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Social cues on stone tools outweigh raw material properties in wild primates

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Tool use is known among many taxa but its frequency in the animal kingdom is rare. The socio-ecological conditions through which tool use is acquired, transmitted and maintained are the subject of extensive study. Understanding these dynamics offers valuable insight into the evolution of tool use in our species. A fundamental requirement of tool use is the ability to select materials suitable for a given task. In extant primates, material selection is influenced by social and ecological factors; their relative roles, however, remain difficult to disentangle. We present an experimental approach to examine the factors influencing tool selection in robust capuchin monkeys. We provided two naturally tool-using populations with nut-cracking tasks that varied in the material properties of stones and visual evidence of previous use. When presented with unused stones, both populations persistently selected tools based on their material properties. When stones showed signs of previous use, they preferably selected those regardless of material properties. These findings suggest that capuchin monkeys can assess raw material properties but prioritize tools that exhibit evidence of previous nut-cracking activities, indicating that tool selection is shaped by indirect social cues and highlighting the importance of culturally transmitted information in the development of technological skill.

1. Introduction

Tool use offers significant advantages by enabling access to a broader range of environments and resources. As a result, the conditions under which the skill is learnt remain a fundamental question for research across many disciplines [1]. A primary requirement of tool use may be the capacity to select materials suitable for the task, which requires an interplay of ecological, cognitive and cultural processes [2,3]. The environment dictates the spatial distribution and abundance of materials suitable for tool-using tasks [4,5], whereas cognition influences the capacity to recognize materials with the necessary physical properties for the task [1,6–8]. For example, ecological studies of Western chimpanzees (*Pan troglodytes verus*; [9]), Burmese long-tailed macaques (*Macaca fascicularis aurea*; [10]) and capuchin monkeys (*Sapajus* spp., *Cebus capucinus imitator*; [11–14]) demonstrate that the frequency of stone tool use is dictated by the availability of suitable stone materials

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combined with their proximity to food sources [4,15]. The physical characteristics of the stones available would also influence the biomechanical actions necessary for their manipulation during use as tools [3,16]. As a result, proficient tool users also select tool materials based on physical properties, such as size, weight and shape, best suited for the task according to the hardness, shape or protective mechanisms of the food [9,17–25]. At Fazenda Boa Vista, where capuchin monkeys (*Sapajus libidinosus*) crack relatively hard and large palm nuts (*Astrocaryum campestre*, *Attalea barreirensis*, *Orbignya* sp. and *Attalea* sp. [26]), individuals preferentially select heavier hammerstones employed in conjunction with anvils used in prior nut-cracking activities. These anvils exhibit pits from previous nut cracking, contributing to the stabilization of the round palm nut [27,28]

Social processes also shape tool selection through the transmission of knowledge between individuals [29–31]. Studies suggest that tool selection is shaped by direct observational learning, during which naive individuals can watch which materials are chosen by competent tool users [32]. In capuchin monkeys, younger individuals have been reported to observe older conspecifics cracking nuts and reusing previous tools, creating specific social learning opportunities [33–35]. However, indirect mechanisms such as local enhancement could also influence tool material selection preferences [29,36,37]. The traces of previous use found on discarded tools or patterns of discarded food may act as valuable cues, facilitating visual associations between specific materials and tasks [38].

Moreover, the continuous selection, transport and discard of tools can result in the accumulation of previously used materials at new locations beyond where the raw materials naturally occur [27,39]. This increases the number of tool sites present and the accessibility of tool materials that novices might intersect with [15,19]. Simulations show that this process can create landscapes in which tool use locations are much more common than locations where stone and food resources naturally co-occur [40]. The frequent and continuous intersection of these new accumulations facilitates additional learning opportunities and structure associations between the characteristics of previously used materials and tool-using behaviours [38,41,42]. Thus, the residual traces of use found on discarded tools may influence the selection preferences of individuals learning to use tools. While experimental studies have demonstrated the influence of ecological constraints on object manipulation and action expression in primates [42], systematic studies of the effect of previous use of stones on the future selection of different tool types remain rare (but see [43]).

Here, we test the influence of material properties and visible cues of previous tool use on stone selection during nut cracking. We applied an experimental approach to two populations of bearded capuchin monkeys (*S. libidinosus*) in their natural environment. Both populations crack nuts using anvils and hammerstones as part of their daily foraging behaviours (figure 1a; [44,45]). We provided subjects with three nut-cracking tasks that involved the material properties of the stones, the visible signs of previous use for nut cracking, or the arrangement of the stones. Through this experimental design, we investigated how selection preferences influenced foraging efficiency over time and their consistency across study groups.

2. Material and methods

(a) Study animals and study sites

This research was conducted with two habituated populations of bearded capuchin monkeys in Serra de Capivara National Park (SCNP) and Park Ecológico do Tietê (PET), Brazil [19,46–49]. Both these populations are known to habitually use stone tools to crack open nuts ([45,50]; figure 1a). The capuchins at SCNP are wild but the park staff provisions food at artificial water holes, which are frequently visited during seasons of low natural food availability in the dry scrub vegetation and deciduous forest [51]. The monkeys at SCNP regularly crack seasonally available cashew nuts using naturally occurring hammerstones and anvils [44]. Available stones in SCNP predominantly include natural quartzite cobbles (recrystallized quartz and polycrystalline quartz with metamorphic foliation and high silica content), which monkeys use as hammerstones. As anvils, the monkeys use predominantly tabular blocks of sedimentary rock, and occasionally concrete of artificially built pathways [52,53].

PET is home to a free-ranging population of capuchins (*Sapajus libidinosus* and *Sapajus nigritus*) that are regularly food-provisioned at a visitor-restricted area by the Centro de Recuperação de Animais Silvestres (CRAS) staff within the park. This group cracks nuts from naturally occurring palm trees (*Syagrus romanzoffiana*). The available stone tool material is partly anthropogenically introduced. The most common raw materials used as hammerstones include concrete and granite blocks, as well as sedimentary rock and ironstone. As anvils, concrete pavements are predominantly used. Given these differences in available nut-cracking material (stones and nuts), the populations differ in their experience with certain raw materials. Furthermore, daily provisioning with high-caloric food sources might affect the motivation to participate in our experiments in PET.

(b) Experimental procedure

To test whether capuchin monkeys from SNCP and PET emphasize material properties or social cues on stones to select tools, we created an artificial nut-cracking site where capuchins could voluntarily crack nuts. We prepared a site provisioned with nuts, stones for use as hammers and anvils, as well as various traces that a site and/or stones had been previously used for nut cracking, depending on the task (see below). The experimental site was set up by clearing an area of approximately 16 m² of all stone or wooden material that could be used for nut cracking to ensure that only the provided stones were used. In the centre of this area, an experimental area of approximately 1 m² was cleared of any leaf litter to minimize distraction and enhance the visibility of the provided material.

The experimental site was provisioned with four stones: two sandstone cuboids and two limestone cuboids. The choice of these materials was based on the variation in the hardness of the materials. The fossiliferous limestone (mean rebound hardness:

