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Material matters: raw material influences stone tool performance in capuchin monkeys

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Identifying the conditions that facilitate and shape tool use is a central focus in the field of human evolution and animal behaviour. Particular interest lies in the use of stone hammers by nonhuman primates to open encased food sources. It is widely theorized that similar behaviours were used by early hominins and provided a foundation for the emergence of stone knapping. Environmental factors are thought to be important in shaping the emergence and progression of tool use. However, there is limited information on whether access to different types of raw tool material for hammerstones and anvils affects the reliability or efficiency with which tool users exploit encased resources. Here, we experimentally provide wild capuchins, *Sapajus libidinosus*, in Brazil with raw materials differing in hardness. Materials were sourced globally from primate and hominin tool use sites. We measured the reliability and efficiency with which monkeys could crack nuts when using different raw materials, and how these metrics changed over the course of the experiment. We further reported variations in the durability of different raw materials, which directly relates to how long a tool remains useable. Our results showed that differences in capuchin nut-cracking performance were largely driven by the ability of the tool material to stabilize the nut on the anvil. Furthermore, there was wide variation in anvil durability during use. These differences appeared to be driven by multiple tool characteristics, including hardness, surface texture and anvil and hammerstone mass. When compared with similar studies, our results also suggest that stone properties, particularly hardness, may have differing effects on nut-cracking outcomes across species. Overall, the differences in raw material performance and durability seen here, respectively, highlight how local raw materials may influence the selective costs and benefits of tool use behaviours, and the accumulation of tools within the landscape.

The adoption of stone tools by early hominins laid the foundation for incremental increases in cognitive and technical abilities culminating in a complex technological culture among humans (De Beaune, 2004; Langley & Suddendorf, 2022). Stone tool use has since been reported for six nonhuman primate species (hereafter 'primates'), including the western chimpanzee, *Pan troglodytes verus* (Boesch & Boesch, 1990), bearded, yellow-breasted, blond and white-face capuchins, *Sapajus libidinosus* (Falótico & Ottoni, 2016), *S. xanthosternos* (Canale et al., 2009), *S. flavius* (Lima et al., 2024), *Cebus capucinus* (Barrett et al., 2018) and Burmese long-tailed macaques, *Macaca fascicularis aurea* (Malaivijitnond et al., 2007). These species use a stone hammer, often combined with a stone or wooden anvil, to crack open encased food sources such as nuts or shellfish (Barrett et al., 2018; Boesch & Boesch, 1990; Falótico & Ottoni, 2016; Luncz et al., 2017). It is widely theorized that this behaviour was also used by hominins and that it formed a foundation from which the behaviour of stone knapping emerged (Marchant & McGrew, 2005; McGrew, 1992; Rolia & Carvalho, 2017). Primate stone tool use thus provides a valuable opportunity to investigate the conditions under

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which early hominin stone technologies may have arisen and persisted and how they may have laid a behavioural and cognitive foundation for more complex technological behaviours (Bandini et al., 2022).

In addition to cognitive and social requisites, such as object manipulation tendencies or the capacity to socially learn, tool use likely requires certain environmental conditions to evolve (reviews: Koops & Sanz, 2022; Sanz & Morgan, 2013; Van Schaik et al., 1999). Evolutionary theories aimed at explaining the presence and absence of primate stone tool use have paid particular attention to the availability of local resources. Thus far, evidence regarding these theories has largely pertained to food resources, including food scarcity (Spagnoletti et al., 2012; Yamakoshi, 1998) and the availability or nutritional value of tool-extractable foods (Fox et al., 2004; Izar et al., 2022; Koops et al., 2013; Sanz & Morgan, 2013). Equivalent literature focused on raw tool materials is less developed. This is despite the knowledge that primate populations have access to and use different types of stones (e.g. across chimpanzees: Proffitt et al., 2022; across bearded capuchins: Visalberghi et al., 2007 versus Falótico & Ottoni, 2016).

Different raw materials may provide tools of different quality. Tool quality can be defined in terms of performance or durability (Schunk, 2021). Performance describes how well a tool achieves an intended task, while durability describes the rate at which performance changes with use (Schunk, 2021). In theory, tool use should be more likely to evolve where it is highly profitable relative to alternative foraging behaviours (Rutz & St Clair, 2012; Sanz & Morgan, 2013). If local tool materials are highly reliable or efficient at extracting food, then this may increase the quantity of food acquired or decrease energetic costs, thereby improving the relative profitability of tool use. Differences in tool quality may also provide a selective pressure for primates to discern between more profitable and less profitable materials or adjust their percussive behaviours to accommodate raw material performance. The ability to discern between high-quality and low-quality material and predict how that material will react when struck is considered an important cognitive component of prehistoric stone knapping technologies (Braun et al., 2009, 2025; Nonaka et al., 2010). If such abilities can evolve, at least in part, through percussive behaviour such as nut cracking, this could help facilitate an evolutionary transition into knapping technologies.

Archaeological studies on hominin cutting-edge stone flakes suggest that both stone tool performance and durability can depend heavily on the raw material they are made of (Abrunhosa et al., 2019; Braun et al., 2009; Key et al., 2020). In comparison, the influence of raw material on the quality of primate percussive tools is poorly understood. Assertions that primate tool performance or durability can be influenced by raw material are commonly inferred from studies of primate tool selection behaviours (Boesch & Boesch, 1983; Fragaszy et al., 2010; Visalberghi, Addessi, et al., 2009; Visalberghi et al., 2015). For instance, the fact that chimpanzees in the Taï National Park, Côte d'Ivoire, prefer stone hammers over wood when cracking hard nuts (Boesch & Boesch, 1983; Luncz et al., 2012; Sirianni et al., 2015) and the tendency for capuchins to transport harder versus softer stones to nut-cracking sites (Visalberghi et al., 2007; Visalberghi, Addessi et al., 2009; Visalberghi, Spanolettie, et al., 2009) may imply that these materials perform better in those contexts. However, preference alone cannot be used to definitively determine that materials differ in quality, as primates also exhibit cultural preferences that are not linked to tool performance (Luncz et al., 2012).

