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RESEARCH ARTICLE

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Adult and juvenile bearded capuchin monkeys handle stone hammers differently during nut-cracking

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Abstract

Wild bearded capuchin monkeys (*Sapajus libidinosus*) habitually use stone hammers to crack open palm nuts and seeds on anvils. This activity requires strength, balance, and precise movement of a large stone with respect to the item placed on an anvil. We explored how well young monkeys cope with these challenges by examining their behavior and the behavior of adults while they cracked palm nuts using a stone. Using video records, we compared actions of six juvenile (2–5 years) and six adult (7+ years) wild monkeys during their first 20 strikes with one unfamiliar ellipsoid, quartzite stone (540 g), and the outcomes of these strikes. Compared with adults, juveniles cracked fewer nuts, performed a more diverse set of exploratory actions, and less frequently placed one or both hands on top of the stone on the downward motion. Adults and juveniles displayed similar low frequencies of striking with a slanted trajectory, missing the nut, and losing control over the nut or stone after striking. These findings indicate that young monkeys control the trajectory of a stone adequately but that is not sufficient to crack nuts as effectively as adults do. Compared with juveniles, adults more quickly perceive how to grip the stone efficiently, and they are able to adjust their grip dynamically during the strike. Young monkeys develop expertise in the latter aspects of cracking nuts over the course of several years of regular practice, indicating that perceptual learning about these aspects of percussion occurs slowly. Juvenile and adult humans learning to use stones to crack nuts also master these features of cracking nuts very slowly.

KEYWORDS

age difference, dexterity, dynamic movement, motor skill, tool

1 | INTRODUCTION

Percussive hammering during feeding in natural settings is documented in several nonhuman primate taxa—common chimpanzees (*Pan troglodytes*; Boesch & Boesch, 1981; Sugiyama & Koman, 1979), long-tailed macaques (*Macaca fascicularis*; Malaivijitnond et al., 2007), and tufted capuchin monkeys (*Sapajus* spp.; Fragaszy, Izar, Visalberghi, Ottoni, & Oliveira, 2004; Moura & Lee, 2004). We know a good deal about the prevalence of the activity and the preferences of individuals for certain kinds of hammers, anvils, and target items to process with percussion (e.g., Carvalho, Biro, McGrew and Matsuzawa (2009), Luncz, Mundry and Boesch (2012), and Sirianni, Mundry and Boesch (2015) for chimpanzees; Tan, Tan, Vyas, Malaivijitnond and Gumert (2015) for macaques; and Ferreira, Emidio and Jerusalinsky (2010), Spagnoletti, Visalberghi, Ottoni, Izar and Fragaszy (2011), and Visalberghi et al. (2007) for capuchins). We know less about how young inexperienced individuals acquire skilled hammering.

In this report we approach using a stone hammer as a perceptuomotor action requiring a firm grip, forceful lifting, and accurate and powerful striking for effective completion. Our aim is to evaluate how young, small, inexperienced individuals manage these aspects of using a stone hammer as compared to more experienced, larger adults. Following Fragaszy and Mangalam (2018), cracking nuts with a stone hammer qualifies as tooling, and we refer to monkeys cracking nuts with hammers as "toolers." The term "tooling" refers to the movements of the body + object system (the body plus a grasped object) to achieve a mechanical effect on another object or surface (in brief; see Fragaszy and Mangalam (2018) for the complete definition of tooling). This term confers a special status on the body + object system, rather than on an object, as does the term "tool use." Our movement-oriented approach to tooling supports comparison across species that use (potentially dissimilar) objects and body parts to achieve particular mechanical effects (Mangalam & Fragaszy, 2016, 2018).

The ontogeny of hammering in the few species of nonhuman primates that tool with stone hammers follows remarkably similar patterns at a gross level. Young chimpanzees from Bossou, Guinea, and the Taï Forest, Ivory Coast learn to use stones to crack nuts of oil palm (*Elaeis guineensis*), panda (*Panda oleosa*), and coula (*Coula edulis*) trees on anvils (Boesch & Boesch, 2000; Inoue-Nakamura & Matsuzawa, 1997). By 2.5–3 years old, young chimpanzees perform each of the basic actions necessary for nut-cracking, but not effectively. Young chimpanzees continue to practice for another 2 to 5 years before they organize actions integrating stones, nuts, and anvils efficiently. Similarly, young long-tailed macaques strike objects and place objects on anvils by 2.5 years of age but often do not organize their actions with stones, shellfish, and anvils correctly for another year (Tan, 2017). When they do begin to crack "correctly" at age 3.5, they have an 83% success rate. Capuchin monkeys also follow this developmental pattern—young monkeys do not systematically relate nut to the anvil, and stone to nut until sometime in their second year or later (Fragaszy et al., 2017; Resende, Ottoni, & Fragaszy, 2008). They do not generate sufficiently forceful strikes to crack palm nuts until more than 2 years old and are not as efficient as adults for several more years (Aiempichitkijkarn, 2017; Resende et al., 2008). They gradually drop inappropriate actions from their repertoire as they improve at cracking nuts (Eshchar, Izar, Visalberghi, Resende, & Fragaszy, 2016; Resende, Nagy-Reis, Lacerda, Pagnotta, & Savalli, 2014). Clearly, instrumental hammering (to open food items) challenges young primates' organizational and motor skills.

