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Mapping nut-cracking in a new population of wild capuchin monkeys (*Sapajus libidinosus*) at Ubajara National Park, Brazil

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Abstract

Populations of bearded capuchin monkeys (*Sapajus libidinosus*) vary in their tool use behaviors, with some of this divergence regarded as culturally determined. The use of stone tools, primarily to crack open encased foods, is widespread among bearded capuchins living in dry habitats (*Caatinga* and *Cerrado*). Significant diversity in targets, processed foods, material, and size of tools is observed across populations. However, so far, only a few sites have been systematically studied, and we are still distant from a representative picture of the range of variation in capuchins' culture. In this study, we did a systematic assessment of stone tool use sites in the Ubajara National Park (UNP), in the *Caatinga* region of Ceará, Brazil, recording and measuring stone tools, processed foods, and available lithic resources as part of an extensive comparative research, the CapCult project. We found indirect and direct evidence that capuchin monkeys at UNP customarily use hammerstones and anvils to process at least two species of palm nuts, macauba (*Acrocomia aculeata*) and the harder babaçu (*Attalea speciosa*). Most of the anvils were rock surfaces and had leftovers of only one palm nut species. The hammerstones used to process both palm nuts were not significantly different in weight, although the ones used for *Ac. aculeata* were longer. We found a higher frequency of nut-cracking sites in the drier lowland area of the park, reflecting differences in the density of the most common palm species, *Ac. aculeata*, and availability of raw stone material. The stone tool use observed in UNP is within the scope of previously reported in savannah capuchin populations. Our study widens the knowledge of stone tool-use diversity in wild capuchin monkeys, which could contribute to shaping conservation policy, including cultural traits.

KEYWORDS
culture, lithics, nut-cracking, percussive technology, tradition

1 | INTRODUCTION

Cultural behavior can be important to animals to allow them to quickly learn from the previous generations' knowledge and adapt to the local environment (Whiten, 2021). Culturally acquired information can even have consequences for the fitness of individuals of that population, as it can be relevant to essential behaviors, such as food acquisition and processing, movement, and communication (Brakes et al., 2021; Whitehead, 2010; Whiten et al., 1999; Whiten, 2021).

Site variance in tool use and behaviors has been suggested as evidence for the presence and diversity of cultural behaviors in nonhuman primates. Broad comparisons across sites have shown behavioral differences among populations with no apparent genetic or ecological causes (method of exclusion) in chimpanzees (Pan troglodytes, Boesch et al., 2020; Whiten et al., 1999) and orangutans (Pongo spp., Schaik et al., 2003). Although these across-site comparisons do not examine the role of social learning, an essential characteristic of cultural behaviors

(Acerbi et al., 2022; Fragaszy & Perry, 2003), they still allow the identification of potential cultural traits. It is even more suitable when the target is a complex behavior, such as tool use, because it can be socially transmitted in primates (Koops et al., 2022; Ottoni, 2021; Schuppli et al., 2016).

Robust capuchin monkeys are proficient tool users in captivity and in the wild (Falótico & Ottoni, 2016; Falótico et al., 2018; Fragaszy et al., 2004; Ottoni & Izar, 2008; Westergaard & Fragaszy, 1987; Westergaard, 1992). For instance, numerous wild populations of bearded capuchins (Sapajus libidinosus), mostly in savannah environments (Cerrado and Caatinga), use tools predominantly to crack open encased foods, such as nuts and seeds (Falótico et al., 2018, 2022; Falótico, 2022; Mendes et al., 2015; Ottoni & Izar, 2008; Visalberghi et al., 2015). The most common resources are palm nuts, which have been observed to be cracked open in several populations, such as Fazenda Boa Vista (FBV, Spagnoletti et al., 2011), Chapada dos Veadeiros (CVNP, Falótico et al., 2022), both in Cerrado, Serra das Confusões (SCoNP, Falótico et al., 2018), in a Cerrado-Caatinga ecotone, and Serra Talhada (Moraes et al., 2014; Figure 1), in

FIGURE 1 Map showing the locations of the six compared medium and long-term study sites that had data on stone tool use split by resource: Ubajara (UNP), Serra da Capivara (SCaNP), Serra das Confusões (SCoNP), Chapada dos Veadeiros (CVNP), Fazenda Boa Vista (FBV), and Serra Talhada (ST). A red star indicates the site described in this paper. Brazil is indicated by the green area, with state divisions. Map designed by Tiago Falótico using QGIS.

the Caatinga biome, among other populations (Ferreira et al., 2010; Mendes et al., 2015). In populations where palm nuts are absent, such as Serra da Capivara (SCaNP), the monkeys use stone tools to crack open seeds, fruits, and cacti (Falótico & Ottoni, 2016; Mannu & Ottoni, 2009). In the case of SCaNP, the monkeys also use lithic tools for other purposes, such as digging (Falótico et al., 2017) and stone-on-stone percussion (Falótico & Ottoni, 2016; Proffitt et al., 2016). The stone tool sizes usually have a strong correlation with the resistance of the food or target being processed with the stone (Falótico & Ottoni, 2016; Ferreira et al., 2010; Spagnoletti et al., 2011; Visalberghi et al., 2009). However, other factors, such as chemical protection, fruit shape, or local tradition can also affect the stone tool choice (Falótico et al., 2022; Luncz et al., 2016).

Other populations of capuchins, such as the *S. libidinosus* living in the Serra Talhada region, also process cactus with stone tools (De Moraes et al., 2014), similar to those observed in SCaNP (Mannu & Ottoni, 2009). The same species can also process snails and crabs in mangrove areas, sometimes using stone or wood hammers (Cutrim, 2013; R. R. dos Santos et al., 2018). Some populations of other species of the same genus (e.g., *S. xanthosternos*) have been reported to crack palm nuts using stone tools in the same manner as *S. libidinosus* (Canale et al., 2009).

Capuchins show a great range in tool use repertoires, suggesting cultural variation (Ottoni & Izar, 2008), but comprehensive and systematic comparisons between more populations are needed. The Capuchin Culture project (CapCult, https://capcult.net/) aims to use standardized protocols as a first attempt to systematically describe and compare robust capuchin populations' tool use repertoire, along with ecological and genetic factors to determine the distribution of cultural diversity on a large geographical scale. As part of this project, one step is to map stone tool use and the possible

resources, encased food items, and potential tools available in new sites and compare the results among them and with previously studied sites (see Figure 1).

The current work aimed to systematically describe the processing sites and assess the use of pounding tools by capuchin monkeys (*S. libidinosus*) in an unstudied site, Ubajara National Park (UNP). We also aim to compare the tools' properties (dimensions and raw material) and exploited encased foods frequency and resistance with those known from other *S. libidinosus* medium or long-term study sites that have data on stone tool use split by resource (Figure 1).