In the first study, to our knowledge, to quantify raw material performance, chimpanzees have been shown to crack nuts more efficiently (i.e. with fewer hammer strikes) when using soft anvils (carbonatite) paired with hard hammers (dacite or granite; Braun et al., 2025). From here on, we define stone hardness broadly as the tendency for a material to rebound force when struck, rather than absorbing it through deformation or fragmentation (e.g. Arroyo et al., 2016; Spagnoletti et al., 2011; Visalberghi, Spagnoletti, et al., 2009). Harder hammerstones may improve efficiency by transmitting more force into the nut on each strike. Softer anvils may also stabilize the nut by absorbing part of the hammer strike and rebounded less force up into the nut. Nut stabilization has previously been identified as an important factor influencing nut-cracking outcomes but predominantly through the formation of pits on anvils (Fragaszy et al., 2010, 2013; Haslam et al., 2014; Liu et al., 2011). As of yet, this research has only addressed a single species and a single measure of tool quality. Further study addressing the influence of stone hardness across different species and a wider array of performance metrics is required. This is especially important, given recent research has demonstrated that nut-cracking techniques differ considerably between chimpanzees, capuchins and macaques (Luncz et al., 2024).

Here, we test if raw materials differing in their hardness confer tools of different quality, as measured in terms of performance and durability, when used by capuchins, *Sapajus libidinosus*, to crack nuts. We provided experimental stone tool sets, varying in their raw material, to semiwild bearded capuchins in Tietê Ecological Park, São Paulo, Brazil. These capuchins habitually use stone tools to crack palm nuts, *Syagrus romanzoffiana* (Luncz et al., 2024). They use a low-precision, two-handed striking technique. In comparison to the techniques used by other nut-cracking species, this technique results in frequent ejection of the nut from the anvil when struck, relatively low efficiency and extensive damage to the tools (Luncz et al., 2024). Capuchins were provided with one of six tool sets at a time, each consisting of different combinations of hard or soft anvil and hammerstone materials. Nut-cracking behaviour was recorded and scored for each tool set. We assessed two measures of performance: the probability of successfully cracking a given nut (i.e. reliability) and the number of hits required to crack a nut and obtain a food reward (i.e. efficiency). We also assessed two measures of durability: the rate at which reliably and efficiency change with use, and how long the tools last. In general, we expect to see similar influences of stone hardness as that seen in chimpanzees, with efficiency being highest with soft anvils paired with hard hammerstones. The hardness of the anvil is expected to be particularly important for stabilizing nuts and preventing them from being ejected from the anvil, thereby improving nut-cracking reliability. We also expect tools to accrue damage, particularly through the formation of pits, resulting in softer anvils having a more variable (but generally improving) performance over time. Our results provide insight into how raw material may influence foraging outcomes for different species. These results also highlight how the type of locally available raw material may influence the cost and benefits of percussive tool use, as well as the accumulation or destruction of tools.

METHODS

Study Group

Data were obtained across 10 days in April of 2017 from a population of 33 semiwild bearded capuchins residing in a 20 ha area at the Tietê Ecological Park of São Paulo, Brazil. This population naturally uses stone tools to crack palm nuts, *Syagrus romanzoffiana*. We provided this group with experimental stone tools and those naturally occurring palm nuts that we collected from their territory (Fig. 1). This nut is harder than other species of palm nuts (e.g. approximately four times harder than *Elaeis*

Figure 1. Capuchin nut-cracking experimental set-up. A semiwild population of bearded capuchins, *Sapajus libidinosus*, was provided with one anvil and three hammerstones at a time (small, medium and large, see Table 1 for exact weights), as well as locally collected palm nuts, *Syagrus romanzoffiana*. Photo credit: T.F.

guineensis; Luncz et al., 2024), and it is round, making it unstable on the anvil compared with flat nuts such as cashew nuts, *Anacardium* spp. and sea almonds, *Terminalia catappa*. This makes it an ideal candidate for the study, as material performance may be particularly influential on foraging outcomes for hard-to-open nuts.

Stone Tool Raw Materials

The capuchins were provided with experimental tool sets differing in the hardness of their raw materials (Table 1). Materials were sourced globally, selecting commonly used rock types from sites of nut-cracking primates and early hominin tool use. This enables testing of a wider diversity of rock types than available at a single site while limiting material combinations to those contextually relevant to hominin and primate tool activity.

Tool set 1 (hard anvil, hard hammer) consisted of a quartzite anvil sourced from Naibor Soit and phonolite hammers sourced from streams originating in the Ngorongoro Volcanic Highlands; both raw materials are found within Olduvai Gorge, Tanzania. Olduvai Gorge has an extensive record of hominin tool use across multiple archaeological sites (Leakey, 1971). A large majority of the lithic assemblages from these sites comprised both quartzite and phonolite. Specifically, the majority of percussive anvils comprised quartzite from Naibor Soit, whereas phonolite river cobbles were commonly used as hammerstones (Leakey, 1971; Mora & de la Torre, 2005). Naibor Soit quartzite is a relatively hard stone, although it can fracture unpredictably along internal faults (Bello-Alonso et al., 2019). Phonolite also has a moderately high surface hardness, indicating a resistance to deformation, although it is brittle and prone to fracturing under enough force (Egeland et al., 2019). Capuchin nut cracking using these Olduvai raw materials has been previously reported by Luncz et al., 2024, where it was compared with nut cracking by chimpanzees and macaques using the same rock types. Here, we compare it with additional nut-cracking materials not previously reported.

Tool set 2 (soft anvil, soft hammer) consisted of a cherty siltstone anvil and hammers of identical material sourced from Boi Island, Phang-Nga National Park, Thailand. The sedimentary stones on this island tend to be soft and friable. This island is resident to long-tailed macaques that use a wide variety of sedimentary stones, including siltstone, to crack nuts and shellfish (e.g. at Yao Noi, Phang-Nga, Thailand; Reeves, Proffitt, Malaivijitnond, & Luncz, 2023; Piak Nam Yai, Laem Son, Thailand; Haslam et al., 2013). However, the anvil degraded rapidly when used by the capuchins. The anvil was replaced by locally sourced concrete, whereas the hammerstones were retained, producing tool set 3 (hard anvil, soft hammer). Concrete is a hard material commonly used by capuchins for nut cracking at Tietê Ecological Park and has the potential to become increasingly available to primates under the spread of anthropogenic landscapes. The concrete anvil was thinner than other anvils tested here (Table 1 for all tool sizes). It fractured after extended use and was replaced with a second, thicker concrete anvil (tool set 4).