Although chimpanzees, long-tailed macaques, and capuchin monkeys share a general pattern of ontogeny in the overall organization of cracking nuts, there are notable differences in the details of their actions (Visalberghi, Sirianni, Fragaszy, & Boesch, 2015). Chimpanzees of all ages crack oil palm nuts in a seated position (Inoue-Nakamura & Matsuzawa, 1997). In the Taï Forest, chimpanzees use wooden hammers to crack softer coula nuts and proportionally more often use stone hammers and larger wood hammers to crack harder panda nuts (Sirianni et al., 2015). Typically, chimpanzees grip the hammer with one hand (Boesch & Boesch, 1981; Inoue-Nakamura & Matsuzawa, 1997). Long-tailed macaques engage in two different modes of hammering—(a) axe-hammering in which a small stone hammer held in one hand is used to crack oysters attached to a substrate and (b) pound hammering in which one or two hands are used to grip a larger stone hammer to crack a food item on an anvil (Gumert, Kluck, & Malaivijitnond, 2009). While pound hammering the monkeys are typically seated (Tan et al., 2015). The bearded capuchin monkeys of Fazenda Boa Vista (hereafter FBV) in Piauí, Brazil using light hammers (e.g., 200–300 g stones) to crack relatively soft food items (e.g., dry cashew nuts) often sit or crouch on or by the anvil, like macaques and chimpanzees. In contrast, they stand bipedally while hammering palm nuts on anvils using stones weighing 500 g or more (Liu, Fragaszy, & Visalberghi, 2016). A bipedal position allows them to lift the hammer stone higher than if they were seated, thus increasing the kinetic energy of their strikes through the action of gravity on the hammer.

The hammers used by capuchin monkeys at FBV on average weigh 1.1 kg, over 50% of an adult female's average body mass (Fragaszy et al., 2016; Visalberghi et al., 2007). The estimated proportion of hammer mass to body mass in other primates is much lower—hammers are usually <12% of the body mass in chimpanzees and <10% of the body mass in long-tailed macaques (Boesch & Boesch, 1984; Gumert et al., 2009; Sirianni et al., 2015; Visalberghi et al., 2015). Capuchin monkeys routinely lift 1 kg stones to a vertical height of 60% of their body length before bringing them down on the nut (Liu et al., 2009). Individual monkeys sometimes increase the kinetic energy of their strike by applying work to the stone during the downward motion (Mangalam & Fragaszy, 2015). Although this manner of bipedal striking allows capuchin monkeys to crack tough nuts, the mass of the stone likely challenges the monkeys to keep their balance, maintain a secure grip on the stone, and orient the stone properly.

How do monkeys perceive and adapt to the challenges of this form of percussive tooling? For instance, how do monkeys determine if their grip on a hammer is effective or anticipate the effort they should use to lift and strike with a given hammer? We adopt the perception-action framework to answer these questions. Gibson's perception-action theory holds that an individual's actions generate perceptual information that can be used to guide subsequent actions and to develop skilled movement (Gibson, 1969). An object affords an individual the opportunity to perform certain actions based on its invariant properties and distinctive features (Gibson, 2000). Perceptual learning occurs when an individual becomes better able to discern and differentiate affordances in the environment (Gibson, 1992). This process is facilitated by exploratory activities such as using the hands to manipulate an unfamiliar object. Such actions inform an individual not only about the object it is handling but also about its own body and movements (Gibson, 2000).

By using their hands to explore objects, humans extract information about texture, mass, temperature, contour, and stiffness, among other properties (Lederman & Klatzky, 1987, 1990, 2009). Humans use a repertoire of species-typical movements for this purpose. For example, when initially handling an unfamiliar object, people use an exploratory procedure called enclosure, which involves gripping the object and molding the hands around its contours to acquire information about the object's shape and contour (Lederman & Klatzky, 1987). Nonhuman primates also frequently explore objects with their hands (Fragaszy & Crast, 2016). Lacreuse and Fragaszy (1997) found that captive tufted capuchin monkeys (*Sapajus* spp.) investigated objects they could not see using many of the same hand movements as humans do in a similar situation, such as contour-following, enclosure, and probing with a finger. Tufted capuchin monkeys also explore objects by tapping them with their fingertips (Visalberghi & Neel, 2003).

A few authors have described manual exploratory actions by wild primates during percussive tooling. While cracking nuts, chimpanzees explore nuts and hammerstones by rolling them on the ground, as well as by pressing them against other objects (Inoue-Nakamura & Matsuzawa, 1997). Similarly, long-tailed macaques roll hammerstones on the ground and manipulate hammers and food items in their hands (Tan, 2017). Bearded capuchin monkeys knock the nut several times in quick succession on the hammer stone or anvil, the latter apparently to gain information about the nut's position on the anvil so as to place the nut in a stable position (Fragaszy et al., 2013). They also tap and partially lift hammer stones to evaluate their composition and mass (Visalberghi et al., 2009).

Natural stones vary in shape and size. Previous study of monkeys cracking resistant piaçava (*Orbignya* spp.) nuts using 1 kg stones has indicated that adult monkeys routinely move the stone by spinning it about its vertical axis as it rests on the anvil, especially when the stone is unfamiliar and when initiating a sequence of strikes (Fragaszy et al., 2019). Spinning the stone results in the monkey touching the stone at several points along its lateral surfaces. This action could aid the monkey to identify the most comfortable place to grip the stone securely. We have interpreted the monkeys' more frequent spinning at the beginning of a nut-cracking bout and when using an unfamiliar stone as supporting the prediction from perception-action theory that an individual will perform exploratory actions to learn about an unfamiliar object (Gibson, 2000).

In the case of percussive tooling, the tooler is expected to perform exploratory actions that are independent but supplemental to the functional actions of hammering. For instance, manually investigating the stone would presumably reveal information about its mass and how it can best be gripped. Manipulating the food item to be hammered might reveal its hardness or shape. The difference between the exploratory actions that experienced adults, with substantial perceptual knowledge about nut-cracking, and inexperienced juveniles, who lack such perceptual knowledge, might perform is unknown. Furthermore, it is unclear how the functional actions of hammering in juveniles compare to the same actions in adults. For example, during striking, adults often switch the position of one or both of their hands at the zenith of the lift from the lateral surfaces of the stone to the top (Fragaszy et al., 2019). Modulation of the grip in mid-strike presumably requires accurate perception of the stone's movement and the pressure of the hands on the stone's surfaces together with the precise timing of the hands' movements. Perhaps refinement of this skill requires extensive practice, and thus it would be less evident in juveniles than in adults.

The present study investigated exploratory actions and functional actions in juvenile and adult monkeys when using a lighter stone (540 g) than used by the adult monkeys in Fragaszy et al. (2019), and less resistant nuts of the tucum palm (*Astrocaryum campestre*) than presented in that study. The lighter stone and the less resistant nuts facilitated participation by juvenile monkeys that did not participate in the study by Fragaszy et al. (2019). We expected that juveniles would use a more diverse set of exploratory actions than adults, that they would shift the position of their hands on the stone during the strike less often than adults, and that they would experience poor outcomes more frequently than adults.

