capuchins normally make several consecutive strikes with the same stone to crack a nut). Finally, we examined if making anticipatory actions with the stone was related to maintaining control of the stone and the nut after the strike. We evaluated the extent to which capuchins achieve consistent grips, produce vertical strikes and maintain control of the stone and the nut following a strike compared to the alternatives (inconsistent grips, slanted strikes, and loss of control of the nut and/or stone).

2 | METHODS

This study complied with protocols approved by the Institutional Animal Care and Use Committee of the University of Georgia, and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates and the legal requirements of Brazil.

The study took place in May and June 2013 and 2014. In 2013, we presented four unfamiliar stones (two 0.5 kg, and two 1.0 kg; within the normal range of mass used by the capuchins at Fazenda Boa Vista to crack nuts). We recorded four individuals proficient at cracking nuts using each of these four stones to crack piaçava nuts. However, most of the capuchins would not use the 0.5 kg stones to crack piaçava nuts. Accordingly, in 2014, we recorded eight additional capuchins using a 1 kg stone to crack palm nuts. In video playback, we coded the behavior of the capuchins with the stones before and during striking, and the outcome of each strike, for the first 20 strikes with each stone they used. For one capuchin, we coded the same data for strikes 1–100 with the 1 kg stone.

2.1 | Site

The study was conducted at Fazenda Boa Vista and adjacent lands (hereafter, FBV) in the southern Parnaíba Basin in Piauí, Brazil (45° West, 9° South). FBV is a flat plain (altitude 420 m asl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m above the plain. Sedimentary rocks of two formations occur in the southern Parnaíba Basin: The Sambaíba Formation (dating from the Triassic era, 250–200 Mya) covers the Pedra de Fogo Formation. The Sambaíba Formation comprises white to reddish fine-grained

TABLE 1 Capuchins that participated in this study, indicating the data set(s) to which they contributed, sex, and mass (kg)

Capuchin	Data set(s)	Sex	mass
Jatobá	I, II, III	M	4.2
Teimoso	II	M	3.5
Mansinho	I, II	M	3.4
Catu	II	M	2.7
Tomate	II	M	2.5
Pati	II	M	2.5
Cangaceiro	II	M	2.4
Dita	I, II	F	2.1
Teninha	II	F	2.1
Chuchu	II	F	2.0
Piaçava	I, II	F	1.9
Doree	II	F	1.8

sandstones with abundant cross-beddings. The lowermost part of the Sambaíba Formation, which is in contact with the Pedra de Fogo Formation, is marked by a conglomeratic level with pebbles of siliceous rocks. The conglomerate contains rounded quartzite blocks and pebbles that loosen from the matrix due to weathering. These rounded stones are favored as hammerstones by the capuchins. The average mass of hammer stones found on a representative sample of anvil sites in the home range of our study group is 1.1 kg (Visalberghi et al., 2007).

The study was conducted in the outdoor laboratory, a flat area with a relatively closed, high canopy, and thin undergrowth affording good visibility, approximately 30 m in diameter. Several natural sandstone and wood anvils are present in the outdoor laboratory (others are scattered across the capuchins' home range; Visalberghi, Haslam, Spagnoletti & Fragaszy, 2013; Visalberghi et al., 2009). Palm trees (*Orbygnia*, *Attalea*, and *Astrocaryum* spp.) are moderately abundant in the surrounding area. The outdoor laboratory is within the capuchins' home range and they visit it frequently.

FIGURE 1 Female bearded capuchin monkey (Piaçava) using a 1,042 g quartzite stone to crack a palm nut. The monkey is in the process of lowering the stone. The nut on the anvil is a fragment of a whole nut. The monkey is holding a whole nut in her left foot. Notice the monkey has her left hand on the top of the stone and grips the edge of the stone with her right hand. Capuchin monkeys commonly lift the stone with both hands gripping the edges, then shift one or both hands from the edge to the top of the stone at the zenith of the lift. The faces of the stone in this photo were marked with numbers to aid in coding the position of the stone (the number 2 shows in the photo). Photo by Michael Haslam

2.2 | Subjects

Twelve capuchins (6 years and older; seven males) living in one group of wild bearded capuchin monkeys (*N* = 23) participated voluntarily in this study (see Table 1). Body masses were obtained at the time of testing when the capuchins stood or sat voluntarily on a digital scale mounted near a bowl of water, using the method described by Fragaszy et al. (2010) and Fragaszy et al. (2016). One capuchin monkey (Mansinho) was missing his left foot following an injury incurred in 2010. One capuchin monkey (Jatobá) had a severed fourth digit on his right hand and was missing the hallux and three toes on his left foot, from 2007 (when he first appeared in the study group). All the other capuchins in the sample had intact limbs and appendages.