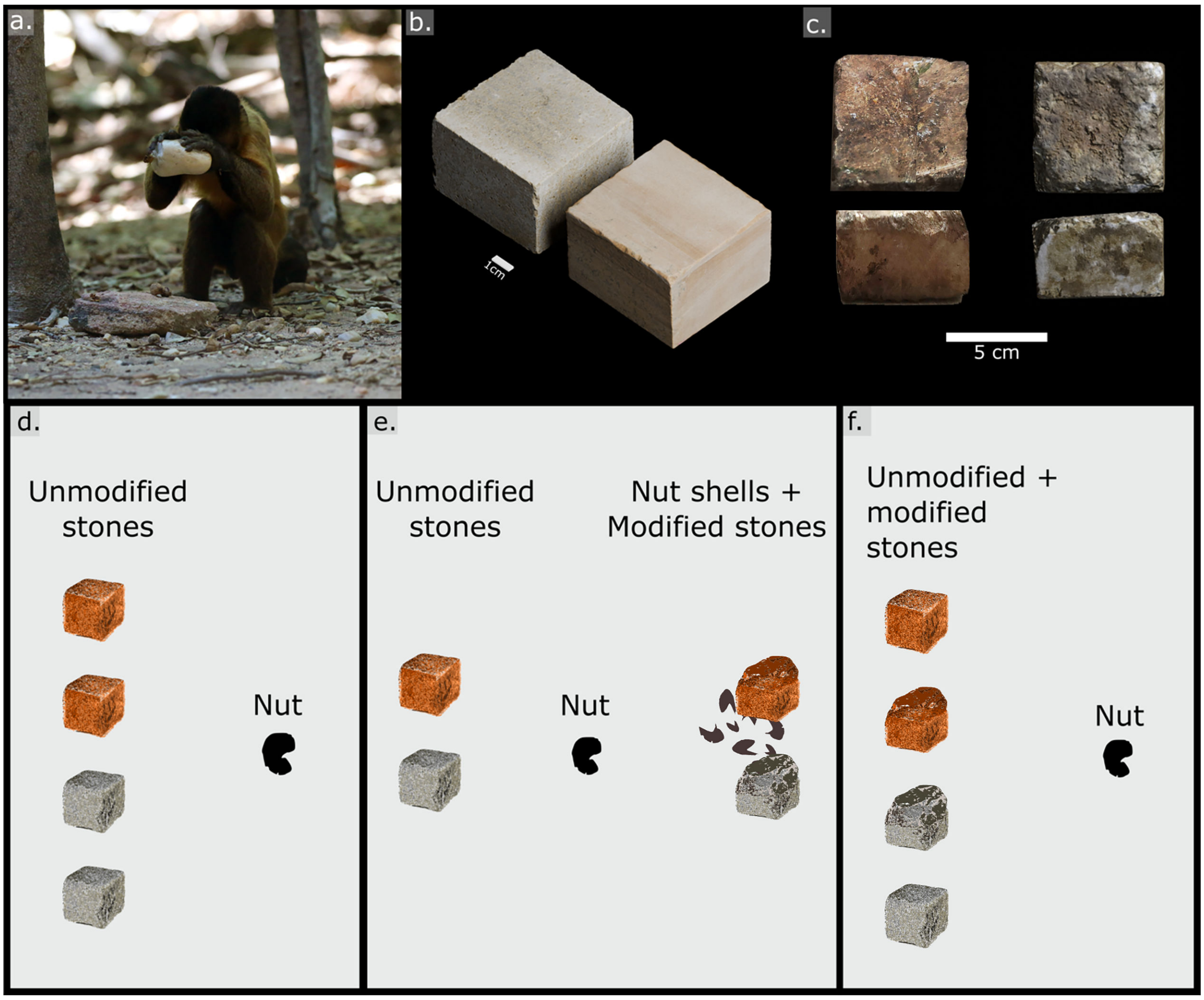

Figure 1. (a) A capuchin monkey cracking a cashew nut using natural stones. (b) Visual comparison of the colours associated with each material provided at nut-cracking sites. (c) Examples of modified hard sandstone and modified soft limestone. (d–f). Experimental tasks ((c) task 1, (d) task 2, (e) task 3) offering nut-cracking sites with stones of different materials (depicted by different colours) and modification (depicted by shapes).

27.05 ± 11.28, n = 69), provided an opportunity for test subjects to choose a soft stone that deforms with relative ease, whereas the sandstone provided an option to choose a hard stone. While sandstones can vary in their hardness, the type chosen for this study is particularly lithified and substantially harder than the limestone option (mean rebound hardness: 57.09 ± 8.39, n = 37). Although these materials are not naturally available in the study sites, their material properties are consistent with the natural stones used for nut cracking by each population (rebound hardness mean, anvils SCNP: 29.35 ± 6.30, n = 23; anvils PET: 32.16 ± 6.56, n = 7; hammerstones SCNP: 69.79 ± 6.96, n = 35; hammerstones PET: 37.67 ± 0.47, n = 3). The stones provided were standardized in size and shape (6 × 6 × 4 cm cuboids) to fit the capuchin's hands (personal experience) and to prevent factors such as size and geometry from influencing the decisions of the participating capuchins (figure 1b). To further remove bias introduced by the experimental setup, we standardized the placement of the stones according to each task (see below, figure 1). The positions of the individual stones were randomized between trials to avoid position or side biases. After placing the stones, a single nut (a cashew nut at SCNP and a palm nut at PET) was placed equidistant from all four stones to prevent the monkeys from simply selecting the stones closest to the nut.

Traces of previous use present at the nut-cracking setup varied depending on the task. Residual traces of previous use ranged from absent (raw, unmodified stones), to traces of battering damage (modified stones) on the surface of a rock that accrues when hammers and anvils are used ([54]; figure 1c), to the presence of broken nut shells indicating that previous individuals had successfully used the site to crack nuts. The modified stones were previously used raw stones that we further manually struck against hard surfaces to induce the typical used pattern on the surface, keeping the general shape similar to the unmodified stones. By systematically varying the presence of residual traces of nut cracking through a series of three tasks, we were able to investigate how factors such as raw material properties and residual traces from previous use influence tool selection patterns in the two study populations.

(i) Task 1, raw material selection. Do capuchin monkeys discriminate between material properties?

To investigate if capuchin monkeys consider stone hardness during tool selection, we provided the experimental site with two stones of either raw material and a single nut per trial (figure 1d, task 1). This allowed the capuchins to choose between four stone combinations for nut cracking (soft anvil and soft hammerstone, soft anvil and hard hammerstone, hard anvil and soft hammerstone, hard anvil and hard hammerstone). The site was devoid of any evidence of previous nut cracking (no discarded, broken nut shells and no evidence of battering or damage on the provided stone material). This allowed us to examine the influence of varying material properties on nut-cracking tool selection.

(ii) Task 2, visual cues. Do capuchin monkeys use signs of previous nut-cracking activity for their selection of a nut-cracking site?

To investigate the role of previously used nut-cracking sites on tool selection, we provisioned the site again with four stones. However, in this task, a soft stone and a hard stone were placed next to each other on each side of the nut (figure 1e). On one side, we placed an unused soft stone and an unused hard stone showing no signs of previous use. On the other side, we placed a soft stone and a hard stone bearing percussive traces of previous use along with broken nut shells as further evidence that these stones were previously used to successfully crack nuts (figure 1c). Thus, upon approaching the setup, capuchin monkeys would need to choose between one of these configurations before selecting stone materials. This setup also allowed the active transportation of stones between sites.

(iii) Task 3, visual cues versus stone properties. Do capuchin monkeys prefer signs of previous tool use over material properties?

To disentangle the influence of visual cues of previous use on the stones (i.e. percussive traces) and the effect of raw material properties on tool selection, we modified the setup in task 1 by exchanging one unmodified stone of either material with one modified stone of that material (figure 1f). The modification presented visual cues of nut cracking on both stone materials. Therefore, capuchin monkeys could choose between stones according to both their material properties and the presence of percussive modification.

(iv) Implementation

All animals' engagement with the setup was voluntary and tested opportunistically when they were motivated to participate. After each trial, we collected all stones and any nut remains to prevent previous encounters from biasing the choices of subsequent individuals. For each subsequent trial, we replaced all used stones with new ones to avoid the capuchin monkeys using any potential (odour or visual) cues left behind from previous use. Before reusing any initially unmodified stones, we removed any traces of nut-cracking activities by abrading their surfaces with sandpaper. If the nut-cracking behaviour resulted in heavy or unremovable percussive damage on an unmodified stone, this stone was excluded from all subsequent trials.

Experimental nut-cracking sites (tasks 1, 2 and 3) were opportunistically set up depending on participating individuals. For example, if individual A has already participated in 10 trials of task 1, we set up task 2. When individual A stopped participating and individual B (which had not yet participated in task 1) approached, we set up task 1 again. This flexible setup was possible as all stones were replaced after every single trial.

To avoid the overrepresentation of specific dominant individuals within one task, additional nut-cracking opportunities were provided away from the experimental task to reduce competition at the testing tool site. In doing so, lower-ranking individuals within the groups were provided with the opportunity to participate in the experimental tasks without being chased by more dominant group members.

(c) Data collection

All experimental trials were recorded using a 4K video camera (Sony FDR-AX700) for later behavioural analyses with BORIS video coding software [55]. Trials started as soon as the subject picked up the provided nut or touched the provided stones and ended when the subject cracked the nut (success) or left the experimental site (failure). For each trial, we recorded the IDs for each participating individual (actively exploring the setup) and demographic information, including sex and age class (adult, subadult). We also recorded each stone ID and whether it was used as a stone anvil or hammerstone (electronic supplementary material, table S1). We also recorded any bystanders (observers or scroungers) within a 2 m distance of the experimental setup. We also noted when the focal was disturbed by any external cues (e.g. group members, other animals), when it used any other objects for nut cracking than the provided stones, or when it transported the provided stones to other nut-cracking sites. Such trials, using other materials than the provided experimental stones ($n = 82$), were excluded from further statistical analyses.