We tested hypotheses related to the capuchin monkey's capacity to choose adequate stones as tools. The first hypothesis was that (1) capuchins actively selected stones by its dimensions to use as tools. We expected that the hammerstones' dimensions would not be chosen at random from the stones available in the environment. The second hypothesis was that (2) palm nut processing needs anvils and hammerstones of different dimensions, as the hard target needs a large flat surface to be placed (anvil) and a mobile stone to be used as a hammerstone, so the monkeys would choose stones with different dimensions for anvils and hammerstones. We predict monkeys would use larger and wider stones as anvils. The last hypothesis was whether (3) capuchin monkeys would choose adequate stones as tools, using bigger and harder hammerstones to process more resistant (harder) resources. We predict larger, heavier, and harder hammerstones associated with harder nuts in the processing sites we mapped. Moreover, as the region studied has two distinct environments (highland and lowland, Figure 2), we descriptively compared the occurrence and resource type on the nut cracking sites between those environments.
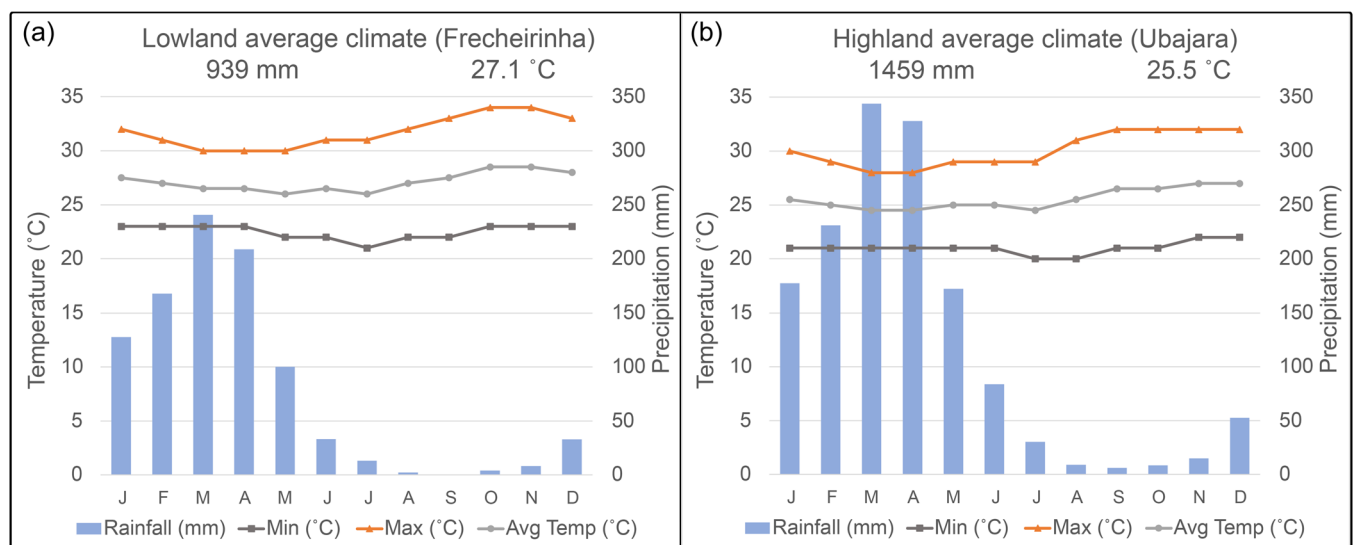
FIGURE 2 Climatic charts for Ubajara National Park, Ceara, Brazil. (a) Frecheirinha (lowland); and (b) Ubajara (highland). Thirty years of historical temperature data from https://www.climatempo.com.br. Precipitation data from Fundação Cearense de Meteorologia e Recursos Hídricos (FUNCEME); Frecheirinha station (GPS −3.758972, −40.810138), 1982–2022; Ubajara station (GPS −3.853444, −40.922583), 1974–2022.

2 | METHODS

2.1 | Study site

UNP is located in the northeast of Ceará state, Brazil, between the coordinates 3°48′–3°50′S and 40°52′–40°55′W (ICM-Bio, 2001). UNP was created in 1959, and it covers 6288 ha. The predominant biome is a dry savannah (*Caatinga*), but it has higher rainfall than a typical *Caatinga*. The climate is semi-arid, with an average annual temperature of 26.1°C, marked by a rainy season (January to June) with lower temperatures and a dry season (July to December) with virtually no rain but higher temperatures (ICMBio, 2001). The annual rainfall average is 1459 mm in the higher area (900–400 m) of the park, with 73.5% of the rain falling between January and April (ICMBio, 2001), and the temperature average is 25.5°C. In the lowland area (below 400 m), the rainfall average is lower, around 939 mm, and the temperature average is higher, 27.1°C, but it has the same monthly variation pattern as the highland (Figure 2).

The terrain stands on a sedimentary sandstone in the higher altitude areas with outcrops of calcareous rocks on the windward slope (Silveira et al., 2020). The park geomorphological domain is at the western peripheral depression (Depressão Periférica Ocidental) of Ceará state and Ibiapaba Plateau (Planalto da Ibiapaba) (Souza, 1988). The slope area comprises conglomeratic quartzites, fine to medium sandstone, fine-grained slates, and limestones (ICMBio, 2001).

The vegetation has remnants of tropical wet forests in the upper region of the hills (highland) and dry forests in the lower parts (lowland), with transitional vegetation in the slope area (ICMBio, 2001; Figure 3). The highlands consist of Tropical Seasonal Evergreen Forest, between 900 and 700 m, and Tropical Seasonal Deciduous Forest, which occurs between 700 and 400 m. In the lowlands (below 400 m), there is the presence of stepic savannah (Silveira et al., 2020).

The park is home to a plant diversity composed of at least 418 taxa, including 213 trees and shrubs, 100 terrestrial herbs, 68 climbing plants, and 33 sub-shrubs (Silveira et al., 2020). Two species of palm trees (Arecaceae) are known to occur in the park: the macauba (*Acrocomia aculeata*) and the babaçu (*Attalea speciosa*). In the park, other plant species that are known to be processed or extracted with stone tools by capuchins in other populations (Falótico & Ottoni, 2016; Falótico et al., 2022), including jatobá (*Hymenaea coubaril*), farinha-seca (*Combretum glaucocarpum*, formerly classified as *Thiloa glaucocarpa*), and louro (*Ocotea* sp.) are present (Silveira et al., 2020). In another list of plant species of UNP, cashew trees (*Anacardium occidentale*) were also reported (ICMBio, 2001).

UNP has a diverse fauna typical of the *Caatinga* biome, including at least 33 species of lizards and snakes, 127 of birds, and 41 of mammals (ICMBio, 2001). Three species of primates are present in

FIGURE 3 Landscape view of the study area (a), showing the wetter highland, the slope of the hill, and the drier lowland. The two insets on the left (b, c) show details of the highland, and the two on the right (d, e) the details of the lowland.

the region: bearded capuchins (*S. libidinosus*), the common marmoset (*Callithrix jacchus*), and the red-handed howler monkey (*Alouata ululata*). Potential terrestrial predators of primates in the area are ocelots (*Leopardus pardalis*), oncillas (*Leopardus tigrinus*), pumas (*Puma concolor*), tairas (*Eira barbara*) and crab-eating foxes (*Cerdocyon thous*; Guedes et al., 2000; T. Valença, personal observation). Domestic dogs and cats can also be a threat to primates in the region, as humans reside at the margins of the park (ICMBio, 2001).