Tool set 5 (soft anvil, hard hammer) is composed of a sandstone anvil and quartzite hammers sourced from Serra da Capivara, Brazil. These materials are some of the most common anvils and hammers used by bearded capuchins across sites (Fazenda Boa Vista; Visalberghi et al., 2007, Visalberghi, Spanolettie, et al., 2009; Serra de Capivara; Falótico et al., 2018). Quartzite hammers used

Table 1
Tool set details and sample sizes

Tool set		Raw material	Hardness class	Tool size	Source location	Sample size (no. of nuts)	
						Total	Cracked
1	Hammer	Phonolite	Hard	257.6, 304.5, 580.6 (g)	Olduvai Gorge, Tanzania	944	544
	Anvil	Quartzite	Hard	16 × 15.5 × 5 (cm)	Olduvai Gorge, Tanzania		
2	Hammer	Siltstone	Soft	334.3, 448.1, 653.2 (g)	Phang-Nga, Thailand	48	21
	Anvil	Siltstone	Soft	23 × 16 × 6 (cm)	Phang-Nga, Thailand		
3	Hammer	Siltstone	Soft	334.3, 448.1, 653.2 (g)	Phang-Nga, Thailand	272	203
	Anvil	Concrete	Hard	27 × 20 × 2.5 (cm)	São Paulo, Brazil		
4	Hammer	Siltstone	Soft	334.3, 448.1, 653.2 (g)	Phang-Nga, Thailand	517	388
	Anvil	Concrete	Hard	26 × 26 × 5 (cm)	São Paulo, Brazil		
5	Hammer	Quartzite	Hard	317.8, 402.5, 625.2 (g)	Serra da Capivara, Brazil	62	35
	Anvil	Sandstone	Soft	31 × 17.5 × 5.5 (cm)	Serra da Capivara, Brazil		
6	Hammer	Quartzite	Hard	317.8, 402.5, 312[a] (g)	Serra da Capivara, Brazil	569	208
	Anvil	Ironstone	Soft	19.5 × 15.5 × 6 (cm)	São Paulo, Brazil		

The raw material, source and nut sample size for each tool set provided to capuchin monkeys. Sample sizes indicate the total number of nuts processed and the number of these nuts which were cracked, after removing nuts processed by juveniles ($N = 499$ total) and nuts for which information was incomplete ($N = 47$).

[a] The large (625.2 g) quartzite hammerstone fractured into two c. 312 g pieces shortly after it was first used on the ironstone anvil.

by capuchins are hard and durable (Visalberghi et al., 2007). Capuchin sandstone anvils tend to be soft; easily fracturing and pitting during nut cracking (Haslam et al., 2014). The sandstone anvil in this study degraded rapidly, necessitating its replacement with locally available ironstone to form tool set 6 (soft anvil, hard hammer). Despite being relatively rare in the environment, ironstone is also frequently used by bearded capuchins (Fazenda Boa Vista; Visalberghi et al., 2007; Visalberghi, Spanolettie, et al., 2009). This ironstone is harder than the sandstone it replaced, based on material surveys at other capuchin sites (Fazenda Boa Vista; Visalberghi, Addessi, et al., 2009). However, as a sedimentary stone, it remains a relatively soft material compared with the quartzite and concrete anvils tested here and is thus classified as a soft anvil.

One tool set was provided at a time, with a new tool set being provided when the material had degraded beyond the point of use or when approximately 1000 nuts had been processed. Each tool set consisted of a stone anvil and three hammer stones. The hammerstones within a tool set were of the same material type. Each anvil was a flat tabular stone block approximately 16—30 cm across. All anvils were approximately 5—6 cm thick, except for the first concrete anvil (tool set 3), which was 2.5 cm thick (Table 1 for all tool sizes). Providing a specific raw material at a time, and anvils of specific dimensions, ensures that differences in material performance are due to intrinsic differences in the raw material rather than material preference. The hammerstones in each tool set included a small (c. 300 g), medium (c. 400 g) and large (c. 620 g) rounded cobble of identical material. This allowed each capuchin to choose their preferred size for nut cracking. The one exception was the ironstone—quartzite tool set (tool set 6), for which the large quartzite hammerstone fractured in half shortly into the study. As a result, the largest hammerstone in this tool set was approximately 400 g.

The final condition of all tools is reported in the study, including those that broke rapidly, to allow for the discussion of differences in observed durability. Damage to some of these tools has been published in detail elsewhere (fragments and surface damage from the ironstone, quartzite and cherty siltstone anvils; Luncz et al., 2022; surface damage to the Olduvai materials; Luncz et al., 2024) and will be briefly reiterated here. We additionally describe damage to the remaining unreported materials and contextualize these results alongside nut-cracking performance and evolution.

Behavioural Observation

Nut-cracking behaviour was recorded in person with a camcorder Canon Vixia HF R52 and a camera Canon EOS 70D. All videos were reviewed by a single person (14 h of footage in total). Recording began from the moment a monkey approached the tool set and ended the moment the last individual left the tool set. From the videos, the following data were collected for each nut-cracking event: the tool set, weight of the hammerstone used by the capuchin, the number of hits applied to the nut, whether the nut was successfully cracked open and the individual's identity, age and sex (see the ethogram in Table S1 and Fig. S1 in the Supplementary Material). These data were used to provide three measures of tool performance: the likelihood of successfully cracking a nut (cracking success), the number of hits required to crack a nut (hits per nut) and the number of hits required to obtain a food reward (hits per reward). Hits per nut excludes unsuccessful cracking attempts. Hits per reward is the combined number of hits in a successful cracking attempt and the preceding unsuccessful attempts, providing a measure of overall efficiency. These metrics were chosen based on prior research. The number of hits required to crack a nut is a common measure of nut-cracking efficiency (Braun et al., 2025). Under experimental conditions with ad libitum nut provision, capuchins commonly fail to crack nuts due to them being ejected off the anvil and not being retrieved (Luncz et al., 2024). This is accounted for by including a 'success' and 'hits-per-reward' metric. A measure of accumulating 'use' was also generated: the cumulative number of hammer strikes applied to the anvil prior to the given nut, including hammer strikes performed by juveniles. This provides an assessment of how much a tool set had been used at each point in the study, thereby enabling an assessment of how tool performance changes over time.