(d) Statistical analyses

The outcomes of these experiments are reported as a series of generalized linear mixed models (GLMMs) using R (v. 4.2.3) [56]. To test the overall significance of the models, we compared the full models (fixed factors, random slopes and interactions if applicable) with respective null models, comprising only the intercept and the random effects, using an analysis of variance (ANOVA) [57]. We assessed statistical significance (α-level: 0.5, significance threshold: 0.05) with χ^2-tests and calculated the effect sizes (R^2) of the full models using the package 'MuMIn' [58] for models with Gaussian error distribution, or calculated Nagelkerke's R^2 for all other models.

We validated each model and its stability (distribution of random effects, variance of fixed and random effects), and controlled for influential cases by controlling the variance inflation factors (function 'vif' applied to standard linear models without any random factors; package 'car') [59], dfbetas (function 'dfbeta'), for overdispersion, as well as normality and homogeneity of residuals (qq-plot for the residuals; scatterplot between residuals and fitted values), where applicable. These tests did not reveal any divergence from the model assumptions or influential cases. A detailed description of each model, diagnostics and results is included as electronic supplementary material.

(i) Task 1, model 1 (raw material selection)

To evaluate whether participating individuals selected stone according to raw material properties (figure 1d, task 1), we used a binomial model with a logit-link function (family 'binomial') for either stone anvil (model 1a; electronic supplementary material, table S4) or hammerstone selection (model 1b; electronic supplementary material, table S5). Whether a stone was selected (1) or not (0) was set as the response variable. The stone material, i.e. either the softer stone (n = 35) or the harder stone (n = 21), the focal's sex, the study site (PET: n = 12 focals, SCNP: n = 10 focals) and the relative trial number (successive trial number per focal within task 1 controlling for a potential learning effect due to retesting) were included as predictor variables and the position of the stone was included as a control variable. As random factors, we included: the stone ID with random slopes for sex, trial and position (outer left, centred left, centred right, outer right); the focal ID with random slopes for material, trial and position and the trial ID per focal with a random slope for the material.

To account for the fact that the selection of stones as hammerstones or anvils inherently implies that the others are not used, we ran permutation tests [60,61] to test the significance of the full model and the individual predictors. To do so, we fitted the respective full and null models n = 999 times with a randomized response variable. To determine the overall significance, we compared the derived test statistics of the randomized data with the test statistics of the original data. Since the stone position encompassed four levels, we included reduced models lacking the position as a fixed effect in the permutation tests. To estimate the overall significance of the position on the stone selection, we compared the differences in the maximum likelihoods between the reduced models and the respective full models.

(ii) Task 2, model 2 (site selection)

To evaluate the role of social cues (in the form of residual traces of previous nut-cracking activity) on the selection of nut-cracking sites (figure 1e, task 2), we again used a binomial GLMM with a logit-link function. Whether a site was selected (1) or not (0) was set as the binary response. We only used the first site selection within a trial. For the full model, we included the foraging site (unmodified stones/nut-cracking site), the focal's sex, the study site (PET: n = 13 focals, SCNP: n = 10 focals) and the relative trial number (successive trial number per focal within task 2, controlling for a potential learning effect due to retesting) as predictor variables. Random factors included the focal ID with random slopes for trial and position and the trial ID per focal. We excluded correlations between random slopes and intercepts as they seemed unidentifiable (model 2a; electronic supplementary material, table S6).

To evaluate the stone anvil (model 2b; electronic supplementary material, table S7) and hammerstone selection (model 2c; electronic supplementary material, table S8) once a site was chosen (figure 1e, task 2), we investigated the effect of the raw material (soft stone/hard stone) and signs of previous nut-cracking activities (unmodified stones/modified stones) on the likelihood that a stone was selected. To do so, we used the same GLMM described for task 1 but also included whether the stone possessed traces of previous use as an additional predictor variable. The relative trial number (successive trial number per focal within task 2 controlling for a potential learning effect due to retesting) was also included alongside the position of the stone as a control factor. The stone appearance, trial and position, and the trial ID per focal with a random slope for material and stone appearance were included as additional random factors using random slopes. We ran permutation tests like task 1 to test the significance of the full model and the individual predictors. To estimate the overall significance of the position (four levels) on the stone selection, we compared the reduced models lacking the position as a fixed factor with the respective full models.

(iii) Task 3, model 3 (social cues)

To evaluate stone tool selection according to raw material properties and signs of previous nut-cracking activities (figure 1f, task 3), we examined the effect of the raw material (soft stone versus hard stone) and signs of previous nut-cracking activities (unmodified stones/modified stones) on the likelihood that a stone was selected. We developed two binomial models with a logit-link function to examine the selection of anvils (model 3a; electronic supplementary material, table S9) and hammerstone selection (model 3b; electronic supplementary material, table S10) separately. Again, whether a stone was selected (1) or not (0) was included as the response variable. The fixed effects were the same as in task 2. The successive trial number of the participating individual was included to account for effects due to retesting. Permutation tests were again used to determine the significance of the full model and individual covariates.

(iv) Model 4 (nut-cracking performance)

To evaluate the nut-cracking performance, we first investigated the effect of the last used stone anvil and hammerstone material, the focal's sex, the study site and the absolute trial number (successive trial number per focal across tasks controlling for a potential learning effect due to retesting) on the success probability (model 4a; electronic supplementary material, table S11). Then, for all successful trials, we evaluated the nut-cracking efficiency, testing the effect of the aforementioned factors on the success latency (nut-cracking duration, model 4b; electronic supplementary material, table S12) and the number of strikes (model 4c; electronic supplementary material, table S13). In all these models, we included random factors: the stone IDs of the stone anvil and hammerstone with random slopes for sex, trial and the material of the respective stone anvil or hammerstone;

the focal ID with random slopes for the stone anvil and hammerstone materials; and trial and the trial ID per focal, in the case of the success probability and the number of strikes.

To evaluate the success probability across trials (tasks 1–3; PET: $n = 189$ trials, $n = 16$ focals; SCNP: $n = 304$ trials, $n = 12$ focals), we calculated a GLMM with binomial error structure and a logit-link function (family 'binomial'). We used a binary response for the success (1) or failure (0) of nut-cracking per trial (model 4a; electronic supplementary material, table S11).

To evaluate the success latency across successful trials (tasks 1–3; PET: $n = 66$ trials, $n = 16$ focals; SCNP: $n = 226$ trials, $n = 12$ focals), we calculated a Gaussian linear mixed model (LMM). As the response, we used the log-transformed success latency as the duration a focal needed to crack the nut (model 4b; electronic supplementary material, table S12).

To evaluate the number of strikes across successful trials (tasks 1–3; PET: $n = 66$ trials, $n = 16$ focals; SCNP: $n = 226$ trials, $n = 12$ focals), we calculated a Poisson GLMM with log-link error function (family = 'Poisson'). As the response, we used the number of strikes a focal needed to crack the nut (model 4c; electronic supplementary material, table S13).

For all these models, we derived individual test statistics and p-values of each predictor by comparing the full model with reduced models, lacking the respective fixed factor, using ANOVA implemented in the function 'drop1'.

3. Results

This study resulted in a total of 304 unique trials at SCNP (task 1: $n = 117$, task 2: $n = 122$, task 3: $n = 65$ trials) and 197 at PET (task 1: $n = 82$, task 2: $n = 105$, task 3: $n = 10$ trials). At SCNP, 12 individuals ($n = 6$ males, $n = 6$ females) out of approximately 40 individuals participated in 2–51 trials ($M = 25.33$, s.d. = 16.90; electronic supplementary material, table S3). At PET, 15 individuals ($n = 7$ males, $n = 8$ females) out of approximately 30 individuals participated in 1–40 trials ($M = 11.81$, s.d. = 10.87; electronic supplementary material, table S3). All individuals were experienced in nut cracking using natural stones.