2 | METHODS

This study was approved by the University of Georgia and meets the American Society of Primatologists' guidelines for the humane care and use of nonhuman primates in research.

2.1 | Site

The study site is privately owned land, FBV located in Piauí, Brazil, near Gilbués (9°39′S, 45°25′W). The landscape consists of a sandy plain (420 m above sea level) with scattered sandstone ridges, pinnacles, and mesas that rise steeply to 20–100 m. The rock formations are made up of sandstone, siltstone, and shale, with quartzite pebbles and cobbles in some layers. Weathering exposes the pebbles and cobbles, rendering them available to the capuchins to use as hammers.

The study took place in an outdoor laboratory (~30 m in diameter) within the home range of the monkeys. This relatively level area has a mostly closed, high canopy with little undergrowth. It contains several natural sandstone and log anvils which the monkeys use regularly to crack several species of palm nuts. Palm trees (*Orbygnia* [piaçava]), *Attalea* (catulè and catulí) and *Astrocaryum* (tucum), are nearby. The study was conducted in May and June 2014.

2.2 | Subjects

Six adults (>7 years; three males) and six juveniles (<6 years; three males) voluntarily participated in the study. The monkeys were all members of a group (N = 24–26) that is well-habituated to human observers and video equipment. The adults ranged in mass from 1.9 to 4.2 kg (see Table 1). Juveniles weighed at least 1.2 kg but did not exceed 2.0 kg. The mass of the monkeys was obtained at the time of testing using a scale with a digital display mounted 1.5 m above the ground in a tree (Fragaszy, Pickering et al., 2010; Fragaszy et al., 2016). Monkeys voluntarily sat on the scale to obtain water. All monkeys that participated in this study had intact limbs and

TABLE 1 Sex, assigned age class, age, and body mass of monkeys that participated in this study

Name	Sex	Age class	Age at time of study (years)	Mass (kg)
Cachaça	M	Juvenile	2	1.29
Chani	F	Juvenile	3	1.25
Thaís	F	Juvenile	3	1.48
Presente	M	Juvenile	3	1.67
Coco	M	Juvenile	4	1.88
Paçoca	F	Juvenile	5	1.81
Tomate	M	Adult	7	2.53
Catu	M	Adult	7	2.73
Jatobá	M	Adult	>7	4.20
Piaçava	F	Adult	>7	1.73
Chuchu	F	Adult	>7	2.00
Dita	F	Adult	>7	2.04

appendages except for one adult male (Jatobá). The fourth digit on his right hand was severed and his hallux and three toes on his left foot were missing.

2.3 | Materials: Stones, anvils, and nuts

One ellipsoid stone (smooth quartzite cobble, 540 g) was used in the study. We chose to use a stone of this mass, rather than a stone of average size (i.e., 1 kg) found on anvils in this region, to accommodate the smaller juveniles, that do not attempt to lift heavier stones. Adults use stones of this mass to crack tucum nuts, although they prefer heavier stones when these are available (Fragaszy, Greenberg et al., 2010). The stone was brought to the site from elsewhere; thus, it was unfamiliar to the monkeys when first presented. However, it was the same material, shape and smoothness as stones typically used by the monkeys at the site. During observation sessions, the hammer was placed near an anvil in the outdoor lab and all other potential hammers were temporarily removed from the site. The experimental hammer was removed at the end of each testing period and nonexperimental hammer stones were returned. We observed nut-cracking at two anvils in this study; both had shallow depressions produced by monkeys' prior cracking (Visalberghi et al., 2007) in which monkeys placed nuts to be cracked.

Tucum nuts (*Astrocaryum* spp.) were collected locally. Tucum nuts are round and contain a single kernel (Visalberghi et al., 2008). They have a soft outer husk and a brittle inner shell (Mangalam & Fragaszy, 2015) which is fairly resistant to fracture (5.57 ± 0.25 kN; Visalberghi et al., 2008). For comparison, walnuts (*Juglans regia*) required 0.37 kN to crack (Schrauf, Huber, & Visalberghi, 2008), and coula nuts (*C. edulis*) 2.72 kN (Peters, 1987). Monkeys typically use a few strikes to fracture the exocarp (outermost fibrous layer), which they usually strip away with their hands or teeth before resuming striking to crack the endocarp (brittle inner shell), exposing the kernel (Mangalam & Fragaszy, 2015). Tucum nuts were used in this study because they are easier to fracture than nuts of other palm species in the area and inexperienced juveniles more often attempt to crack them (Fragaszy, Greenberg et al., 2010). Participation by juveniles was essential for this study.

2.4 | Procedure

Videos were recorded when the monkeys appeared at the outdoor laboratory and a monkey approached an anvil to crack nuts with the experimental hammer. Using a Casio EX-ZR700 camera mounted to a tripod, the monkey was filmed from 6 to 6.5 m from the anvil and 40 cm above the anvil at 120 frames per second with a resolution of 640 × 480 pixels.

2.5 | Behavioral coding

We coded each monkey's activity during its first 20 strikes using Observer™ 10.0 (Noldus Inc.) and using an ethogram adapted from Fragaszy et al. (2019), which examined adult monkeys' use of a 1 kg hammer to crack piaçava nuts (see Table 2). The ethogram was expanded to include behaviors and outcomes not seen in the previous study (e.g., sniff stone, tap stone, breach hull). We identified exploratory actions, functional actions and grips, and outcomes of strikes (see Supporting Information Video Samples S1 and S2). A strike was deemed slanted when the angle of the lower surface of the stone to the nut at the frame before impact was >15° off vertical as measured by a protractor placed on the computer screen during behavioral coding.

