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Stone selection by wild chimpanzees shares patterns with Oldowan hominins

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ABSTRACT

The use of broad tool repertoires to increase dietary flexibility through extractive foraging behaviors is shared by humans and their closest living relatives (chimpanzees, *Pan troglodytes*). However, comparisons between tool use in ancient human ancestors (hominins) and chimpanzees are limited by differences in their toolkits. One feature shared by primate and hominin toolkits is rock selection based on physical properties of the stones and the targets of foraging behaviors. Here, we document the selectivity patterns of stone tools used by wild chimpanzees to crack nuts at Bossou, Guinea, through controlled experiments that introduce rocks unknown to this population. Experiments incorporate specific rock types because previous studies document hominin selection of these lithologies at Kanjera South 2 Ma. We investigate decisions made by chimpanzees when selecting stones that vary in their mechanical properties—features not directly visible to the individual. Results indicate that the selection of anvils and hammers is linked to task-specific mechanical properties. Chimpanzees select harder stones for hammers and softer stones for anvils, indicating an understanding of specific properties for distinct functions. Selectivity of rock types suggests that chimpanzees assess the appropriate materials for functions by discriminating these 'invisible' properties. Adults identify mechanical properties through individual learning, and juveniles often reused the tools selected by adults. Selection of specific rock types may be transmitted through the reuse of combinations of rocks. These patterns of stone selection parallel what is documented for Oldowan hominins. The processes identified in this experiment provide insights into the discrete nature of hominin rock selection patterns in Plio-Pleistocene stone artifact production.

1. Introduction

The study of human evolution has long associated the emergence of our genus (*Homo*) with the origins of tool use (Leakey, 1975). However, recent discoveries of fossilized bones bearing butchery marks dated to around 3.4 million years ago (McPherron et al., 2010; Dominguez- Rodrigo et al., 2010) and 3.3-million-year-old Lomekwian tools (Harmand et al., 2015; Archer et al., 2020) add to a growing body of evidence that places the origins of tool use much further back in time than the earliest recognized fossils of the genus *Homo* (Panger et al., 2002; Key et al., 2021; Plummer et al., 2023). At present, the origin of tool use in our lineage is subject

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of debate (Toth and Schick, 2018; Archer et al., 2020), yet it is clear that evidence for tool use in the past will provide insights into uniquely human features associated with our technological dependence (Hill et al., 2009; Laland and O'Brien, 2010; Tennie et al., 2017). Recent reviews of both anatomical and behavioral variation in the Pliocene indicate that tool use may have very deep roots among hominoids (Almecija et al., 2010; Almécija et al., 2015; Carvalho and Beardmore-Herd, 2019; Prang et al., 2021). This older extension of hominoid tool use is potentially expected, given the numerous examples of tool use as an adaptive strategy in the animal kingdom and in particular, the primate order (Biro et al., 2013). The field of primate archaeology has expanded upon this by linking the material record to the complex dynamics of behavior and biology that cannot be observed in the archaeological record (Haslam et al., 2017; Carvalho and Beardmore-Herd, 2019; Proffitt et al., 2023). Understanding the parallels between hominin and nonhuman primate tool use is critical as the archaeological record continues to extend further back in time (McPherron et al., 2010; Benito-Calvo et al., 2015; Harmand et al., 2015; Harmand and Arroyo, 2023; Plummer et al., 2023).

Significant morphological differences exist between hominin (usually focused on producing sharp edges) and chimpanzee tools (usually focused on percussive actions), which limit the value of direct comparisons of the material record of these behaviors (Davidson and McGrew, 2005; Bandini et al., 2022). Technology-related behaviors such as selection and transport provide greater avenues for comparison (Visalberghi et al., 2015; Luncz et al., 2016b) and may offer novel insights into behavioral adaptations signifying distinctions or similarities within the primate order (Carvalho et al., 2012).

Chimpanzees (*Pan troglodytes*) incorporate size and weight of tools in selection decisions (Biro et al., 2003; Carvalho et al., 2008). Furthermore, within chimpanzee nut-cracking, tool selection appears to be dependent on the interplay between multiple variables, reflecting a large set of conditional rules for the optimal use and transport of tools suggestive of the anticipation of future events (Sirianni et al., 2015). Despite these findings, at the community level, selection of certain types of tools (e.g., rock type, wooden vs. stone tools) has been shown to be pervasive within a group and is maintained even when group-wide patterns result in efficiency costs (Luncz et al., 2012, 2018; Luncz and Boesch, 2015). Such patterns are further indicative of a strong influence of the social environment on tool selection, in line with the broadly held view that chimpanzee tool use is at least in part culturally transmitted (Biro et al., 2003; Luncz et al., 2012; Koops et al., 2014). Investigations of shared technological characteristics between hominin and primate tool use (i.e., selection) may provide insights into the possible influence of information transfer on patterns of tool use in the past (Sakura and Matsuzawa, 1991; Biro et al., 2003, 2006, 2013; Luncz and Boesch, 2015).

The selection and transport of task-appropriate tools is a feature that is shared between Pleistocene hominins and nonhuman primates (Carvalho et al., 2008; Rolian and Carvalho, 2017). Although there is great variety in the technology used by various Pleistocene hominins, the selection of specific rock types for tool production remains one of the few features consistent across these industries (Braun et al., 2019). Studies of Oldowan stone tool technology have highlighted that human ancestors selected specific lithologies for tool manufacture based on distinct properties of the rocks including their ability to fracture and their resistance to wear during use (Stout et al., 2005; Braun et al., 2009b; Harmand, 2009; Plummer and Finestone, 2018). Understanding these selection features is especially important when the properties of stone are not directly evident from the macroscopic visual properties of the objects. Although this behavior seems ubiquitous across the entire African continent, there is little understanding of how hominins acquired information about the properties of rocks in the past (Braun et al., 2009b; Plummer and Finestone, 2018).

The concurrence of tool use (especially percussive tool use) among primate and hominin lineages remains a topic that needs further investigation if we aim to explain the ubiquity of this behavior among nonhuman primate tool users (Carvalho and McGrew, 2012; Benito-Calvo et al., 2015; Visalberghi et al., 2015; Carvalho and Beardmore-Herd, 2019; Proffitt et al., 2023). Chimpanzee choices of stone types for nut-cracking may provide insights into the mechanisms at play in the selection of rocks used for the production of stone artifacts in the earliest hominin assemblages and thus merits further attention (Stout et al., 2005; Braun et al., 2008; Goldman and Hovers, 2009; Plummer and Finestone, 2018). It is important to re-emphasize that the selection decisions by chimpanzees of specific rock types will be distinct from hominins, largely because tool use is different in the two species (Proffitt et al., 2018; Bandini et al., 2022). However, the degree of selectivity and the mechanisms of identifying appropriate rock types should have clear parallels.

The chimpanzees of Bossou in Guinea, West Africa, are well known for their diverse tool repertoire and, in particular, for their use of moveable stones as hammers and anvils to crack open oil palm nuts (Matsuzawa et al., 2001; Biro et al., 2003). No other extant nonhuman primate communities are known to systematically combine movable hammer and anvil stones for the cracking of hard-shelled nuts, making Bossou a site of particular relevance for addressing questions regarding stone tool selectivity patterns (Supplementary Online Material [SOM]). The Bossou context combines components of the ecological reality of studies of wild subjects with a level of experimental control typically possible only in captive experimental work. This setting allows for investigation of the details of stone tool selection and use and the production of the material record of chimpanzee tool use behaviors in a naturalistic setting (Carvalho et al., 2008; Benito-Calvo et al., 2015). Nut-cracking by Bossou chimpanzees is the result of a complex learning process that involves both social and individual learning over an extended period (Matsuzawa et al., 2001; Biro et al., 2003). Acquisition involves mastering components of tool selection and transport as well as identification of suitable rock types for use as hammers and anvils (Carvalho et al., 2008, 2009; Carvalho and McGrew, 2012).

A major impediment to comparisons of tool selection between the hominin stone artifact record and chimpanzee tool use relates to stone availability (Carvalho et al., 2008; Luncz et al., 2012, 2016b). The diversity of rock types in the natural settings where chimpanzees use stone to crack nuts is rarely as varied as that seen among Pleistocene hominins (Braun et al., 2009b; Harmand, 2009; Goldman-Neuman and Hovers, 2012; Plummer and Finestone, 2018). This is also true for the site of Bossou, where a limited number of rock types (amphibolite and quartz) are available for nut-cracking in the chimpanzee's natural habitat (Carvalho et al., 2008). In contrast, numerous Oldowan archaeological sites have documented the incorporation of more than 10 different lithologies in the technological repertoire of Oldowan hominins (Stout et al., 2005; Braun et al., 2009b; Harmand, 2009; Plummer and Finestone, 2018).

We overcome this limitation by introducing a diverse array of rocks transported from East Africa to the Bossou research site. This enables us to directly compare stone tool selection between extant nut-cracking chimpanzees and Oldowan hominins from Kanjera South. Kanjera South is a well-studied ~2.0 Ma Oldowan locality from western Kenya. The archaeological record at Kanjera South indicates hominins selected specific rock types and transported them over 10 km to the site. These rock types were used to access large mammalian carcasses and process underground storage organs (Plummer, 2004; Bishop et al., 2006; Braun et al., 2008, 2009b; Plummer et al., 2009; Ferraro et al., 2013; Lemorini et al., 2014). Selection of specific rock types is a feature that is well studied in Oldowan hominins (Stout et al., 2005; Harmand, 2007; Braun et al., 2008; Goldman-Neuman and Hovers, 2012; Plummer and Finestone, 2018). Hominins at the Kanjera South locality selected rock types specifically from distant parts of the landscape and transported rocks that had mechanical properties that are ideal for making chipped stone tools (Braun et al., 2009b).

We investigated the ability of individuals in the Bossou community to discriminate between rock types with significant differences in mechanical properties (Stout et al., 2005; Braun et al., 2009b; Harmand, 2009). We introduced specific rock types that varied in their mechanical properties into a specially designed outdoor laboratory at Bossou where nut-cracking activities can be investigated (Matsuzawa, 2011). We chose certain rock types for the experiment that vary in properties that may impact their suitability as a hammer or anvil during nut-cracking behaviors (Fig. 1). Critically, these rocks had mechanical properties that are significantly different from many of the rock types naturally available at Bossou (SOM Tables S1–3). The major rock types available at Bossou (amphibolite/diorite and quartz) are heavily weathered and break frequently. This is in stark contrast to the introduced rocks. None of the local rock types were incorporated into the experiments, so we did not explore selection patterns of these materials. Furthermore, the color of the introduced rocks provides no external indication of the mechanical properties of these stones (Fig. 2). The experimental setting followed protocols previously established for the outdoor lab at Bossou. This investigation of chimpanzee stone selection followed two phases. The first phase (Condition 1) introduced the rock types that had the highest values for the various mechanical properties (dacite), as well as the rock with the lowest values (carbonatite). Rocks were then introduced in the experiment in a randomized matrix to prevent placement of stones from influencing selection patterns. We conducted six experimental sessions in Condition 1. The second phase (Condition 2) introduced two further rock types (granite, phonolite) with intermediate properties. We conducted nine experimental sessions in Condition 2. Through these naturalistic experiments, we investigated the variables driving chimpanzee raw material selection and reported patterns that parallel those documented in the Oldowan (Plummer, 2004; Braun et al., 2008; Plummer et al., 2009; Plummer and Finestone, 2018). We also explore how patterns of selection change over the course of our experiment. This allows us to explore the mechanism for how rock material properties are ascertained by the Bossou chimpanzees. We also compare the patterns of selection with estimates of selection in Oldowan hominins based on data collected from previous studies of rock selection in Oldowan assemblages.