(a) Capuchin monkeys discriminate between stones based on material properties

When provided with a choice of two standardized blocks of harder stone and two blocks of softer stone as nut-cracking tools ($n = 152$ trials; task 1, figure 1d), the material had a significant effect on the subjects' selection for both anvils (model 1a: $\chi^2(4) = 15.03$, $p = 0.022$; $R^2 = 0.04$; electronic supplementary material, table S4) and hammerstones (model 1b: $\chi^2(4) = 1.56$, $p = 0.004$; $R^2 = 0.02$; electronic supplementary material, table S5). Capuchin monkeys selected the softer stone as anvils more frequently than the harder stone (model 1a: $E_{\text{hard}} = –0.64 \pm 0.24$, $p = 0.002$; figure 2; electronic supplementary material, table S4). Conversely, the harder stone was more often selected for hammerstones compared with the softer stone (model 1b: $E_{\text{hard}} = 0.82 \pm 0.32$, $p = 0.001$; figure 2; electronic supplementary material, table S5). This suggests that the hardness of raw material plays a substantial role in the selection patterns of these tool types for capuchin monkeys.

(b) Capuchin monkeys select previously used nut-cracking sites

When provided with a choice of two separate nut-cracking sites ($n = 221$ trials; task 2, figure 1e), the presence of previous nut-cracking activities had a significant effect on site selection (model 2a: $\chi^2(4) = 14.19$, $p = 0.007$; $R^2 = 0.05$; electronic supplementary material, table S6). Capuchin monkeys preferentially chose nut-cracking sites that bear traces of previous use compared with sites containing only unmodified stones ($E_{\text{unmodified}} = –1.86 \pm 0.40$, $p < 0.001$; figure 3A), suggesting that local enhancement plays a crucial role in initial nut-cracking site selection.

Furthermore, capuchin monkeys showed a clear preference to also use modified stones as both anvils (model 2b: $\chi^2(5) = 23.87$, $p = 0.001$; $R^2 = 0.08$; $n = 189$ trials; figure 3B; electronic supplementary material, table S7) and hammerstones (model 2c: $\chi^2(5) = 6.81$, $p = 0.016$; $R^2 = 0.03$; $n = 189$ trials; figure 3C; electronic supplementary material, table S8) while maintaining the same preference for raw material properties. They continued to select softer stone to use as anvils (model 2b: $E_{\text{hard}} = –0.91 \pm 0.20$, $p = 0.001$; figure 3B; electronic supplementary material, table S7) and harder stone as hammerstones (model 2c: $E_{\text{hard}} = 0.68 \pm 0.34$, $p = 0.022$; figure 3C; electronic supplementary material, table S8).

(c) Capuchin monkeys discriminate between stone tools based on social cues rather than material properties

In task 3 ($n = 73$, figure 1f), when one hard and one soft stone block was modified to mimic traces of previous nut-cracking activities, the subjects repeatedly discriminated between these stones for their anvil (model 3a: $\chi^2(5) = 5.00$, $p = 0.004$; $R^2 = 0.07$; electronic supplementary material, table S9) but not hammerstone selection (model 3b: $\chi^2(5) = 2.63$, $p = 0.107$; $R^2 = 0.02$; electronic supplementary material, table S10). Unlike the previous tasks, no single raw material was preferentially selected based on its properties (anvils: model 3a: $E_{\text{hard}} = –0.37 \pm 0.35$, $p = 0.255$; figure 4A; electronic supplementary material, table S9; hammerstones: model 3b: $E_{\text{hard}} = 0.50 \pm 0.37$, $p = 0.247$; figure 4B; electronic supplementary material, table S10). Instead, modified stones were more frequently selected as anvils (model 3a: $E_{\text{modified}} = 1.08 \pm 0.30$, $p = 0.003$; figure 4A; electronic supplementary material, table S9). However, no preferential selection was observed for hammerstones (model 3b: $E_{\text{modified}} = –0.65 \pm 0.39$, $p = 0.112$; figure 4B; electronic supplementary material, table S10).

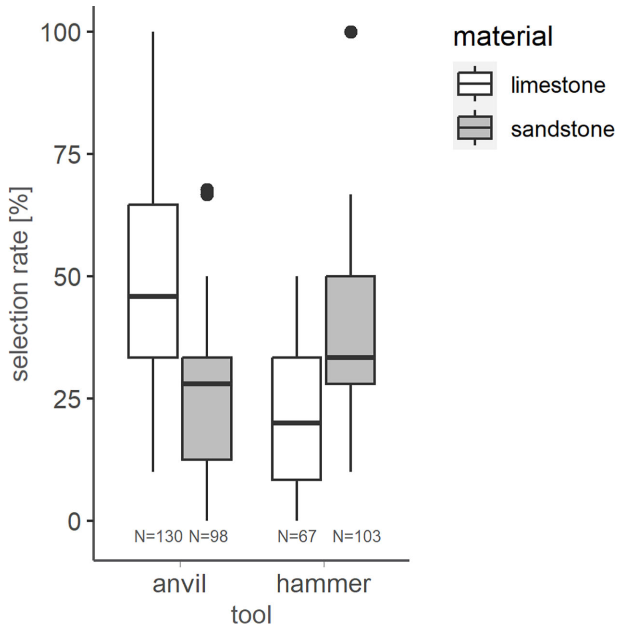

Figure 2. Task 1: selection rate of raw materials for anvils and hammerstones. Capuchin monkeys selected softer anvils (binomial linear mixed model (LMM), model 1a, $p = 0.002$) and harder hammers (binomial LMM, model 1b, $p = 0.001$). Shown are median and standard error bars. Sample sizes are given below each box plot. The black dots represent outliers.

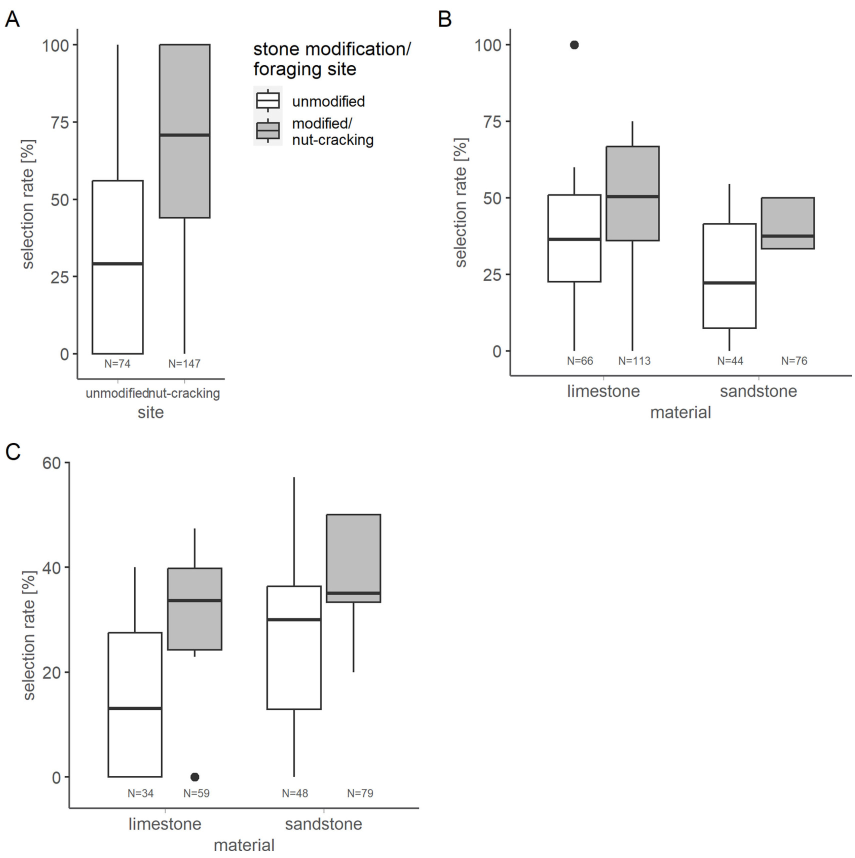

Figure 3. Task 2: selection rates for foraging sites (A), anvils (B) and hammerstones (C). Subjects first oriented towards previously used nut-cracking sites (binomial linear mixed model (LMM), model 2a, $p < 0.001$). Then, they selected modified stones (grey), softer stone anvils (binomial LMM, model 2b, $p = 0.001$), but harder stone hammers (binomial LMM, model 2c, $p = 0.022$). Shown are median and standard error bars. Sample sizes are given below each box plot. The black dots represent outliers.

