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The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil

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Abstract

The use of pounding stone tools (PSTs) is a customary behaviour in several wild populations of capuchin monkeys; most of these monkeys use PSTs primarily to open hard palm nuts. Here, we describe the use of PSTs in two not previously studied groups of capuchin monkeys (*Sapajus libidinosus*) in Serra da Capivara National Park (SCNP), northeastern Brazil, and compare them to other groups and populations. Capuchins from SCNP are one of the only known population that habitually use PSTs for several purposes other than nut processing, including cracking seeds and fruits, breaking and/or enlarging holes in tree trunks or rocks, and pulverizing pebbles. Moreover, they use PSTs sequentially with probe stick tools to access hidden prey. The average size of PSTs was larger than the average locally available stones, suggesting active choice. The two groups exhibited more diversity in the use of PSTs than any other known population to date.

Keywords

tool use, capuchin monkey, pounding stone tool, Caatinga, *Sapajus libidinosus*, *Cebus libidinosus*.

1. Introduction

Tool use in animals has been observed in several groups of animals, from arthropods to vertebrates, but in most cases, it is species-specific and stereotyped (Shumaker et al., 2011). Among tool-using primates, tool use tends to be more flexible, diverse and is socially biased, as reflected in the inter-population variation in toolkits of chimpanzees (Whiten et al., 1999, 2001) and orangutans (van Schaik et al., 1996, 2003; Shumaker et al., 2011). The customary use of lithic tools by wild non-human primates, however, is apparently restricted to chimpanzees (Boesch & Boesch, 1983; Luncz & Boesch, 2014), long-tailed macaques (*Macaca fascicularis*; Malaivijitnond et al., 2007) and capuchin monkeys (Ottoni & Izar, 2008).

Several wild populations of robust capuchin monkeys (*Sapajus* spp.) use stones as tools to pound and crack open palm nuts (Fragaszy et al., 2004; Ottoni & Izar, 2008; Canale et al., 2009; Ferreira et al., 2010; Spagnoletti et al., 2012; De Moraes et al., 2014; Mendes et al., 2015). Although palm nut cracking appears to be the most widespread form of stone tool use in capuchins (Ottoni & Izar, 2008), there are reports that capuchins also use stones to crack manioc seeds (Ferreira et al., 2010; De Moraes et al., 2014) and cashew nuts (Spagnoletti et al., 2012; Sirianni & Visalberghi, 2013). The frequency of tool-aided processing of these food items, however, is low compared to that of palm nuts in groups that use this resource. In some of the best studied capuchin groups in Fazenda Boa Vista (FBV, Brazil), palm nuts are, by far, the resource the most frequently processed with the aid of stone tools (Spagnoletti et al., 2012). Given the heavy weight of the stones employed to crack high-resistance palm nuts (median 1059 g), body mass requirements are likely the reason for the highly male-biased frequency of stone use and success rate (Spagnoletti et al., 2011).

The customary use of pounding stone tools (PSTs) to acquire several kinds of resources (other than nuts) has been systematically reported only in wild groups of bearded capuchin monkeys (*Sapajus libidinosus*) in Serra da Capivara National Park (SCNP). These monkeys use stones to crack open a diversity of encapsulated foods (Moura & Lee, 2004; Mannu & Ottoni, 2009). There is indirect evidence that this is a common behaviour in other locations, as well (Ferreira et al., 2010; De Moraes et al., 2014). However, in SCNP, the use of PSTs also occurs in other foraging contexts, such as cracking trunks and branches, enlarging openings in rocks, and loosening soil to aid digging (Mannu & Ottoni, 2009). The SCNP capuchins also use stones in communicative contexts, including banging them against the substrate in threat displays (Moura, 2007) and throwing them during sexual displays (Falótico & Ottoni, 2013). They employ other materials as tools as well, such as wooden twigs used as probes (Mannu & Ottoni, 2009; Falótico & Ottoni, 2014; Haslam & Falótico, 2015). There are also a few reports of multiple and sequential tool use in some groups in SCNP, including the use of different tools during the same episode (Mannu & Ottoni, 2009).

Most of the PST use in SCNP is not obligatory, that is, it is not needed to obtain the resource, but might be a way to save processing time for some resources or to circumvent plant defences. The use of stone tools can be an energy-consuming behaviour (Liu et al., 2009); therefore, it is expected that capuchins would use tools of different sizes for different food resources (i.e., smaller stones for low-resistance targets and heavier stones for high-resistance ones). This has been demonstrated in Fazenda Boa Vista (FBV) (Spagnoletti et al., 2011), Serra Talhada (De Moraes et al., 2014), and other groups in Rio Grande do Norte, Brazil (Ferreira et al., 2010).