Statistical Analysis

Differences in tool performance and durability across materials were assessed using generalized linear mixed models (GLMMs). Models were designed and implemented using the package 'glmmTMB' (Brooks et al., 2017) in R (v 4.3.1; R Core Team, 2018). Three models were used, each addressing a different performance metric: (1) cracking success (yes/no), (2) hits per nut and (3) hits per reward were compared across tool sets. The sample size for cracking success (model 1) corresponds to the total number of nuts processed ($N = 2302$) and includes 12 individuals (eight males and four females). The sample size for hits per nut (model 2) and hits per food reward (model 3) corresponds to the number of nuts successfully cracked ($N = 1343$) and includes 11 individuals (eight males and three females). Nuts processed by juveniles ($N = 499$ nuts, eight male juveniles < 5 years old) were excluded from analysis, as these individuals may still be developing their nut-cracking abilities. The tool sets with the siltstone and sandstone anvils (tool sets 2 and 5, respectively) were also excluded due to low sample sizes, resulting from the rapid destruction of their anvils (Table 1 for sample size of each material).

All models had the same predictor variables: material, use, hammer weight and sex. There were two variables of interest: 'material' as a categorical variable reflecting the tool set and 'use' as measured in cumulative prior hammer strikes. An interaction between material and use was included to test if the rate at which tool performance changes with use depends on the material the tool is made of. Hammer weight and sex were included as control variables. Also included was a random effect of subject ID on the intercept and on the slope of the material effect. The inclusion of such a random slope is shown to reduce type I errors, providing a conservative estimate of significance (Matuschek et al., 2017). When assessing hits per reward (model 3), hammer weight reflects the mean weight of hammers used across the successful nut and its unsuccessful predecessors. Hammer weight and use were scaled by subtracting from the mean and dividing by the SD. The cracking success model (model 1) used a binomial distribution and logit link function. The hits per nut and hits per reward models (models 2 and 3) used a zero-truncated negative binomial distribution to correct for overdispersion and a right skew, with a log link function. We also investigated if it was warranted to account for the fatigue of the individuals during nut-cracking sessions. However, sessions tended to be short (median = 10 s, mean = 2.9 min). Including a fatigue variable (cumulative number of hits within a single nut-cracking session) was also not supported by statistical investigation: for each of the three models (success, hits per nut and hits per reward), the full model did not differ significantly from a reduced model where fatigue was removed (see section 2 'Exploratory Analysis' in the Supplementary Material). This variable was therefore dropped from the analysis.

All models performed well when tested for homoscedasticity of residuals, overdispersion, collinearity of predictor variables and model stability (see Figs. S2, S3, S4 in section 3 'Model Diagnostics' in the Supplementary Material). Homoscedasticity was assessed by visually inspecting plots of residual values against predicted values. Residuals were found to vary equally across the range of predicted values. Dispersion was assessed using the 'DHARMa' package (Hartig, 2022). The dispersion ratios were close to 1 (0.89–1.02 depending on the model), and models were not significantly over- or underdispersed ($P > 0.05$). Collinearity was low with VIF values of 1.66 or less. Model stability was assessed by dropping one individual at a time, with all variables of interest found to be reasonably stable. The binomial cracking success model (model 1) was also checked for complete separation by visually checking sample sizes across groups.

The significance of each model was tested by comparing it with a null model using the ANOVA function in R. Thereafter, the significance of the effect of each individual predictor variable was assessed by dropping the variable from the model and comparing the resulting reduced model with the full model. This reduced versus full model comparison was done, one at a time, for material, use, hammer weight, and the interaction of material and use. The predicted influence of material and use was plotted for each response variable using the predict function.

Ethical Note

This research complied with protocols approved by the Animal Research Ethical Committee of the Institute of Psychology, University of São Paulo (CEUA 3036140715), fully adhered to Brazilian law under authorization from agencies IBAMA/ICMBio 37609-6 and CNPq 001375/2015-60, complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, and adheres to the ARRIVE guidelines. No stress or adverse effects were observed or anticipated from the procedures performed in this study. All subjects were free-living animals participating at will in the experiment. This population was habituated to and comfortable around human presence. The nut species and size of tools provided reflected those naturally available to the species, and the observed nut cracking was within their typical behavioural repertoire.

RESULTS

Material Durability

Hammer durability was relatively constant across materials, with all hammers except one remaining useable throughout the study with minimal change to their mass. The large quartzite hammer was the sole exception, fracturing in half after 166 strikes (Fig. S5). In contrast, anvil durability, measured as the length of time tools remained useable, was much more variable and closely matched our prior knowledge of the material hardness, broadly defined here as their tendency to resist deformation or fragmentation. The softest anvils (sandstone and siltstone) fractured into numerous small pieces (>30 each) in less than 84 and 129 strikes, respectively (Fig. S6). The slightly harder ironstone anvil developed a large depression and eventually split in half after 536 strikes. However, both halves remained viable anvils. One half was retained for the remaining duration of the study, accumulating a further 974 hammer strikes (1510 total for the anvil). Anvil thickness also influenced durability. The hard but thin concrete anvil had its first large piece break off after only 16 strikes, and after 700 strikes, it had been broken into six pieces (7.5–14 cm long). The hard quartzite and thicker hard concrete anvils were the only anvils that remained predominantly intact by the end of the study, after sustaining 1758 and 1052 hammer strikes, respectively. Although both anvils lost pieces along their outer edge up to 14 cm in length, these pieces were generally thin and did not alter the overall size of the anvils by more than a few centimetres in either direction.

Model Overview

GLMM analysis reveals that tool performance is influenced by the tool attributes included in the models. All three models differed significantly from their respective null model (see Table S2 for all model comparisons). Further full versus reduced model comparison for all three models did not find support for the presence of an interaction between material and use. This indicates the rate at which tool performance changes with use does not differ depending on the material the tool is made of. However, material, hammerstone weight and the prior use of the tool all had important effects on the aspects of tool performance investigated. These are discussed in detail below. These influences were consistent across individuals, although individuals themselves differed in their nut-cracking performance (predictive plots of conditional effects: Fig. S7). We report model outputs (effect sizes and predicted values) using the reduced version of each of the three performance models, where there is no interaction (full model results in Table S3; Figs. S8 and S9). Unless stated otherwise, all predicted values assume a male capuchin, an unused tool (prior uses = 0) and a hammer weight of 518 g (the mean for this study).