(d) Stone tool selection patterns did not affect the nut-cracking performance across capuchin populations

Despite the clear preference for specific raw material properties for both anvils and hammerstones, this selection pattern had little effect on foraging efficiency. Instead, the probability of success was influenced more by the subjects' characteristics (model 4a: $\chi^2(5) = 22.28$, $p < 0.001$; $R^2 = 0.08$; $n = 405$ trials; electronic supplementary material, table S11), with capuchin monkeys from SCNP being more likely to succeed than those from PET (model 4a: $E_{\text{SCNP}} = 1.54 \pm 0.43$, $p < 0.001$; figure 5A; electronic

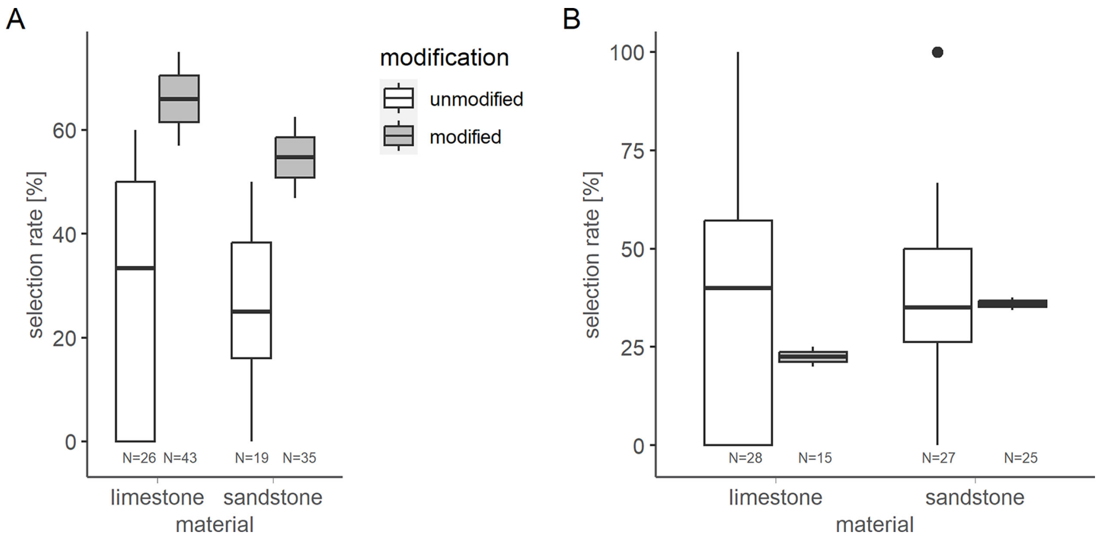

Figure 4. Task 3: selection rates for anvils (A) and hammerstones (B). As anvils, subjects selected modified stones (grey; binomial linear mixed model (LMM), model 3a, $p = 0.003$), irrespective of the material ($p = 0.255$). As hammers, subjects did not discriminate between materials or stone modifications (binomial LMM, model 3b, $p = 0.107$). Shown are median and standard error bars. Sample sizes are given below each box plot. The black dot represents an outlier.

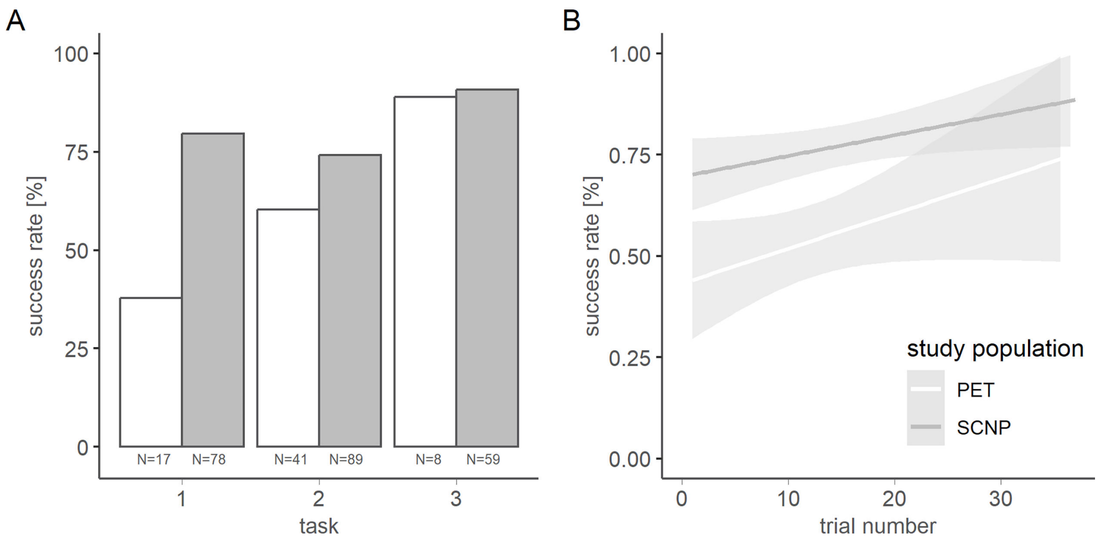

Figure 5. (A) Success rates in the individual tasks and (B) success probabilities across trials for capuchin monkeys at Serra de Capivara National Park (SCNP, grey) and Park Ecológico do Tietê (PET, white). Individuals at SCNP were more successful than individuals at PET (result model 4a; $p < 0.001$). Individuals of both populations were more successful in later trials ($p = 0.005$). Sample sizes are given below the bar plots.

supplementary material, table S11). The primary cause of failure for PET individuals was loss of the nut during nut cracking leading to the subject abandoning the experimental site. At SCNP, individuals primarily left the experimental site with the nut, continuing nut processing at natural anvils (electronic supplementary material, table S14). In both groups, individual success probability increased across trials ($E = 0.51 \pm 0.17$, $p = 0.005$; figure 5B; electronic supplementary material, table S11), suggesting the presence of a learning curve for handling previously unknown raw material. However, the materials of the chosen stone tools did not affect the success probability (anvil: $E_{\text{hard}} = 0.04 \pm 0.40$, $p = 0.920$; hammerstone: $E_{\text{hard}} = 0.16 \pm 0.34$, $p = 0.632$). The nut-cracking efficiency in successful trials was not influenced by any of the subjects' or stones' characteristics (nut-cracking speed, model 4b: $\chi^2(5) = 2.15$, $p = 0.826$; $R^2 = 0.34$; $n = 292$ trials; electronic supplementary material, table S12; number of strikes, model 4c: $\chi^2(5) = 4.18$, $p = 0.525$; $R^2 = 0.01$; $n = 292$ trials; electronic supplementary material, table S13).

4. Discussion

Studying the selection of materials for tool use provides insight into the cognitive abilities of tool users. Previous research has predominantly focused on documenting the choices individuals make during tool use. However, studies of human and non-human primates, past and present, show that the mere exploitation of stone for tool use can lead to landscape-wide modifications in the accessibility of raw materials [40,62,63], which likely influenced the learning opportunities of novice tool users [38]. However, how socially mediated information embedded at previously used tool sites influences selection is less clear. Through a three-task experimental design, this study investigated how ecological and social factors influence tool selection patterns in wild capuchin monkeys.

Our findings highlight a complex interplay between material properties and social cues on stone material related to tool selection, providing insight into the cognitive capacities of technological primates. In the absence of social cues on stone material, capuchin monkeys consistently preferred softer stones as anvils, while harder stones were selected as hammerstones. This observation suggests that capuchin monkeys distinguish between raw materials for specific tasks based on their hardness.

However, previous studies have shown that primates select percussive tools according to both their geometric attributes [19] and the properties of the target nut [20]. This result indicates that capuchin monkeys are discerning of material properties in their selection process. Such work is important to discuss in light of our experimental setup. In contrast with the rounded cobbles that naturally occur in the study area, our study provided each group with cuboids. During the modification process and use, some of the stones experienced a rounding of their edges. It could be argued that this rounding of edges might have influenced selection choices, as the stones would be slightly more like what occurs in their natural environment. However, we argue that this is likely not the case, as none of the stones lost their cuboid shape, and they remained far more like their original geometry than what naturally occurs in the study area.