Some of the palm nuts (*Attalea* spp.) cracked by FBV groups are harder than seeds and fruits consumed by SCNP capuchins, and the stones used as tools are heavier, averaging 1096 g (Fragaszy et al., 2004; Visalberghi et al., 2007). The heavier tools needed to break harder nuts may be the reason for females (which are on average smaller than males) to be less effective, and, indeed, the weight of monkeys is the best predictor for success, not the sex (Fragaszy et al., 2010a). This is also evident when episodes involving only low-resistant fruits or nuts were compared because, in this cases, sex-based differences were not found (Visalberghi et al., 2007; Spagnoletti et al., 2011).

Here, we describe the PSTs of two previously non-studied groups of capuchin monkeys from SCNP, report the diversity of tools selected and the frequency of their use, and compare them to previously described behaviours in other groups in the park and other populations. The aims of our study were to: (i) describe PST use, in particular the presence of sequential tool use, in two groups not yet studied in SCNP; (ii) compare the dimensions of the PSTs used for each type of resource to identify variation in the processing of those resources; (iii) compare PST dimensions with locally available (control) stones to identify any choice bias; and (iv) compare each group's PST use behaviour to that of other groups and populations previously studied.

Our first hypothesis (H1) is that the selection of PSTs is related to the hardness of the target. Based on H1, we predicted (1) a positive correlation between PST weight and the resistance of the target, (2) because SCNP capuchins do not process high resistance food items such as palm nuts, the PSTs they use will be smaller than those used to process hard palm nuts in other capuchin populations, and (3) indication of a potential degree of active selection of PSTs from the available stones on the area.

Hypothesis 2 (H2) is that sex differences in PST use frequency and efficiency are caused by body size differences. When harder resources are processed, larger individuals (males) will be more efficient than smaller ones (females). Accordingly, we predicted that because SCNP capuchins do not process high-resistance items, such as palm nuts, there will be lower or no sex bias regarding frequency and efficiency of PST use.

2. Material and methods

2.1. Study site and subjects

The study was conducted at SCNP, in Piauí State, northeastern Brazil. The SCNP area is classified in the geoclimatic domain called Caatinga: a mosaic of xerophytic vegetation with patches of deciduous forest along the narrow, more humid valleys surrounded by high cliffs within a semi-arid climate. The study area was located near the southeastern border of the park (limiting coordinates: North: 8°49′S, 42°33′W; South: 8°51′S, 42°33′W; East: 8°50′S, 42°32′W; West: 8°50′S, 42°34′W).

We observed two partially sympatric groups. The Pedra Furada (PF) group was composed of 45 individuals (8 adult males, 13 adult females, 6 subadult males, 5 juvenile males, 5 juvenile females, 6 juveniles, and 2 infants) at the beginning of the study. The Bocão (BC) group was composed of 27 individuals (5 adult males and 7 adult females, 2 subadult males, 10 juveniles, 3 infants). Age was estimated by body size/proportion when birth date was unknown. These groups were systematically followed for 20 days per month, from the initial contact early in the morning to sunset or until contact was lost. Data for the PF group were collected for 23 months (September 2007–July 2009, total of 226 days), and for the BC group for 12 months (March 2008–February 2009, total of 99 days).

Capuchin monkeys at SCNP obtain most of their food by exploiting naturally occurring resources. The groups studied were also provisioned in the dry months of July to November by the park staff (approximately 3–4 dozen bananas every two days), and spent less than an hour per day eating the provided food. The caloric value of each banana is around 398 kJ (95 cal) (NHS, 2014) and the total energetic value for the estimated quantity of bananas provided was 9552 kJ per day. For PF group, the caloric input of the bananas was 212 kJ/individual and for BC group, it was 354 kJ/individual. The daily energy expenditure for brown capuchin monkeys (*S. apella*) is estimated between 1200 and 1400 kJ (Janson, 1988).

2.2. Data collection

We recorded all observed occurrences (Altmann, 1974) of tool-related behaviours (following the definition from Shumaker et al., 2011). Because some of the tool use behaviours were infrequent, we recorded ‘all occurrences’ to increase the number of tool-use episodes observed. Based on previous research in the same location (Mannu & Ottoni, 2009), we were aware of the difficulty of using interval individual sampling. In our opinion, any randomized sampling would not provide enough data, especially for the rarer types of tool-use behaviour also investigated, such as stone throwing and stick tool use.