2. Materials and methods

2.1. Rock mechanical properties

We measured a variety of properties of the stones introduced in the experiment (Leeb hardness, Young's modulus of elasticity, rebound hardness) to explore the variability in rock properties that

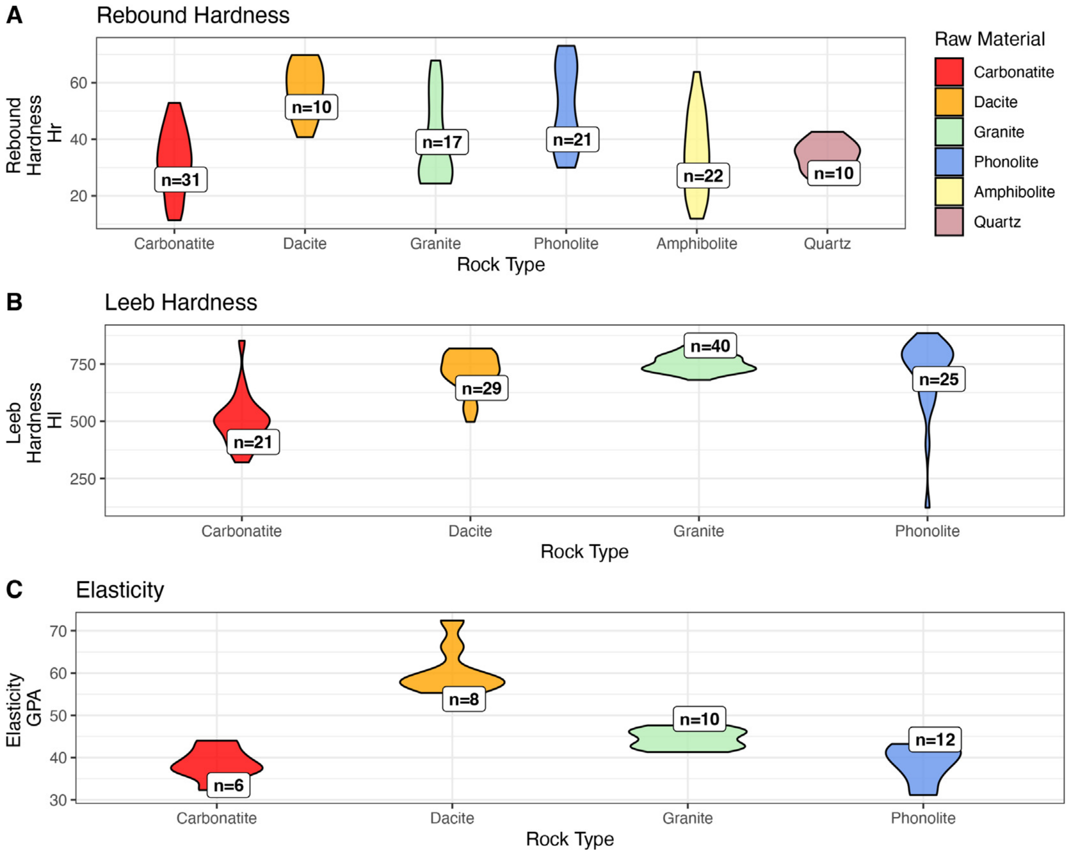

Figure 1. Rock hardness of experimentally introduced lithologies and local rock types. Data are presented as a violin plot. The width of the shape reflects the relative proportion of the data in the dataset at a specific point along the y-axis. Section A represents value of rebound hardness. Section B represents values of Leeb hardness (H_L) for experimental samples. Section C represents values for modulus of elasticity (N/m^2) for experimentally introduced lithologies. Abbreviation: GPA = Gigapascal.

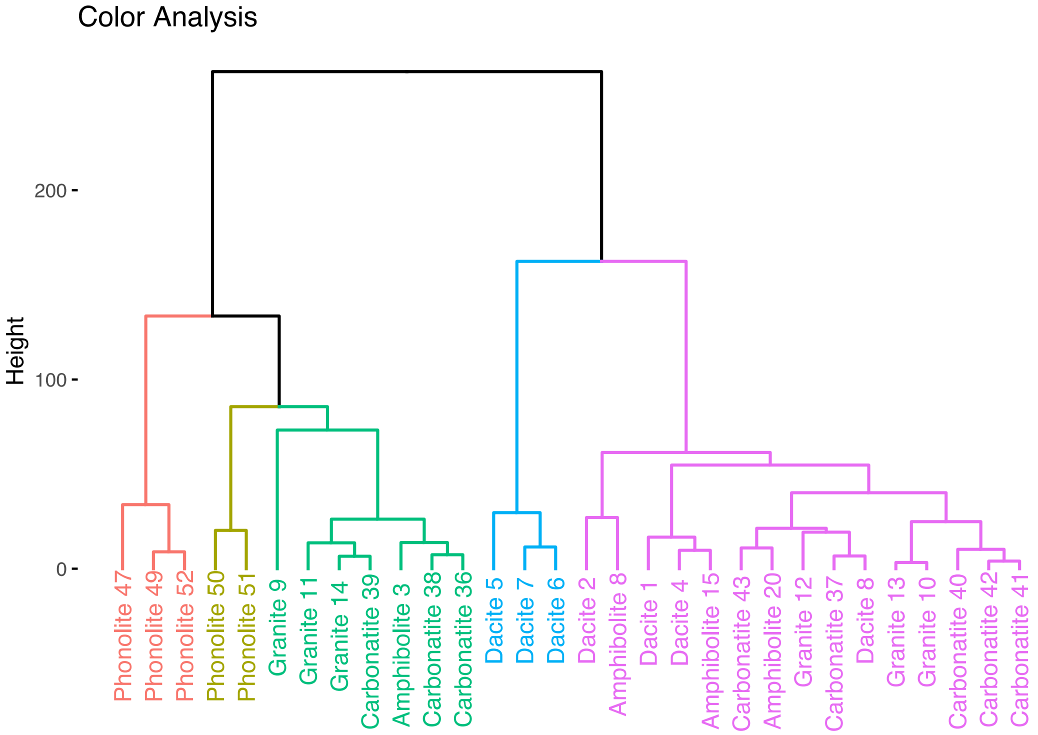

Figure 2. Dendrogram of a K-mean cluster analysis of RGB color values from the rock types used in this study. Note that although many clusters include a single rock type, numerous rock types can be found in separate clusters (e.g., granite, carbonatite, and amphibolite (local) in the same cluster). Also, note that rocks of vastly different mechanical properties (e.g., granite, carbonatite) are often clustered together. This emphasizes the fact that the properties of stones are not easily identified from visual inspection of the stones themselves. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) RGB: red, green, and blue.

may influence rock selection. Analysis of these various mechanical properties indicates that the rock types introduced in this experiment are usually harder and more durable than those available in the Bossou Forest (except for carbonatite). The different mechanical properties are not correlated such that selection related to a specific mechanical property is likely independent of other mechanical properties (Fig. 1; SOM Tables S1–S3). All of the stones in the study also conformed to four standardized size categories (SOM Table S4). The hardness and elasticity of rocks used in the various experiments were measured at the field station in Guinea, West Africa. Subsequent testing of blocks of stones from the same outcrops as those used in the experiments was conducted at the Stone Age Archaeology Lab at George Washington University. We measured rocks using three different standard mechanical tests. Although these measures were not all developed for stones, they have been adapted to allow for measurements of fine-grained rocks (Braun et al., 2009b).

Rebound hardness Rebound hardness is a measure of rock hardness originally devised for field-based geomorphological applications (Katz et al., 2000; Goudie, 2006; Viles et al., 2010). The test is largely nondestructive and includes a calibrated spring-loaded plunger. Here we used the Proceq Silverschmidt Rebound Hammer, which uses an internal calibration to account for the potential effects of friction on the plunger when used at different angles (Hannachi and Guetteche, 2014). Each stone was measured using the standard American Society for Testing and Materials (ASTM) methodology by placing the stone on a solid steel plate. The hardness of these stones was only recorded when it was clear that the sample was large enough and stable enough that vibrations in the measured stone did not impact the values recorded. Samples that cracked or were broken during the process of measurements were removed from the analysis. A subset of the smallest samples in this study were not used included in the data because the samples were too small to measure. Values of rebound hardness were based on ASTM D-5873, which requires multiple testings and subsequent discarding of the upper and lower quartile of values. The second and third quantiles were averaged for each specimen to produce the values reported here.

Leeb hardness The Leeb hardness tester is a non-destructive test of surface strength. It is known for high accuracy, precision, and portability (Leeb, 1979; Kompatscher, 2004). The Leeb hardness tester fires an impact body with an indenter made of very high known hardness (carbide) which impacts the surface of the material. The impact body goes through a stage of movement toward the surface and then passes through an impact phase where the testing surface deforms plastically and elastically. The elastic recovery of the tested surface causes the rebound of the indenter into the Leeb hardness tester. The velocity of the travel of the indenter is directionally proportional to the force of the indenter after the initial impact phase. The Leeb hardness value (H_L) is the ratio between rebound velocity and the impact velocity multiplied by 1000. When no plastic deformation takes place, then the value is recorded at 1000 (complete recovery of initial impact force). When energy is consumed in the plastic deformation of the test surface, less of the original impact energy is recovered in the rebound phase. The high accuracy and precision of these measurements allow for direct comparison with other measures of surface hardness (e.g., Rockwell hardness: HRC). Calibrated reference blocks were measured before and after each measurement process to insure standard calibration within the experiments. All materials were measured using standard measurement techniques outlined in ASTM 956-96.

Elastic modulus The measurement of elasticity of rocks is often assumed to be equivalent to the bulk modulus of elasticity because most crystalline rocks are isotropic. As such, we measured Young's (or stiffness) modulus and attributed it to the general elasticity of the rock being measured (without separately measuring a modulus of shear strength or rigidity). This property reflects the ability for a rock to deform under stress and return to its original shape. As such, we hypothesize that rocks that have high rock stiffness are likely to transfer more of the energy to a nut during nut-cracking than those rocks that may undergo some plastic deformation. We measured rock stiffness using an ultrasonic instrument (Pundit Lab+; Proceq). This test measures the speed of the transmission of ultrasonic waves through a rock. Conversion of ultrasonic values to Young's modulus values requires an understanding of rock density and the length of a rock specimen. A standard P-wave and S-wave transducer was used to investigate the speed of P and S waves through the samples. We used a standard couplant to ensure consistent transmission of ultrasonic waves through the specimens. Prior to each test, the system was calibrated using a standard calibration rod with a known value for elastic modulus. The measurement of P- and S-wave values was averaged over three measurements to remove potential variation caused by the security of the manual coupling of transducers to the samples. S-wave velocity was measured five times using varied pulse intervals and rotation of transducers to identify possible courses of error. Values were averaged and the specific values for the elastic modulus were calculated using Punditlink software.

2.2. Selectivity

To investigate the selection process of specific rock types, we used a measure of selectivity that was modified from dietary selectivity (Leighton, 1993). In this measure, each individual instance of selection is calculated using a) the total number stones available for selection by the individual at the time of selection and b) the number of stones available of the same raw material as that being selected.

[selectivity = # of stones available for selection of a specific raw material at the time of selection/total # of stones available for selection at the time of selection].

At each instance of selection, we determined which stones were available for selection (based on which tools were currently used by other individuals). This measure allows for each individual selection to be ranked as high selectivity (when the rock type that is being selected is rare at the point of selection) or low selectivity (when the rock type being selected is abundant at the point of selection). These events of selection were investigated using linear mixed models to understand the impact of various factors (fixed and random effects) on selection (response variable). This includes details of the individual animal that is selecting a stone (age, sex, ID) as well as contextual factors (rock type, rock size). As rock type did not vary consistently with color, we used pixel color values from digital images with standardized lighting to create color groups (Fig. 2). We also included a variable that related to whether individuals were reusing a toolset (the combination of a specific hammer and anvil) from another individual. This feature we refer to as toolset 'reuse.' We only counted reuse when an entire set (hammer and anvil) was reused by and individual.

2.3. Color analysis

Due to the varied color of the experimental stones and the inconsistent relationship between lithology type and color designation, we created experimentally determined color groupings. We took digital photos of each of the stones used in the experiment under identical lighting conditions. We then selected a single 5 cm × 5 cm square from the center of the specimen. The average values for red, green, and blue for the pixels in this selection were calculated using Image J 1.51f. These values were then used in a K-means cluster analysis using Euclidean distances. The resulting k-means clustering algorithm identified five major clusters with distinct color signatures (Fig. 2). Note that although most clusters are dominated by a particular rock type, certain rock types are found in numerous clusters. These clusters identified in this analysis were used in the subsequent generalized linear mixed models to assess the influence of color on chimpanzee selection decisions. Note that there is no relationship between color distinctions and any raw material properties (correlation between cluster group and rank order Leeb hardness: Kendall's Tau = 0.018; p = 0.94). Although material properties can also be assessed from the grain size and phenocrysts present in rocks, these are usually visible only in rocks with fresh breaks (all of the experimentally selected cobbles had smooth cortex on all surfaces). In addition, the rock types selected in this study are all fine-grained rocks (Braun et al., 2009b).