2.2 | Stone tool use site mapping

For 10 days in October 2020, four researchers walked the main park tracks, in the center part of the park, looking for stone tool use processing sites on the ground. A "processing site" was characterized by the following items: (1) "anvil," a flat surface used as a substrate for the processed encased food, (2) "hammer," a stone or wood with traces of usage—such as marks or food remains attached—, on top of the anvil, and (3) remains of the processed encased-food on top or adjacent (within 30 cm) to the anvil (Falótico et al., 2018).

When we identified a processing site, we recorded the following variables: GPS coordinates, anvil material and size (maximum length and width—weight and thickness of the anvils could not be measured as they were embedded in the substrate), hammer material, hammer weight and size (maximum length, width, and thickness; see Falótico & Ottoni, 2016 for details on the tool measurements), processed encased-foods (if more than one type of resource was present, the most abundant one was noted as the main resource and it was the only one considered in the analysis), the distance of anvil to the nearest encased-food tree, the estimated number of processed items on the anvil, and their approximate age (fresh or old, based on color and integrity). We used digital scales (to the nearest 0.1 g) to measure weight, calipers (to the nearest 0.1 mm) to measure lengths up to 15 cm (our calipers maximum extent), and measuring tapes (to the nearest 1 mm) to measure length and distance bigger than 15 cm.

We visually identified the processed items in each site and collected samples from nearby trees for botanical identification and for the resistance to fracture test.

2.3 | Resources availability

To describe the overall distribution of trees and stones in the area and the potential raw resources for percussive tool use, we did a plot survey sampling of 45 points across the two main regions (highland and lowland), where we did the processing site mapping. Each plot was 10 by 10 m, and each was 100 m away from the next one. The first point was subjectively chosen near the eastern entrance of the park, and the following points were drawn westward on Google Earth every 100 m, fitting a transect. The transect should ideally be a square grid; however, because of terrain restrictions (steepness, river, and streams), we designed the grid following the valley bottom and the top of the hills. We did not sample the transition between lowland and highland areas because the inclination prevented it (Figure 3).

In each plot, we measured the DBH (diameter at breast height) of trees larger than 3 cm and tried to identify the trees that could be resources for the monkeys, particularly those they processed with stone tools in this or other populations.

To sample the availability of stones in the area, we did a 50 × 50 cm subplot in the SW corner of each plot, measuring the quantity, dimensions, weight, and composition of every rock with a length of more than 3 cm. We applied the same sampling protocol to other sites in the scope of the CapCult project (Falótico et al., 2022).

2.4 | Fruit resistance

To describe and compare within and across populations, the food resources processed with stone tools (i.e., whose remnants were found on a "processing site"), we tested the resistance to fracture of those following Visalberghi et al. (2008).

The fruit samples were collected on the ground, in the same area where capuchin monkeys live, and crack those fruits with stone tools. We tried to collect fruits that appeared to be mature, whole, and with no signs of parasites or rot. We tested 46 macauba fruits (*Ac. aculeata*) and 22 babaçu nuts (*At. speciosa*), which were the two targets identified in the processing sites during this study. In addition, we tested 16 jatobá pods (*Hymenaea courbaril*), which was a resource we only identified in one processing site in this study but was observed being cracked with stone tools in UNP during a subsequent study (T. Valença, personal observation).

We used two types of universal testers to measure our samples. For the softer *Hymeanaea* (jatoba), we used a custom universal mechanical tester at the Laboratory of Plant Anatomy at the Institute of Biosciences, University of São Paulo, which has a test limit of 2 kN but has a higher sensitivity. For the harder fruits (macauba and babaçu), we used a universal tester TONI COMP III, which has an upper limit of 50 kN, at the Associação Brasileira de Cimento Portland (ABCP), São Paulo. The samples were collected in October/2021 and stored in plastic bags, and the tests were carried out in early November/2021. The samples were positioned on the lower metal plate of the apparatus, and the upper probe was a plane and larger than the contact area with the nuts (Figure 4). The fruits were placed on their flat or stable side on the metal plate. The rate of compressive loading was 1 mm/min for the jatobá, 0.24 kN/s for macauba, and 0.48 kN/s for babaçu (the units do not match because the two machines had different configurations). We used a slower rate of compressive loading for the less resistant macauba than the more resistant babaçu to identify more precisely the point of fracture initiation. Compression terminated when the force abruptly dropped when the first crack was initiated in the shell. The force at failure is in kNewton ($1 N = kg\ m/s^2$).

Before the compression test, we took the measurements of length and diameters (one for round fruits and two for fruits with elliptical equatorial sections) with a caliper, and weight with a digital

FIGURE 4 (a) Babaçu nut (*At. speciosa*) being tested at the Universal tester TONI COMP III, at the Associação Brasileira de Cimento Portland (ABCP), São Paulo, Brazil. (b) Jatobá (*H. courbaril*) being tested by the custom universal mechanical tester at the Laboratory of Plant Anatomy at the Institute of Biosciences, University of São Paulo. A fracture can be seen in the fruit.

scale. After the fruits were cracked open, the kernels were counted and weighed, and the thickness of the shell was assessed in its mid position, i.e., as close as possible to its measured diameter. We also noted if the kernel was parasitized (presence of larvae). We estimated the volume of each nut with the following formula for ellipsoids: volume = $4/3\pi d^1 d^2 l$ (where d^1 and d^2 are the diameters, and l is the length).

2.5 | Statistical analyses

To test if the stones used as tools differed in weight, length, width, or thickness from the stones available in the plot survey (Hypothesis 1), showing a potential active choice of dimensions and shape by the monkeys, we used General Linear Models (GLM) with the independent variables being the type of stone (raw material sample or used stone tool) and the dependent variables stone dimensions (weight, length, width or thickness) in each model. We analyze the dimensions separately because those measures do not necessarily covary because of the different shapes of the stones.

To test whether the monkeys chose stones of different sizes and shapes to use as hammers or anvils (Hypothesis 2), we ran GLM tests with the independent variables being the type of tool (anvil or hammer) and the dependent variables stone length and width.

To test whether features of hammers and anvils differed according to the resistance of the food item processed, showing a potential choice by the monkeys of stone tools regarding the target resistance (Hypothesis 3), we used GLMs to test the effect of the independent variables (encased-food species, hammer rock type, and anvil material) on the dependent variables (hammer-stones tool dimensions). Gamma distribution for the dependent variable with a log link function was used for all of the above GLM tests.