To investigate the relationship between the analysis of hand position and the work added to the stone on the strike, we coded videos of Jatobá and Tomate (two adults) and Coco and Presente (two juveniles) collected during the same time period of this study (May–June 2014) using the same 540 g stone and cracking tucum nuts. These videos were collected for a different study (Mangalam & Fragaszy, 2015). From this corpus of videos, we examined, per monkey, the first 10 strikes for which the hands remained in the same position on the stone during the lift and the downward strike, and the first 10 strikes for which one or both hands moved from the lateral edge(s) of the stone during the lift to the top of the stone during the downward strike. Data for the maximum height of the stone and the velocity of the stone at the moment of impact on the downward strike for these strikes were used to compute work added to the stone through the equation work = kinetic energy − potential energy (work = [1/2 mv^2] − [mass × 9.8 m/s × height]).

Three people coded the videos (S. A. B, R. P., and S. K.). To establish the reliability of coding, each person independently coded video of two monkeys (40 strikes total) until their coding agreed for 85% of events and positions for both monkeys, after which point they

TABLE 2 Actions and outcomes coded per strike

	Description
Exploratory actions	
Preparatory lift	Stone hammer is lifted off the anvil to no more than half the height of a full lift but does not result in a striking bout
Smell/lick stone	Stone hammer is brought to the nose or mouth
Handling nut	Nut is manipulated in one or both hands
Knock	The nut is held in one hand and is tapped gently on the anvil. Was scored as a single action if more than three seconds passed between knocks
Soft release nut	Similar to the functional action "release nut" (see below) except the monkey cups its hands around the nut and watches it wobble
Smell/lick nut	The nut is brought to the nose or mouth
Shake/tap nut	One or two hands manipulate the nut through shaking it, tapping it, or spinning it on the anvil
Strike nut on stone	Monkey strikes the nut on the stone
Spin stone	Monkey manually rotates the stone horizontally on the anvil at least 90°. The vertical orientation of the stone remains the same
Partial spin	Monkey manually rotates the stone with hands at least 30°, but stone returns to the original position
Direct percussion of stone on the anvil	Monkey strikes the anvil (absent the nut) with the stone
Direct percussion of nut on anvil	Monkey strikes the anvil with the nut (rather than the stone)
Functional actions	
Lift	Stone hammer is raised off the anvil to strike the nut. Hammer can be gripped by the lateral edge(s) or the top
Down	Monkey ceases to lift the stone hammer and the stone begins to approach the nut on the anvil. Hammer can be gripped by the lateral edge(s) or the top
Strike	Moment when stone comes into contact with the nut
Release nut	Nut is returned to the anvil after handling or knocking
Modifiers	
Lateral edge grip	Modifies lift or down. The hand is grasping a stone hammer at the point of the stone that is least central (most outer edge). The fingers tend to be under the stone and the palm tends to be on top of the stone
Top grip	Modifies lift or down. The hand, including the palm and at least two-thirds of the length of the fingers, are on the surface of the stone, facing upward
Under grip	Modifies lift or down. Stone hammer is gripped by its underside
Outcomes	
Straight strike	Stone hammer hits the nut between a 75° and 105° angle from vertical
Slanted strike	Stone hammer hits the nut outside of the 75–105° angle range
Missed strike	Stone hammer misses the nut entirely
Crack	Outer and inner layers of nut's shell are split open. The kernel is accessible
Breach hull	Exocarp of nut is split open. The shell is not cracked
Nut fly	Monkey loses control over the nut after striking it and leaves position on the anvil to retrieve it
Stone drop	Monkey loses control of the stone during a strike and the stone falls off the anvil to the ground below

each began coding the videos. S. A. B. coded five individuals. S. K. coded three individuals. R. P. coded four individuals. S. A. B. additionally coded eight videos with kinetic data.

2.6 | Analysis

The frequency of each behavior and outcome was tallied per monkey and converted to rate per strike for statistical analysis. We report means and 95% confidence intervals (CIs). We compared values for adults and juveniles using *t*-tests for independent samples. To examine the effect of shifting the position of the hand(s) between lift and strike on the work done on the stone by individual monkeys we used independent *t*-tests. Cohen's *d* statistic served as a measure of effect size for *t*-tests. To examine age-related changes in behavior, we plotted the data by age, treating all adults as having the same age.

3 | RESULTS

Tables 3 and 4 present the frequency counts of exploratory behaviors, grip types, and strike outcomes per monkey.

TABLE 3 Frequency per individual of exploratory behaviors across 20 strikes

Monkey (sex)	Exploratory behavior: Knock	Handling nut	Smell/lick nut	Shake/tap nut	Strike nut on stone	Soft release nut	Smell/lick stone	Preparatory lift
Cachaça (male)	8	1	4	0	4	3	0	0
Chani (female)	7	3	2	0	0	0	2	0
Thaís (female)	17	3	4	0	0	0	0	1
Presente (male)	4	4	4	0	0	0	0	0
Coco (male)	15	6	2	0	0	6	0	7
Paçoca (female)	0	7	8	0	0	3	0	3
Juvenile mean	8.50	4.00	4.00	0.0	0.66	2.00	0.33	1.83
Juvenile *SD*	6.47	2.19	2.19	0.00	1.63	2.45	0.82	2.79
Tomate (male)	8	3	4	0	0	3	1	0
Catu (male)	2	1	0	0	1	1	0	0
Jatobá (male)	16	4	1	0	0	0	0	1
Piaçava (female)	14	2	0	0	0	1	0	0
Chuchu (female)	43	6	1	0	0	0	0	0
Dita (female)	10	4	0	1	0	0	0	1
Adult mean	15.50	3.33	1.00	0.17	0.17	0.83	0.17	0.33
Adult *SD*	14.34	1.75	1.55	0.41	0.41	1.17	0.41	0.52