2.4. Efficiency

We investigated levels of nut-cracking efficiency by tallying the total number of strikes required to crack a single nut. This is calculated for each nut cracked, and then average values are computed for specific rock combinations (hammer and anvil) to create efficiency values for rock combinations (e.g., dacite hammer, carbonatite anvil). These efficiency measures were calculated from videos of experimental sessions. A subset (15%) of the experimental sessions were used to calculate efficiency with two different observers. Inter-rater correspondence is high (correlation between observers: Spearman's rho = 0.90, $p < 0.001$). Previous experiments indicate that primates routinely identify the most efficient hammers and anvils depending on properties such as size, and weight (Visalberghi et al., 2009; Massaro et al., 2012; Luncz and Boesch, 2015). As such, we expect members of the Bossou community to select hammers and anvils based on their hardness and elasticity. Furthermore, we expect size, age, and sex to also influence selection patterns (Carvalho et al., 2008, 2009).

2.5. Statistical analysis

We outline the details of the linear models that are used to explore the impacts of other variables in each experimental setting. All linear models were conducted in R (4.1) using the following packages: lme4, MASS, lmertest, and visreg. Separate linear models were explored for each condition (Condition 1 and Condition 2) and separate models for Hammers and Anvils because the response variable is selectivity, which is dependent on availability. Availability varies for each individual selection, so hammers are analyzed separately from anvils. The selectivity value is transformed to a z-score within each condition.

2.6. Experimental setting

The field site of Bossou has been the target of a field experimental approach since 1988. The Bossou field site is a long-term field study in the southeastern part of the Republic of Guinea. At the summit of Mt. Gban in the study area, a natural clearing of approximately 7 × 20 m has been established as a field laboratory for observing tool use behavior (Biro et al., 2003). Researchers provide wild chimpanzees with various objects and resources in this natural clearing referred to as the 'outdoor laboratory' (Matsuzawa, 1994) to observe behaviors and interactions from a close range, with good visibility and longitudinally over consecutive years. Data for this study were collected from January to March of 2012. The area is largely small hills of secondary and primary forest surrounded by savannah ecosystems (Hockings et al., 2010). The field study area is situated within the foraging radius (~6 km^2)

Table 1
Details of the experimental sessions. Only those sessions with greater than five chimpanzees are included in this analysis. PAB is a term used by the Bossou research project to refer to "Party at the Bureau" which describes an individual instance when the Bossou community enters the outdoor laboratory.

PAB #	Date	Time in	Time out	Duration	Nut sp.	# Chimpanzees	Demographics	Condition
1	Mon, Jan 30, 2012	16:15	16:28	00:13	E.g	1	M = 1	1
2	Mon, Jan 30, 2012	16:47	17:15	00:28	E.g	1	M = 1	1
3	Tue, Jan 31, 2012	14:46	15:04	00:18	E.g/C	1	M = 1	1
4	Wed, Feb 1, 2012	08:51	08:53	00:02	E.g/C	1	M = 1	1
5	Wed, Feb 1, 2012	09:19	09:26	00:07	E.g/C	0		1
6	Wed, Feb 1, 2012	09:32	10:12	00:40	E.g/C	5	F = 3; J = 2	1
7	Thu, Feb 2, 2012	14:59	16:49	01:50	E.g/C	9	M = 3; F = 3; J = 3	1
8	Sat, Feb 4, 2012	17:07	17:37	00:30	C	5	M = 3; F = 1; J = 2	1
9	Sun, Feb 5, 2012	07:11	08:12	01:01	C	9	M = 4; F = 3; J = 2	1
10	Sun, Feb 5, 2012	15:50	16:45	00:55	C	12	M = 4; F = 5; J = 3	1
11	Sun, Feb 5, 2012	16:59	17:25	00:26	C	2	F = 2	2
12	Sun, Feb 5, 2012	17:36	17:43	00:07	C	4	M = 2; F = 1; J = 1	2
13	Mon, Feb 6, 2012	07:08	08:13	01:05	C	8	M = 3; F = 2; J = 3	2
14	Mon, Feb 6, 2012	09:30	10:27	00:57	C	4	M = 1; F = 2; J = 1	2
15	Mon, Feb 6, 2012	12:02	13:06	01:04	C	8	M = 3; F = 2; J = 3	2
16	Mon, Feb 6, 2012	17:33	18:05	00:32	C	11	M = 4; F = 4; J = 3	2
17	Thu, Feb 9, 2012	16:16	17:10	00:54	C	0		2
18	Thu, Feb 9, 2012	17:50	18:15	00:25	C	10	M = 3; F = 4; J = 3	2
19	Fri, Feb 10, 2012	07:04	08:23	01:19	C	5	M = 3; F = 2	2
20	Fri, Feb 10, 2012	14:22	15:42	01:20	C	10	M = 3; F = 4; J = 3	2
21	Sat, Feb 11, 2012	07:45	11:29	03:44	C	1	F = 1	2

F = female; J = juvenile; M = male.
The Bossou community cracks two species of nuts. We refer to these here as E.g. for *Elaeis guineensis* and C for *Coula edulis*.

of this community. Within the region, *Elaeis guineensis* nuts are the only nuts locally available, and the community routinely uses locally available rock types to crack these nuts. The outdoor laboratory described here has been used for >25 years, and the documentation of this tool use is well established in this setting (Matsuzawa et al., 2001).

Experimental sessions began when the first individual entered the experimental setting. None of the locally available amphibolite or quartz was placed in the outdoor lab so that the chimpanzees were required to select from the stones provided. The current experiment included 22 experimental sessions totaling about 13 h of recorded footage (Table 1). In each experimental session, seven separate piles of coula nuts (*Coula edulis*) were positioned at the entrance to the experimental area (Carvalho et al., 2008). In Condition 1, a rock from each size class within the two rock types (dacite and carbonatite, 8 in total) was positioned in a matrix at one end of the outdoor lab to allow for identification of the selection process of stones. In Condition 2, a rock from each size class within the four rock types (carbonatite, dacite, phonolite, and granite; 16 in total) was positioned in a random placement based on size and rock type. The position of the different stones was randomized by size and raw material, at the beginning of each session, so that each experimental session had a different matrix of stones. This prevented individuals from consistently selecting rocks from one portion of the matrix. Each stone was labeled with a letter and number combination identifying the rock type as well as the size of the stone (e.g., D8 was the medium-sized dacite specimen). The matrix at the front of the experimental area stones was an evenly spaced arrangement of stones. The chimpanzees consistently entered the outdoor laboratory from a single entrance. The matrix was arranged in a randomized order prior to the entrance of any individual into the experimental area**.** The activities of the chimpanzees were recorded using two to three video cameras (Sony Digital Handicam, DCR-VX 100, and Sony Digital Handicam DCR-PC 110). Videos were used to document the details of selection processes and efficiency subsequent to fieldwork.

At the time of this study, 12 individuals were consistently cracking nuts in the experimental setting. We recorded a stone selection every time an individual picked up a stone to begin nut-cracking. At each selection, we documented which stones were available for selection and which stones were currently in use.

2.7. Exploring social information transfer

To determine how chimpanzees made these selections, we observed the sequence of selections through the course of the

Table 2
Details of archaeological collections described in the analysis of comparisons with chimpanzee selection patterns. Note that the Kanjera South assemblages includes numerous raw material types (>20); however, we focus here on rock types that represent a significant percentage of the assemblage and those that were also incorporated into this experimental study.

Region	Site	Age (Ma)	Raw materials
Gona, Afar (Ethiopia)	DAN-1	2.55	rhyolite, basalt, latite, trachyte
Gona, Afar (Ethiopia)	OGS-6	2.58	rhyolite, basalt, quartz, latite, trachyte
Gona, Afar (Ethiopia)	OGS-7	2.58	rhyolite, basalt, quartz, latite, trachyte
Gona, Afar (Ethiopia)	EG-13	2.55	rhyolite, basalt, quartz, latite, trachyte
Nachukui Fm., West Turkana (Kenya)	Lokalalei 2C	2.33	phonolite, basalt, trachyte, rhyolite
Koobi Fora Fm., East Turkana (Kenya)	FxJj 50	~1.5	transitional basalt, alkali basalt, rhyolite (pantellerite), crypto-crystalline silica (chalcedony)
Kanjera Formation, Nyanza Rift (Kenya)	Kanjera South	2.0	carbonatite, basalt, phonolite, granite, dacite, quartzite
Hadar Fm., Afar (Ethiopia)	AL-666	2.4	rhyolite, basalt, trachyte, quartz, chert
Hadar Fm., Afar (Ethiopia)	AL-894	2.4	rhyolite, basalt, trachyte
Ledi-Geraru, Afar (Ethiopia)	Bokol Dora 1	2.6	rhyolite, dacite, basalt, crypto-crystalline silica (chalcedony)

Table 3
Details of the various assemblages used for comparison between Oldowan hominin selectivity and measures of selectivity observed during the experiment. Data collected here is derived from diverse sources (Semaw, 2000; Semaw et al., 2003; Stout et al., 2005; Harmand, 2007, 2009; Braun et al., 2008, 2009a, 2009b, 2019; Goldman and Hovers, 2009; Arroyo et al., 2020).