2.3 | Materials

2.3.1 | Stone, anvils, and nuts

Four experimental stones were presented in 2013. All were quartzite and roughly elliptical in shape (see Figure 1). These stones were brought from outside the study area (and thus initially were unfamiliar to the capuchins). The stones were classed as larger (1,042 and 1,100 g) and smaller (455 and 524 g). A single experimental stone was placed by the anvil during a given test day and removed at the end of each testing period. In 2014, only the 1,042 g stone was presented, and it was removed at the end of each test day.

Anvils used by the capuchins have distinctive shallow depressions (hereafter, pits; 1–2 cm deep) produced by capuchins cracking nuts (Visalberghi et al., 2007). The capuchins were recorded using two wood anvils in this study (designated A and B). A was 0.9 m long and 25 cm wide on its top surface, and had one pit in its center (see Figure 1). B was 0.7 m long and 0.2 m wide, with three pits in the central area.

For this study, we collected piaçava nuts (*Orbygnia* spp) and tucum nuts (*Astrocaryum campestre*). Piaçava nuts are irregular in shape, roughly ovoid, 4 x 6 cm on average, and contain one to six kernels in individual locules encapsulated in a thick, woody shell contained in a fibrous husk and edible thin mesocarp. The husk and (edible) mesocarp had been fully or mostly removed by other animals before the nuts were collected. Tucum nuts are round, roughly 3 cm in diameter, with a thin husk and contain a single kernel. The nut shells of these two species of palms differ considerably in their resistance to fracture: Tucum is less resistant (5.57 ± 0.25 kN) than piaçava (11.50 ± 0.48 kN; Visalberghi et al., 2008). Both of these nuts are considerably more resistant to fracture than the orally processed food provided to nonhuman primates in captivity (Williams, Wright, Truong, Daubert, & Vinyard, 2005) and the species of nuts that humans commonly crack, such as almonds, *Prunus dulcis* (Aktas, Polat, & Atay, 2007) and walnuts, *Juglans regia* (ca. 0.5 kN; Sharifian & Haddad derafshi, 2008). One kind of nut was presented exclusively on one testing day. In the data reported here, ten capuchins cracked piaçava nuts only, one capuchin monkey (Chuchu) cracked both kinds of nuts, and one capuchin monkey (Doree) cracked only tucum nuts.

2.4 | Procedure

Video recording occurred opportunistically when the capuchins came to the outdoor laboratory area. During these periods capuchins were cracking nuts at other anvils in the vicinity, as well as at anvils A and B. Experimenters distributed nuts (60–80/day) intermittently until the capuchins' interest in cracking nuts waned and they traveled away from the outdoor laboratory.

We filmed activity at the selected anvil from 6 to 6.5 m, with an oblique angle (approximately 45°). We used a Casio EX-ZR700 camera mounted on a tripod and set at 120 fps with 640 × 480 pixels resolution. The field of view encompassed the top of the anvil to 40 cm above the anvil.

2.5 | Data processing

The data were processed in three sets. Data set I comprised the first 20 strikes on whole nuts with each of the four stones by the four most proficient individuals in our study group (Jatobá and Mansinho, males, and Piaçava and Dita, females), recorded in 2013. Exceptions were that we recorded just 16 strikes for Mansinho with the 455 g stone, and 10 and 14 strikes for two individuals (Dita and Piaçava, respectively) with the 1,100 g stone, producing 300 strikes total for the four capuchins across the four stones. Data set II comprised the first 20 strikes on whole nuts with the 1,042 g stone by 12 capuchins (with two exceptions: Pati provided 19 strikes; Teninha provided 15 strikes) thereby producing 234 strikes. Eight individuals were recorded in 2014. For this data set, we used the data from 2013 for Jatobá, Mansinho, Piaçava, and Dita. Data set III comprised the first 100 strikes on whole nuts by one capuchin monkey (Jatobá) using the 1,042 g stone, recorded in 2013. Following extensive review of the video corpus, we developed an ethogram specifying actions with the stone before each strike, the position of the hands on the stone during the lift and during the downward trajectory, the trajectory of the stone during the downward strike, and outcomes of the strike (the stone hits or misses the nut, the nut cracks, the nut flies off the anvil, and/or the stone drops off the anvil; see Table 2). Three actions with the stone (Spin, Flip, and Preparatory Lift) were identified. A Spin was defined as the capuchin monkey rotating the stone in the horizontal plane 180° about its center as the stone rested on the surace of the anvil. A Flip was defined as rotating the stone in the vertical plane 180° about its center (i.e., turning it over). A Preparatory lift occurred when the capuchin monkey lifted the stone off the anvil less than half the height of a normal strike, did not move it toward the nut, and put it down again at the point where it lifted it off the surface of the anvil (see Video Samples S1, S2, S3). Subsequently, we coded each capuchin monkey's sequence of actions with the stone and outcomes of each strike from video playback using Observer 10.0 (Noldus Corp.) for all three data sets using this ethogram.