When an individual was observed using a tool, that monkey became the focal animal and the tool-use event was recorded until the resource target was broken and consumed or the focal animal left the site without success. We did not use a regular focal animal sampling (e.g., sampling all individuals for a same period) because this kind of sampling would not provide enough samples of the less frequent tool-use behaviours. TF and a field assistant conducted the observations. The initial identification of the groups was made by TF and a field assistant, and during the research, the identification of individuals by the field assistant was checked by TF on a regular basis. TF also trained the field assistant to collect data, overseeing the data collection during the first month to evaluate and correct the field assistant’s data collection procedures. For all these reasons, we did not perform statistical reliability tests.

Stone tool use was recorded using audio and video equipment, when possible. For the data presented in this manuscript, video and audio records were equivalent. Most information (ID, resource, substrate) was recorded by narrating the episode, even when filming. The video was used for more detailed analyses of tool use (including other forms of stone and stick probe tool use) not covered here.

The identity of the monkeys was recorded when possible; when it was not, we recorded sex and age category. We used the following categories for age: infant (0–2 years), juvenile (2–5 years), subadult (only males, 5–7 years), and adult (more than 7 years or following the first pregnancy). For most monkeys, we estimated ages at the beginning of the study, because the groups were not previously studied.

For each episode, we recorded the function of the tool, the target substrate/resource, and success in acquiring the food. When identification was possible (24% of the episodes), the stones used as tools were collected, measured, and weighed. For valid comparison with other groups and populations, we used the absolute frequency relativized by the contact time with the group and group size.

To describe the stone tools, the longest axis was recorded as the stone's length, and three measurements were taken for both width and thickness. The measurements of width were taken at 1/4, 1/2 and 3/4 of the length, perpendicular to the length, and on the widest size of the stone. Similarly, three thickness measurements were taken perpendicular to the width and length (Figure 1).

To compare the PSTs to the available stones, the latter were sampled at 44 randomly selected GPS coordinates inside the limiting coordinates of the home ranges of the capuchin monkey groups studied. If a location was inaccessible (e.g., a mountain top), then sampling was done at the nearest attainable position. At each location, an area with a 50 cm radius was drawn, and all loose hard stones (quartzite, quartz and sandstone) longer than 2 cm at their major axes were measured following the same method as described for the stone tools.

2.3. Statistics

To determine if the PSTs used to crack the same kind of food items were different in the two groups, we used a t-test to compare measurements of the PSTs collected from each group. To compare PST dimensions between pebble pulverization and other targets we used the Mann–Whitney test because we had too few episodes of pulverization to permit the use of the parametric test. To compare the PST weight employed to process different resources, we used the Kruskal–Wallis test, analysing only data from resources with more than five recorded episodes. These last analyses were conducted with data from both groups combined because we had fewer episodes and variety for BC group, the groups used an overlapping area (thus, used largely the same environment), and comparing the PST sizes between the two groups (Mood's median test) showed no significant difference (see Results). All tests were two-tailed with alpha set at 0.05 and performed in SPSS 22.

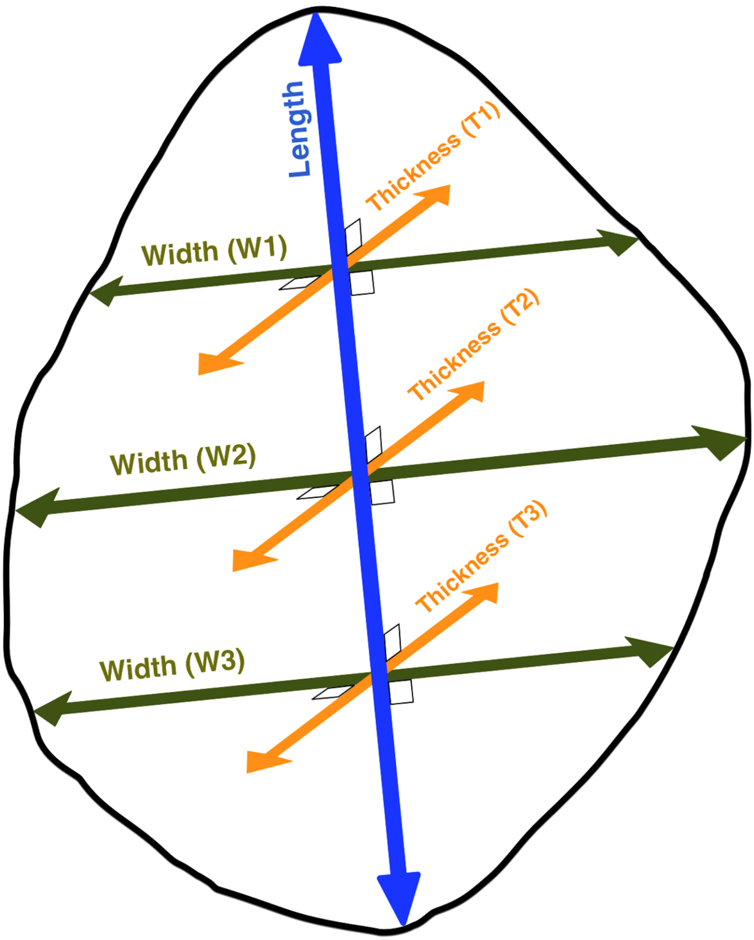

Figure 1. Measurements for assessment of stone dimensions. The width was measured at the widest axis, perpendicular (90°C) to the length. The thickness was measured perpendicular to the width and length. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