Furthermore, studies have shown that raw material properties can affect the efficacy of percussive stone tools [20,64]. Specifically, softer raw materials gradually form pits on the anvil's surface through persistent use, which act to stabilize the nut during percussion. Palm nuts at PET were more prone to dislodging from the anvil, causing individuals to cease further nut cracking (electronic supplementary material, table S14). While the pits present on the previously used materials included in the study were shallow, this wear pattern could, thus, enhance the efficiency of nut-cracking behaviour [65]. Given that the soft stone is more likely to undergo this type of alteration during use, the preference to select previously used materials as anvils (task 3) could be explained by this phenomenon. Conversely, the use of soft hammerstones, which absorb force or deform through use, is likely to be less efficient compared with harder materials that transmit a larger portion of the tool user's force onto the nut. Theoretically, this could reduce the number of strikes required to successfully crack the nut.

Given that the stones used in our study were standardized, how capuchin monkeys differentiate between hardness remains unclear. Although the weight difference between the stones was minor (electronic supplementary material, table S2), the monkeys may have relied on it as a determining factor in their choice, given that the harder tools were slightly heavier, and capuchin monkeys have demonstrated their ability to assess weight [66,67]. However, they never lifted stones without subsequently using them as anvils or hammerstones, indicating that it was unlikely that they evaluated stone weight before use. Our observations suggest that capuchin monkeys may have been frequently assessing the material properties through more subtle exploratory behaviours, such as tapping (see electronic supplementary material, video S1), a behaviour that capuchin monkeys also use to assess the ripeness of uncracked nuts [66].

However, when two potential nut-cracking sites were offered (task 2), the monkeys consistently selected the one with clear evidence of previous successful nut-cracking activity. The presence of both visible nut debris and used tools together may encourage the reuse of these sites compared with unused localities. The repeated use of these sites, coupled with their increasing visibility, potentially reinforces ongoing tool-related behaviours. This, in turn, may contribute to the persistence of nut-cracking practices within primate populations once established and condition how individuals recognize materials and sites where tools can be used. This result supported the findings of previous studies [38] that social cues of tool use embedded in the environment contribute to shaping knowledge about the selection of tool materials.

The importance of social cues on stone material in shaping tool selection is further supported by the results of our third experiment. In task 3, tools could be selected from a sample of unmodified and modified stones. Here, capuchin monkeys based their choice of an anvil on the prior modification of the stone rather than the raw material itself. This preference for selecting materials modified by previous behaviours supports the hypothesis that the social context of tool use acquisition may extend beyond direct observation. However, the results of our study cannot determine whether it is the presence of broken nut shells or damaged tools that influences this preference. It might be that the presence of broken nut shells may indicate that the stones present at the site were successfully used as hammers and anvils and therefore there is less need to be selective when choosing a hammer. This could be investigated through additional experimentation. Nevertheless, our results highlight the complex interplay between social cues of previous use and nut cracking.

Our findings further allow us to discuss the implications of tool selection for cultural evolution. One of the main tenets of cultural evolutionary theory is that individuals inherit not only their genes but also the environments and social practices of their ancestors [68]. The combination of discarded tools and residual nut debris may serve as learning opportunities for future generations, even in the absence of direct demonstrations of the behaviour. Therefore, tool accumulations may help to reinforce the selective preferences of the older, more skilled group members, creating path-dependent behaviours within a given group. Such a process would not only reinforce the types and attributes of materials individuals associate with suitable tools, but over time may also result in group-specific behaviours across social groups [33,34,38].

Our results contribute to a growing body of evidence that shows how tool use in primates is socially influenced. Previous research has shown that female chimpanzees (*Pan troglodytes verus*), upon immigrating into a new group, exhibit a propensity to conform to the tool selection patterns practised by the new host group members [69]. It is thought that conformity to local traits allows primates to quickly adopt the most efficient behaviour within a specific environmental context [70], enhancing their foraging success, overall fitness and survival. In addition, different social groups of wild long-tailed macaques (*Macaca fascicularis*) show distinct selection patterns concerning stone tool properties [71]. This group's selection of visually identifiable percussive damage on stone tools highlights the potential importance of social cues for persistent reuse of group-specific tools.

Furthermore, stone selection patterns were persistent across our study groups, despite different experiences with local materials (stones as well as nuts). However, nut-cracking proficiency varied between the different populations of capuchin monkeys, with wild individuals at SCNP exhibiting higher success rates in nut cracking compared with the semi-wild individuals from PET. Individuals at PET were found to switch more often between stones within one trial, whereas individuals at

SCNP usually continued to crack nuts with the selected anvil and/or hammer once they chose a specific stone. This may imply variation in population-specific motivation for nut cracking, owing to reduced food availability during the dry season at SCNP, while individuals at PET were provisioned with high-quality food (e.g. fruits). This may explain why SCNP individuals were more efficient nutcrackers than PET individuals. Additional effects of sex may reflect variances in individual experience either in nut cracking or within the experiments, as well as variances in social learning opportunities, which have been investigated in more detail in previous studies [72,73]. For instance, male capuchin monkeys were found to use tools more frequently than females, suggesting more experience, although nut-cracking efficiency did not vary between sexes [72]. Therefore, respective nut-cracking skills are likely shaped by a combination of individual, environmental and social factors, as well as differences in the mechanical properties of the presented nuts [20].

Despite a preference for specific tool materials and indicators of prior use, we found no significant effects of tool selection on the success or efficiency of nut cracking. Since the participating individuals were already proficient tool users, their extensive experience likely overshadows improvements in nut-cracking efficiency due to material selection. Since all material combinations could lead to nut-cracking success, a learning effect that a certain combination (e.g. soft anvil, hard hammer) was more efficient than another (e.g. hard anvil, soft hammer) may be hidden. Alternatively, individuals learned over the course of the experiments that they would succeed no matter which material combination they chose, resulting in the elimination of initial preference (task 1 compared with task 3). Instead, the monkeys based their stone selection on the presence of social cues indicating prior use, which we interpret as a more important factor for experienced nutcrackers than the mere stone material in our experiment.

These results have implications for interpreting hominin tool selection, where the social context of tool production is often debated. The repeated use of specific locations in the landscape is also a characteristic feature of the Plio-Pleistocene Oldowan toolmakers [62]. Previous research emphasizes the role of landscape modification through repeated tool activities as a potential contributing factor to the recurrent use of favoured locations by Plio-Pleistocene hominins [62]. Once a behavioural location became visually distinguishable owing to the material presence or modification by hominins, it may have served as a visual cue to both contemporaneous and future hominin groups of the suitability of the location for tool use [62]. Given the limited availability of direct behavioural and cognitive evidence associated with past hominin species, there are few data to directly support this hypothesis. Nonetheless, our results indicate that the visual identification of successful past behaviours and respective discrimination between raw materials can motivate the reuse of specific locations and materials in the landscape.

The ability to identify and exploit favourable material properties for specific tasks is also a fundamental characteristic of early hominin tool behaviours. During the Plio-Pleistocene, Oldowan hominins routinely displayed a preference for high-quality isotropic stones with morphologies advantageous to stone tool production [74]. Our study suggests that the ability to discern stone material properties may be a shared capacity across tool-using primates, including hominins, regardless of phylogenetic divergence, and drives primate technological culture.

Ethics. We strictly adhered to the guidelines set out for the ethical treatment of primates established by the American Primatological Society and the Association for the Study of Animal Behaviour. Additionally, the Instituto Brasileiro do Meio Ambiente and Instituto Chico Mendes de Conservação da Biodiversidade approved this research (Sisbio authorization 60134). The fieldwork was conducted under permit 60134 from Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and portaria CNPq no. 846/2022 from the Brazilian Ministry of Science, Technology and Innovation (MCTI).