Reliability of coding between the two coders, K.M. and R.B., was established by the coders independently coding a subset of the video. Coders trained until their codes on two consecutive novel video segments agreed for >85% of coded events and positions. Subsequently, K.M. coded the first 20 strikes of the four capuchins that used all four stones; K.M., R.B., and E.U. coded the first 20 strikes of the other eight capuchins using the 1,042 g stone. Discrepancies in coding were resolved by joint examination. R.B. coded strikes 21–100 for Jatobá with the 1,042 g stone.

2.6 | Analysis

The frequency of each behavior, hand position, and the outcome were summed per individual and calculated as a percentage of strikes. For Data Set I, because of the *n*, we present descriptive data only. For Data Set II, correlations of the proportional frequency of Spin, Flip, and Preparatory Lift with each other were tested using the Pearson product-moment

TABLE 2 Variables coded during nut-cracking by bearded capuchin monkeys

I. Anticipatory behaviors
A. Preparatory lift: Capuchin lifts stone and immediately puts it down again; usually lifts less than half the height of a full strike. Does not include lifting stone onto anvil from ground
B. Spin: Capuchin manually rotates stone with hands at least 180 degrees; orientation of stone surfaces to the anvil remain the same
C. Flip: Capuchin manually turns stone over with hands; surfaces of stone are re-oriented with respect to the nut and anvil
II. Position of the hands on the stone; scored separately for each hand
A. End: Hand grasps the stone at lateral edges; fingers tend to be at lower edge and palm at upper edge.
B. Top: Palm and at least 2/3 of the length of the fingers are on the upper surface of stone
C. Under: Fingers and at least 2/3 of the length of the palm are on lower surface of stone
III. Events in the strike cycle when hand positions were scored
A. Lift: Scored when stone is lifted above anvil
B. Down: Scored when stone begins moving downward from the zenith of the lift
C. Strike: Scored when stone contacts the nut
IV. Trajectory of the stone to the nut during downward motion of the stone
A. Straight – stone moves vertically downward
B. Slanted – stone moves at a perceptible angle (more than 5°) off vertical
V. Possible Outcomes (these are not mutually exclusive)
A. Nut fly: Nut comes off anvil after strike and must be retrieved or is lost
B. Stone drop: Stone falls off anvil
C. Crack: Nut is cracked open

TABLE 3 Occurrence (expressed as percent of strikes) of anticipatory actions and particular outcomes of strikes in 12 capuchins during their first 20 strikes using an unfamiliar 1,042 g stone to crack nuts. Capuchins are ordered by body mass in descending order. Values >100 indicate that the behavior occurred more than once per strike, on average

	Behaviors				Outcomes			
Subject	Flip	Spin	Prep Lift	Sum	Drop Stone	Nut fly	Slanted Strike	Crack
Jatoba	30	140	55	225	20	35	5	15
Teimoso	70	35	10	115	35	45	10	0
Mansinho	105	85	45	230	5	45	0	10
Catu	55	0	0	55	0	0	0	20
Tomate	15	5	70	90	0	15	5	20
Pati[a]	84	20	160	264	35	50	5	5
Cangaceiro	65	5	35	105	40	45	20	10
Dita	125	5	15	145	10	35	5	30
Teninha[b]	105	30	35	170	35	45	5	5
Chuchu	35	45	0	75	10	25	20	5
Piaçava	30	15	15	60	15	55	15	10
Doree	85	5	25	105	0	10	5	0
Mean	67.0	32.6	38.8	136.6	17.1	33.8	7.9	10.8
SD	35.0	41.6	43.9	70.7	15.4	17.5	6.9	9.0