3.1 | Exploratory actions

On average, adults performed 1.08 exploratory actions per strike and juveniles performed 1.07 exploratory actions per strike. Adults knocked the nut on the anvil more frequently than all other exploratory actions combined (mean = 15.50, knock vs. 5.57, all others; $t(10) = 1.64$, $p = 0.08$; $d = 0.068$), whereas juveniles performed all other actions about as often as knocking the nut on the anvil (mean = 11.00, all others, vs. 8.50, knock; $t(10) = 0.778$, $p = .454$; $d = 0.450$; see Figure 1). Juveniles performed all exploratory actions (excluding knock) at approximately twice the rate of adults (0.55 per strike, juveniles, vs. 0.28 per strike, adults); $t(10) = 2.42$, $p < .05$; $d = 0.069$). Aside from knock, handling nut and smell/lick nut were the most common exploratory actions for juveniles (mean = 4.00 strikes/monkey, both handling nut and smell/lick nut). A soft release of the nut and preparatory lift occurred about half as often as the two previous behaviors for juveniles (mean = 2.00, soft release, and 1.83, preparatory lift). The frequency of smell/lick nut differed the most between adults and juveniles (mean = 4.00, juveniles, vs. mean = 1.00, adults; $t(10)= 2.74$, $p < .05$; $d = 1.58$). Strike nut on stone, smell/lick stone, and shake/tap nut were rare among both age groups; no individual performed one of these actions more than four times across 20 strikes. No individual ever performed the actions spin or partial spin of the stone, or direct percussion of the nut on the anvil, which have been observed in previous studies (Fragaszy et al., 2017, 2019). There were no differences in the frequency of use of left versus right hand for these unimanual actions for adults ($t(10) = 0.565$, $p = .58$) or juveniles ($t(10) = 2.03$, $p = .79$). Furthermore, there was no difference in the rate of exploratory actions performed by males and females ($t(10) = −0.70$, $p = .502$; $d = 0.402$).

3.2 | Functional actions and grips

For 15% of lifts by juveniles and 28% of lifts by adults, one hand was not visible. The following results are from data collected when both hands were visible. Adults and juveniles lifted the stone while gripping its lateral edges with both hands on the majority of their strikes (see Figure 2). Adults gripped the top of the stone with at least one hand on one-quarter of all lifts. Juveniles, however, gripped the top of the stone with one hand on <10% of their lifts. Two juveniles occasionally gripped the stone from underneath with both hands, one for three lifts and the other for fewer. Juveniles gripped the stone on the lateral edges to lift it on 83% of strikes, and adults on 57% of their strikes ($t(10) = 5.75$, $p < .05$; $d = 3.32$). There was no difference between males and females for gripping the stone by the lateral edges during the lift ($t(10) = 0.137$, $p = .894$; $d = 0.0792$).

On the downward motion, juveniles usually continued to grip the lateral edges of the stone, whereas adults typically shifted one or both hands to the top of the stone. Adult shifted their grip more often than juveniles (67% of strikes, adults, vs. 42% of strikes, juveniles; $t(10) = −2.92$, $p < .01$; $d = 1.69$). Males and females did not shift

TABLE 4 Frequency per individual of specific grips during 20 strikes and outcomes of these strikes

	Grips[a]					Outcomes						
Monkey (sex)	Lift lateral edge	Lift under	Lift top	Down lateral edge	Down top	Straight strike	Slanted strike	Missed strike	Nut fly	Breach hull	Crack nut	Stone drop
Cachaça (male)	17	0	1.5	13.5	3.5	4	5	0	2	1	0	3
Chani (female)	13.5	3	0	4	14	19	0	1	2	0	0	2
Thaís (female)	19	1	0	11	9	17	3	0	0	2	0	0
Presente (male)	19.5	0	0.5	8.5	11.5	8	11	1	4	1	0	0
Coco (male)	19	0	1	15	4	8	6	6	8	1	1	0
Paçoca (female)	12.5	0	3.5	8.5	8	4	10	1	8	1	0	2
Juvenile mean	16.75	0.67	1.08	10.08	8.33	10	5.83	1.50	4.00	1.00	0.17	1.17
Juvenile *SD*	3.05	1.21	1.32	3.97	4.12	6.48	4.17	2.26	3.35	0.63	0.41	1.34
Tomate (male)	11.5	0	8.5	2.5	17.5	10	10	0	6	3	0	0
Catu (male)	13.5	0	2	0	15.5	18	2	0	1	6	1	1
Jatobá (male)	5	0	10.5	9.5	10	18	2	0	2	3	2	0
Piaçava (female)	6.5	0	12.5	0.5	19.5	12	8	0	4	4	2	1
Chuchu (female)	11.5	0	1.5	5.5	10.5	20	0	0	5	3	1	1
Dita (female)	20	0	0	0.5	19.5	14	6	0	9	3	2	0
Adult mean	11.33	0.00	5.83	3.08	15.4	15.33	4.67	0.00	4.50	3.67	1.33	0.50
Adult *SD*	5.35	0.00	5.31	3.75	4.27	3.93	3.93	0.00	2.89	1.21	0.82	0.55

[a]Average frequency of grip for both hands.

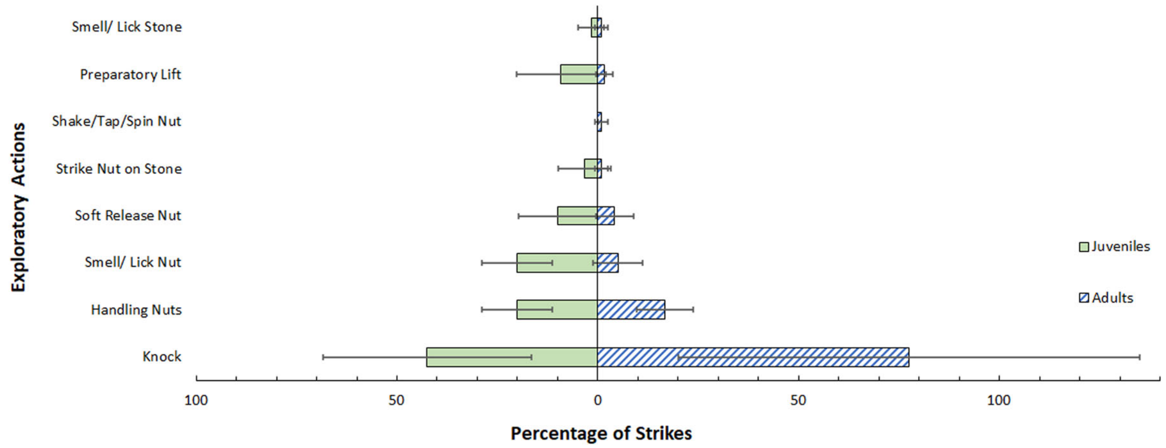

FIGURE 1 Percentage of strikes in which juveniles (left) and adults (right) performed specific exploratory actions. Error bars represent 95% confidence intervals