Archaeological site/experiment	Raw material	Count of artifacts/selections	Region	Assemblage type	Assemblage name
LA2C	Phonolite	1916	Nachukui Fm.	All artifacts	LA2C_ALL
LA2C	Basalt	350	Nachukui Fm.	All artifacts	LA2C_ALL
LA2C	Trachyte	175	Nachukui Fm.	All artifacts	LA2C_ALL
LA2C	Rhyolite	5	Nachukui Fm.	All artifacts	LA2C_ALL
AL894	Rhyolite	76	Hadar	All artifacts	AL894_ALL
AL894	Basalt	9	Hadar	All artifacts	AL894_ALL
AL894	Trachyte	10	Hadar	All artifacts	AL894_ALL
EG13	Rhyolite	48	Gona	All artifacts	EG13_ALL
EG13	Basalt	9	Gona	All artifacts	EG13_ALL
EG13	Latite	11	Gona	All artifacts	EG13_ALL
EG13	Trachyte	88	Gona	All artifacts	EG13_ALL
OGS6a	Rhyolite	14	Gona	All artifacts	OGS6a_ALL
OGS6a	Basalt	11	Gona	All artifacts	OGS6a_ALL
OGS6a	Latite	11	Gona	All artifacts	OGS6a_ALL
OGS7	Rhyolite	68	Gona	All artifacts	OGS7_ALL
OGS7	Basalt	5	Gona	All artifacts	OGS7_ALL
OGS7	Latite	43	Gona	All artifacts	OGS7_ALL
OGS7	Trachyte	15	Gona	All artifacts	OGS7_ALL
DAN1	Rhyolite	28	Gona	All artifacts	DAN1_ALL
DAN1	Basalt	2	Gona	All artifacts	DAN1_ALL
DAN1	Latite	10	Gona	All artifacts	DAN1_ALL
DAN1	Trachyte	37	Gona	All artifacts	DAN1_ALL
AL666	Rhyolite	86	Hadar	All artifacts	AL666_ALL
AL666	Basalt	15	Hadar	All artifacts	AL666_ALL
AL666	Trachyte	5	Hadar	All artifacts	AL666_ALL
AL666	Quartz	18	Hadar	All artifacts	AL666_ALL
Kanjera South	Carbonatite	65	Kanjera Fm.	All artifacts	KJS1_ALL
Kanjera South	Basalt	131	Kanjera Fm.	All artifacts	KJS1_ALL
Kanjera South	Phonolite	586	Kanjera Fm.	All artifacts	KJS1_ALL
Kanjera South	Granite	148	Kanjera Fm.	All artifacts	KJS1_ALL
Kanjera South	Dacite	290	Kanjera Fm.	All artifacts	KJS1_ALL
Kanjera South	Quartzite	248	Kanjera Fm.	All artifacts	KJS1_ALL
BD1	Rhyolite	130	Ledi Geraru	All artifacts	BD1_ALL
BD1	Dacite	75	Ledi Geraru	All artifacts	BD1_ALL
BD1	Basalt	39	Ledi Geraru	All artifacts	BD1_ALL
BD1	Ccs	25	Ledi Geraru	All artifacts	BD1_ALL
FxJj50	Basalt	53	Koobi Fora Fm.	All artifacts	FxJj50_ALL
FxJj50	Basalt	198	Koobi Fora Fm.	All artifacts	FxJj50_ALL
FxJj50	Rhyolite	114	Koobi Fora Fm.	All artifacts	FxJj50_ALL
FxJj50	Ccs	7	Koobi Fora Fm.	All artifacts	FxJj50_ALL
Bossou hammers Condition 1	Carbonatite	37	Bossou	All instances of selection	BOSSOU_HAMMMER
Bossou hammers Condition 2	Dacite	28	Bossou	All instances of selection	BOSSOU_HAMMMER
Bossou anvils Condition1	Carbonatite	49	Bossou	All instances of selection	BOSSOU_ANVIL
Bossou anvils Condition1	Dacite	16	Bossou	All instances of selection	BOSSOU_ANVIL
Bossou hammers Condition 2	Carbonatite	35	Bossou	All instances of selection	BOSSOU_HAMMERS
Bossou hammers Condition 2	Dacite	61	Bossou	All instances of selection	BOSSOU_HAMMERS
Bossou hammers Condition 2	Granite	49	Bossou	All instances of selection	BOSSOU_HAMMERS
Bossou hammers Condition 2	Phonolite	19	Bossou	All instances of selection	BOSSOU_HAMMERS
Bossou anvils Condition 2	Carbonatite	101	Bossou	All instances of selection	BOSSOU_ANVILS
Bossou anvils Condition 2	Dacite	23	Bossou	All instances of selection	BOSSOU_ANVILS
Bossou anvils Condition 2	Granite	34	Bossou	All instances of selection	BOSSOU_ANVILS
Bossou anvils Condition 2	Phonolite	6	Bossou	All instances of selection	BOSSOU_ANVILS
AL894	Rhyolite	214	Hadar	Only whole flakes	AL894_FLAKE
AL894	Basalt	79	Hadar	Only whole flakes	AL894_FLAKE
AL894	Trachyte	17	Hadar	Only whole flakes	AL894_FLAKE
BD1	Rhyolite	29	Ledi Geraru	Only whole flakes	BD1_FLAKE
BD1	Dacite	30	Ledi Geraru	Only whole flakes	BD1_FLAKE
BD1	Basalt	15	Ledi Geraru	Only whole flakes	BD1_FLAKE
BD1	Ccs	10	Ledi Geraru	Only whole flakes	BD1_FLAKE
Kanjera South	Carbonatite	22	Kanjera Fm.	Only whole flakes	KJS1_FLAKE
Kanjera South	Basalt	66	Kanjera Fm.	Only whole flakes	KJS1_FLAKE
Kanjera South	Phonolite	150	Kanjera Fm.	Only whole flakes	KJS1_FLAKE
Kanjera South	Granite	44	Kanjera Fm.	Only whole flakes	KJS1_FLAKE
Kanjera South	Dacite	127	Kanjera Fm.	Only whole flakes	KJS1_FLAKE
Kanjera South	Quartzite	67	Kanjera Fm.	Only whole flakes	KJS1_FLAKE
FxJj50	Basalt	47	Koobi Fora Fm.	Only whole flakes	FxJj50_FLAKE
FxJj50	Basalt	165	Koobi Fora Fm.	Only whole flakes	FxJj50_FLAKE
FxJj50	Rhyolite	100	Koobi Fora Fm.	Only whole flakes	FxJj50_FLAKE
FxJj50	Ccs	8	Koobi Fora Fm.	Only whole flakes	FxJj50_FLAKE
LA2C	Phonolite	45	Nachukui Fm.	Only cores	LA2C_CORE
LA2C	Basalt	9	Nachukui Fm.	Only cores	LA2C_CORE

(*continued on next page*)

Table 3 (*continued*)

Archaeological site/experiment	Raw material	Count of artifacts/selections	Region	Assemblage type	Assemblage name
LA2C	Trachyte	8	Nachukui Fm.	Only cores	LA2C_CORE
OGS7	Rhyolite	2	Gona	Only cores	OGS7_CORE
OGS7	Latite	1	GONA	Only cores	OGS7_CORE
OGS7	Trachyte	1	Gona	Only cores	OGS7_CORE
BD1	Rhyolite	11	Ledi Geraru	Only cores	BD1_CORE
BD1	Dacite	13	LEDI_GERARU	Only cores	BD1_CORE
BD1	Basalt	5	Ledi Geraru	Only cores	BD1_CORE
BD1	Ccs	3	Ledi Geraru	Only cores	BD1_CORE
KJS1	Carbonatite	2	Kanjera Fm.	Only cores	KJS1_CORE
KJS1	Basalt	5	Kanjera Fm.	Only cores	KJS1_CORE
KJS1	Phonolite	52	Kanjera Fm.	Only cores	KJS1_CORE
KJS1	Granite	16	Kanjera Fm.	Only cores	KJS1_CORE
KJS1	Dacite	16	Kanjera Fm.	Only cores	KJS1_CORE
KJS1	Quartzite	20	Kanjera Fm.	Only cores	KJS1_CORE
FxJj50	Basalt	4	Koobi Fora Fm.	Only cores	FxJj50_CORE
FxJj50	Basalt	36	Koobi Fora Fm.	Only cores	FxJj50_CORE
FxJj50	Rhyolite	9	Koobi Fora Fm.	Only cores	FxJj50_CORE
FxJj50	Ccs	7	Koobi Fora Fm.	Only cores	FxJj50_CORE
LA2C	Phonolite	2	Nachukui Fm.	Only pounding tools	LA2C_POUNDING
LA2C	Basalt	3	Nachukui Fm.	Only pounding tools	LA2C_POUNDING
LA2C	Trachyte	22	Nachukui Fm.	Only pounding tools	LA2C_POUNDING

experiment. We characterize certain rock combinations based on certain mechanical properties that are ideal for specific purposes (e.g., harder dacite hammer and softer carbonatite anvil). The diversity of different rock combinations (especially in Condition 2 where the number of combinations results in 16 options) makes identifying the optimal rock combination difficult. We ranked the rock combinations based on efficiency of nut-cracking (# of strikes per cracked nut). We ranked those rock combinations where fewer strikes resulted in the cracking of a single nut as the highest efficiency. We consider those combinations with the lowest average strikes per nut as the most efficient combinations.

To assess changes in selection decision through the course of the experiment, we assigned each rock combination a rank score of efficiency. We then calculated the changes in the average efficiency rank over the course of the experiment. To calculate these general changes, we combined every four instances of selection into an average efficiency score. We assume that if chimpanzees rapidly acquire knowledge about the efficiency of rock combinations, then the average efficiency score should increase quickly through the experiment and then plateau at the highest-efficiency values. If chimpanzees are not able to assess the relative values of efficiency in rock combinations, then we expect the average efficiency value should remain roughly consistent throughout the experiment. To further explore these patterns, we identify selection patterns that are associated with reuse (when a chimpanzee reuses a tool set previously used by another individual). We also distinguish rock selections from the matrix (i.e., the randomized positioning of rocks at the beginning of each experimental session), which represents first selections by individuals.

2.8. Comparison with Oldowan selectivity

Direct comparisons between chimpanzee stone tool use and hominin stone tool use are hampered by the dramatic differences between these technologies (e.g., an emphasis on cutting tools in hominins and percussion in chimpanzee toolkits; Proffitt et al., 2018). Numerous studies have emphasized that Oldowan technology is guided by technical rules that structure the formation of Oldowan stone tools that is absent from the materials produced by primates (Schick et al., 1999; Delagnes and Roche, 2005; Bandini et al., 2022). Here we attempt to compare measures of selectivity, which presumably reflect patterns of behavior between hominins and chimpanzees that are more analogous than decisions regarding the manufacture of artifacts (i.e., the selection of appropriate rocks for tool use). However, it is important to note that hominin selection of rocks for chipped stone tool production will differ markedly from selection by chimpanzee for percussive behaviors (Carvalho et al., 2008; Proffitt et al., 2022). Primates, in general, have been shown to select specific types of percussive tools in relation to the target items that tools are used for (Carvalho et al., 2008; Visalberghi et al., 2009; Massaro et al., 2012; Sanz and Morgan, 2013; Koops et al., 2014; Proffitt et al., 2022). Although there are a number of recent studies that explore the details of percussive technology in hominin toolkits (Chavaillon, 1979; Goren-Inbar et al., 2002; Arroyo and de la Torre, 2016, 2018; Arroyo et al., 2020), the vast majority of evidence on raw material selectivity in hominins derives from chipped stone tool technology. Many of the assemblages where percussive activities have been intensively investigated (e.g., Gesher Benot Ya'aquov, Gombore IB) are not associated with information on the availability of specific rock types to allow for an investigation of selectivity specifically for pounding activities. Lokalalei 2C and Kokiselei 4 both have reported information about the availability of raw materials as well as the availability of certain rock types. However, these assemblages have very small samples sizes, making it difficult to compare to chimpanzee selection patterns (LA2C: $n = 30$; KS4: $n = 4$) (Harmand, 2007; Arroyo et al., 2020).

To compare the levels of rock selectivity between chimpanzees and Oldowan hominins, we collated the selection rock types at 10 Oldowan sites, where published information on the frequency of raw material in excavated samples are provided. To make the investigation of selectivity comparable to the chimpanzee data, we only explored raw material selection at sites that have published information about conglomerates where the rocks were selected by hominins for artifact manufacturing. It is important to note that almost every study that has explored the availability of certain rocks on ancient landscapes has also included a geological exploration of when these rocks were available (Stout et al., 2005; Harmand, 2007; Braun et al., 2008, 2019).

Data for rock availability as well as total artifact counts were available for Oldowan sites from Gona (DAN-1, OGS-6a, OGS-7, EG-13); Nachukui Formation (Lokalalei 2C); Koobi Fora Formation (FxJj50); Kanjera Formation (Kanjera South); Hadar Formation (AL 666, AL 894); and Ledi-Geraru (Bokol Dora 1) (Stout et al., 2005; Braun et al., 2008, 2009a, 2019; Harmand, 2009; Goldman-Neuman and Hovers, 2012; see Table 2 for details of archaeological sites). We