We tested whether the occurrence of cracking sites, resource type, and nearest distance from the resource tree to the anvil site differed between highland/wet and lowland/dry areas using Kruskal–Wallis and Chi-Square tests. All tests were performed in R 4.2 (R Core Team, 2021).

2.6 | Ethical note

The research regarding the monkeys was indirect and observational and complied with protocols approved by the Animal Research Ethical Committee of the School of Arts, Sciences, and Humanities, University of São Paulo (CEUA/EACH 002/2019); all methods were performed in accordance to the Brazilian law, under authorization from environmental agencies IBAMA/ICMBio (authorization 60134) and complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. The same authorization also gave permission to collect plants and seeds, and our study complies with national and University of São Paulo guidelines regarding experiments on plants.

3 | RESULTS

3.1 | Stone tool use site mapping

We did a 10-day survey (October 6–20, 2020), walking twice (round trip) 23.9 km of trails on the west border of the park (Figure 5). We found 209 processing sites and 270 stone hammers (Figure 6).

We identified two distinct resources processed by the capuchins: macauba nuts (*Ac. aculeata*), being the predominant resource, and babaçu nuts (*At. speciosa*, Figure 7). We also identified remains of jatobá fruit (*H. courbaril*) in one processing site in the area (Figure 7d). However, we only considered the main resource in the anvil for the analysis, so the jatobá is not present in the comparative analysis. Nevertheless, in later observations of the capuchins for ongoing studies (Valença & Falótico, 2023), one of us (T. Valença, personal observation) observed the capuchins cracking jatobá fruits with stone tools in the lower area of the park in at least ten processing sites.

Table 1 gives the mean dimensions of the stone hammers and anvils. Anvils were longer and wider than hammers (GLM length: Chi-square = 29.8, df = 465, p < 0.001; GLM width: Chi-square = 27, df = 465, p < 0.001). The height from the ground to the active plane of the anvils had an average of 347 mm. However, in the highland area, we found three *Ac. aculeata* anvils that were "aerial," meaning the active surface was on tree branches out of the ground (Figure 6c).
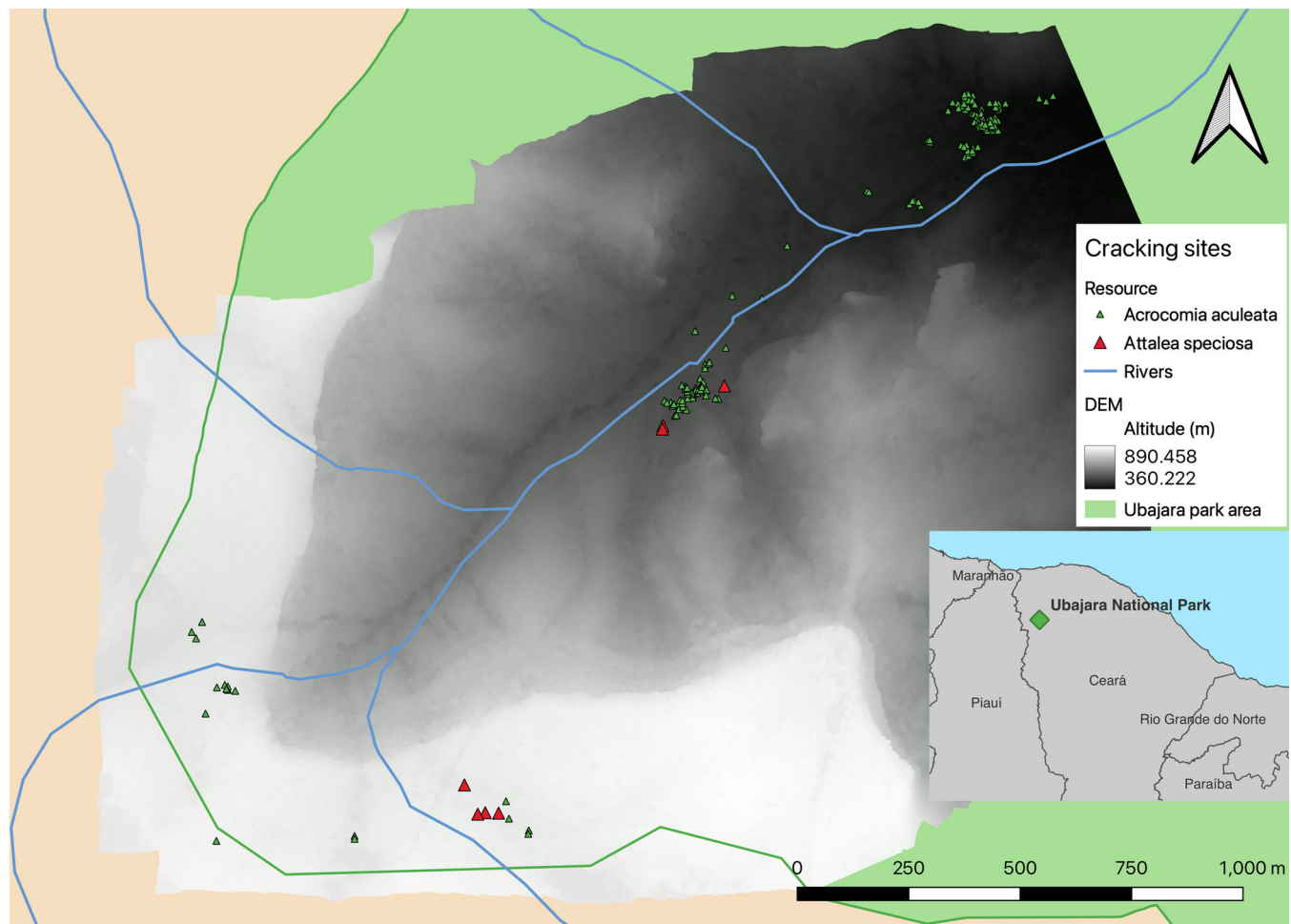
FIGURE 5 Map of processing sites recorded during the mapping, indicating the main resource identified in each site. Terrain elevation in the sampled area is indicated by the grayscale values of the digital elevation model (DEM). The location of Ubajara National Park in Brazil is shown in the inset. Map by Tiago Falótico using QGIS.

The highest one was at 3.2 m. We were not actively looking for aerial anvils, so the frequency can be underestimated.

Regarding the number of hammers, 171 (81.8%) of the processing sites had one hammer, 29 (13.9%) had two hammers, and 9 (4.3%) had three to seven hammers. 121 of the anvils (58%) had fresh remains, indicating that most anvils were active at the time of the sampling. A total of 195 anvils (93%) had remains of only one kind of resource visible, and 13 anvils (6%) had remains of *At. speciosa* and *Ac. aculeata*, three of those had *At. speciosa* as the main resource, and 10 had the main resource classified as *Ac. aculeata*. One anvil (<1%) had fresh remains of *Ac. aculeata* and old remains of *H. courbaril*. This later anvil was considered as *Ac. aculeata* anvil for the analysis.