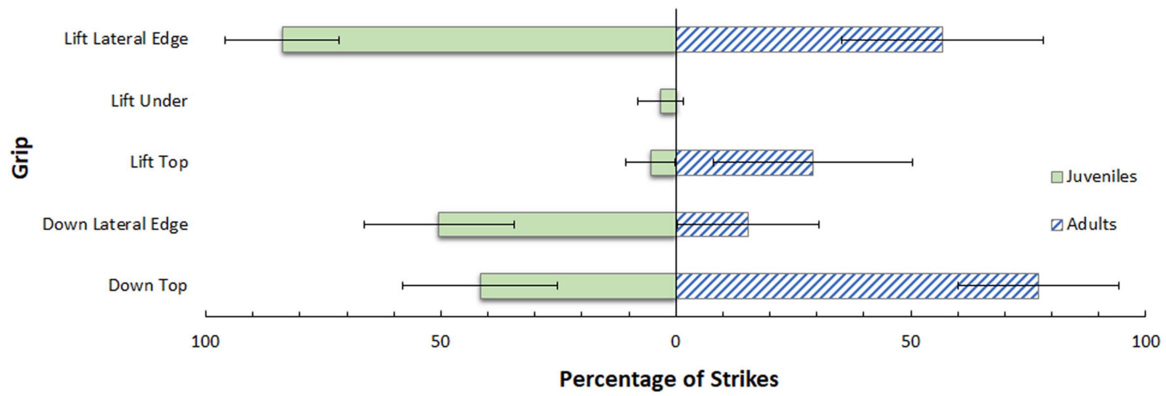

FIGURE 2 Percentage of strikes in which juveniles (left) and adults (right) used specific grips while lifting (lift) and lowering (down) the stone. Error bars represent 95% confidence intervals

their grip on a different percentage of trials ($t(10) = -0.441$, $p = .670$; $d = 0.0249$). Adults gripped the stone on the top on a greater proportion of downward motion during strikes than did juveniles (adults, 86% for the left hand and 68% for the right hand; juveniles, 36% left and 48% right; $t(10) = 3.25$, $p < .01$; $d = 1.87$).

3.3 | Shifting the grip and work on the stone

Across the four monkeys for which we could examine this variable, the average work added per strike when the hands remained on the lateral edges of the stone was 0.0342 J, CI (−0.235, 0.304) and 0.546 J, CI (0.330, 0.761) when the hands shifted to the top of the stone for the downward strike (see Table 5). One of the four monkeys, Tomate, added significantly more work to the stone when he shifted his grip than when he did not ($t(9) = 5.81$, $p < .001$; $d = 2.21$). All four monkeys subtracted work from the stone (slowing it down) for at least 1 of the 10 strikes when they shifted their grip to the top of the stone (range, 1–4) and one of their 10 strikes when their hands remained on the lateral edge of the stone (range, 1–7).

3.4 | Outcomes

Both adults and juveniles experienced similar proportions of straight and slanted strikes (see Figure 3). Juveniles missed striking the nut on a few strikes; adults never missed the nut. The angle of 13% of juveniles' strikes could not be determined and these strikes were not included in this analysis.

Adults breached the hull and cracked the nut more often than juveniles (breach hull, 22 vs. 6, $t(10) = -4.78$, $p < .05$, $d = 2.76$; crack nut, 8 vs. 1, $t(10) = -3.13$, $p < .05$, $d = 1.81$; see Figure 3). Males and females did not differ on the number of nuts cracked ($t(10) = -0.319$, $p = .756$, $d = 0.191$). There was little difference between the two groups for other outcomes. Monkeys rarely dropped the stone, though juveniles did this more often than adults (juveniles 7 times vs. adults 3 times).

4 | DISCUSSION

We compared percussive tooling by juvenile and adult bearded capuchin monkeys using a perceptuomotor perspective. Compared with

TABLE 5 Kinetic energy and work (calculated via the equation work = kinetic energy − potential energy (work = [1/2 mv^2] − [mass × 9.8 m/s × height]) added to strikes with the hammer stone as a function of whether the monkey shifted its grip to the top of the stone at the apex of the lift

Monkey (sex)	Average kinetic energy (J)		Average work added (J)	
	Shift grip	No shift grip	Shift grip	No shift grip
Presente (male)	1.82	1.30	−0.249	0.39
	1.22	1.78	−0.345	0.0748
	0.983	1.01	0.613	−0.104
	1.06	1.75	0.724	−0.478
	1.08	1.75	0.115	−0.385
	2.11	1.43	0.156	0.0595
	2.20	1.04	−0.149	0.322
	2.62	1.35	0.443	−0.272
	1.14	2.25	−0.0632	0.0991
	1.11	1.58	0.0201	−0.0905
Coco (male)	1.85	0.673	0.582	−0.436
	1.01	1.30	−0.201	−0.186
	1.50	0.963	−0.453	−0.305
	1.29	2.17	0.0248	0.219
	1.33	1.63	0.0605	0.258
	1.53	2.14	0.104	0.506
	1.50	2.04	0.022	−0.022
	2.02	2.43	0.33	0.365
	2.41	1.75	0.508	0.221
	1.78	1.88	0.143	0.295
Juvenile mean	1.58	1.61	0.119	0.0266
Juvenile *SD*	0.485	0.463	0.320	0.291
Jatobá (male)	2.38	2.33	0.581	0.534
	2.86	2.85	1.015	0.839
	2.71	3.08	0.807	1.23
	1.34	1.01	−0.332	−0.158
	3.38	3.45	1.74	1.61
	2.67	2.92	1.037	1.17
	2.59	2.73	0.9	0.824
	2.90	2.66	1.31	0.914
	3.87	3.42	1.92	1.62
	2.36	2.59	0.248	0.794
Tomate (male)	1.84	1.08	0.41	0.022
	2.51	1.46	0.87	0.248
	3.63	2.88	1.623	1.086
	3.17	0.0168	1.586	−1.304
	2.49	0.0227	0.906	−1.509
	3.87	0.0119	2.202	−1.097
	1.67	0.0259	−0.403	−1.612
	3.32	0.0227	1.42	−1.509
	2.64	0.0259	0.950	−1.612
	2.28	0.0155	0.645	−1.252
Adult mean	2.72	1.63	0.972	0.0419
Adult *SD*	0.666	1.34	0.666	1.16

other primates, bearded capuchin monkeys use proportionally heavy stone hammers. Striking with heavy stones presumably challenges their balance, grip, and control of the stone. They would benefit from organizing their actions precisely in accord with the particular features of a given stone, just as they apparently benefit from placing nuts precisely in certain positions before striking them (Fragaszy et al., 2013).