Data accessibility. The data and R code are openly available on Dryad [75]. A private link is provided here: https://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/aQ_gfld5oS6tQygMyudHN_yv9c5KAmWLXIjiGaYcFB8. Supplementary material is available online [76].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.H.d.M.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; J.S.R.: investigation, methodology, writing—original draft, writing—review and editing; T.P.: conceptualization, data curation, writing—original draft, writing—review and editing; T.F.: conceptualization, data curation, writing—review and editing; H.R.: data curation, writing—review and editing; L.V.L.: conceptualization, methodology, project administration, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Hunt GR, Gray R, Taylor AH. 2013 Why is tool use rare in animals? In *Tool use in animals: cognition and ecology* (eds C Sanz, J Call, C Boesch), pp. 89–118. Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511894800.007)
2. Boyd R, Richerson PJ. 1985 *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
3. Newell KM. 1986 Constraints on the development of coordination. In *Motor development in children: aspects of coordination and control* (eds MG Wade, HTA Whiting), pp. 341–360. Dordrecht, TheNetherlands: Martinus Nijhoff. (doi:10.1007/978-94-009-4460-2_19)
4. Koops K, McGrew WC, Matsuzawa T. 2013 Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Anim. Behav.* **85**, 175–185. (doi:10.1016/j.anbehav.2012.10.022)

5. Lee PC, Moura A de A. 2015 Necessity, unpredictability and opportunity: an exploration of ecological and social drivers of behavioral innovation. In *Animal creativity and innovation* (eds AB Kaufman, JC Kaufman), pp. 317–333. London, UK: Academic Press. (doi:10.1016/B978-0-12-800648-1.00011-5)
6. Meulman EJM, Seed AM, Mann J. 2013 If at first you don't succeed… Studies of ontogeny shed light on the cognitive demands of habitual tool use. *Phil. Trans. R. Soc. B* **368**, 20130050. (doi:10.1098/rstb.2013.0050)
7. Harmand S. 2007 Economic behaviors and cognitive capacities of early hominins between 2.34 Ma and 0.70 Ma in West Turkana, Kenya. *Mitt. Ges. Urgesch.* **16**, 11–23.
8. Gibson JJ. 1979 *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.
9. Boesch C, Boesch H. 1983 Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour* **83**, 265–286. (doi:10.1163/156853983X00192)
10. Malaivijitnond S, Lekprayoon C, Tandavanittj N, Panha S, Cheewatham C, Hamada Y. 2007 Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *Am. J. Primatol.* **69**, 227–233. (doi:10.1002/ajp.20342)
11. Fragaszy D, Izar P, Visalberghi E, Ottoni EB, de Oliveira MG. 2004 Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am. J. Primatol.* **64**, 359–366. (doi:10.1002/ajp.20085)
12. Canale GR, Guidorizzi CE, Kierulff MCM, Gatto CAFR. 2009 First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). *Am. J. Primatol.* **71**, 366–372. (doi:10.1002/ajp.20648)
13. Ferreira RG, Jerusalinsky L, Silva TCF, de Souza Fialho M, de Araújo Roque A, Fernandes A, Arruda F. 2009 On the occurrence of *Cebus flavius* (Schreber 1774) in the Caatinga, and the use of semi-arid environments by *Cebus* species in the Brazilian state of Rio Grande do Norte. *Primates* **50**, 357–362. (doi:10.1007/s10329-009-0156-z)
14. Barrett BJ, Monteza-Moreno CM, Dogandžić T, Zwyns N, Ibáñez A, Crofoot MC. 2018 Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *R. Soc. Open Sci.* **5**, 181002. (doi:10.1098/rsos.181002)
15. Elisabetta V, Haslam M, Spagnoletti N, Fragaszy D. 2013 Use of stone hammer tools and anvils by bearded capuchin monkeys over time and space: construction of an archeological record of tool use. *J. Archaeol. Sci.* **40**, 3222–3232. (doi:10.1016/j.jas.2013.03.021)
16. Lockman JJ. 2000 A perception–action perspective on tool use development. *Child Dev.* **71**, 137–144. (doi:10.1111/1467-8624.00127)
17. Ferreira RG, Emidio RA, Jerusalinsky L. 2010 Three stones for three seeds: natural occurrence of selective tool use by capuchins (*Cebus libidinosus*) based on an analysis of the weight of stones found at nutting sites. *Am. J. Primatol.* **72**, 270–275. (doi:10.1002/ajp.20771)
18. Gumert MD, Malaivijitnond S. 2013 Long-tailed macaques select mass of stone tools according to food type. *Phil. Trans. R. Soc. B* **368**, 20120413. (doi:10.1098/rstb.2012.0413)
19. Luncz LV, Falótico T, Pascual-Garrido A, Corat C, Mosley H, Haslam M. 2016 Wild capuchin monkeys adjust stone tools according to changing nut properties. *Scient. Rep.* **6**, 33089. (doi:10.1038/srep33089)
20. Falótico T, Valença T, Verderane MP, Fogaça MD. 2022 Stone tools differences across three capuchin monkey populations: food's physical properties, ecology, and culture. *Scient. Rep.* **12**, 14365. (doi:10.1038/s41598-022-18661-3)
21. Visalberghi E, Barca V, Izar P, Fragaszy D, Truppa V. 2021 Optional tool use: the case of wild bearded capuchins (*Sapajus libidinosus*) cracking cashew nuts by biting or by using percussors. *Am. J. Primatol.* **83**, e23221. (doi:10.1002/ajp.23221)
22. Sakura O, Matsuzawa T. 1991 Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils: an experimental analysis. *Ethology* **87**, 237–248. (doi:10.1111/j.1439-0310.1991.tb00249.x)
23. Carvalho S. 2011 Extensive surveys of chimpanzee stone tools: from the telescope to the magnifying glass. In *The chimpanzees of Bossou and Nimba* (eds T Matsuzawa, T Humle, Y Sugiyama), pp. 145–155. Tokyo, Japan: Springer Japan. (doi:10.1007/978-4-431-53921-6_16)
24. Falótico T, Proffitt T, Ottoni EB, Staff RA, Haslam M. 2019 Three thousand years of wild capuchin stone tool use. *Nat. Ecol. Evol.* **3**, 1034–1038. (doi:10.1038/s41559-019-0904-4)
25. Proffitt T, Reeves JS, Pacome SS, Luncz LV. 2022 Identifying functional and regional differences in chimpanzee stone tool technology. *R. Soc. Open Sci.* **9**, 220826. (doi:10.1098/rsos.220826)
26. Visalberghi E, Sabbatini G, Spagnoletti N, Andrade FRD, Ottoni E, Izar P, Fragaszy D. 2008 Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *Am. J. Primatol.* **70**, 884–891. (doi:10.1002/ajp.20578)
27. Visalberghi E, Spagnoletti N, Ramos da Silva ED, Andrade FRD, Ottoni E, Izar P, Fragaszy D. 2009 Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys. *Primates* **50**, 95–104. (doi:10.1007/s10329-008-0127-9)
28. Visalberghi E, Fragaszy D, Ottoni E, Izar P, de Oliveira MG, Andrade FRD. 2007 Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *Am. J. Phys. Anthropol.* **132**, 426–444. (doi:10.1002/ajpa.20546)
29. Fragaszy DM, Visalberghi E. 1989 Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* **103**, 159–170. (doi:10.1037/0735-7036.103.2.159)
30. Stout D. 2011 Stone toolmaking and the evolution of human culture and cognition. *Phil. Trans. R. Soc. B* **366**, 1050–1059. (doi:10.1098/rstb.2010.0369)
31. Haslam M, Falótico T, Luncz L. 2018 Recognizing culture in wild primate tool use. In *Evolution of primate social cognition* (eds L Di Paolo, F DiVincenzo, F De Petrillo), pp. 199–209. Cham, Switzerland: Springer International Publishing. (doi:10.1007/978-3-319-93776-2_13)
32. Tan AWY, Hemelrijk CK, Malaivijitnond S, Gumert MD. 2018 Young macaques (*Macaca fascicularis*) preferentially bias attention towards closer, older, and better tool users. *Anim. Cogn.* **21**, 551–563. (doi:10.1007/s10071-018-1188-9)
33. Eshchar Y, Izar P, Visalberghi E, Resende B, Fragaszy D. 2016 When and where to practice: social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Anim. Cogn.* **19**, 605–618. (doi:10.1007/s10071-016-0965-6)
34. Fragaszy DM, Eshchar Y, Visalberghi E, Resende B, Laity K, Izar P. 2017 Synchronized practice helps bearded capuchin monkeys learn to extend attention while learning a tradition. *Proc. Natl Acad. Sci. USA* **114**, 7798–7805. (doi:10.1073/pnas.1621071114)
35. Resende B, Ballesteros-Ardilla A, Fragaszy D, Visalberghi E, Izar P. 2021 Revisiting the fourth dimension of tool use: how objects become tools for capuchin monkeys. *Evol. Hum. Sci.* **3**, e18. (doi:10.1017/ehs.2021.16)
36. Sanz CM, Morgan DB. 2013 Ecological and social correlates of chimpanzee tool use. *Phil. Trans. R. Soc. B* **368**, 20120416. (doi:10.1098/rstb.2012.0416)
37. Ottoni EB, de Resende BD, Izar P. 2005 Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Anim. Cogn.* **8**, 215–219. (doi:10.1007/s10071-004-0245-8)
38. Fragaszy DM, Biro D, Eshchar Y, Humle T, Izar P, Resende B, Visalberghi E. 2013 The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Phil. Trans. R. Soc. B* **368**, 20120410. (doi:10.1098/rstb.2012.0410)
39. Luncz LV, Proffitt T, Kulik L, Haslam M, Wittig RM. 2016 Distance–decay effect in stone tool transport by wild chimpanzees. *Proc. R. Soc. B* **283**, 20161607. (doi:10.1098/rspb.2016.1607)
40. Reeves JS, Proffitt T, Luncz LV. 2021 Modeling a primate technological niche. *Scient. Rep.* **11**, 23139. (doi:10.1038/s41598-021-01849-4)