Cracking Success

Overall, only slightly more than half of all nuts were cracked successfully (58%). Unsuccessful nut-cracking events were largely the result of the nut flying off the anvil when struck. The likelihood of cracking a given nut depended heavily on the tool material and hammer weight. Material was shown to have a highly significant effect (model 1: full versus reduced model comparison: $\chi^2_6 = 25.9$, $P < 0.001$), with nuts being cracked more reliably using some materials over others (effect size E between −1.06 and 1.04; Table 2). The best-performing material was a hard anvil paired with soft hammerstones (tool set 4: thick concrete anvil, siltstone hammerstones, predicted likelihood of 0.83; Fig. 2a). This material was over three times more likely to crack a given nut than the worst material (tool set 6: soft anvil, hard hammer: ironstone anvil, quartzite hammerstones; predicted likelihood of 0.25 Fig. 2a). Larger hammers were also significantly more effective at cracking nuts ($\chi^2_1 = 5.5$, $P < 0.05$). The likelihood of successfully cracking a nut increased significantly with hammer weight (E ± SD = 0.11 ± 0.051). When comparing the smallest hammer (c. 260 g) with the largest (c. 650 g), the chance of cracking a nut rose by 20% (predicted likelihood of 0.52 versus 0.62; Fig. S10). Although 20% is still a notable difference, this is much less than the 300% difference between materials. The influence of hammer weight may be somewhat muted by the fact that capuchins were able to choose their preferred hammer. Capuchins chose the largest available hammer 77% of the time. Although the exact frequency at which the largest hammerstone was selected differed between individuals, all individuals tended to prefer larger hammerstones (Fig. S11). Tools did not get better or worse at cracking nuts over time: the full model did not differ from the reduced model where prior use was removed ($\chi^2_4 = 6.4$, $P = 0.17$).

Table 2
GLMM outputs for cracking success, hits per nut and hits per reward

Parameter	Model 1: Cracking success			Model 2: Hits per nut			Model 3: Hits per reward		
	Estimate	(SD)	*Z*	Estimate	(SD)	*Z*	Estimate	(SD)	*Z*
Intercept	0.31	(0.24)	1.26	−0.25	(0.15)	−1.70	0.44	(0.077)	5.67
Material									
Tool set 3	0.81	(0.21)	3.87	0.86	(0.14)	6.02	0.36	(0.12)	2.96
Tool set 4	1.04	(0.37)	2.84	0.28	(0.16)	1.81	−0.00035	(0.10)	−0.0034
Tool set 6	−1.06	(0.30)	−3.54	−0.58	(0.24)	−2.41	0.34	(0.19)	1.80
Use	0.0087	(0.013)	0.67	0.032	(0.012)	2.66	0.041	(0.0088)	4.65
Hammer weight	0.11	(0.051)	2.07	−0.27	(0.039)	−6.78	−0.24	(0.037)	−6.58
Sex female	−1.49	(0.51)	−2.90	0.67	(0.31)	2.18	0.87	(0.22)	4.05

Outputs reflect the model where the interaction between material and use is removed. Estimates for hammer weight and use have been scaled to reflect change per 100 g and 100 cumulative hammer strikes, respectively. The base material was tool set 1, which had a hard quartzite anvil and hard phonolite hammerstones. Material effects are from tool set 3 (hard anvil, soft hammer: thin concrete anvil, siltstone hammerstones), tool set 4 (hard anvil, soft hammer: thick concrete anvil, siltstone hammerstones) and tool set 6 (soft anvil, hard hammer: ironstone anvil, quartzite hammerstones).

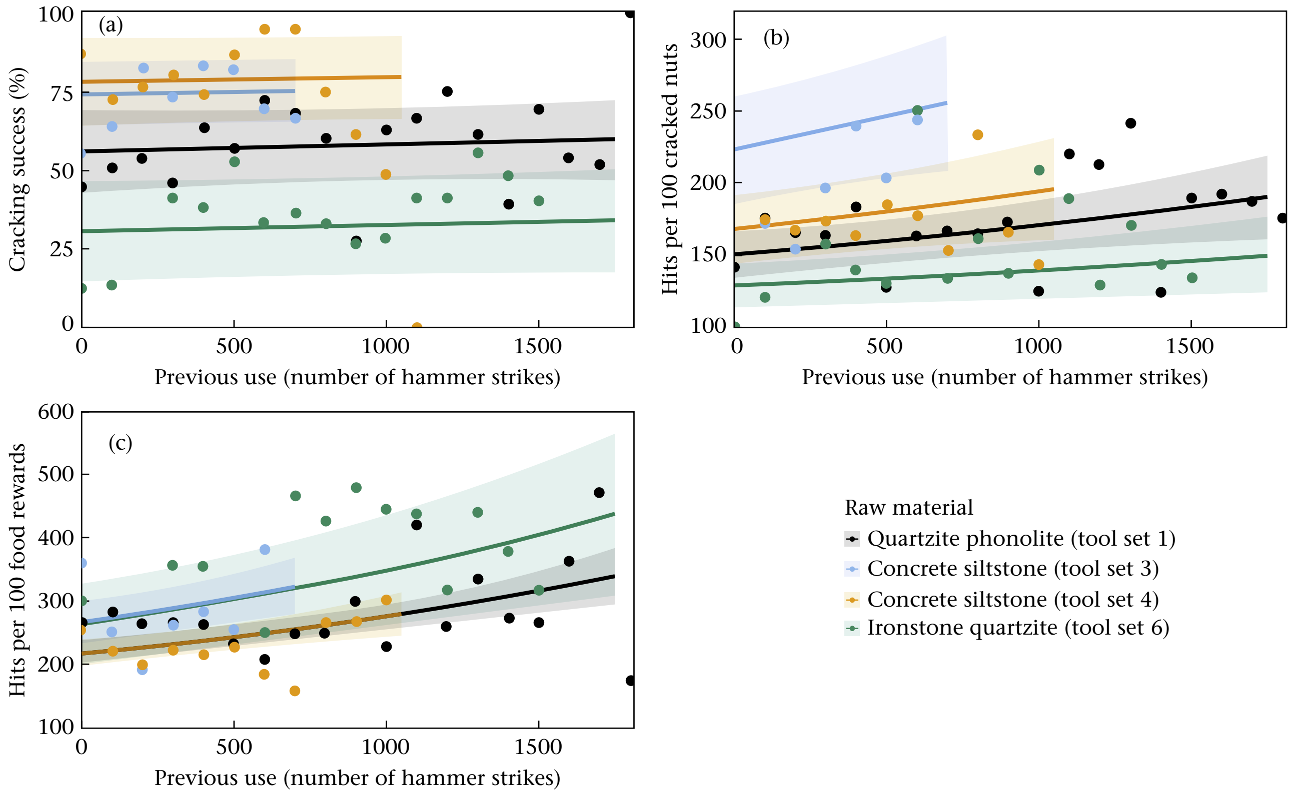

Figure 2. Influence of raw material and prior use on tool performance. Tool performance as measured by the likelihood of successfully cracking a nut (a, model 1), hits to open a nut (b, model 2) and hits to obtain a food reward (c, model 3). Performance varies with increasing use and across tool sets of different raw material (listed as anvil then hammerstone, with tool set 3 containing the first, thinner concrete anvil). Quartzite, phonolite and concrete are hard materials, whereas siltstone and ironstone are soft. Each point indicates the observed data, averaged across 100 hammer strikes. Three outlying points are excluded to improve interpretation of the slope (visible in Fig. S12). Lines reflect model predictions, assuming a male capuchin and hammer weight of 518 g, with no interaction between raw material and use. Shaded areas reflect one standard error either side of the estimate.