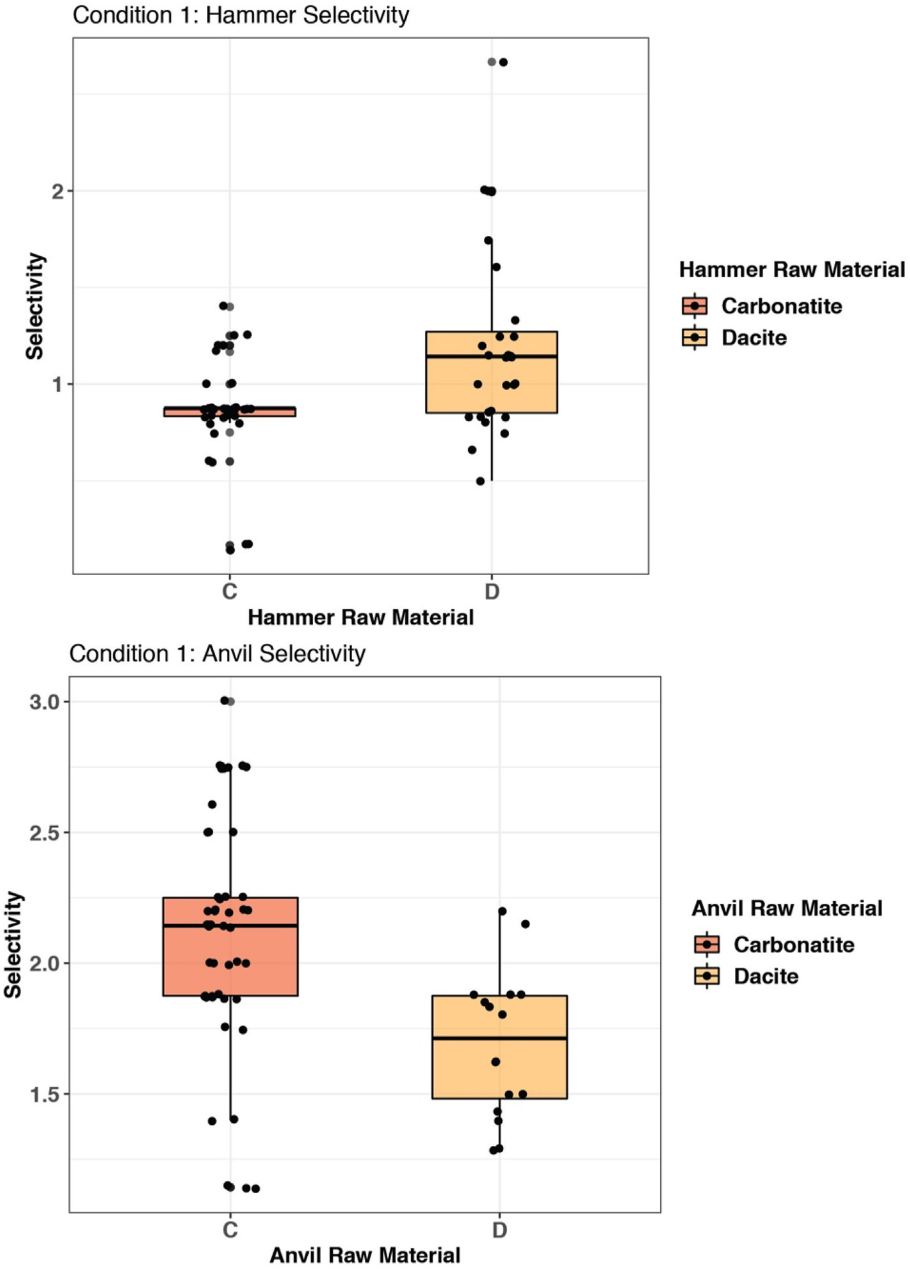

Figure 3. Selection values for Condition 1. This plot reflects the interquartile range (box) and 1.5 times the interquartile range (lines) of the selectivity values for each raw material. Selectivity values are provided separately for anvils and hammers as the selectivity values reflect the availability of specific stone at the time of selection.

calculated selectivity based on the difference between the prevalence of certain rock types in the archaeological assemblages and their appearance in nearby conglomerates. In this way, we are able to calculate measures that are similar to the selection values we used for the selection of rocks in the Bossou chimpanzee experimental setting. Thus, overall selection values combine the availability of certain rock types (as calculated from the presence of similar rock types in nearby conglomerates) as well as the frequency of that rock type in an assemblage. We calculated selectivity for the archaeological sites using several different metrics. Our first assessment used all artifacts in an assemblage as an indicator of selection. We calculate a selectivity value for each artifact (percentage of each rock in an assemblage relative to its percentage in nearby conglomerates). To compare overall values of selectivity between archaeological assemblages and the experimental setting (e.g., Kanjera Fm compared to Bossou Hammers), we compared the assemblage of selectivity values between hominin assemblages and the assemblage of selectivity values in the Bossou experiment.

However, not every artifact represents an individual event of selection. Indeed, many artifacts are flakes and are discarded after cobbles have been tested for material properties. These may not reflect actual instances of selection in the archaeological record. We evaluate selection using three other metrics. Each cobble that has been flaked and resulted in a core can be used as a measure of selection because hominins selected a particular cobble for reduction, and therefore, this is an instance of selection. We calculate selectivity in core assemblages based on the relative frequency of cores from a particular raw material compared to the total

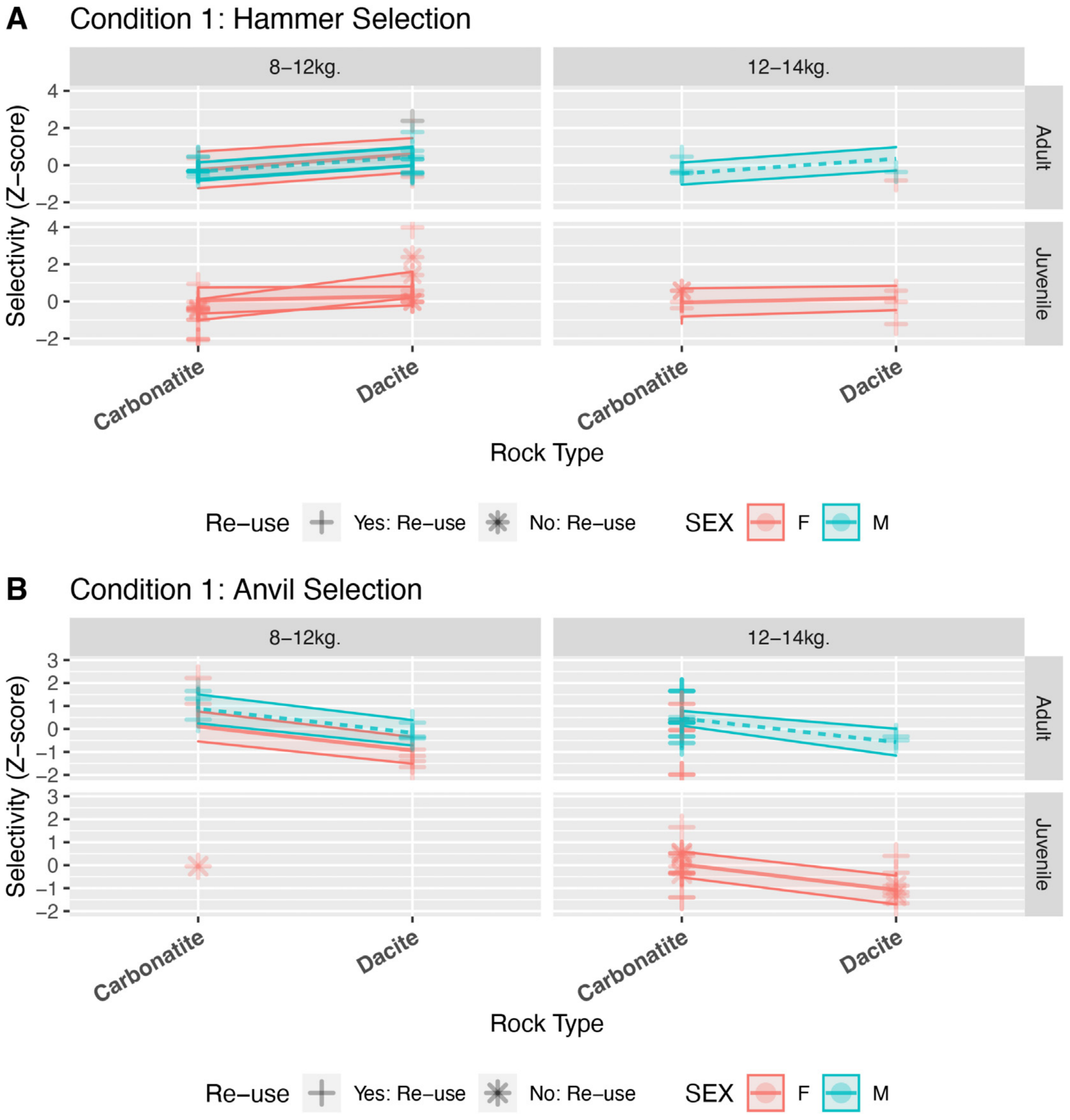

Figure 4. Plots of selection values for different rock types in Condition 1. A. Selection values plotted for each rock type. Note similar patterns regardless of age, sex, or reuse. Dacite is consistently selected at a higher level than carbonatite. Size of hammer shows no significant differences in this model, yet the highest selection values are attributed to relatively smaller hammers. B. Plots of selection values for anvils of each rock type. Carbonatite is consistently selected at higher selectivity values. However, unlike hammers, the size of anvils is clearly influencing these patterns with the largest anvils (12–14 kg) selected more often than others. Polygons reflect 95% confidence intervals of the linear mixed model.

assemblage of cores. This is then compared to the availability of that rock type in nearby conglomerates. These data were only available for a select number of assemblages: (LA2C—Nachukui Fm.; OGS7—Gona; BD1—Ledi-Geraru; Kanjera South—Kanjera Fm.; FxJj 50—Koobi Fora Fm.).

We also calculated selection in hominin archaeological assemblages using each whole flake as an instance of selection. This is based on the assumption that the production of a flake represents an instance of selecting a specific raw material to initiate fracture. Selectivity was calculated based on the relative proportion of a particular rock type in the entire assemblage of flakes. This relative proportion is then compared to the availability of this rock type in nearby conglomerates. Data on the raw material distribution of flakes were available only for a select number of assemblages: (AL 894—Hadar; BD1—Ledi-Geraru; Kanjera South—Kanjera Fm.; FxJj 50—Koobi Fora Fm). The final metric we used to compare selectivity between hominins and chimpanzees used data on raw material availability in Oldowan pounding tools from the site of Lokalalei 2C in the Nachukui Formation (Arroyo et al., 2020). This is the only available data on raw material selection of pounding tools available for an Oldowan locality. Similar to the previously described comparisons of flakes and cores, we calculated selectivity based on the proportion of certain raw materials relative to the complete assemblage of pounding tools in the assemblage. These proportions were compared to the overall availability of this rock type in nearby conglomerates.

To compare measures of Oldowan selectivity with chimpanzee selectivity measured in our experiment, we conducted pairwise Dunn's tests between the values of selectivity for each assemblage (see Table 3). The significance of these comparisons is corrected for multiple comparisons using the Bonferroni adjustment of *p* values. We separate the assemblage of selectivity values in the data from the Bossou experiment with chimpanzees by experimental condition (e.g., Condition 1 vs. Condition 2) and tool type (e.g., hammers vs. anvils). This is based on different parameters of selection between Condition 1 and Condition 2.

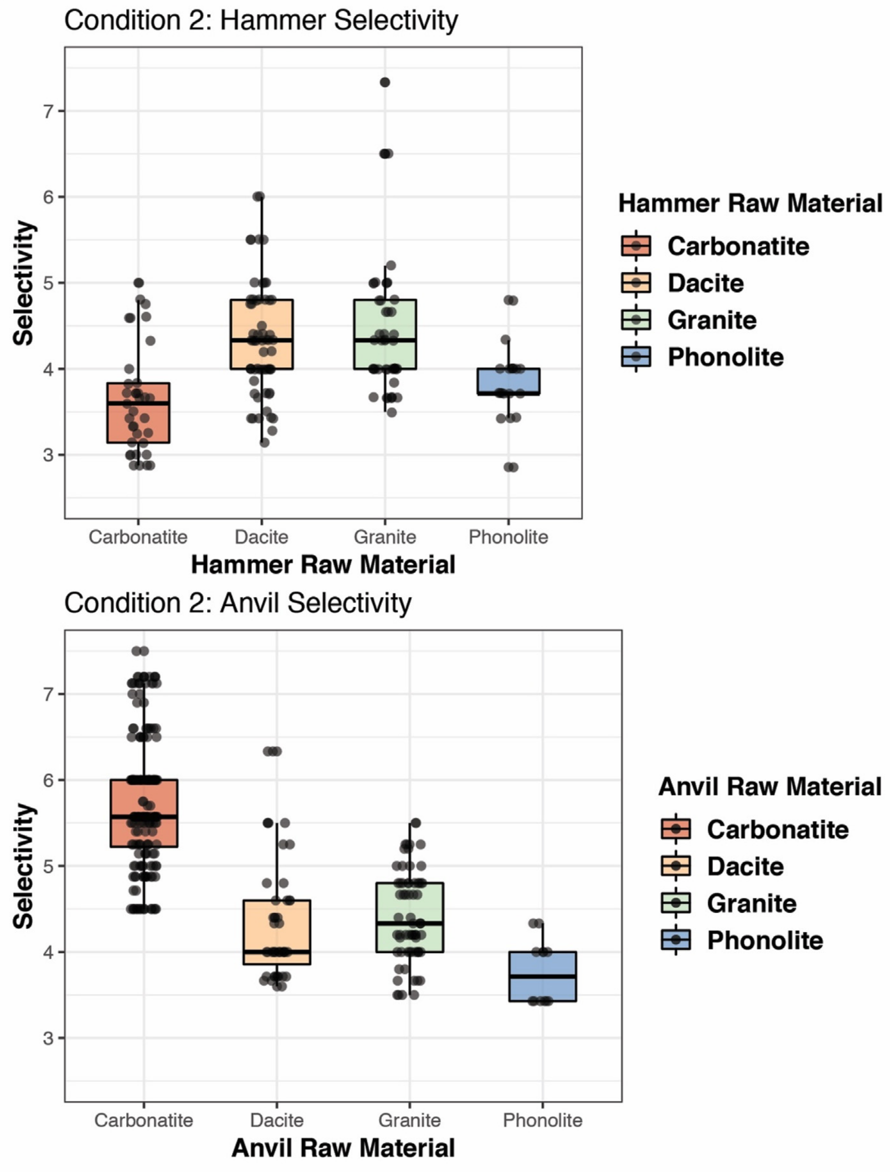

Figure 5. Selection values for Condition 2. Chimpanzees at Bossou select dacite as a hammer with higher selection values than other rock types. Chimpanzees select carbonatite as an anvil with higher selection values.