Anvils were mostly composed of conglomerate, sandstone, and limestone (Table 2). The hammers were all stones (no wooden hammers were observed), mainly from sandstone and limestone, but quartzite and conglomerate hammers were also found during the mapping (Table 2). Wooden surfaces were rarely used as anvils, only being observed in five sites, although at least two of them were heavily used.

Most of the processing sites (90.7%) were located in the lower (and drier) area of the park (darker areas in Figure 5).

We calculated the mean dimensions of the hammers used for each encased food (Figure 8). The GLMs testing the differences in each stone hammer dimension between the two encased foods showed that the only GLM with a significant effect was the one for resource species on the hammerstone length. The stones used to process *Ac. aculeata* were longer than the ones used to process *At. speciosa* (Table 3). None of the other variables had any significant effect on the stone tools' dimensions. The sample of *At. speciosa* hammers was small, so the results of this comparison would need to be confirmed with a larger sample.

The mean distance from the nearest encased-food tree to the anvils was 7.5 m, similar for both analyzed resources (Table 4) (Kruskal–Wallis Chi-squared = 0.002, $df = 1$, $p = 0.964$). There was also no significant difference in distances between lowland and highland (Kruskal–Wallis Chi-squared = 3.796, $df = 1$, $p = 0.051$).

There was a difference in the frequency of cracking sites per resource and per area (Table 5). The lowland area presented more processing sites in general (Chi-square = 52.175, $df = 1$, $p < 0.001$), and *Ac. aculeata* cracking sites were more frequent in both areas. However, *At. speciosa* cracking sites were more frequent in the highland areas.

FIGURE 6 Examples of processing sites observed in Ubajara National Park. (a) *Attalea speciosa* (babaçu) nut processing site, (b) *Acrocomia aculeata* (macauba) nut (b) terrestrial and (c) aerial processing sites. Scales 10 cm.
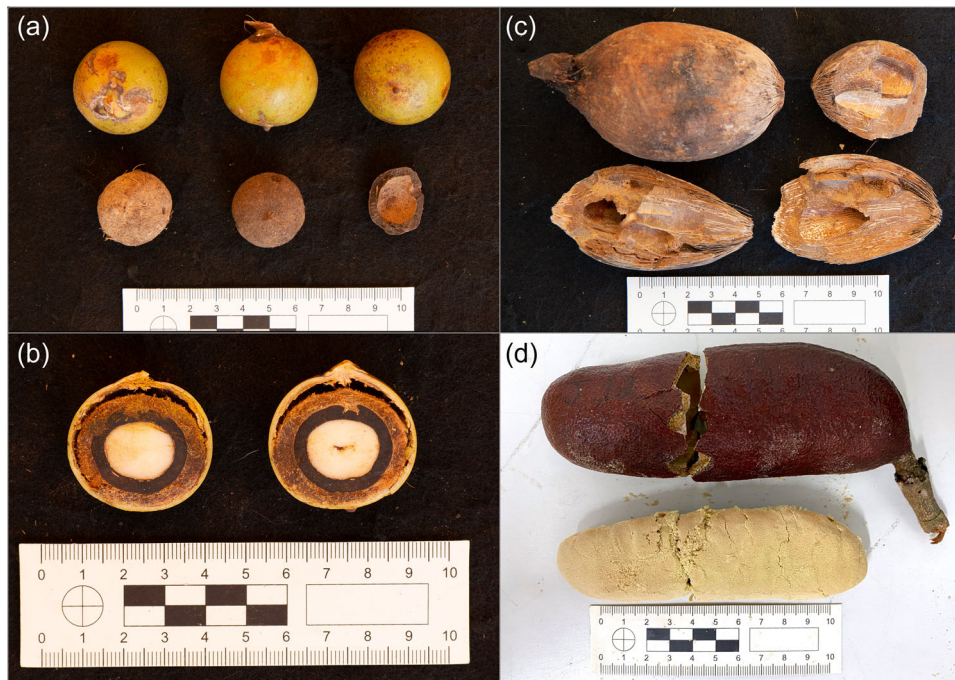
FIGURE 7 Sample of the fruits processed with stone tools by capuchin monkeys in Ubajara National Park. (a, b) Macauba nuts (*Acrocomia aculeata*); (c) babaçu palm nuts (*Attalea speciosa*); (d) Jatobá fruit (*Hymenaea courbaril*). Scales in cm.

3.2 | Resources availability

We counted 511 trees in the plot sampling. The average DBH was 13.6 cm, and 49 trees (9.6%) were fruiting at the time. *At. speciosa* trees were present at a higher density in the higher (wet) part of the

park (0.83 indiv/ha) than in the lower (dry) region (0.33 indiv/ha), and *Ac. aculeata* were more frequent in the lower part of the park (0.19 indiv/ha) than in the higher area (0.083 indiv/ha).

The overall lithic raw material density was 6.1 stones/m². However, we had no lithics sampled in the highland plots, indicating

TABLE 1 Dimensions (mean ± SD, range) of hammers and anvils from the tool using sites mapped at Ubajara National Park.

	Weight (g)	Length (mm)	Width (mm)	Thickness (mm)	Height from the ground (mm)
Anvil (N = 209)	–	643 ± SD 364 75–3000	378 ± SD 224 37–1670	–	347 ± SD 323 0–3200
Hammer (N = 270)	1142 ± SD 718.5 97–4500	141 ± SD 87 43–1430	94 ± SD 25 39–180	61 ± SD 18 16–130	–

Note: The full dataset is presented in Supporting Information Material S1.

TABLE 2 Frequency of material composition of anvils and hammers tools from Ubajara National Park area mapping.