41. Bourgeois KS, Khawar AW, Neal SA, Lockman JJ. 2005 Infant manual exploration of objects, surfaces, and their interrelations. *Infancy* **8**, 233–252. (doi:10.1207/s15327078in0803_3)
42. Cenni C, Pellis SM, Wandia IN, Leca JB. 2021 Stone affordances as potential for action expression in object play in long-tailed macaques (*Macaca fascicularis*). *J. Comp. Psychol.* **135**, 430–438. (doi:10.1037/com0000283)
43. Gunst N, Boinski S, Fragaszy DM. 2008 Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour* **145**, 195–229. (doi:10.1163/156853907783244701)
44. Falótico T, Ottoni EB. 2016 The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. *Behaviour* **153**, 421–442. (doi:10.1163/1568539X-00003357)
45. Ottoni EB, Mannu M. 2001 Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *Int. J. Primatol.* **22**, 347–358. (doi:10.1023/A:1010747426841)
46. Coelho CG, Falótico T, Izar P, Mannu M, Resende BD, Siqueira JO, Ottoni EB. 2015 Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* sp.). *Anim. Cogn.* **18**, 911–919. (doi:10.1007/s10071-015-0861-5)
47. Corat C, Siqueira J, Ottoni EB. 2016 Sequential organization and optimization of the nut-cracking behavior of semi-free tufted capuchin monkeys (*Sapajus* sp.). *Primates* **57**, 113–121. (doi:10.1007/s10329-015-0491-1)
48. Cardoso RM, Ottoni EB. 2016 The effects of tradition on problem solving by two wild populations of bearded capuchin monkeys in a probing task. *Biol. Lett.* **12**, 20160604. (doi:10.1098/rsbl.2016.0604)
49. Falótico T, Luncz LV, Svensson MS, Haslam M. 2017 Cashew nut positioning during stone tool use by wild bearded capuchin monkeys (*Sapajus libidinosus*). *Folia Primatol.* **87**, 392–397. (doi:10.1159/000459621)
50. Falótico T, Ottoni EB. 2023 Greater tool use diversity is associated with increased terrestriality in wild capuchin monkeys. *Am. J. Biol. Anthropol.* **181**, 312–317. (doi:10.1002/ajpa.24740)
51. Santos JC, Leal IR, Almeida-Cortez JS, Fernandes GW, Tabarelli M. 2011 Caatinga: the scientific negligence experienced by a dry tropical forest. *Trop. Conserv. Sci.* **4**, 276–286. (doi:10.1177/194008291100400306)
52. de OM, Santos JC. 2019 GPR stratigraphy and quaternary morphogenesis in the semiarid Brazil. *Mercator* **19**, e18027. (doi:10.4215/10.4215/rm2019.e18027)
53. Arroyo A, Falótico T, Burguet-Coca A, Expósito I, Quinn P, Proffitt T. 2021 Use-wear and residue analysis of pounding tools used by wild capuchin monkeys (*Sapajus libidinosus*) from Serra da Capivara (Piauí, Brazil). *J. Archaeol. Sci.* **35**, 102690. (doi:10.1016/j.jasrep.2020.102690)
54. Luncz LV, Slania NE, Almeida-Warren K, Carvalho S, Falótico T, Malaivijitnond S, Arroyo A, de la Torre I, Proffitt T. 2024 Tool skill impacts the archaeological evidence across technological primates. *Scient. Rep.* **14**, 16556. (doi:10.1038/s41598-024-67048-z)
55. Friard O, Gamba M. 2016 BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* **7**, 1325–1330. (doi:10.1111/2041-210X.12584)
56. R Core Team. 2016 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org.
57. Forstmeier W, Schielzeth H. 2011 Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* **65**, 47–55. (doi:10.1007/s00265-010-1038-5)
58. Burnham KP, Anderson DR. 2022 *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
59. Fox J, Weisberg S. 2011 *Multivariate linear models in R. An appendix to An R companion to applied regression*. Thousand Oaks, CA: Sage Publications.
60. Berry KJ, Johnston JE, Mielke PW. 2011 Permutation methods. *Wiley Interdiscip. Rev. Comput. Stat.* **3**, 527–542. (doi:10.1002/wics.177)
61. Anderson MJ, Robinson J. 2001 Permutation tests for linear models. *Aust. N. Z. J. Stat.* **43**, 75–88. (doi:10.1111/1467-842X.00156)
62. Shick KD. 1987 Modeling the formation of Early Stone Age artifact concentrations. *J. Hum. Evol.* **16**, 789–807. (doi:10.1016/0047-2484(87)90024-8)
63. Potts R. 1984 Home bases and early hominids. *Am. Scient.* **72**, 338–347.
64. Fragaszy D, Pickering T, Liu Q, Izar P, Ottoni E, Visalberghi E. 2010 Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Anim. Behav.* **79**, 321–332. (doi:10.1016/j.anbehav.2009.11.004)
65. Haslam M, Cardoso RM, Visalberghi E, Fragaszy D. 2014 Stone anvil damage by wild bearded capuchins (*Sapajus libidinosus*) during pounding tool use: a field experiment. *PLoS ONE* **9**, e111273. (doi:10.1371/journal.pone.0111273)
66. Fragaszy DM, Greenberg R, Visalberghi E, Ottoni EB, Izar P, Liu Q. 2010 How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Anim. Behav.* **80**, 205–214. (doi:10.1016/j.anbehav.2010.04.018)
67. Visalberghi E, Addessi E, Truppa V, Spagnoletti N, Ottoni E, Izar P, Fragaszy D. 2009 Selection of effective stone tools by wild bearded capuchin monkeys. *Curr. Biol.* **19**, 213–217. (doi:10.1016/j.cub.2008.11.064)
68. Richerson PJ, Boyd R. 2008 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.
69. Luncz LV, Mundry R, Boesch C. 2012 Evidence for cultural differences between neighboring chimpanzee communities. *Curr. Biol.* **22**, 922–926. (doi:10.1016/j.cub.2012.03.031)
70. Luncz LV, Boesch C. 2014 Tradition over trend: neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *Am. J. Primatol.* **76**, 649–657. (doi:10.1002/ajp.22259)
71. Luncz LV, Gill M, Proffitt T, Svensson MS, Kulik L, Malaivijitnond S. 2019 Group-specific archaeological signatures of stone tool use in wild macaques. *eLife* **8**, e46961. (doi:10.7554/eLife.46961)
72. Spagnoletti N, Visalberghi E, Ottoni E, Izar P, Fragaszy D. 2011 Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *J. Hum. Evol.* **61**, 97–107. (doi:10.1016/j.jhevol.2011.02.010)
73. Visalberghi E, Albani A, Ventricelli M, Izar P, Schino G, Fragazsy D. 2016 Factors affecting cashew processing by wild bearded capuchin monkeys (*Sapajus libidinosus*, Kerr 1792). *Am. J. Primatol.* **78**, 799–815. (doi:10.1002/ajp.22545)
74. Braun DR, Plummer T, Ferraro JV, Ditchfield P, Bishop LC. 2009 Raw material quality and Oldowan hominin toolstone preferences: evidence from Kanjera South, Kenya. *J. Archaeol. Sci.* **36**, 1605–1614. (doi:10.1016/j.jas.2009.03.025)
75. Henke-von der Malsburg J. 2026 Data from: Social cues on stone tools outweigh raw material properties in wild primates. Dryad Digital Repository. (doi:10.5061/dryad.wm37pvn38)
76. Henke-von der Malsburg J, Reeves JS, Proffitt T, Falótico T, Rufo H, Luncz LV. 2026 Supplementary material from: Social cues on stone tools outweigh raw material properties in wild primates. Figshare. (doi:10.6084/m9.figshare.c.8572282)