2.4. Ethics

The research in SCNP was exclusively observational and the researchers had only visual contact with the monkeys. The research was previously approved by the Instituto Brasileiro do Meio Ambiente (IBAMA) and Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), authorizations 037/2007/DIREC and 14825-1, and adhered to the Animal Behavior Society Guidelines for the Use of Animals in Research, and followed all ethical guidelines for animal research of the Institute of Psychology-USP.

3. Results

Capuchins in SCNP used PSTs to access hidden resources or to process encapsulated food (Table 1). The overall rates of PST-use episodes (ep) were 0.035 ep/h per individual (BC group) and 0.021 ep/h per individual (PF group). Tool transport was observed during 217 episodes, for a distance of 3.14 ± 3.1 m (average ± SD). The maximum transport distance was estimated to be 20 m. Because there were only 39 stones collected for BC group and the overall PST size was not significantly different between the two groups (Mood's median size, $\chi^2 = 1.6$, $p = 0.199$), we combined group data for stone size analysis.

Table 1.
Targets of the pounding stone tools used by SCNP capuchin monkeys.

Target	*N*	%
Cashew nut (*Anacardium occidentale*)	854	50.9
Manihot spp. seed	189	11.3
Cordia rufescens fruit/seed	110	6.6
Embedded quartz pebble[a,b]	96	5.7
Trunk/branch[a,c]	91	5.4
Rock crevice[a,d]	58	3.5
Thiloa glaucocarpa tuber	48	2.9
Invertebrate	4	0.2
Provided food (corn/pumpkin seed)	28	1.7
Mango seed (*Mangifera indica*)	24	1.4
Unknown seed	67	4
Unknown root	16	0.9
Other[e]	93	5.5
Total	1678	

When not possible to identify the item we searched for, we classified the event according to the targeted material.

[a] Food item not always identified.

[b] Target could be prey or the dislodgement/pulverization of pebbles.

[c] Food item was usually insect larvae, carpenter bees or honey.

[d] Food item was usually preys (e.g., lizards, scorpions, spiders). These crevices are common hiding places for these animals.

[e] Items not in any other categories and in low frequency (< 2) of occurrence (e.g., cactus, other fruits, termite mounds, cement pavement).

Table 2.
Dimensions of the collected pounding stone tools ($N = 304$) and the ratios between these measurements.

	Mean	SD	Median	Range
Weight (g)	221.4	236.4	150.0	18–1550
Length (cm)	7.4	2.8	6.8	3.1–21
Width (cm)	4.7	1.7	4.4	2.2–13.4
Thickness (cm)	3.5	1.1	3.3	1.3–8.4
Length/width	1.6	0.3	1.5	1.1–2.6
Length/thickness	2.2	0.7	2.0	1.2–7.9
Width/thickness	1.4	0.4	1.3	0.8–6.3

We collected 304 PSTs and their average dimensions are shown in Table 2. Adults used bigger and heavier stones than juveniles (t-test: $t = -2.1$, df $=$ 376, $p = 0.036$), but there were no sex differences in these variables (mean $\pm$ SD: males $= 255.7 \pm 325$ g; females $= 201.6 \pm 226.5$ g; t-test: $t = 1.49$, df $= 326$, $p = 0.137$).

3.1. Targets processed

Table 3 shows the number of episodes and the success of PST use to open the five most frequent target items: cashew nuts (*Anacardium occidentale*), *Manihot* seeds, *Cordia rufescens* seeds, trunks and rock crevices.

The overall PST use success rate was of 70.8%; however, there were substantial differences according to the targeted resource. The monkeys were more successful when targeting seeds and nuts than when trying to obtain food from trunks or crevices (Table 3).

Stone-aided processing of cashew nuts, both ripe and unripe, was observed 840 times. Cashew nuts were the main items processed with PSTs in the studied groups. The weight of the stones used to crack cashew nuts was 233.6 ± 260 g (average $\pm$ SD, $N = 131$).