We expected that juveniles would engage in more diverse and more frequent exploratory actions with stones than adults, given their lesser experience at handling stone hammers. We further expected this to be the case because captive juvenile tufted capuchin monkeys perform a more diverse set of manipulations on familiar objects than do adults (Fragaszy & Adams-Curtis, 1991). We found support for the first part of this prediction, but not the second. Juvenile capuchin monkeys performed all exploratory actions except for knock about twice as frequently as adults, although overall, adults and juveniles explored the stones in similar ways. Perhaps our ethogram was not sufficiently refined to capture differences in actions performed by individuals of different ages. Alternatively, perhaps by the time that juveniles had mastered hammering sufficiently to participate in this study, they had already dropped most of the ineffective (perhaps also exploratory) actions characteristic of young monkeys learning to crack nuts. Resende et al. (2014) similarly reported that older tufted capuchin monkeys performed less variable actions when cracking nuts of *Syagrus* palms than younger monkeys (age range, 1–5 years). A third alternative is that the exploratory actions towards stones that we observed in this study are not particular to percussive tooling per se, and thus not altered as monkeys master this activity.

Interestingly, monkeys used different exploratory actions in this study than in a previous study of adults using a heavier (1.0 and 1.5 kg) stone to crack more resistant *Orbygnia* nuts (Fragaszy et al., 2019). In that study the only exploratory actions observed were preparatory lift (lifting the stone slightly, then resetting it on the anvil momentarily before striking) and spin (rotating the stone, as it rests on the anvil, around its vertical axis). In the current study, spinning the stone was not observed. Fragaszy et al. (2019) proposed that the exploratory action spin allows the monkey opportunities to grip the stone at different points and choose an effective grip. That spin did not occur in this study suggests that monkeys practice certain exploratory actions in response to the mass of the stone they are handling. Spin might be informative for lifting a heavy or large stone but may not be as important when using a smaller, lighter stone.

The grips used to lift and bring down the stone on the nut differed between the two age groups. Juveniles and adults both tended to grip the stone by the lateral edges during the lift. Juveniles typically maintained this grip when bringing the stone down. Adults, however, typically shifted their grip of one or both hand(s) to the top of the stone. Fragaszy et al. (2019) proposed that shifting the grip to the top of the stone on the downward motion may allow the monkey to add more force to the stone, thus increasing the kinetic energy at impact of the stone with the nut. We were able to examine the kinetic force of two adult and two juvenile monkeys' strikes when

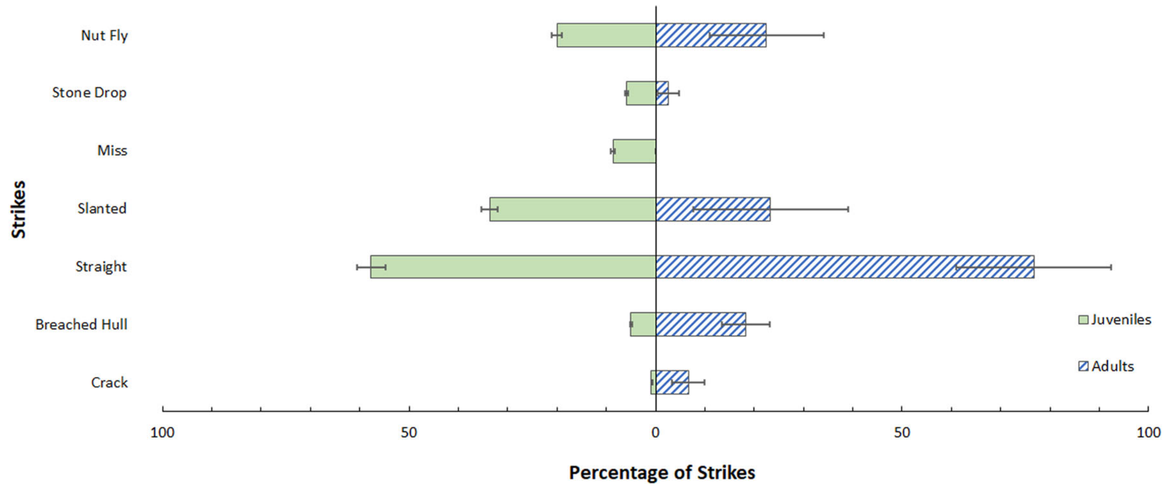

FIGURE 3 Percentage of outcomes from 20 strikes made by juveniles (left) and adults (right). Error bars represent 95% confidence intervals

they shifted their grip to the top of the stone and when they did not. All four monkeys tended to add more work to the stone when they gripped it at the top for the downward motion, although the probability that work was increased when the monkeys' hands gripped the stone on top as opposed to laterally was significant for only one monkey. In fact, we found that independent of the position of the hands, both adult and juvenile monkeys occasionally subtracted work from the stone on the downward motion. This unexpected pattern invites further exploration. One possible explanation is that they did so to reduce the force of the strike, so as not to smash the kernel and render it inedible. This seems unlikely, however. Mangalam, Izar, Visalberghi, and Fragaszy (2016) reported that adult capuchin monkeys in the same study population lowered a heavier stone to crack piaçava nuts (*Orbygnia* spp.) with a slower velocity than they produced with a lighter stone to crack tucum nuts. Yet piaçava nutshells are considerably more resistant to fracture than are those of the tucum nuts (Visalberghi et al., 2008), and the kernels of piaçava nuts are tough and not susceptible to smashing (Fragaszy, personal observation). Thus, they put zero to negative work into the stone when cracking piaçava nuts using a heavier stone, compared with largely positive work into the stone when cracking tucum nuts with a lighter stone (as we found in the present study). This contrast suggests that monkeys add (positive or negative) work into the stone to control the stone and/or their balance during striking, rather than (or more than) to influence the kinetic energy of the stone at impact with the nut. Field experiments could aid us in evaluating this hypothesis. In general, we do not yet understand the range or functional consequences of the monkeys' modulation of the body + object system during hammering. Indeed, we are just beginning to explore these topics in humans' actions with objects (Mangalam, Chen, McHugh, Singh, & Kelty-Stephen, 2020).