[a] Nineteen strikes recorded.
[b] Fifteen strikes recorded.

correlations. Subsequently, these behaviors were pooled to derive a single measure called Anticipatory actions. The correlations between the capuchins' proportional frequency of Anticipatory actions and the frequency of a slanted strike, the nut flying, dropping the stone, or cracking the nut were evaluated using the Pearson product-moment correlations. The proportional frequencies of these same variables were compared between males and females using Wilcoxon–Mann–Whitney tests with alpha set at 0.05 (2-tailed). The proportional frequency of occurrence of Anticipatory actions, slanted strikes, nuts flying, and stone drops in first strikes in a bout versus in continuing strikes was compared using Wilcoxon signed-rank tests with alpha set at 0.05 (one-tailed, as we made a directional prediction that these actions and outcomes would be more frequent on initial strikes). Nonparametric tests were used for the latter analyses given the *n* values in our study and unequal sample sizes of first strikes compared to continuing strikes.

To evaluate changes in behaviors and outcomes over 100 strikes for one capuchin, frequencies of these variables were summed across ten blocks of ten strikes each. We examined the relationship between the order of blocks and the frequency of exploratory actions using linear regression.

3 | RESULTS

3.1 | Data set I: Using larger and smaller stones to crack piaçava nuts

Table S1 presents the count data for four proficient nut-crackers using larger and smaller stones, and Video S1 illustrates a proficient adult female cracking a piassava nut using the 1100 g stone. The capuchins cracked 0–5 nuts in 20 strikes with each of the larger stones and 1–3 nuts in 20 strikes with each of the smaller stones. They regularly performed Spin (0.31/strike), Flip (0.69/strike), and Preparatory lift (0.25/strike). The capuchins used all three actions more often with larger stones than smaller stones (rate per strike, larger vs. smaller, respectively: Preparatory lift: 0.37 vs. 0.14; Spin: 0.61 vs. 0.03; Flip, 0.82 vs. 0.58). Three of four capuchins occasionally lifted a larger stone with one hand underneath it (34 times across all strikes; 0.24/strike) but no capuchin monkey ever did so with a smaller stone. The capuchins primarily struck the nut with a vertical strike (0.94/strike) and hit the nut on 99% of strikes. Given the rarity of missing the nut, we do not address this outcome further.

3.2 | Data set II: Using a 1,042 g stone to crack piaçava and tucum nuts

Out of the 12 capuchins, each cracked zero to six nuts across their first 20 strikes. Individual capuchins' Anticipatory actions, hand positions on the stone and outcomes are presented in Table 3. Anticipatory actions occurred on an of average 1.4 times/strike. Flip occurred the most often (0.7/strike) and all individuals flipped the stone multiple times (see Table 3). The percentages of strikes with Preparatory Lift and Flip, Flip and Spin, and Spin and Preparatory Lift were not correlated across individuals (r_{xy} [12] = −0.001 to + 0.08). The relative frequencies of each of these Anticipatory actions did not differ significantly between males and females (n_1= 7, n_2= 5, all values of U > 9, $p > .05$). Spin correlated modestly positively with Crack

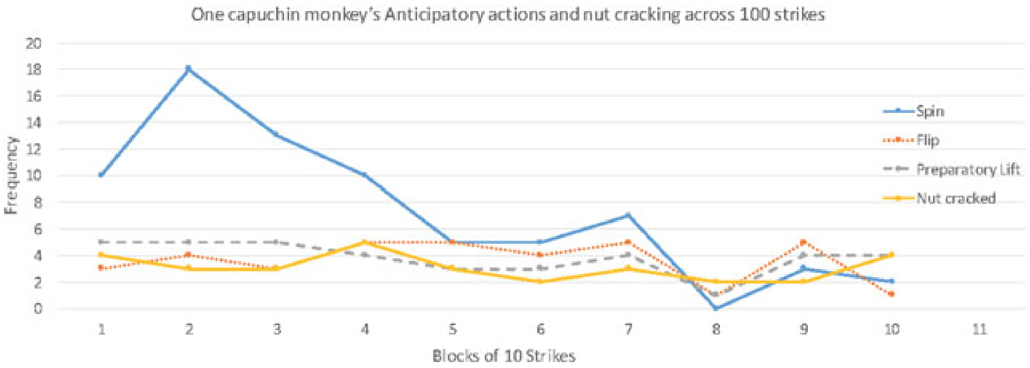

FIGURE 2 The frequency of three forms of Anticipatory actions (Spin, Flip, and Preparatory lift) and cracking nuts across 100 strikes by a male bearded capuchin monkey (Jatobá) using an initially unfamiliar 1,042 g stone to crack palm nuts. Notice that for the first four blocks (40 strikes, total), the monkey spun the stone at least once per strike. He spun it increasingly less often in later blocks