The genus *Manihot* includes several species known for latex production (Wisniewski & de Melo, 1983). Capuchins eat the kernel of *Manihot* spp. seeds, which are 1–2 cm in length. The seed is so small that it was not opened by capuchins with their hands, but was cracked with their molars. Most observations of *Manihot* seed cracking happened during a 2–3-week period near the end of the research period when the monkeys from the PF group were foraging in an area rich with these plants (189 episodes, Table 3).

Table 3.
Observed episodes and frequency of success of acquisition and ingestion of food items with pounding stone tools by capuchin monkeys from PF and BC groups at SCNP.

	Anacardium nuts		*Manihot* seeds		*Cordia* fruit/seed		Rock/trunks	
	N	Success (%)	*N*	Success (%)	*N*	Success (%)	*N*	Success (%)
Male	552	75.7	73	97.3	73	90.4	113	17.7
Female	225	73.7	103	99.0	30	90.0	17	17.6
Unknown	63	65.1	13	100	7	85.7	19	22.2
Total	840	74.4	189	98.4	110	90.0	149	18.1
Adult	397	80.6	129	100	37	89.2	32	15.6
Subadult	95	76.8	13	100	12	100	26	11.5
Juvenile	347	66.8	47	93.6	61	88.5	91	20.9
Infant	1	0	0	–	0	–	0	–
Total	840	74.4	189	98.4	110	90.0	149	18.1

Rock crevices ($N = 58$) and trunks ($N = 91$) were treated together in the analyses, as hiding places for prey.

No PSTs were collected for these episodes because they happened in areas of thorn bush vegetation that were hard to access and the tools were small and difficult to tell apart from the other stones at the site.

The third most consumed resource was *Cordia rufescens*, a 4–8 m-tall tree with 1.5–2 cm-long fruits. The monkeys ate the ripe fruits or broke the unripe ones and the seeds with PSTs. The seeds were sometimes collected by the monkey from its own faeces, just after producing it. This behaviour appeared to be to collect the seeds, and not a faeces re-ingestion behaviour. We observed 110 episodes of *C. rufescens* seeds and fruit cracking, and the average weight of the collected PSTs was 136.1 ± 145.4 g (average $\pm$ SD, $N = 39$).

In 149 events pounding tools were used to crack or enlarge openings in trunks and rock crevices, hiding places for prey (arthropods and small vertebrates). Trunks and rock crevices were analysed together because they were similar targets, hiding places of prey, and not the food item itself. The success rate (proportion of ingested prey) was lower than for other food items, being 26.4% ($N = 91$) when targeting tree trunks and branches, and only 5.2% ($N = 58$) for rock crevices. The PSTs had a weight of 228.75 ± 75.2 g (average $\pm$ SD, $N = 37$).

Table 4.
Observed episodes of capuchin monkeys using pounding stone tools (PSTs) to pulverize or dislodge quartz pebbles at SCNP.

	Sniff	Lick	Rub	Total
Male	30	7	12	60
Female	1	0	0	3
Unknown	15	5	3	33
Total	46	12	15	96
Adult	16	3	6	33
Subadult	4	0	1	11
Juvenile	26	9	8	52
Total	46	12	15	96

Frequency of the total episodes were powder direct behavior (sniff, lick and rub) was observed. More than one of these behaviors could happen in the same episode.

We observed 96 events in which the capuchin monkeys struck stones against sandstone-embedded pebbles, with the apparent purpose of pulverizing, breaking, or dislodging them from the sandstone conglomerates. It was frequently difficult to distinguish the goal, and sometimes the behaviours happened sequentially, with the monkey pulverizing and then dislodging the stones. We never observed the monkeys using the dislodged stones, but other groups were observed using them to continue the pulverization (Mannu & Ottoni, 2009). The monkeys sometimes licked, sniffed, and rubbed the percussion spot, apparently for the resulting stone powder (Table 4, Figure 2). The purpose was difficult to identify, and in most of our observations it was not possible to distinguish, but the locale and tool use were similar. Therefore, we pooled both contexts of tool use together. This behaviour leaves many marks on the target stones, which sometimes broke, even producing flakes by fracturing the embedded stone (Figure 2). Flake production did not seem intentional, as the flakes were never used by the monkeys. The PSTs used for this task (weight: 635 ± 589 g, average ± SD, $N = 6$) were significantly heavier than the PSTs used for cracking encased food (Mann–Whitney: $N_1 = 296$, $N_2 = 6$, $U = 1599$, df $= 335$, $p = 0.009$). Juveniles and adults were observed performing this behavior to a similar degree, with 54.2% of the episodes by juveniles and 45.8% by adults. For the episodes where sex identification was possible, 95.2% of the individuals were males.