Hits Per Nut

Tool material, hammer weight and prior use were all important variables in determining the number of hits required to crack a nut. Tools made of different materials varied considerably in the number of hits required to open a nut (model 2: E between −0.58 and 0.86; full versus reduced model comparison: $\chi^2_6 = 25.5$, $P < 0.001$). Larger hammers also required fewer hits than smaller hammers ($E \pm SD = -0.27 \pm 0.039$; $\chi^2_1 = 39.8$, $P < 0.001$). Although the majority of nuts were opened in one (59%) or two (24%) hits, capuchins in our study could crack as many as 99 nuts in one sitting. In these circumstances, small differences in effort on a per-nut basis may have large cumulative effects. We thus report our results in terms of hits per 100 nuts, as calculated by multiplying the predicted hits-per-nut by 100. Comparing the predicted number of hits across different materials and hammer weights shows both these factors are similarly important. The worst performing material (tool set 3: hard anvil, soft hammer: thin concrete anvil, siltstone hammerstones) required almost twice as many hits compared to the best material (tool set 6: soft anvil, hard hammer: ironstone anvil, quartzite hammerstones) with a respective 223 versus 128 predicted hits per 100 nuts (Fig. 2b).

Similarly, the smallest hammer required almost twice the number of hits compared with the largest hammer (predicted hits: 240 versus 147). Tools also appeared to perform worse as they accumulated use. The predicted number of hits increased from 167 to 220 when comparing an unused tool with a heavily used tool (0 versus 1750 prior strikes; E ± SD = 0.032 ± 0.012; $\chi^2_4 = 12.3$, $P < 0.05$). However, this result appears to be driven by one tool set. The comparatively thin concrete anvil in tool set 3 splits in half partway through the study. When nuts were placed along the fracture, the anvil would move when struck, likely dissipating the force of the hammerstone. Rerunning the full versus reduced model comparison without tool set 3 showed performance did not significantly degrade with use ($\chi^2_3 = 4.7$, $P = 0.19$).

Hits Per Reward

The energetic efficiency of nut cracking varied according to tool material, hammer weight and prior use. Full versus reduced model comparisons show these effects were significant. As with the hits-per-nut model, the results for this model are discussed in terms of hits per 100 food rewards. Materials differed in their efficiency, although this difference was not as strong as for the other performance metrics (model 3: E between 0 and 0.36; $\chi^2_6 = 17.6$, $P < 0.01$). Efficiency increased by 18% from the worst materials (tool sets 3 and 6: thin concrete anvil with siltstone hammerstones, ironstone anvil with quartzite hammerstones; c. 265 predicted hits) to the best materials (tool sets 1 and 4: quartzite anvil with phonolite hammerstones, thick concrete anvil with siltstone hammerstones; 217 hits each; Fig. 2c). Poor performing materials had either thin (tool set 3) or soft anvils (tool set 6), whereas high-efficiency tool sets had hard anvils paired with either hard (tool set 1) or soft hammerstones (tool set 4). Hammer weight was important for efficiency, with larger hammers requiring substantially fewer hits (E ± SD = −0.24 ± 0.037; $\chi^2_1 = 40.7$, $P < 0.001$). Efficiency increased by 45% from the smallest (366 hits) to the largest (203 hits) hammer. Tools became less efficient over time as they accumulated use (E ± SD = 0.041 ± 0.0088; $\chi^2_4 = 24.6$, $P < 0.001$). The predicted number of hits per 100 food rewards increased by 61% (242 versus 390 hits) when comparing an unused tool (0 prior strikes) with a heavily used tool (1750 prior strikes). Unlike in the hits-per-nut model, the effect of use in this model does not appear to be due solely to tool set 3 (thin concrete anvil, siltstone hammerstones). Even if this material is removed, there is a significant difference between the full model and a reduced model which excludes an effect of use ($\chi^2_3 = 20.6$, $P < 0.001$).

DISCUSSION

Most studies investigating the environmental context of stone tool use in nonhuman primates have focused heavily on the quality and availability of extractable food resources (Fox et al., 2004; Izar et al., 2022; Koops et al., 2013; Sanz & Morgan, 2013; Spagnoletti et al., 2012; Yamakoshi, 1998). There has been comparatively little emphasis on the effect of available raw tool material on foraging outcomes. Here, we investigated if raw material affects the performance and durability of tools used by capuchins for nut cracking, particularly with regard to material hardness.

All raw materials provided to the monkeys were successfully used to crack nuts. However, raw materials differed significantly in performance. The strongest difference was in the likelihood of successfully cracking open a nut (i.e. reliability). Reliability was lowest when pairing a soft anvil with hard hammerstones (tool set 6: ironstone anvil with quartzite hammerstones) and highest when pairing a hard anvil with soft hammerstones (tool sets 3 and 4: concrete anvil, siltstone hammerstones). Failure to crack a nut was typically due to the nut flying off the anvil when struck, indicating this is an issue of nut stability. The influences of material hardness on nut stability were counter to our expectations, wherein soft anvils were predicted to improve nut stability by exerting less force upwards onto the nut as the anvil absorbs more force from the hammer strike. Instead, surface friction may have been more important for stabilizing nuts. In this study, the hard concrete anvils had a visibly rough surface and exhibited the greatest nut stability. In comparison, the soft ironstone anvil provided the least stability to the nut and had a weathered surface that scratched and subsided easily when struck.