(r_{xy} [12] = +0.42); Flip and Preparatory Lift correlated modestly negative with Crack (r_{xy} [12] = −0.17, both variables). All of these correlations have 2-tailed probabilities >0.10.

The summed percentage of strikes, in which a capuchin monkey used the three Anticipatory actions, correlated modestly with the number of nuts cracked (r_{xy} [12] = +0.06), the percentage of slanted strikes (r_{xy} [12] = −0.25), and the percentage of strikes, in which the stone dropped (r_{xy} [12] = +0.33; $p > 0.10$, 2-tailed, all these correlations). The summed percentage of strikes, in which a capuchin monkey used the three Anticipatory actions, correlated most strongly with the percentage of strikes, in which the nut flew off the anvil (r_{xy} [12] = +0.61; $p = 0.05$).

Eleven capuchins spun the stone at least once. Recall that this action, like Flip and Anticipatory lift, is bimanual. The monkeys spun the stone in a clockwise direction 28 times and in a counter-clockwise direction 50 times. Individuals' bias to one direction ranged from 100% to 57%. Four monkeys produced more clockwise spins and seven produced more counter-clockwise spins. All of the 11 spun the stone proportionally more often before the first strike on a new nut (i.e., beginning a cycle of strikes) than before continuing to strike the same nut again (median, % of first strikes = 0.33 vs. 0.07, continuing strikes, Wilcoxon signed-ranks, T (11) = 0; $p < .01$). Flip occurred at similar rates in the two conditions (median, % of first strikes = 0.55 vs. 0.60, continuing strikes, as did Preparatory lift (median, % of first strikes = 0.40 vs. 0.31, continuing strikes). Wilcoxon tests revealed no significant differences in rates between first and continuing strikes for these two variables.

3.3 | Outcomes

Ten capuchins produced one or more slanted strikes but overall slanted strikes were uncommon (8% of strikes). The percentage of a capuchin's strikes which were slanted and correlated modestly with the percentage of strikes in which it dropped the stone (r_{xy} [12] = +0.35; $p > .20$) and the nut flew off the anvil (r_{xy} = +0.34; $p > .20$). Eight capuchins dropped the stone off the anvil at least once, and 11 capuchins made the nut fly off the anvil at least once. Of these poor outcomes, the nut flying off the anvil was the most common, occurring on more than a third of strikes (34%; individual range: 0–55%). Capuchins that produced more strikes where the nut flew off the anvil were also more likely to produce strikes in which the stone dropped off the anvil (r_{xy} (12) = +0.80; $p = .001$). The relative frequencies of each of these outcomes did not differ significantly between males and females ($n_1 = 7$, $n_2 = 5$, all values of $U > 12$, $p > .05$).

Initiation of a bout of striking was associated with poor performance most clearly in that the proportion of slanted strikes was higher for strikes initiating a bout than for continuing strikes (median = 0 vs. 0; Wilcoxon T [8] = 6, $p = 0.05$). The nut flew off the anvil proportionally more often on first strikes than on continuing strikes, although not significantly so (median = 0.52, first strikes, vs. 0.31, continuing strikes; Wilcoxon T (11) = 16, $p > .05$). Capuchins dropped the stone off the anvil at roughly equivalent rates in these two conditions (median = 0.07, first strikes, and 0.11, continuing strikes; T (9) = 18, $p > .05$).

3.4 | Hand positions

The capuchins predominantly gripped the stone with fingers spread wide at the lateral edges to lift it (88% with the Left hand; 86% with the Right hand), but capuchins sometimes gripped the top of the stone or (least often) the underside of the stone with one hand while gripping the edge with the other. One capuchin, Teimoso, gripped the top of the stone with his left hand and gripped the underside of the stone with his right hand on ten strikes, and on one strike, gripped the edge of the stone with his left hand and the underside of the stone with his right hand. He kept his hand on the underside of the stone during the downward strike on two of these 11 strikes and moved his hand from the edge to the underside of the stone in one strike. Not surprisingly, this capuchin monkey experienced frequent poor outcomes from his strikes, dropping the stone on 35% of strikes and causing the nut to fly on 45% of strikes, both values above the average for the group (17% and 34%, respectively). Mansinho, the capuchin monkey missing his left foot, gripped the underside of the stone with his right hand on 14 out of 20 strikes while lifting, but always moved his hand to the edge or top of the stone in the downward portion of the strike. This capuchin monkey never struck at a slant and dropped the stone just once.