Why might adult monkeys regularly shift their grip when they are not adding positive work to the stone? It is possible that positioning the hands on the top of the stone during the downward strike allows the monkey to add work to the stone when greater kinetic energy at impact is useful and they can do so without compromising control and balance, but that greater kinetic energy is not needed when cracking the relatively less resistant *Astrocaryum* nuts used in this study. In other words, perhaps moving the hands to the top of the stone at the zenith of the lift is a habit that is useful in some circumstances but performed outside of those circumstances as well. Alternatively, perhaps moving the hands to the top of the stone allows the monkey to manage some other feature of the task, such as controlling the trajectory of the stone during rebound, or to protect the fingers from striking the anvil. These are not mutually exclusive alternatives.

On occasion, adults would lift the stone with a top grip, but they did not lift from underneath. One juvenile lifted the stone from underneath on one occasion, and another, three times. The juveniles' lifting from underneath the stone may reflect less strength or smaller hands compared with adults, or it may simply reflect more variable grips by juveniles. Overall, individual monkeys in both groups used idiosyncratic combinations of grips for lifting and bringing down the stone. Adults tended to be more consistent in the grips they used for each strike. Thus, gripping the stone is a component of nut-cracking where juveniles are more variable than adults.

Adults and juveniles produced similar frequencies of straight strikes (strikes in which the stone touched the nut within 15° of vertical). Straight strikes were more frequent than slanted strikes for both age groups. However, slanted strikes accounted for roughly a quarter of strikes for both age groups. Both age groups also experienced loss of control of the nut (nut fly) or the stone (stone drop) at similar rates. This suggests that maintaining control over the stone upon impact might be difficult for bearded capuchin monkeys of all ages.

Contrary to our expectations, we found that the exploratory actions, functional actions, and strike outcomes of juvenile and adult monkeys during nut-cracking with a 540 g stone were largely the same. It appears, by these measures, that even the 2-year-old bearded capuchin monkey in our sample was competent at using stone hammers. Similarly, we have some evidence that juveniles place nuts into pits, apparently using haptic information, with the same positional precision as adults (Fragaszy et al., 2013). However, the juveniles in this study had minimal success at breaching the hulls or cracking tucum nuts, in line with findings from the study by Resende et al. (2008) of young (<3 years old) tufted capuchin monkeys (*Sapajus* spp.) attempting to crack relatively smaller, less resistant nuts of the palm *Syagrus romanzoffiana*. It appears that juvenile tufted capuchins aged 5 years and younger, even after they master the basic actions of placing the nut, lifting the stone and striking the nut are still mastering the finer points of using stone hammers to crack nuts, even nuts of those species relatively less resistant to fracture.

What about cracking nuts might challenge juvenile capuchins? Some candidate features of skilled action that were not assessed in this study, but that have been documented in adults, include (a) lifting the stone to an individually consistent amplitude across stones of varying mass, (b) subtle variations in the amplitude and velocity of strikes in accord with the state of the tucum nut following each strike (hull intact, hull breached but nut uncracked, or fully cracked) and (c) strong joint synergies in the lower body that presumably stabilize the monkeys' dynamic balance in bipedal stance, and thus stabilize the trajectory of the hammer (Mangalam & Fragaszy, 2015; Mangalam, Pacheco, Izar, Visalberghi, & Fragaszy, 2018; Mangalam, Rein, & Fragaszy, 2018). Perhaps juveniles have not yet mastered these aspects of controlling their own bodies during effortful lifting and striking as fully as adults. To that list we add the one notable difference in actions between adults and juveniles observed in this study: repositioning the hands on the stone during the striking action, which the adults do routinely but the younger monkeys do less often. The functional consequence for cracking the nut of this action is unknown but deserves investigation, along with variations in work added or subtracted from the stone during the downward strike.

We note that our analyses are based upon a small sample of juveniles and adults (six of each) in one group of monkeys. Clearly replication of this study is warranted to confirm the findings and to examine interactions of independent variables (body mass, age, sex) that we were unable to address.

Bril (1986) examined how young children (2.6–9 years) and adult humans in Mali used pestles to pound cereals while standing upright, a percussive task sharing with nut-cracking (as capuchin monkeys perform it) the requirement for stable bipedal stance while lifting and striking with a heavy object. Among several differences noted, adults performing this task stood with one foot in front of the other and did not change the position of their feet between strikes. Children, in contrast, shifted the positions of their feet frequently between strikes. Adults sequentially extended the hip, shoulder, and elbow to lift the pestle; children did not. Bril suggested that adults used a coordinative structure of movements that kept the center of gravity of the pestle as near as possible to the body, a position that reduced the effort required to lift and lower it. Children developed their own optimal coordinative structure during this activity across several years of practice and growth. Although the parallels between pounding cereals as practiced in Mali at the time of Bril's study and capuchin monkeys cracking nuts are not complete, the comparison does highlight that the motoric components of the actions in these tasks continue to challenge young individuals of both species for years after mastery of the sequence of actions and the orientation of objects. A full understanding of percussive tooling as practiced by adult bearded capuchins (and by other nonhuman primates) requires understanding the mastery of control of vigorous actions with a held object, as well as mastery of sequences of actions and orientation of objects to each other, that have been the focus of previous studies (Aiempichitkijkarn, 2017; Inoue-Nakamura & Matsuzawa, 1997; Resende et al., 2008; Tan, 2017).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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