	Sandstone	Limestone	Conglomerate	Quartzite	Limonite	Wood
Anvil (N = 209)	29%	20%	31%	7%	12%	2%
Hammer (N = 270)	38%	25%	13%	13%	11%	0%
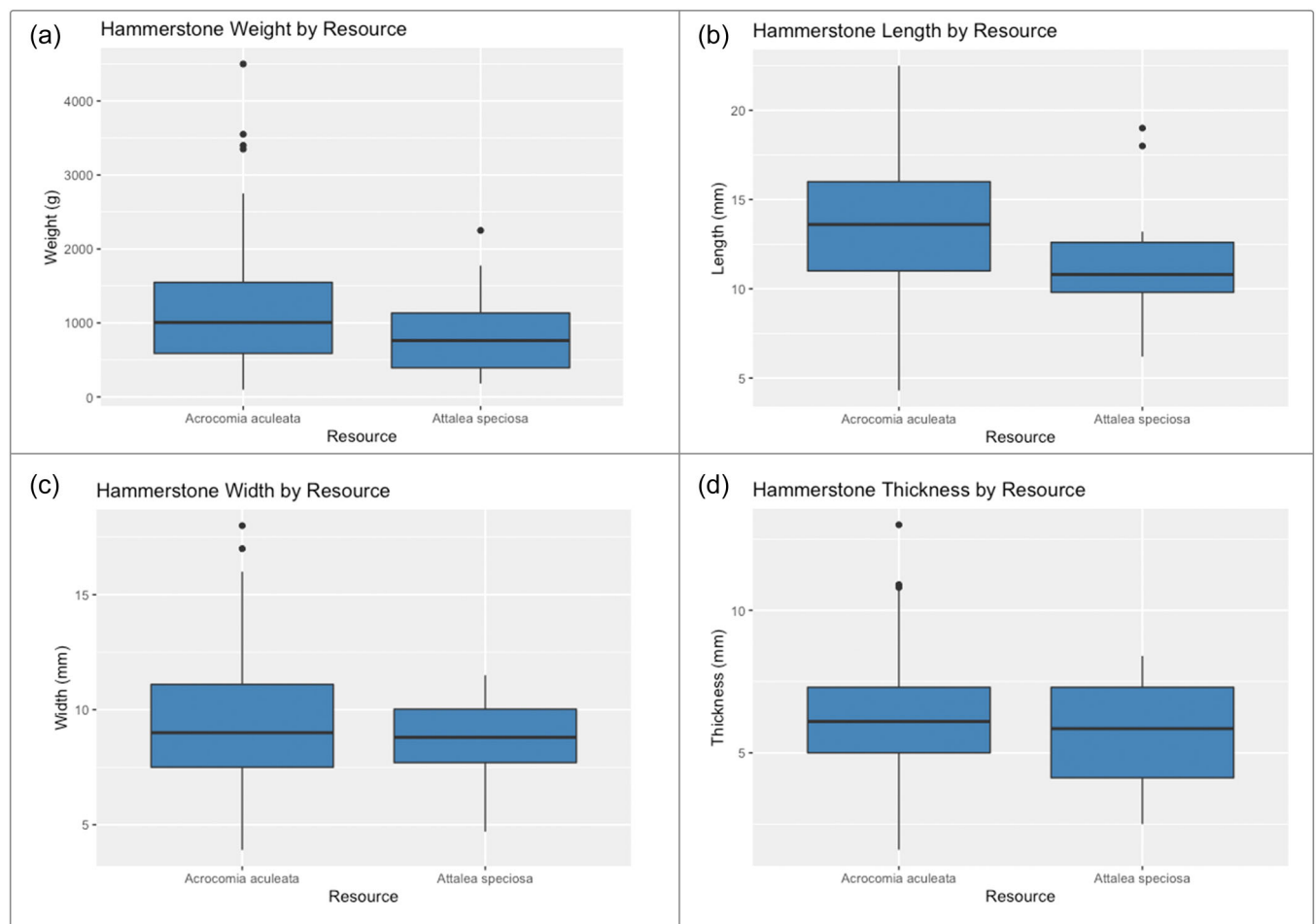
FIGURE 8 Hammerstone tools dimensions per encased food exploited by the capuchin monkeys from Ubajara National Park. (a) Weight, (b) length, (c) width, and (d) thickness.

Dependent variable	Effect	Chi-square	df	p value	Odds ratio
Weight	Intercept	2.847	263	**0.005**	1.000
	Encased-foods	1.162		0.246	1.000
	Hammer rock type	0.320		0.749	1.000
	Anvil rock type	−0.491		0.624	0.999
Length	Intercept	7.401	263	**<0.001**	1.060
	Encased-foods	1.999		**0.046**	1.013
	Hammer rock type	−0.015		0.988	0.999
	Anvil rock type	0.220		0.826	1.000
Width	Intercept	8.774	263	**<0.001**	1.101
	Encased-foods	1.250		0.212	1.011
	Hammer rock type	−0.508		0.612	0.999
	Anvil rock type	−0.047		0.963	0.999
Thickness	Intercept	8.273	263	**<0.001**	1.200
	Encased-foods	0.837		0.404	1.045
	Hammer rock type	0.865		0.388	1.005
	Anvil rock type	−0.446		0.656	1.002

TABLE 3 GLM results for comparison of hammer dimensions across encased foods, hammer, and anvil rock type. Hammers were sampled at tool-use sites in Ubajara National Park.

Note: N = 265. Significant *p* values (*p* < 0.05) in bold.

Encased-food	N sites	% of anvils with fresh remains	Distance to the nearest resource tree (m)
Acrocomia aculeata	201	58%	7.5 ± 5.0
Attalea speciosa	8	50%	7.7 ± 3.8

TABLE 4 Number of tool using sites, percentage of anvils with fresh remains, and distance to the nearest identifiable resource tree (mean ± SD) for each encased food target.

Note: Sample taken at Ubajara National Park.

TABLE 5 Density of tool use processing sites per km sampled during the mapping at Ubajara National Park, split by area and resource processed.

Area	*Acrocomia aculeata* processing site/km	*Attalea speciosa* processing sites/km	Total processing sites/km
Highland	2.4	0.6	3.0
Lowland	11.4	0.2	11.6
Total	8.4	0.3	8.7

TABLE 6 Lithic raw material availability in the study area at Ubajara National Park.

Lithic raw material	Avg length	Avg weight	SD	N	% Material
Quartz	19.0	3550.0	–	1	1.4%
Sandstone	6.6	167.0	261.8	26	37.7%
Limonite	6.4	74.2	89.0	7	10.1%
Conglomerate	9.9	453.3	557.8	17	24.6%
Limestone	8.0	330.7	789.3	18	26.1%

Note: Data from plot survey sampling.

TABLE 7 Physical characteristics of the fruits processed with stone tools by the capuchin monkeys at Ubajara National Park.

Resource	N	Peak force at failure (kN)	Fruit weight (g)	Length (mm)	Estimated vol (cm³)	Shell thickness (mm)	# kernels	Meat weight (g)
Acrocomia aculeata	46	4.15 ± 0.64	17.53 ± 1.86	37.74 ± 1.27	195.51 ± 17.61	3.14 ± 3.16	1.15 ± 0.36	1.65 ± 0.29
Attalea speciosa	22	18.8 ± 3.90	110.35 ± 23.63	80.26 ± 9.35	814.27 ± 183.01	7.60 ± 1.12	5.05 ± 0.95	15.98 ± 3.8
Hymenaea courbaril	16	0.94 ± 0.20	82.74 ± 21.65	113.75 ± 17.92	783.12 ± 206.89	4.49 ± 0.45	1	29.77 ± 10.40

Note: Averages (±SD) of peak force at failure (kNewton), whole fruit weight (g), length(mm), estimated volume (cm³), shell thickness (mm), number of kernels, and kernel meat weight (g).

that in that region the availability of stones is very low. In the lowland area, the density of lithic raw material was 13.1 stones/m². The stones were a mix of sandstone, limestone, and conglomerates (Table 6), with an average weight of 319.9 ± 654 g.