Also counter to our expectations was the fact that nut stability did not change as anvils accrued damage. Previous research has shown that anvil pits formed through nut-cracking behaviour improve foraging outcomes by stabilizing nuts (Fragaszy et al., 2010, 2013; Haslam et al., 2014; Liu et al., 2011). Anvils in this study accumulated surface damage, including shallow, wide depressions (Luncz et al., 2022 for details). However, these depressions were likely not deep or narrow enough to effectively stabilize the hard, round nut being cracked. The anvils in this study may not have formed effective pits in part due to their small size: large sedimentary anvils used by capuchins at Fazenda Boa Vista can form several pits on a single anvil surface (Haslam et al., 2014). Based on these results, although material properties such as hardness can be expected to influence nut-cracking outcomes, this effect is likely to depend on other factors such as mass or surface texture.

Raw materials also differed significantly in the number of hits required to crack open a nut. This performance metric is often used to infer energetic efficiency of nut cracking (Boesch et al., 2017; Falótico et al., 2024; Luncz et al., 2024). However, in this study, the number of hits per nut appeared to be influenced by nut stability. The hits per nut for a given material was inversely proportional to its cracking success, the latter of which was directly influenced by nut stability as discussed above. When nut stability is low, then there is a high chance of losing a nut each time it is struck. Harder nuts that require more hits are therefore more likely to be lost and will not contribute to the hits per nut for that material. This can make low-stability materials appear more 'efficient' than they are. Instead, efficiency can be accurately described by the number of hits required to obtain a food reward. This performance metric differed significantly across materials, with an approximately 20% difference between the best materials (tool set 1: quartzite anvil and phonolite hammerstones, and tool set 4: thicker concrete anvil and siltstone hammerstones) and the worst materials (tool sets 3: thinner concrete anvil and siltstone hammerstones, and tool set 6: ironstone anvil and quartzite hammerstones).

Comparison between tool sets suggests that multiple factors influence efficiency. Tool sets 1 and 4 had similarly high efficiencies. Tool set 4 achieved its high efficiency by having a high nut stability, which can be attributed to the surface roughness of the anvil as previously discussed. In comparison, tool set 1 achieved a high efficiency by cracking nuts in a small number of hits, suggesting this material had a highly effective hammer strike. This is likely due to its hard anvil and hard hammerstone combination exerting more force on the nut per strike. Increased hammer mass also significantly reduced the number of hits required to open a nut. Additionally, a comparison between tool sets 3 and 4 reveals an influence of anvil mass: both tool sets had a concrete anvil with siltstone hammers, but the anvil in tool set 4 was twice as thick and required far fewer hits per nut. This is likely because the larger anvil was more stable when struck by the hammerstone. Although prior research has identified an influence of hammer mass on nut cracking (chimpanzees; Boesch et al., 2017), anvil mass has largely been disregarded. Our results ultimately point to combined influences of surface friction, stone hardness and hammer and anvil mass on nut-cracking efficiency in capuchins.

The patterns of raw material performance observed here have implications for the conditions under which tool use may be expected to evolve. All raw materials provided to the monkeys were successfully used to crack nuts, suggesting a wide array of materials are suitable for this tool use behaviour. This aligns with prior studies, where percussive artefacts used by extant primates can consist of a wide range of rock types (Reeves, Proffitt, Malaivijitnond, & Luncz, 2023, 2024). It is also consistent with the fact that stone-mediated nut cracking has evolved in a wide variety of material landscapes (e.g. capuchins; Falótico et al., 2022; macaques; Proffitt et al., 2018; chimpanzees; Proffitt et al., 2022). As such, the type of stones available to a primate population may not present a major barrier to the emergence of tool use and is unlikely on its own to explain the absence or presence of tool use. However, differences in raw material performance may subtly augment the likelihood of percussive behaviours emerging in a given population. In this study, materials differed in the number of hits required to obtain a food reward, and the rate at which nuts were ejected from the anvil when struck. In a competitive species where food scrounging is common (Coelho et al., 2015; Vogel, 2005), the nut may not be retrievable once lost, which might result in a lower overall food yield. Raw materials thus differed in both the potential food yield and energetic efficiency they confer: two factors likely to affect the profitability (i.e. cost to benefit ratio) of tool use. The relative profitability hypothesis states that tool use should only be retained where it is more profitable than foraging without tools (Rutz & St Clair, 2012; Sanz & Morgan, 2013). Based on this study, the local relative profitability of tool use may depend on the raw materials available. Furthermore, capuchins may require more time to forage when using raw materials that frequently lead to the loss of the nut. Stone tool use is predominantly observed on the ground in capuchins (Falótico & Ottoni, 2023), macaques (Luncz et al., 2017; Malaivijitnond et al., 2007) and chimpanzees (Boesch & Boesch, 1983). Many primate populations face ground-based predation (Ferrari, 2009; Zuberbühler & Jenny, 2002), which has been theorized to limit opportunities for terrestrial tool use (Monteza-Moreno et al., 2020). Where ground-based predation is prevalent, the trade-off between tool use and predation risk may be partially alleviated by having access to highly reliable and efficient raw materials. Similar evolutionary pressures have been suggested for hominins, which faced predation by large mammals and may have reduced this predation risk by using tool materials that allowed for more efficient foraging techniques (Caruana, 2020).

These results also have implications for the cognitive evolutionary processes underpinning stone tool use. Where rock types differ in the foraging profitability they afford, there should be selective pressure for primates to be able to identify and select more profitable stone materials. Although prior studies have shown that primates sometimes prefer certain materials over others (chimpanzees; Boesch & Boesch, 1983; Luncz et al., 2012; Sirianni et al., 2015; capuchins; Visalberghi et al., 2007, Visalberghi, Addessi et al., 2009, Visalberghi, Spanolettie, et al., 2009), it was only recently that rock types have been conclusively shown to differ in nut-cracking performance (chimpanzees; Braun et al., 2025). Here, we demonstrate that raw material can influence capuchin nut-cracking performance according to multiple metrics (reliability and efficiency). Materials that perform well in one metric may not perform well in another. Furthermore, our study shows that raw material performance is likely influenced by a combination of stone properties. As such, primates likely need to consider many factors when selecting profitable stone material. This builds on the array of information primates are already known to use when selecting tools, including food type and tool mass, size or durability (e.g. capuchins; Fragaszy et al., 2010; Luncz et al., 2016a; Spagnoletti et al., 2011; Visalberghi, Addessi et al., 2009; chimpanzees; Sirianni et al., 2015; macaques; Gumert & Malaivijitnond, 2013). The specific criteria used to select materials will likely depend on the primate species in question. Although chimpanzee nut-cracking efficiency has been shown to be highest with soft anvils and hard hammers (Braun et al., 2025), capuchin nut-cracking efficiency in our study was highest for tool sets with hard anvils, regardless of the hardness of the hammerstone. Additionally, the nut stability afforded by different raw materials is likely to be more important for capuchins than for other nut-cracking primate species, as the two-handed nut-cracking technique used by capuchins leads to nuts frequently being ejected from the anvil when struck (Luncz et al., 2024). In addition to selecting appropriate materials, primates may benefit from being able to adjust their nut-cracking technique to account for differences in raw material performance. Capuchins have previously been shown to maximize energetic efficiency by dexterously altering the amount of force in each hammer strike depending on nut properties (Mangalam et al., 2016; Mangalam & Fragaszy, 2015). Capuchins may also benefit from using less force in their hammer strikes when using materials on which the nut is less stable. Collectively, this body of research highlights the cognitive flexibility required for percussive tool use. Many of these cognitive demands are also important to hominin stone knapping, including raw material selection and dexterously modulating how stones are struck against each other (Braun et al., 2009, 2025; Nonaka et al., 2010). This reinforces the theory that simple percussive behaviours in hominins, similar to nut cracking, could have provided a foundation for stone knapping to emerge. It may have done this, not only by incidentally producing cutting-edge flakes that hominins could have come into contact with (as demonstrated in Luncz et al., 2022) but also by scaffolding necessary cognitive abilities.