3. Results

3.1. Selectivity

We measured selectivity by documenting the frequency with which a specific rock type was selected, given the availability of that rock type relative to other rock types in the experiment at the time of selection. During Condition 1 (only dacite and carbonatite provided), Bossou chimpanzees consistently exhibited higher selectivity when choosing the hardest rock type (dacite) for hammers (Kolmogorov-Smirnov Test or K-S Test; D = 0.435; $p = 0.004$, Fig. 2). Also, during Condition 1, the chimpanzees consistently exhibited higher selectivity when selecting carbonatite as an anvil (K-S Test; D = 0.568; $p < 0.001$, Fig. 3).

We developed a linear mixed model to test the influence of variables on the selection patterns during Condition 1. Separate models were developed for anvils and hammers, as selectivity is based on the availability of a specific rock type at the time of selection and thus is different for hammers and anvils. The response variable was the selectivity value for individual selection events (adapted to z-scores, SOM Fig. S1). We investigated the impact of rock type, rock size, sex, age, and reuse (i.e., the use of a set of tools previously used by a different individual) as fixed effects. We also included the color of the rock and the individual as random effects in the model (SOM Fig. S1). Comparisons between the full model and null model found significant differences in both the hammer and anvil models in Condition 1 (SOM Tables S4–5). The stability and dispersion of the model was investigated using a bootstrapping method. We bootstrapped the model 1000 times to ascertain if variance in predicted values of selectivity was stable in bootstrapped samples. We assessed predicted values and residuals in the bootstrapped samples to determine if the pattern in the response variable was stable. Comparisons between residuals and leverage values indicated no overdispersion in either the anvil or the hammer model in Condition 1 (Kuznetsova et al., 2017). Predicted values of selectivity (response variable) show no variance in

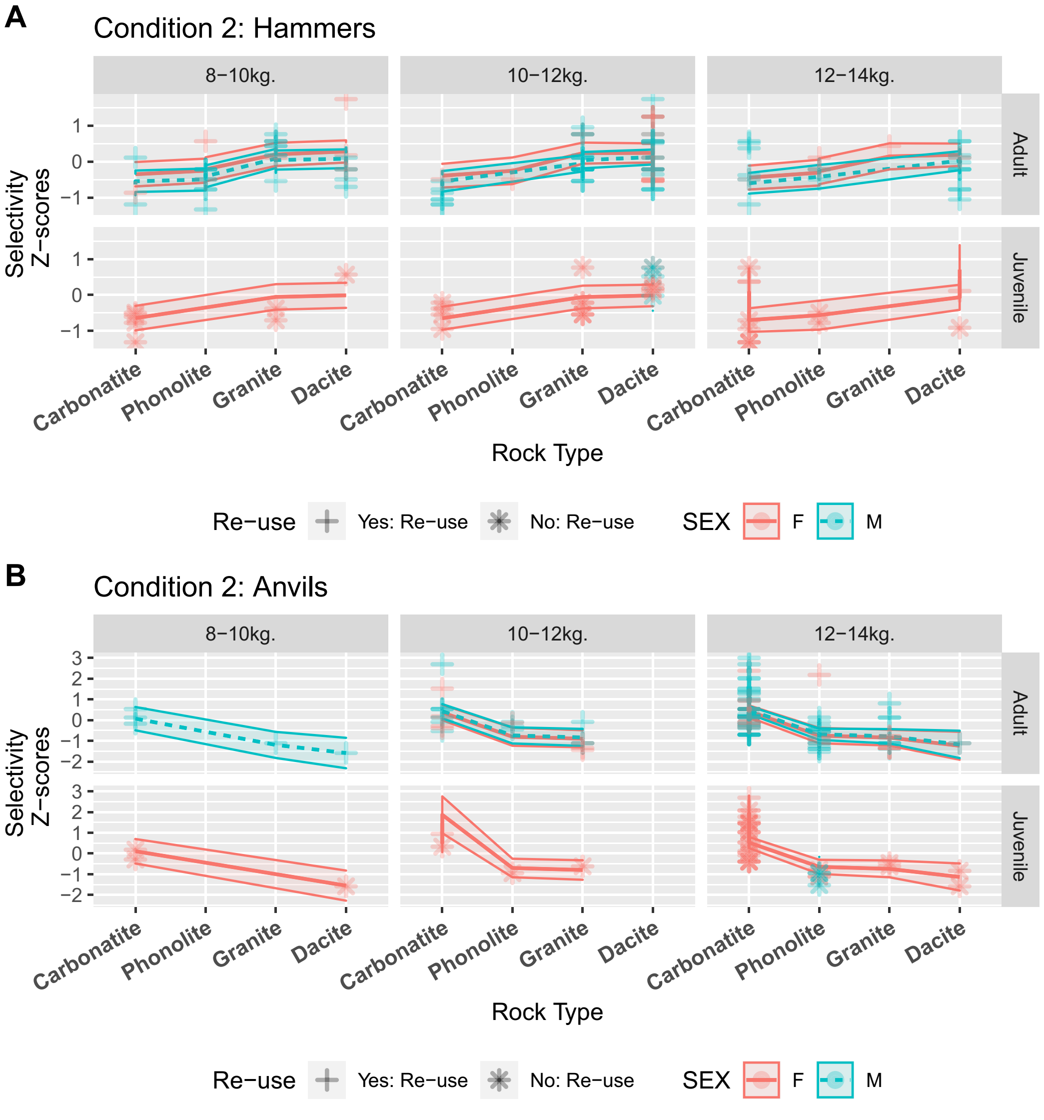

Figure 6. Plots of selectivity values (as z-scores) for Condition 2 in hammers and anvils. The values are divided based on the different fixed effects of the GLMM described in the text. Note the high selectivity of granite and dacite hammers as well as carbonatite anvils among juveniles (especially the largest size class). This is especially the case in instances where individuals are reusing sets used by adult individuals. Transparent polygons represent 95% confidence intervals of the linear mixed model. Abbreviation: GLMM = generalized linear mixed model.

bootstrapped models, indicating little effect of outliers on model stability for both the hammer and anvil models. Tests of the significance of fixed effects indicated that only rock type significantly influences selection of hammers. Similar tests in the anvil model showed that while rock type has the most significant impact on selection, both sex of the tool user and anvil size also contribute (Fig. 4). Larger anvils have higher selectivity values. Males appear to exhibit higher selectivity values when selecting carbonatite anvils. The models indicate that although other variables appear to influence selection, rock type is the most significant factor.

During Condition 2, selection was based on the four different rock types that have variable properties (dacite, carbonatite, granite and phonolite; Fig. 1). The Bossou chimpanzees consistently exhibited significantly higher levels of selectivity when selecting the two hardest rock types as hammers (granite and dacite; SOM Table S7; Fig. 5). Selection for rock type among anvils shows that carbonatite was selected at significantly higher levels from all other rock types except phonolite (SOM Table S8; Fig. 5). We used a linear mixed model to explore the impact of fixed (rock type, rock size, sex, age, and reuse) as well as random effects (color and individual; SOM Fig. S6). The structure of these models followed that described for Condition 1, with selection as the response variable and fixed and random effects that parallel Condition 1. Models were checked for overdispersion by assessing the relationship between leverage and residuals (Kuznetsova et al., 2017). Residuals of the model conform to the expectations of a normal distribution (SOM Fig. S1). Linear models developed to investigate the same fixed and random effects as described in Condition 1 show similar patterns in Condition 2. The residuals of both the hammer and anvil models in Condition 2 show no outliers, and there is no relationship between leverage and residuals for either the hammer or the anvil model. Model stability was further checked using similar bootstrapping methods described for Condition 1. Comparisons between the full and null models found significant differences in the hammer and anvil models (SOM Tables S9−10).

Tests of the significance of the fixed effects show that hammer raw material consistently has the highest impact on the response variable (selection). As seen in the analysis of Condition 1, in

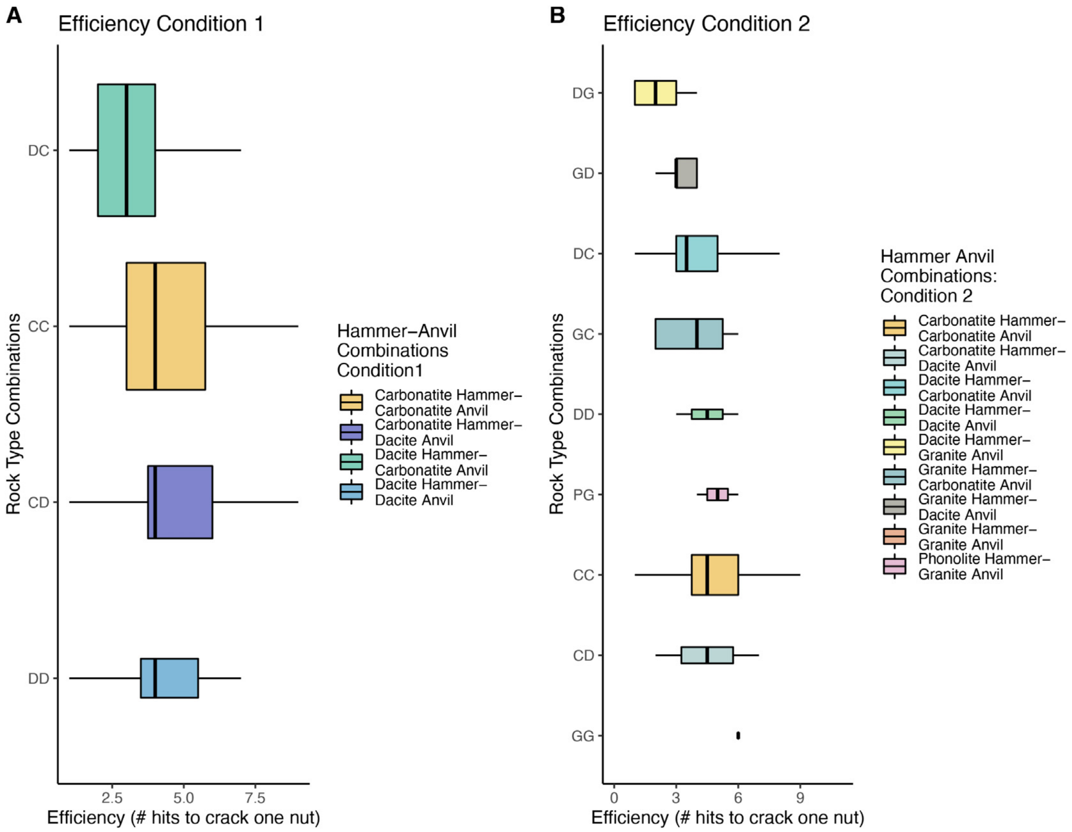

Figure 7. Values of nut-cracking efficiency with different rock combinations for hammers and anvils. Boxplots reflect the median and interquartile range and 1.5 times the interquartile range (whisker). Lower values represent more efficient tool combinations (i.e., fewer strikes per nut). The width of the boxplots is scaled to the square-root of sample size. Significance values are provided in SOM Tables S11–12.