At the zenith of the lift, nine capuchin monkeys shifted their grips with both left and right hands to the top of the stone for the downward strike for 75–100% of their strikes (mean = 92%, left, and 96%, right; see Figure 1). The three heaviest individuals kept their right hand on the edge of the stone for 40–90% of their strikes, but their left hand on the top of the stone for 90–100% of strikes, as did the lighter capuchins. The lightest capuchin monkey gripped the stone with her right hand three times on the underside and eight times on the top to lift it, and kept her left hand on the edge of the stone on the downward strike eight times and the right hand on the edge of the stone five times. For her remaining downward strikes, she moved her hands to the top of the stone.

3.5 | Data set III: Changes across 100 strikes in one capuchin monkey using a 1,042 g stone

Jatobá cracked 31 nuts in 100 strikes with the initially unfamiliar 1,042 g stone. He cracked two to six nuts/block of ten strikes and the number of nuts cracked did not vary systematically with the order of blocks. He made four slanted strikes (in Blocks 2 and 9) and dropped the stone five times (in Blocks 1, 2, and 7). The nut flew off the anvil 2.2 times/block on average (range 0–4). Overall this capuchin monkey was relatively proficient at cracking nuts among members of this group and this data set is typical of his performance.

Jatobá produced 1.5 Anticipatory actions/strike across 100 strikes, very close to the rate that the full sample of capuchins produced in their first 20 strikes (1.4 Anticipatory actions/strike). He spun the stone less frequently in later blocks ($F = 57.89$, $df = 9$, $p < .001$, adjusted $r^2 = 0.86$) but produced the other two actions and cracked nuts at a consistent rate across blocks (see Figure 2).

4 | DISCUSSION

We studied wild bearded capuchin monkeys experienced at using natural stones on natural anvils (both of which vary enormously in size, shape, composition, and other features) to crack nuts of several species of palms (Visalberghi et al., 2007). Thus, we regard them as skilled toolers. We presented the capuchins with unfamiliar stones and palm nuts near a familiar log anvil. Using a stone to crack palm nuts requires achieving a strong grip on the stone and producing precisely aimed vertical strikes within a zone of kinetic energy at impact (Bril et al., 2010; Mangalam et al., 2018). The capuchins consistently maintained control of the stone while using it to strike a nut. They made considerable use of three particular actions with the stone before striking, which we labeled Anticipatory actions. They did so at a rate of more than one action per strike through 20 strikes. What do these actions indicate how the capuchins approach the task?

4.1 | Anticipatory actions

Spin, where the capuchin monkey moved the stone 180° or more in the horizontal plane with both hands as the stone rested on the anvil, occurred more often when the capuchin monkey initiated a striking bout than when it continued a striking bout, and more often when the stone was less familiar. This action was energetically rather easy, as the stone's mass rested on the anvil throughout the action. Spinning the stone allowed different surfaces to come to hand. We hypothesize that moving the stone in this way afforded an opportunity to grip the stone lightly at different points and to identify grips that were more comfortable or secure without the risk of dropping the stone and/or expending much effort. It might be that the capuchin monkeys sense torque (that causes rotational acceleration) when they grip the stone lightly, and explore different grip locations to minimize this force.

The second Anticipatory action, Preparatory lift, occurred when the capuchin monkey lifted the stone a short distance above the anvil, then set it down, and then immediately afterward lifted the stone for the strike. This movement is reminiscent of preliminary movements humans make before strenuous actions, such as tapping a hammer lightly against a hard surface before initiating a full strike, or a counter-swing of a baseball bat before the pitch. Biomechanical studies of humans have shown that using a prestretch, or countermovement (an eccentric movement, that is, lengthening the muscle under load) increases the power of subsequent concentric movements (i.e., shortening the muscle under load) through the natural elastic components of muscle and tendon and the stretch reflex (Baechle, 2008; Newton et al., 1997). In the case of the capuchin monkey lifting and lowering the stone, both components of the strike are alternately performed. Therefore, this action may increase the power of the subsequent strike. A preparatory lift followed by placing the stone down again may also provide proprioceptive information via muscles and tendons about force needed to lift the stone—muscular "tuning" for the effort to follow. It is interesting that a nonhuman primate exhibits similar preparation strategies as humans facing similar striking tasks, but we cannot as yet evaluate to what extent these actions impact the qualities of the strikes that follow them, for humans or for nonhuman primates.