Besides tool performance, our results also revealed notable differences in tool durability, depending on raw material. As expected, soft sedimentary anvils saw the highest rates of fracturing. This is consistent with prior analysis regarding the rate at which different materials produce stone flakes and fragments (Luncz et al., 2022). This pattern of durability also matches what has previously been reported across wild primate populations. Natural sandstone anvils used by capuchins can lose large proportions of their mass in short periods of time (Haslam et al., 2014). In comparison, quartzite anvils used by captive chimpanzees show limited fracturing and prolonged durability (Arroyo et al., 2016). However, the rate at which the sandstone and siltstone anvils were destroyed was much faster than expected, given these materials are commonly used as anvils in their respective locations of origin. The degradation of these anvils may have been partially exacerbated by their small mass. The sandstone anvil is similar in size to other sandstone anvils used at the Serra da Capivara site from which it was obtained, but there is little published information on how long such anvils last. In comparison, at Fazeda Boa Vista, capuchin sandstone anvils are typically large (c. 1.89 m^2) and last for years despite losing mass when used (Haslam et al., 2014; Visalberghi et al., 2007). Unexpectedly, changes in performance were uniform across raw materials, despite anvils fracturing at different rates. As previously discussed, this is likely because the small mass of the anvils prevented them from forming deep pits before fracturing.

Differences in material durability have implications for the processes that shape technological landscapes in the long term. Prior research has shown that repeated short-scale transport of stones to tool use sites can lead to large-scale redistribution of stones away from their source location, expanding the availability of tool material within a population's home range (Luncz, Proffitt, et al., 2016; Reeves et al., 2021). Through processes such as these, primates may unintentionally improve opportunities for future generations to access and learn how to use tools. However, computer simulations indicate that this effect is more limited for low-durability materials that break quickly and thus have limited capacity for repeated use (Reeves et al., 2021, Reeves, Proffitt, Almeida-Warren, & Luncz, 2023). Our study demonstrates that stones available to primates can vary widely in how long they remain useable, with particularly rapid destruction of certain soft, sedimentary materials. Based on the aforementioned simulations, in environments dominated by low-durability sedimentary materials, tool use opportunities may be more geographically limited to areas near sources of stone. Conversely, even in environments where durable stones are rare, the geographical spread of tools could in theory be enhanced if primates preferentially transport these durable stones. This would increase the frequency, and potentially the cumulative distance, such tools were transported. Capuchins at Fazenda Boa Vista (FBV), Brazil, have been shown to preferentially transport more durable tools to palm nut-cracking sites: selecting Brazilian siltstone hammers over friable, weathered sandstone (Visalberghi, Addessi, et al., 2009). Similar stone selection processes have been used to explain the abundance of high-durability quartzite hammers at FBV nut-cracking anvils, despite their rarity in the surrounding landscape (Visalberghi et al., 2007). Capuchin selection of durable materials may be an indirect result of selecting more effective materials: Visalberghi, Addessi, et al. (2009) report that more friable materials at FBV (particularly sandstone) are not as effective at opening high-resistance palm nuts. In our study, the higher-durability quartzite anvil and phonolite hammerstones were also more reliable and efficient at cracking nuts than the lower-durability ironstone anvil and quartzite hammerstones. Selection for these effective materials could indirectly support the transport of durable longer-lasting materials throughout the landscape.

Cumulatively, this study provides evidence that raw materials differ in their performance and durability as primate nut-cracking tools. However, the influence of raw material on nut-cracking outcomes likely also depends on the food type being targeted. The palm nut species used here are moderately difficult to open. It is harder than some other species of oil palm nuts (e.g. 5 times harder than *Elaeis guineensis*; Luncz et al., 2024). It is also round, making it less stable than flat nuts such as cashew nuts, *Anacardium* spp. and sea almonds, *Terminalia catappa*. This combined hardness and roundness may have heightened how frequently nuts were lost when struck and made the ability of tools to stabilize nuts particularly important. The hardness of the nut may have also exacerbated differences in material durability. This is supported by prior research showing that stone tools used by chimpanzees are more likely to fracture when used on harder nuts (Reeves et al., 2024).

In conclusion, this study demonstrates that primate percussive tools differ in quality depending on the raw materials they are made of. Raw materials differ in their performance and durability as nut-cracking tools, with the precise pattern of this effect depending on the nut-cracking species. The specific material properties influencing tool quality are likely to be diverse. Here, we indicate that nut-cracking outcomes may be influenced by stone hardness, surface texture and their interaction with tool mass. Ultimately, differences in durability across materials may help shape the emergence of tool use by altering the local profitability of tool use, selecting for cognitive flexibility and augmenting the dynamic processes shaping technological landscapes.

Author Contributions

Ignacio de la Torre: Writing – review & editing, Funding acquisition. **Jonathan S. Reeves:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Lydia V. Luncz:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Nora E. Slania:** Writing – review & editing, Formal analysis. **Theo D.R. O'Malley:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Tiago Falótico:** Writing – review & editing, Funding acquisition, Data curation. **Tomos Proffitt:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization.

Data Availability

All relevant data are available in the supplementary material.

Declaration of Interest

The authors declare no competing interests.

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Supplementary Material

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