Condition 2 males tend to have higher selectivity values in the selection of larger anvils. This is less evident in the selection of hammers. Reuse also appears to increase selectivity, whereby reused toolsets (hammer and anvil) tend to have higher selectivity values than toolsets used for the first time. Most reuse is by juveniles who reuse toolsets previously used by adults. In the anvil model, adults appear to have higher selectivity values than juveniles. Selectivity is greater when toolsets are reused. (SOM Tables S8–S9; Fig. 6).

3.2. *Exploring social information transfer*

Although the chimpanzees at Bossou selected stones of optimal hardness for specific functions (hammer vs. anvil), there is substantial variation in the selection process. There are four possible combinations in Condition 1 with average efficiency values for the different rock combinations of 3.4–7.9 strikes per nut. In Condition 2, there are 16 possible combinations. Average efficiency values range from an average of 2.0 strikes per nut (dacite hammer–granite anvil) to an average of 6.0 strikes per nut (carbonatite hammer–dacite anvil). Some combinations in Condition 2 occurred too infrequently to include in the analysis, so we focused on only those rock combinations that appeared more than eight times in the experiment. In Condition 1, the combination of dacite hammers and carbonatite anvils allowed the Bossou chimpanzees to crack nuts with significantly fewer strikes (Fig. 7; SOM Table S11). In Condition 2, harder rock types (granite and dacite) when paired with carbonatite anvils consistently resulted in higher levels of efficiency (Fig. 7). These differences in efficiency are consistent across individuals and not the product of individual differences in efficiency.

Chimpanzees at Bossou appear to identify and incorporate aspects of these mechanical properties from the beginning stages of the experiment. Adults appear to identify high-efficiency toolsets relatively quickly and maintain these combinations for the duration of Condition 1. The order of selections is correlated with the average efficiency rank (Spearman's rank correlation rho = 0.29; $p < 0.05$; Fig. 8). During Condition 1, adults select more efficient rock combinations more frequently at the end of the experiment than at the beginning of the experiment. This is not the case for juveniles who do not consistently select the most efficient combinations throughout Condition 1 of the experiment (Spearman's rank correlation between sequence number and average efficiency rank of rock combinations; rho = −0.32; $p = 0.17$).

In the later stages of the experiment (Condition 2), both adults and juveniles consistently select the most efficient rock combinations (adult: Spearman's rank correlation rho = 0.31; $p < 0.001$; juveniles: Spearman's rank correlation rho = 0.48; $p = 0.001$; SOM Fig. S8). Juveniles specifically use more efficient combinations of rocks when they are reusing a rock set than their own initial selections from the matrix (Fig. 9; reuse: Adult: Spearman's rank correlation rho = 0.39; $p < 0.001$; re-use: juveniles*:* Spearman's rank correlation rho = 0.53; $p = 0.001$, juvenile matrix: Spearman's rank correlation rho = 0.3; $p = 0.95$).

3.3. *Comparison with Oldowan selectivity*

The comparisons of assemblage-level selectivity compared all of the assemblages described in Table 3. Most assemblage-level

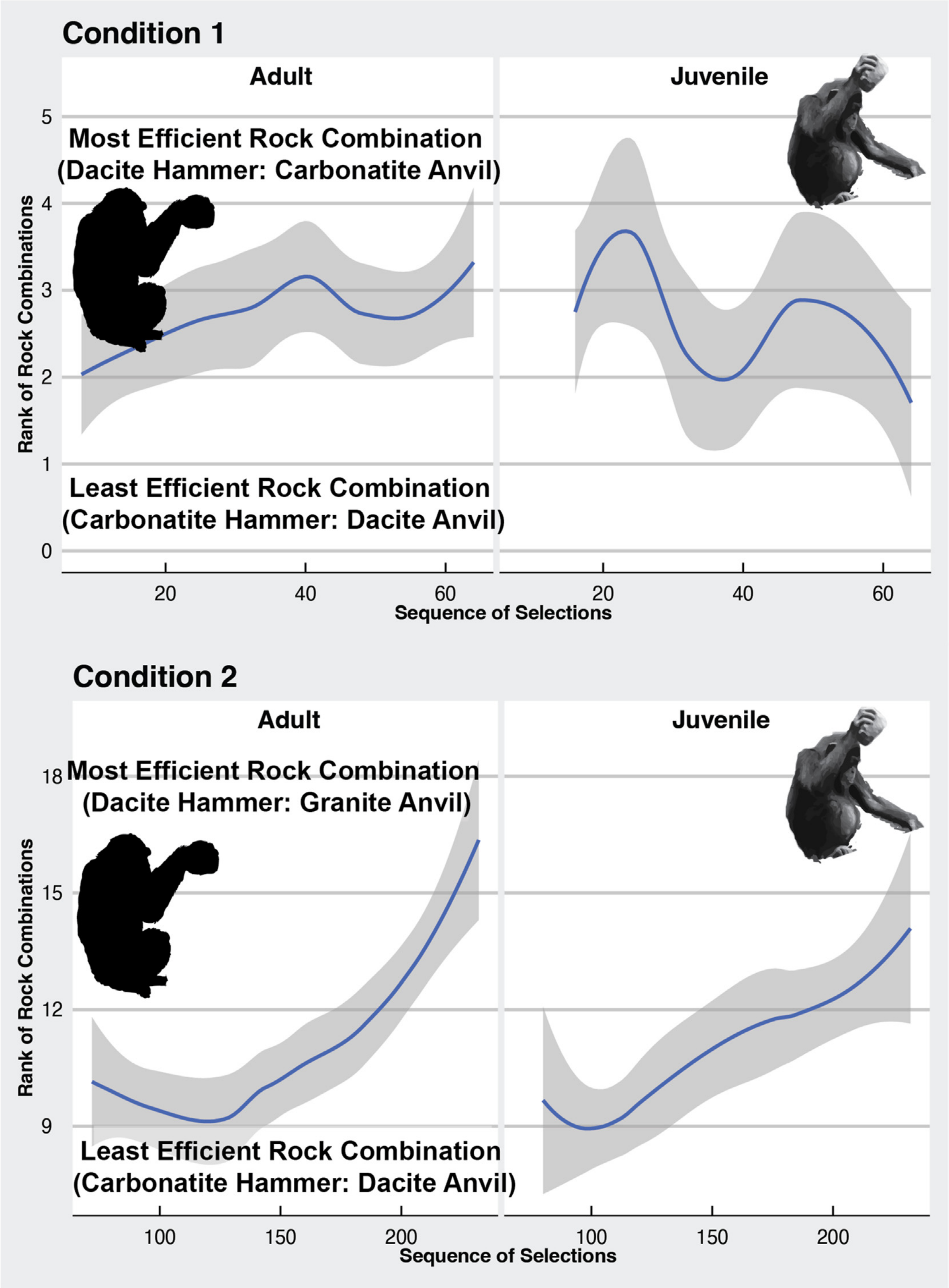

Figure 8. Plots of the average efficiency rank of rock combinations (hammer:anvil) through the course of the two portions of the experiment (Condition 1, Condition 2). The experiment is divided into a sequence of individual rock selections (defined as an instance where the hammer or anvil is changed) to investigate general patterns through the course of the experiment. Spearman's rank correlation is conducted on the efficiency rank value through the sequence of selections (see main text for Spearman's rank correlation values of rho).

measures of selectivity in Oldowan assemblages are similar to that seen in the experiment with Bossou chimpanzees (Fig. 10). This resulted in 276 individual assemblage-scale comparisons, the majority of which are not significant (Bonferroni-corrected p values > 0.05). Only 147 comparisons resulted in significant differences, most of these are significant differences between Oldowan assemblages. In 32 of these assemblage-level comparisons, there are significant differences (Bonferroni-corrected $p < 0.05$) between an Oldowan assemblage and the chimpanzee assemblages of selectivity values. In each of these 32 instances, the chimpanzee measure of selectivity is significantly higher than that seen in the Oldowan assemblages. The selectivity values of the Bossou chimpanzees when selecting anvils in Condition 1 is significantly higher than 10 Oldowan assemblages (DAN1 [all artifacts]; FxJj 50 [all

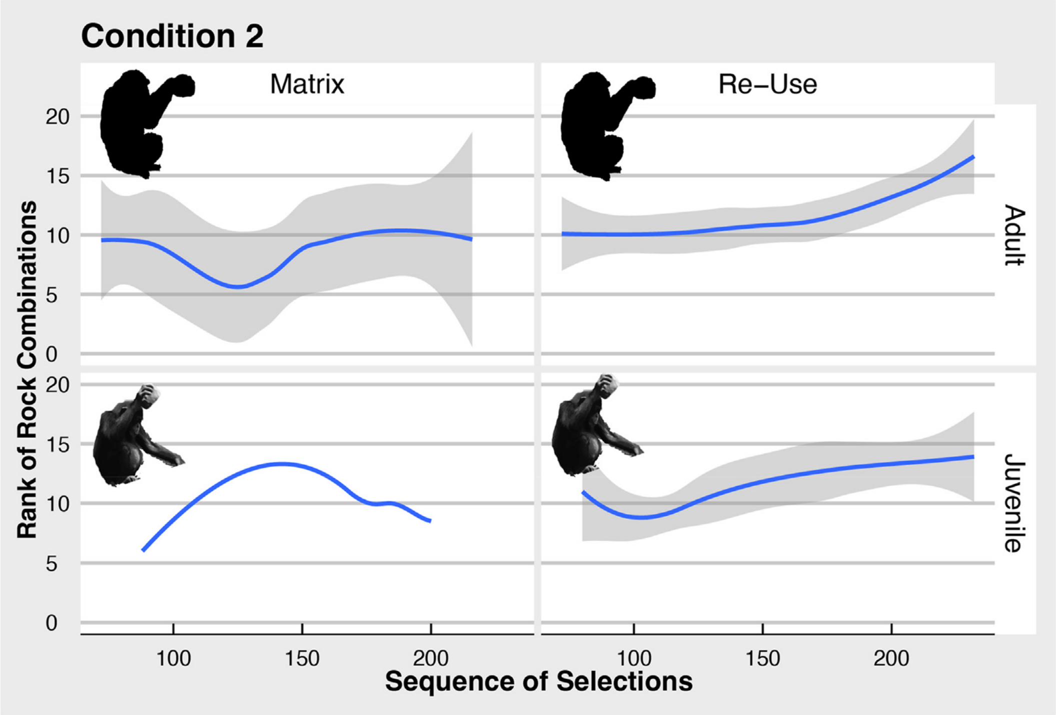

Figure 9. Plots of the average efficiency rank of rock combinations (hammer:anvil) through the course of Condition 2. The experiment is divided into steps of four separate rocks selections (defined as an instance where the hammer or anvil are changed) to investigate general patterns through the course of the experiment. Spearman's rank correlation is conducted on the average efficiency rank value and each group of four selections (see main text for Spearman's rank correlation values of rho). Note the selection of higher efficiency rock combinations during reuse compared to initial selections from the matrix of stones laid out at the beginning of the experiment.

artifacts and core and flake assemblages]; LA2C [cores]; OGS6a [all artifacts]; OGS7 [all artifacts and the core assemblage]). The selectivity of Bossou chimpanzees when selecting hammers in Condition 1 is significantly higher than 2 Oldowan assemblages (BD1 [all artifacts]; DAN1 [all artifacts]). The selectivity values of Bossou anvils in Condition 2 is significantly higher than 8 Oldowan assemblages (BD1 [all artifacts and the flake assemblage]; EG13 [all artifacts]; Kanjera South [all artifacts, as well as the core and flake assemblage]; LA2C [all artifacts]; OGS6a [all artifacts]). The selectivity values of the Bossou hammers in Condition 2 is significantly higher than 8 Oldowan assemblages (BD1 [all artifacts and the core assemblage]; DAN1 [all artifacts]; EG13 [all artifacts]; Kanjera South [all artifacts, as well as the core and flake assemblage]; LA2C [all artifacts]).