Figure 2. Juvenile capuchin monkey using a PST on a pebble conglomerate. The stone tool broke when hitting the targeted embedded pebble. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

3.2. Sequential tool use

During most pounding tool-use events, only one kind of tool was used, but in 22 events, we observed the sequential use of PSTs and stick probes to reach a single resource (Table 5). Typically, the individual was chasing prey (e.g., lizards or scorpions) or searching their potential hiding places. They used probe tools in rock crevices or carpenter bee (*Xylocopa* spp.) nests to flush out the prey (Falótico & Ottoni, 2014), alternating them with the stone tools employed to enlarge the openings of the prey hiding places. Only males were observed performing this behaviour and only three episodes (13.6%) were successful.

3.3. Stone tools dimensions

There were size differences between PSTs used for each of the six targets analysed (cashew nuts, *Cordia* seeds, *Thiloa glaucocarpa* tuber, mango seeds, tree trunks and crevices) (Kruskal–Wallis test $= 24.2$, $df = 5$, $p < 0.001$). Pairwise comparison, however, revealed that the only significant dif-

Table 5.
Episodes ($N = 22$) of sequential tool use.

Sequence of tools	Sex	Age	Target	Success
PST; SP; PST; SP; SP	M	Adult	Rock crevice	No
SP; SP; PST; SP	M	Juvenile	Rock crevice	No
PST; PST; SP	M	Juvenile	Rock crevice	Yes
PST; SP; SP	M	Adult	Trunk	No
PST; SP; PST	M	Juvenile	Trunk	No
PST; SP; SP	M	Adult	Trunk	No
SP; SP; PST	M	Subadult	Trunk	Yes
SP; PST; SP	M	Juvenile	Rock crevice	No
SP; PST; PST	–	Juvenile	Rock crevice	No
PST; SP	M	Juvenile	Rock crevice	No
PST; SP	M	Juvenile	Termite nest	No
PST; SP	M	Juvenile	Termite nest	No
PST; SP	M	Adult	Trunk	No
PST; SP	–	Juvenile	Rock crevice	No
PST; SP	M	Subadult	Trunk	Yes
SP; PST	M	Adult	Rock crevice	No
SP; PST	–	Juvenile	Rock crevice	No
SP; PST	M	Juvenile	Trunk	No
SP; PST	M	Juvenile	Trunk	No
SP; PST	M	Juvenile	Rock crevice	No
SP; PST	M	Adult	Rock crevice	No
SP; PST	M	Juvenile	Trunk	No

PST, pounding stone tool; SP, stick probe.

ferences were between PSTs used to process *Cordia* seeds and all of the other resources/targets (cashew nuts: Kruskal–Wallis $= 32.7$, $p = 0.006$; tree trunks, Kruskal–Wallis $= 51.9$, $p = 0.002$; Crevices, K–W $= 32.7$, $p = 0.006$; mango seeds, Kruskal–Wallis $= -93.5$, $p = 0.001$; *T. glaucocarpa* tuber, K–W $= -69.5$, $p = 0.004$). PSTs used with *Cordia* seeds were significantly smaller than those used with all other seeds.

The size and shape of the collected PSTs were compared with those of the available stones collected in the home range of the groups. We collected 1480 'control' stones and compared them to those used as tools. There were significant differences between these samples. The stones selected for use as tools were, on average, heavier, larger and rounder than the average of available stones (Table 6).

Table 6.
Size and shape (ratios) measurements of stones used as tools and locally available (background) stones.

	Stone tools (mean ± SD)	Locally available stones (mean ± SD)	*t*-test		
			t	df	*p*
N	304	1480			
Weight (g)	221.4 ± 236.4	85.6 ± 156.5	8.9	1147	<0.001
Length (cm)	7.4 ± 2.8	5.2 ± 2.8	15.9	1147	<0.001
Width (cm)	4.7 ± 1.7	3.2 ± 1.3	19.8	1147	<0.001
Thickness (cm)	3.5 ± 1.1	2.2 ± 0.9	24.9	1147	<0.001
Length/width	1.6 ± 0.3	1.6 ± 0.5	−0.9	1147	0.38
Length/thickness	2.2 ± 0.7	2.4 ± 1.3	−3.7	1147	<0.001
Width/thickness	1.4 ± 0.4	1.5 ± 0.5	−4.5	1147	<0.001

4. Discussion

The contexts of PST use by SCNP capuchin monkeys are manifold. The wild groups of SCNP capuchin monkeys are the only ones known to use stone tools customarily for reasons other than cracking encased food items, including use as a digging aid (Mannu & Ottoni, 2009).