The raw material was significantly lighter and smaller in the dimensions compared to the stones used as tools (GLM weight: $t = 7.71$, $df = 334$, $p < 0.001$; GLM length: $t = 24.39$, $df = 334$, $p < 0.001$; GLM width: $t = 24.3$, $df = 334$, $p < 0.001$; GLM thickness: $t = 19.52$, $df = 334$, $p < 0.001$).

3.3 | Fruit resistance

The peak force at failure for the fruits tested was variable. The more resistant (harder) resource was the *At. speciosa* nut (Table 7).

3.4 | Population comparison

The stone tool use behavior observed so far at UNP appears to fit the most usual pattern of cracking hard-shelled resources we observe in other *Caatinga* and *Cerrado* populations previously studied (Table 8). For this comparison, we used populations that had more than 5 days of surveys or longer studies (Chalk et al., 2015; Coutinho, 2021; De Moraes et al., 2014; Falótico & Ottoni, 2016; Falótico et al., 2018, 2022; Ferraz et al., 2003; Mannu & Ottoni, 2009; L. P. C. dos Santos, 2015; Visalberghi et al., 2008, 2016). For lack of space and simplicity, this comparison table does not include the behaviors of stone tools to aid in digging, stone on stone, or stone-throwing, which are behaviors, so far, only customarily registered at the SCaNP capuchin population (Haslam et al., 2018).

4 | DISCUSSION

4.1 | Stone tool use site mapping

Our investigation showed that capuchin monkeys living at UNP customarily use stone tools to process at least two species of palm nuts. A third non-palm fruit (*H. courbaril*) was also registered in one anvil site. Macauba nut is by far the most exploited of those resources in UNP, and it was most frequently exploited in the lowland/dry part of the park. On the contrary, babaçu was more frequently registered at the anvils in the highland/wet part of the mapped region. That seems to be directly related to the availability of resources in each area. The distance from the anvil to the nearest resource tree was, on average, 7.5 m and was not significantly different between resource species, suggesting that the capuchins do not transport resources far from the source.

Most of the anvils had only one hammer, some of them heavily used, implying that after a proper site is established, the monkeys can reuse it for a long period, with few new stone tools brought to the

TABLE 8 Comparison between *S. libidinosus* populations from semi-arid biomes regarding the processing of encased food resources using stone tools. Frequency categories according to the definition by Whiten et al. 2001: Customary, Habitual, Present, Absent; (E) ecological explanation, e.g., resource not present, or (C) potential cultural difference, no evident ecological explanation.

Population	Study duration	Biome[a]	Resource processed						Stone tool average weight (g, ±SD, range)	References
			Palm nuts (Attalea sp. and Syagrus sp.)	Macauba nut (Acrocomia aculeata)	Cashew nuts (Anacardium sp.)	Jatobá fruit (Hymenaea sp.)	Manihot sp. seed	Cactaceae		
Ubajara (UNP)	12 months	Caatinga	Customary	Customary	Absent (C)	Habitual	Absent (E)	Absent (C)	1142 ± 718, 97–4500	This study
Serra da Capivara (SCaNP)	>10 years	Caatinga	Absent (E)	Absent (E)	Customary (fresh and dry nuts)	Customary	Customary	Customary	202 ± 209, 18–1900	Falótico & Ottoni (2016); Mannu & Ottoni (2009)
Serra Talhada	15 months	Caatinga	Customary	Absent (E)	Absent (E)	Absent (E)	Customary	Customary	396 ± 559, 10–4000	Nogueira Ferraz et al. (2003); de De Moraes et al. (2014)
Serra das Confusões (SCoNP)	2 years	Caatinga/Cerrado	Present	Absent (E)	Absent (C)	Customary	Customary	Unknown	316.0 ± 254, 31–1409	Coutinho (2021); Falótico et al. (2018)
Chapada dos Veadeiros (CVNP)	5 months	Cerrado	Customary	Absent (E)	Absent (E)	Present	Absent (E)	Absent (E)	1672 ± 1051, 266–5700	Falótico et al. (2022)
Fazenda Boa Vista (FBV)	>10 years	Cerrado	Customary	Absent (E)	Customary (dry nuts)	Absent (C)	Present	Absent (C)	1168 ± 489, 250–2530	Chalk et al. (2015); dos Santos (2015); Visalberghi et al. (2008), 2016

[a]According to IBGE (Brazilian Federal Geography Institute). https://ibge.gov.br/apps/biomas/.

anvil. As expected, the stones used as hammerstones were different from the average available lithic material; the tools were bigger and heavier. Also, as expected, the anvils were larger and wider than hammerstones. The niche construction of a profusion of stable nut-cracking sites (anvil, hammers, and resources) could facilitate the learning of stone tool use by naive individuals, as it can increase the chance of interaction with the relevant and functional objects to learn the behavior (Ottoni, 2021).

The three aerial anvils surveyed were used to crack open *Ac. aculeata*. This can be related to the size of the resources, as macauba is smaller, making it potentially easier to transport and position it on a trunk than *At. speciosa*. Moreover, the transportation of hammers together with the food resource, a pattern that capuchin monkeys usually do to secure the food, then transporting nut and hammer together to the anvil (Corat et al., 2015), may be difficult (or even impossible) in the case of *At. speciosa* and aerial anvils. Despite trunks being used as anvils to crack other species of *Attalea* in the FBV population, these trunks are not reported to be aerial (Spagnoletti et al., 2011). In contrast, aerial trunks are used as anvils to crack softer resources such as cashew nuts in SCaNP (Falótico, 2011) and FBV (Visalberghi et al., 2021), and crabs in mangroves (R. R. dos Santos et al., 2018).

4.2 | Fruit resistance

Macauba is softer (4.15 kN) and easier to crack than babaçu (Table 7), and the peak force to crack babaçu (18.8 kN) is higher than that necessary to crack any other palm nuts processed with stones in FBV (nut species average peak-force-at-failure ranging from 5.15 to 11.5 kN), the only other population where the resistance of palm nuts has been tested so far (Spagnoletti et al., 2011; Visalberghi et al., 2007, 2008). That fact led us to hypothesize that stone hammers to crack babaçu would be heavier. However, our data showed no differences in weight between the hammers to process the two resources, nor differences regarding the type of material, although we did find that hammers used for macauba were longer. This difference in length implies that the shape of the tool could have been selected by the monkeys, such as flatter tools to process macauba. Although our sample for babaçu processing sites was small (N = 8), the stone tools for this resource were heavily used, evidenced by the huge amount of babaçu leftovers around those sites and the wear marks on the hammers and anvils, suggesting the monkeys reused those sites successfully over the years.

The location of babaçu sites only in the highlands is also revealing. The park highland had fewer stones available (no stone was sampled in our plots in that area), probably forcing the monkeys to use smaller stones to process the harder *At. speciosa* nut, although we cannot yet rule out that they can use other behavioral adjustments to maximize nut cracking. The ongoing analysis of the video-recorded nut-cracking events will give us more information about the efficiency of babaçu nut-cracking by this population, and future experimental approaches exploring tool selection might also help to

clarify the factors affecting stone choice in this population. Another factor, not exclusive, that could influence the stone choice could be a cultural bias to the smaller stone size used for the most frequent food resource exploited with it, as observed in the other direction (bigger stone tools to process softer resources) in the *S. libidinosus* of CVNP (Falótico et al., 2022).