In the third action, Flip, the capuchin rolled the stone 180° about one axis, which, like Spin, resulted in the stone moving on the anvil without the capuchin monkey lifting it. Therefore, it was an ergonomic way for the capuchin monkey to move the stone toward or away from itself. The capuchin monkeys usually have to move the stone away from the nut between strikes, as it comes to rest on or near the nut after a strike. Moving the stone by flipping it over with both hands is a common way that they accomplish this and this was the most common of the three actions with a stone that preceded a strike.

The relative frequency of Anticipatory actions per individual correlated positively with the percentage of strikes in which the nut flew off the anvil, modestly positively ($p > .10$) with the percentage of strikes in which the, stone dropped, and the number of nuts cracked, but modestly negatively with the percentage of slanted strikes. Thus we do not see in our data a strong relationship between the relative frequency of these actions and specific outcomes.

Spinning and flipping the stone, preparatory lifts, and other actions with the hammer stone performed in advance of striking have not been described for long-tailed macaques or chimpanzees. Perhaps these other species do not use these actions because on average they use proportionally much lighter stones (estimated average to be 14–17% of body mass, chimpanzees, and 1–9% of body mass, long-tailed macaques) compared to the bearded capuchins at Fazenda Boa Vista (estimated to be 25–40% of body mass for adult males, higher for females and juveniles; Aempichitkijkarn, 2017; see also Visalberghi, Sirianni, Fragaszy, & Boesch, 2015). Alternatively, perhaps researchers have simply not reported these actions.

Our findings expand the known repertoire of haptic exploratory actions demonstrated by tufted capuchins beyond those previously described by Lacreuse and Fragaszy (1997), Visalberghi and Neel (2003), Visalberghi et al. (2009), Phillips, Goodchild, Haas, Ulyan, and Petro (2004), and Fragaszy et al. (2010). Lacreuse and Fragaszy described how capuchins moved the fingers of one hand over an unseen irregular surface to retrieve sunflower seeds using actions that in humans have been linked to detecting surface contour and hardness (Lederman & Klatzky 1984, 1990, 2009). The other reports describe capuchins tapping nuts or woody surfaces, such as tree branches, with their fingertips, apparently to detect something about the density of the material (for example, relevant for detecting hidden invertebrate prey, or whether a nutshell contained kernels, or whether a stone is heavy or light). Tapping actions in these reports were unimanually or bimanually complementary (such as one hand holding the nut while the other tapped it). The bimanual character of Spin is different in that both hands are moving concurrently and in opposite directions. In this sense, it requires a different form of motor coordination than the other exploratory actions described for capuchins.

4.2 | Effect of practice

Improvement with practice was evident at the group level in the higher incidence of slanted strikes in initiating strikes compared to continuing strikes and in the decline of Spin over 100 strikes in one capuchin's record. The incidence of Preparatory lift and Flip did not change in either of these comparisons. These findings, in conjunction with those above, suggest that Spin informs the actor about how to grip the stone but that when the stone is familiar, this action is less useful. Preparatory lift apparently serves other purposes, perhaps bodily preparation for the strenuous action to follow, and this action is apparently unaffected by familiarity with the stone. Flip is likely to be used to space the stone with respect to the body and/or the nut, and like Preparatory Lift, it seems not about informing the actor about how to grip the stone.