4.1. Resource processing

Regarding the resources/targets, as predicted by H1, we found significant size differences between PSTs used to process *Cordia* seeds and those used to process other resources; the tools used for cracking very low-resistance seeds were smaller. This result supports our prediction that the monkeys selected PST weights according to the resistance of the food items they process. PSTs in PNSC are on average smaller than the ones used in FBV to process hard palm nuts.

On the other hand, the mean weight of the PSTs used for food processing in our study (238 g) was higher than that of PSTs used by other capuchin groups and populations to process resources other than palm nuts: FBV, 127 g (Spagnoletti et al., 2011); Luis Gomes, 65 g (Ferreira et al., 2010); and Serra Talhada, 189 g (De Moraes et al., 2014). However, they were much smaller than the average size of PSTs for cracking palm nuts, which is around 1 kg (Ferreira et al., 2010; Spagnoletti et al., 2011; De Moraes et al., 2014). The PSTs used to pulverize or dislodge pebbles (a high-resistance target), as we predicted, were on average much larger (the biggest PSTs registered in this study).

Overall, the monkeys exhibited greater success rates in obtaining food when using PSTs to process plant items than when using probes to hunt animal prey in trunks or rock crevices (Falótico & Ottoni, 2014). We observed higher success rates by adults/subadults in the acquisition of resources than by juveniles, as expected based on ontogeny development (Table 3).

As predicted by H2, we found no difference in the success rates between males and females. This result differs from that reported for groups of *S. libidinosus* from FBV that dealt with high-resistance nuts, where males were much more efficient (Fragaszy et al., 2010a; Spagnoletti et al., 2011), but it is similar to the results for processing low-resistance nuts at the same site, where the sex bias was also absent (Spagnoletti et al., 2011).

The capuchins of SCNP exhibited several tactics in response to the challenges of hunting hiding prey. They used PSTs to facilitate access to the hiding places and probing tools to expel the prey, sometimes using both tools together. Capuchin monkeys use tools sequentially to solve problems in laboratory settings (Westergaard & Suomi, 1993; Westergaard et al., 1997), but to date this has only been observed in the wild in the SCNP population (Mannu & Ottoni, 2009; present study). The sequential use of percussive tools and probes, however, was only exhibited by males, as expected based on previous results because females almost never use probe tools (Falótico & Ottoni, 2014). In reports of multiple tool use by other groups in SCNP (JB and OT groups), three out of the four episodes were performed by males (unknown sex in one case) (Mannu & Ottoni, 2009).

4.2. Stone selection

The differences in size and weight between the stones used as tools and locally available stones suggest that the capuchins select a restricted size range from the available stones to use as tools (Table 6), supporting H1's third prediction. The selection of PSTs has been naturalistically observed or experimentally tested in other groups of *S. libidinosus*. The monkeys appeared to adequately select stone tool weights that positively correlated to the hardness of the item to be processed and the size of the monkey (Liu et al., 2009; Ferreira et al., 2010; Fragaszy et al., 2010a, b). The same appears to happen in SCNP. The PST sizes do not simply reflect the average size of available stones; instead, the monkeys seem to select a narrower range of dimensions. There were shape differences between the selected stones and the locally available ones (Table 6). The comparison of the means of the length/width/thickness ratios (a proxy of shape) between selected and locally available stones samples revealed significant differences on most of them.

4.3. Group and population comparisons

In the two groups previously studied, Jurubeba (JB) and Oitenta (OT), the frequencies and contexts of PST use were different (Mannu & Ottoni, 2009). In these groups, PSTs were used mostly (47.8%) to crack jatobá fruits (*Hymenaea courbaril*), a resource not abundantly available in the home range of the PF and BC groups (we found only one abandoned processing site of this item at the limits of BC group home range; TF, personal observation). Cashew trees and *C. rufescens* occur in both areas, but there are no reports of use of PSTs to process these species by JB or OT groups (Moura & Lee, 2004; Mannu & Ottoni, 2009).

On the other hand, other groups in the park and in other *Caatinga* areas process *Manihot* seeds with stone tools (Moura & Lee, 2004; Ferreira et al., 2010; De Moraes et al., 2014), and use stones to open or enlarge trunk and rock crevices (Mannu & Ottoni, 2009). Three cases of sequential tool use (similar to the events described here) were also observed in the JB and OT groups, as well as the use of stones to pulverize or dislodge pebbles (Mannu & Ottoni, 2009). The purpose of this latter behaviour is still unknown. Although it occasionally seemed that the monkeys were looking for food items, dislodging the stones to access something, most of the time they merely rubbed or sniffed the stone powder with no obvious consequences. An explanation for the latter behaviours could be the search for some mineral, such as sodium chloride, but preliminary tests done by F. Andrade (unpublished data) did not identify any biologically active substance in the collected powder samples, only silica. An alternative hypothesis would involve the pulverization of lichens on the stones. Capuchins from genus *Cebus* and *Sapajus* anoint themselves with several substances to repel ectoparasites (Valderrama et al., 2000; Verderane et al., 2007; Alfaro et al., 2011). Although we did not test this hypothesis, we know that some lichens have active substances (e.g., antibiotics) (Huneck, 1999), and we did occasionally record monkeys rubbing against lichen-covered rocks.