At least some capuchin groups travel between highlands and lowlands in the area (TF, personal observation), and there is presumably migration between groups living in each area. This leads to the possibility of individuals growing and learning tool-use behaviors in one area and later transferring to another ecological condition, forcing them to adapt to new resource availability, learning from the local group, or, eventually, being a model of novel behaviors for them. The use of trunks as anvils only in the highland could be an adjustment of the nut-cracking behavior to the local conditions of scarcity of adequate stone anvil materials.

4.3 | Population comparison

From the two palm nut resources we identified in this study, macauba nut (*Ac. aculeata*) is present and processed with stone tools in other *S. libidinosus* populations (Mendes et al., 2015; Waga et al., 2006), showing that cracking open macauba nuts is not a unique behavior of UNP capuchins. However, there are many reports on the same and other species of capuchin monkeys (*S. cay*, *S. flavius*, *S. apella*, *C. imitator*) who live in areas where this resource is available but only the mesocarp is consumed, and no use of tools to process and consume the endocarp is reported (Freitas et al., 2008; Hogan & Melin, 2018; Junior, 2013; Montenegro, 2011; Rodrigues, 2013; Sanz & Márquez, 1994; Smith et al., 2017). Although we do not have information about other ecological factors that can influence the occurrence of the behavior (e.g., stone availability and terrestriality), that variation points to the use of stones to crack open macauba as a potential cultural behavior in the UNP capuchin population. Among the medium and long-term studied capuchins populations (Table 8), none of them have macauba available in their home range.

Babaçu palm nut (*At. speciosa*) is not cited in any previous work, but other capuchin populations process the same genus *Attalea*, with nuts of similar size and shape, that, in certain cases, could be the same species. Indeed, capuchins from CVNP (Falótico et al., 2022) may be processing the same species, and capuchins from FBV (Visalberghi et al., 2008) process the species *Attalea barreireinses*, which is a similar palm nut, has the same common name (babaçu) and form hybrids with *At. speciosa* (Cavallari et al., 2019).

Moreover, as far as we know, no population has been described to process those two species with tools. Populations from *Caatinga* and *Cerrado* that use stone tools usually process *Attalea* nuts when this resource is present in the area. This indicates that the presence of very hard nuts could be one of the drives to the innovation and maintenance of this behavior by the capuchins. However, it is important to point out that this factor may not be essential, as the SCaNP population does not have palm nuts in the area, whereas its

capuchins have the most diverse stone tool use known for non-human primates (McGrew et al., 2019). This specialization on hard nuts could, in fact, be a barrier to diversification. The specialization on cracking very hard resources, which requires heavier stones, could restrict the innovation of smaller stone tools in other contexts. At least, that is the pattern indicated so far by comparing those populations. The extreme cases of SCaNP (high stone tool use diversity) and FBV (low stone tool use diversity) appear to fit that "specialization hypothesis." Although FBV capuchins also process low-resistant items, most stone tools in that population are aimed at palm nuts (86% of episodes in Spagnoletti et al., 2011). UNP population appears to be in the middle but closer to FBV. Although the monkeys in UNP also crack very hard nuts, the main resource explored is the easier-to-access macauba, compared to the babaçu nuts in UNP and all FBV palm nuts (Visalberghi et al., 2008). In this line, we can predict that populations more specialized in cracking very hard nuts would be less inclined to innovate on the use of stone tools to process other resources or targets, and the opposite would hold for more generalist populations. We do not have enough data to discuss this hypothesis at this time, but data from other populations that use stone tools can help test this in the future.

The absence of cashew nut processing in UNP could be a population behavioral variation in an area where the resource is available. Compared to other populations, this appears to be a likely situation, as cashew nut processing, with or without tools, appears to be absent. Cashew nut processing with stone tools has been observed, so far, only at FBV and SCaNP, and with variations of the nut stages being processed (Luncz et al., 2016; Sirianni & Visalberghi, 2013). At least one site (SCoNP) have cashew trees in the environment, but the capuchins have not been observed to process the nuts with or without stone tools. Our present mapping did not sample areas with cashew trees, but later work with the monkeys has not, so far, observed them processing cashews, with or without tools, when they are near areas with that resource (T. Valença, personal observation).

The comparison of average tool weight between the populations (Table 8) shows a variation of up to 8 times in the extreme cases. The values appear to be positively correlated with the resistance of the main resources processed with stone tools in each area. However, since resistance values with universal testers are not available for all of the food resources, future analyses are needed to confirm this interpretation. Nevertheless, we know that there is an active selection of stone tools to process different resources in some of those populations (De Moraes et al., 2014; Falótico & Ottoni, 2016; Ferreira et al., 2010; Spagnoletti et al., 2011).

4.4 | Conclusion

This information on the stone tool use in this newly studied population of *S. libidinosus* widens the mapping of stone tool use diversity and potential cultural variance in wild capuchin monkeys and presents a comparison of this new population to others already known. Furthermore, UNP was found to have two different areas (highland and lowland), with distinct ecological and stone tool activities that could be of future interest to the study of the ecological effect on tool use innovation and learning by capuchins living or migrating between those neighboring areas.

Lately, the concept of "culturally significant units" has been considered in the policy-making of chimpanzees' conservation to stress that, for species that depend on socially transmitted information for their survival, conservation plans must rely on comprehensive descriptions of behavioral diversity as much as on assessments of genetic structure (Kühl et al., 2019). Two species of *Sapajus* are classified as endangered and one as critically endangered in the IUCN levels for risk of extinction (Canale et al., 2021; Martins et al., 2021; Valença-Montenegro et al., 2021), and expanding agriculture jeopardizes an increasing number of populations (Presotto et al., 2020). Results from the current study contribute to uncovering cultural diversity in tool-using robust capuchins, hopefully contributing to shaping conservation policy for capuchin monkeys.

This mapping was an indirect approach that only taps into the potential diversity of capuchin monkeys' tool use at UNP. To uncover more subtle and rare behaviors, a more direct approach needs to be taken in the future, including camera traps, direct observation, or field experiments. Part of this approach is already being done, and future data will hopefully help to fill the gaps in our knowledge.

AUTHOR CONTRIBUTIONS

Tiago Falótico: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Supervision (lead); Writing—original draft (lead). **Tatiane Valença**: Formal analysis (supporting); Investigation (equal); Methodology (supporting); Project administration (supporting); Writing—original draft (equal). **Michele P. Verderane**: Investigation (equal); Methodology (supporting); Writing—original draft (supporting). **Beatriz C. Santana**: Data curation (supporting); Investigation (equal); Writing—original draft (supporting). **Giulia Sirianni**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing—original draft (equal).

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