4.3 | Grips

The capuchin monkeys mainly gripped the lateral edges of the stone to lift it, although the larger capuchins sometimes placed one hand on the top of the stone to lift it. Capuchin monkeys, especially the larger individuals, usually moved one or both hands to the top of the stone at the zenith of the lift, at the initiation of the downward phase of the strike. Moving the hand to the top of stone for the downward portion of the strike likely allows the capuchin to add work to the stone most easily, increasing its downward velocity and thus its kinetic energy at impact. The capuchin monkey's grip on the stone determines which face of the stone and which area of the face strikes the nut. If the capuchin monkey consistently gripped the stone in the same place, it would consistently strike the nut in the same way. Thus precise positioning of the face of the stone with respect to the nut that these capuchin monkeys can achieve (documented by Haslam & Fragaszy, 2014 unpublished data) might be a consequence of the choice of grips, rather than a goal of the actor. Future work is needed to sort out these possibilities. One could test experimentally the extent to which contours of the stone or the location of its center of mass govern the position of the hands. This aspect of skilled action can be expected to differ across species in accord with details of hand morphology and goniometry, that influence how the hand conforms to the shape of the stone, and in accord with sensibility of the individual to torque (perceived through dynamic touch; Carello & Turvey, 2000; Turvey & Carello, 2011). We do not as yet have normative data about the perception of torque for any species handling dense, roughly spherical objects like stones, although we do have such data for humans wielding objects composed of rods (Fitzpatrick, Carello, & Turvey, 1994; Pagano & Turvey 1992).

We have more information with regard to hand morphology and goniometry across species. Historically, most attention with respect to humans' hand morphology in relation to manual dexterity has concerned the role of the opposable thumb, which allows the pad of the thumb to contact the pads of the other digits (Napier & Tuttle,1993). However, when humans grip a stone hammer (roughly spherical or elliptical), the thumb does not contact the other digits; instead, several different grips allow human hands to exert and to withstand strong forces (Marzke, 2013). While there are details of anatomy of the human hand and wrist and associated movements that have been suggested to reveal evolutionary adaptations in humans for striking while holding a spherical object, as when using a club (Young, 2003) or knapping stone (Key & Dunmore, 2015; Williams, Gordon, & Richmond, 2012), some of these anatomical features apparently predate the use of tools in the fossil record (Skinner et al., 2015). They may be associated with the use of the hands in diverse strenuous percussive activities, and accordingly, they may be distributed more widely among primates rather than restricted to the hominin lineage. We hope that comparative anatomists will determine if there is an anatomical signature in the hands associated with using percussive stone tools evident in the three genera (*Macaca*, *Sapajus*, and *Pan*) that have percussive technology.

Our findings show that capuchin monkeys achieve adequately strong grips in varied positions on stone hammers, including (perhaps surprisingly) lifting and lowering the hammer with one or both hands on the top of the stone. The placement of a hand underneath the stone during striking is puzzling. The capuchin monkey that held the stone from underneath during the downward portion of several strikes dropped the stone the most frequently and cracked no nuts over 20 strikes. Perhaps this capuchin monkey has never learned to move his grip on the stone during the downward portion of the strike, but why he persisted in lifting the stone from underneath is unclear.

4.4 | Effects of the mass of the stone

Although the small number of subjects (four) that used both larger and smaller experimental stones to crack palm nuts limits the generalizability of our findings, our findings indicate that capuchin monkeys use anticipatory actions more frequently with larger stones (1 kg) than with smaller stones (0.5 kg). This pattern is in accordance with the hypothesis that anticipatory actions aid the capuchin to secure a firm grip on the stone and to prepare for the strenuous action of lifting the stone (both are more challenging to achieve with a heavier stone). It also indicates that actions with smaller stones are not more frequent even though they would require less effort to accomplish.

In conclusion, our findings suggest that bearded capuchin monkeys actively explored where they could grip a hammerstone securely and/or comfortably by moving their hands on the stone and by moving the stone around on the anvil. As expected, these actions occurred more frequently when initiating a bout of striking, when the stone was heavier, and when the stone was less familiar. Sometimes they lifted the stone a short distance before lifting it to strike, and they usually adjusted their grip on the stone during a strike, while the stone was in the air. These anticipatory and modulatory actions reveal new dimensions of skill in nut-cracking, although individuals that performed more of them in this sample of strikes did not have better outcomes nor did they crack nuts in fewer strikes. They also reveal that the monkeys gripped the stone in variable ways to lift it. Further studies are needed to evaluate how manual haptic information generated through anticipatory actions (with the stone or with the nut) helps a monkey recognize that the various sub-goals of nut-cracking (placing the nut in a stable position on the anvil; gripping the stone in a firm grip and in an appropriate orientation and position) have been achieved. It is worth exploring if the perceptuomotor traits supporting anticipatory actions and skillful adjustments of grips and movements with objects that are evident in these monkeys are shared among primates, as are many other features of manual action (Fragaszy & Crast, 2016), or are shared only among species that forage extractively using strenuous actions, together with anatomical features associated with generation of percussive forces.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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