Processing of cashew nuts with PSTs is not required to open the nuts (especially the unripe ones, which can be opened with hands and/or teeth), but we recorded several individuals using stone tools to process them. The caustic substance present in the cashew nut (cashew nut shell liquid, composed primarily of anacardic acids) apparently causes chemical burns on the monkeys' lips (Figure 3), but did not seem to inhibit them from processing and eating the nuts. This substance stained the repeatedly used tools, creating an easily identifiable, long-lasting dark coating on the stones.

The rubbing of unripe cashew nuts against the substrate to avoid the caustic liquid, as described in FBV, 322 km from PNSC (Sirianni & Visalberghi, 2013), was less frequent in the SCNP groups observed. In contrast, they did not appear to avoid the caustic liquid as did the FBV monkeys, which could suggest a potential advantage to its consumption. This is possible considering that the cashew nut oil has active ingredients, such as anacardic acids and tannins, with many alleged properties, including antimicrobial effects (Himejima & Kubo, 1991; Gonçalves & Gobbo, 2012). Unlike FBV capuchins (Sirianni & Visalberghi, 2013), the monkeys at SCNP used PSTs to process these nuts in all their maturational stages, not just the ripe nuts.

Figure 3. Adult male capuchin monkey with possible cashew nut oil chemical burn on his lips. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

PST use, virtually absent in *Sapajus* species in forest habitats (Ottoni & Izar, 2008; Ferreira et al., 2009) but widespread in *S. libidinosus* groups inhabiting savanna environments, may be explained as a function of their degrees of terrestriality (Visalberghi et al., 2005). Much of the variation, in the case of *S. libidinosus*, is due to the availability of resources in each location. The frequencies of resource processing using PSTs differed even between neighbouring groups, such as PF and BC (this study); these differences were more pronounced when distant groups in the same park were compared (Mannu & Ottoni, 2009), and greater again in comparison to other populations such as FBV. This indicates that environment may explain at least some of the differences.

However, the SCNP capuchins appear to have a particular set of behaviours different from other *S. libidinosus* groups studied to date. Most previous reports show that capuchins use PSTs to crack nuts in areas of Cerrado (Spagnoletti et al., 2011; Mendes et al., 2015), but there is great variation in PST use in the groups from the Caatinga environments (Ferreira et al., 2010; De Moraes et al., 2014). The food resources consumed reflect these environmental differences in most cases, but not all. Some of these areas are similar to SCNP, such as Serra Talhada (De Moraes et al., 2014), where the capuchins also crack *Manihot* seeds. Nevertheless, there are no reports from these locations on PSTs used to crack trunks, enlarge crevices, or pulverize pebbles. This could be due to shorter observation times, but some of these behaviours are too conspicuous to miss, if present. Moreover, in at least one of these sites, FBV, capuchin monkeys have been observed for as long and thoroughly as SCNP groups (Visalberghi & Fragaszy, 2013).

The patterns of PST use by the two groups studied here are far more diversified than those observed in other populations, not only regarding the contexts for the use of stone tools, but also in their combination with other tools, such as stick probes, to achieve a single goal. Some of the differences may be due to ecological affordances (available food resources and stones), but behavioural traditions may foster some of these differences in the toolkits.

The use of stones as tools for multiple functions perhaps also further drives the appearance of innovative forms of stone tool use, such as the novel behaviour of stone throwing as a part of female oestrus display in PF group, which has never before been reported for this species in the wild (Falótico & Ottoni, 2013). Similarly, SCNP monkeys tried to solve a probing problem box using stones (but quickly changing to sticks), whereas FBV capuchins rarely tried any tool-use solutions for the same box (Ottoni & Cardoso, 2014). Arguably, the more diversified the use of a given kind of tool, the easier it would be for such behaviour to be further generalized, so innovative variations may appear and spread in the groups (Harlow, 1949; Kummer & Goodall, 1985). On this basis, we predict that stone tool using capuchin monkey populations with greater availability of raw stone material, as seems to be the case in SCNP, would exhibit more diversity in stone tool use than capuchins in areas with a lower abundance of adequate lithic material, like FBV (Visalberghi et al., 2007).

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