4. Discussion

Chimpanzees at Bossou discriminated mechanical properties when they selected rocks for nut cracking. Importantly, these decisions were not based on properties of the stones that were easily visible (i.e., color did not influence selectivity and rock types with divergent mechanical properties had similar color values e.g., carbonatite and granite). Furthermore, these differences in mechanical properties appear to influence the overall efficiency of tool use (Fig. 7). Although rock type is the most significant factor influencing selection, it does appear that larger stones are frequently selected for anvils. In addition, males tend to select these larger anvils at higher levels of selectivity (SOM Fig. S4 and Fig. S6). Our study was not able to confirm the influence of social interactions on selection patterns. This would require information about which individuals observed specific instances of selection. At present, the current experiment does not include this information. As such, it is not possible to ascertain if the pattern described here is directly the result of social enhancement or individual learning (Sanz and Morgan, 2013). However, the increased levels of selectivity associated with reused toolsets, as well as the increase in more efficient tool combinations during reuse seems to indicate that social information use may be at least partially responsible for these patterns.

Many current accounts of chimpanzee tool use indicate that some social learning is responsible for the transfer of information between individuals (Luncz and Boesch, 2014; Koops et al., 2015). However, many indications suggest that high-fidelity information transfer is limited in nonhuman primates (Call and Tennie, 2009; Tennie et al., 2009; Dean et al., 2012). Although there is some evidence of active tool transfers during chimpanzee tool use that may be interpreted as teaching (Musgrave et al., 2020), none of the tool transfers documented in our study were associated with direct information transfer. A conservative estimate is that, at most, stimulus enhancement resulted in the patterns of selection in this study. Bossou chimpanzees seem to be able to use their previous knowledge of tool properties and some social enhancement to canalize selection patterns relatively quickly (<2 months).

When we compare overall selectivity between hominins and chimpanzees, the levels of selection seen in the chimpanzees at Bossou are rarely significantly different from most Oldowan chipped-stone assemblages (Fig. 10). Importantly, the levels of selection seen in Oldowan hominins for pounding tools as seen at Lokalalei 2C are not significantly different from that seen in chimpanzees. We emphasize that selection values for specific rock types is not the focus of this comparison. Differences in selectivity for certain rock types (e.g., carbonatite) between hominins and chimpanzees are likely due to the different presumed uses for these rocks (e.g., percussive tools by chimpanzees, sharp-edged flake production in hominins). However, the overall degree of selection is comparable between hominins and chimpanzees.

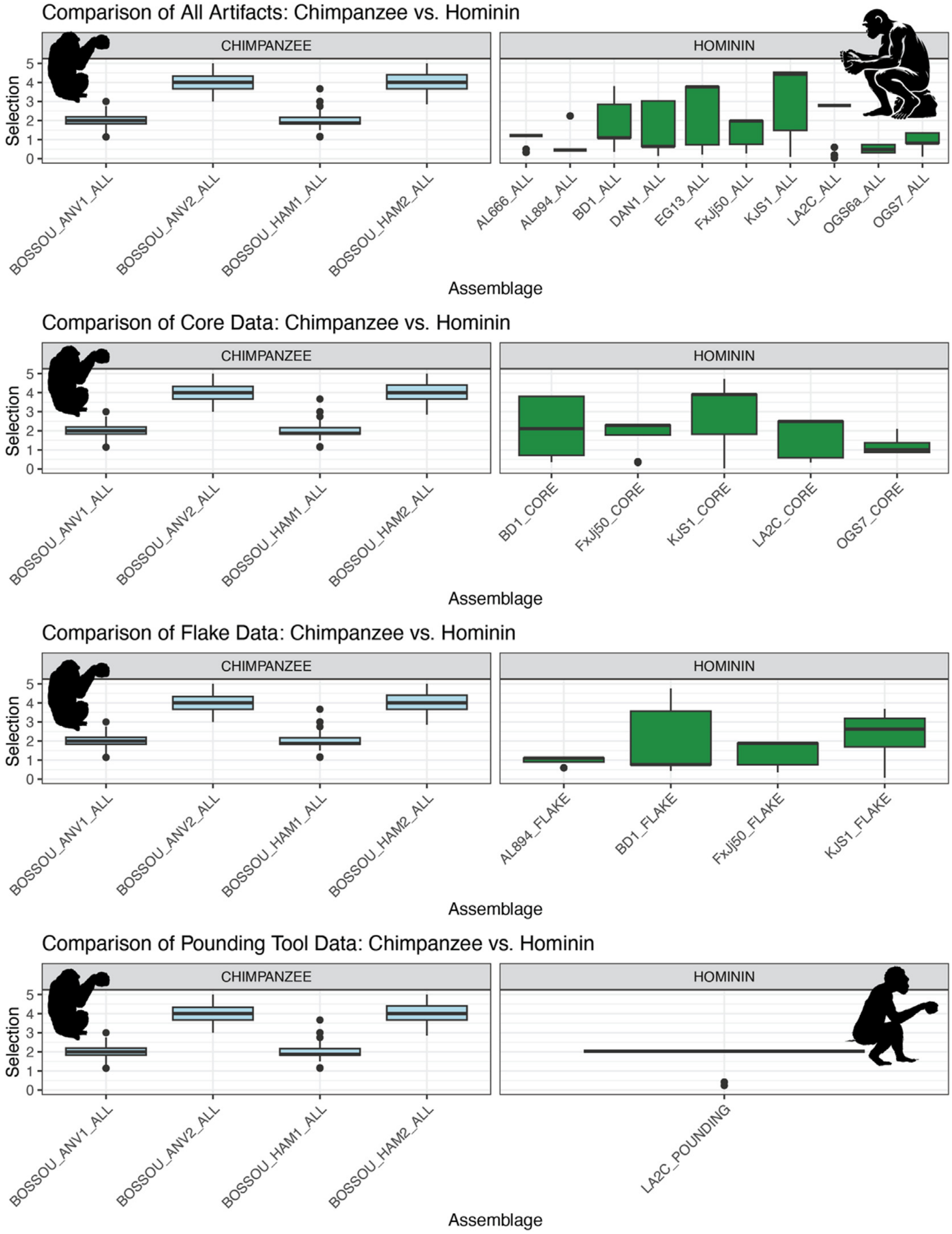

Figure 10. Comparison of selectivity between Bossou chimpanzees and Oldowan hominins. Selection for hominins is based on the availability of rocks at various Oldowan sites as compiled from various sources and described in Braun et al. (2019). Boxplots reflect the median and interquartile range and 1.5 times the interquartile range (whisker). Despite the differences in impetus behind selection, the levels of selectivity in hominins are rarely significantly different between those exhibited at Bossou (levels of selection described as mean values for each rock type, separated into hammers and anvils) and any of the archaeological assemblages. Significant differences between chimpanzee selection and Oldowan assemblages are described in the text.

Selection of task-specific materials for extractive foraging is a feature seen across multiple species, including hominins (Braun et al., 2009b; Harmand, 2009; Sanz et al., 2009; Luncz et al., 2016a). However, selection of certain material properties in percussive tool use may be transmitted via social mechanisms in a similar manner as different types of tool use (e.g., stone vs. wooden tools; Biro et al., 2003; Luncz et al., 2012; Luncz and Boesch, 2014). The selection of certain rock types for stone artifact production is a consistent feature of hominin tool use from some of the earliest instances of tool use (Stout et al., 2005; Harmand et al., 2015; Braun et al., 2019; Plummer et al., 2023). Hominins may not have needed to directly understand the mechanical properties of stone to canalize the selection patterns on only a few specific rock types. Instead, as seen here in this experiment, a combination of individual learning with some social enhancement can lead to rapid enforcement of the most efficient tool use. This suggests that relatively simple social learning mechanisms can underlie the broad-based adoption of rock types that are best adapted for a specific tool use behavior. Oldowan hominins may not have implemented the kind of high-fidelity social learning evident in modern humans to create the archaeological patterns of selection that are visible in earliest industries (Braun et al., 2009b; Tennie et al., 2017; Plummer and Finestone, 2018).

The selection of appropriate tools for extractive foraging behaviors has been shown to increase feeding efficiency among primate (Visalberghi et al., 2009) and nonprimate species (*Corvus moneduloides* ;St Clair et al., 2018). Appropriate selection of tool forms will provide an adaptive benefit for animals that routinely engage in extractive foraging. Task-specific selection has been documented in extant nonhuman primates in both perishable and stone technologies (Sanz et al., 2004; Carvalho et al., 2008; Visalberghi et al., 2009; Sirianni et al., 2015; Almeida-Warren et al., 2017; Pascual-Garrido, 2018; Pascual-Garrido and Almeida-Warren, 2021). Tool selection can involve the selection of certain shapes for certain prey items (e.g., *Macaca fascicularis aurea*; Gumert and Malaivijitnond, 2013; Tan et al., 2015). Selection may also involve certain properties of food item and a variety of details of tool morphology and physical characteristics such as tool mass and friability (e.g., *Sapajus libidinosus*; Ferreira et al., 2010; Spagnoletti et al., 2012; Haslam, 2014; Luncz et al., 2016a). Chimpanzee percussive tool use may represent a shared trait present in the last common ancestor of chimpanzees and hominins (Rolian and Carvalho, 2017; Proffitt et al., 2023). Percussive activity has been suggested as a precursor to the intentional production of knapped technology (Goren-Inbar et al., 2002; Davidson and McGrew, 2005; Marchant and McGrew, 2005; Luncz et al., 2022), which appears to be a derived feature so far unique to the hominin clade (although unintentional flake production has been observed in non-human primates; Proffitt et al., 2016, 2023). The use of stone as a medium for tool use may indicate an underlying shared capacity to identify mechanical properties that is inherent in primate tool use.

5. Conclusions

The ability of primates to select tools for specific activities has been strengthened by the emergence of the archaeology of primate tool use (Carvalho et al., 2008; Visalberghi et al., 2009; Massaro et al., 2012; Luncz et al., 2016a). Here, we show that rock types similar to those found at Oldowan archaeological sites can be distinguished by chimpanzees (Plummer, 2004; Braun et al., 2008, 2009b; Plummer et al., 2023). The patterns of selection by the chimpanzees at Bossou show levels of selectivity that are similar to those identified in the earliest hominin toolmakers (Fig. 10). In fact, selection for pounding tools in the Oldowan archaeological record (Lokalalei 2C) shows lower levels of selectivity than that seen in chimpanzees (although the reasons for selection may be governed by different activities that hominins at Lokalalei 2C were engaged in). Patterns of selection seen in some of the earliest toolmakers may be a socially mediated phenomenon (Morgan et al., 2015). However, this study indicates that archaeologically visible patterns of selection can result through relatively simple means of information transfer. It is important to note that we do not rule out the possibility that chimpanzees use social learning mechanisms to identify the properties of stones. Indeed, some aspects of social enhancement are very likely to have played a role in the experimental setting, as exhibited by the frequent reuse of tool sets. In addition, the frequent selection of more efficient tool sets when tool sets are reused supports the assertion that social enhancement reinforced the individual learning by some chimpanzees. Bossou chimpanzees converged on the use of efficient tool combinations even when presented with rock types that they had never seen before.

It is possible that Pleistocene hominins also reused toolsets on ancient landscapes (Turq et al., 2013). Accumulations of stones on ancient landscapes may have provided the necessary information about rock selection even in the absence of direct observation (Schick, 1986; Rezek et al., 2020). Rock selection in percussive behaviors in chimpanzees provides insights into the possible mechanisms of information transfer in antiquity (Biro et al., 2003, 2006; Stout, 2011). As the archaeological record extends further back in hominin evolution (Harmand et al., 2015; Plummer et al., 2023), we may find greater similarities between the technology of modern nonhuman primates and ancient hominins. Exploring selection of appropriate raw materials is a fruitful mechanism to compare across technologies.

Author contributions

D.R. Braun: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **S. Carvalho:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **R.S. Kaplan:** Writing – review & editing, Methodology, Formal analysis, Data curation. **M. Beardmore-Herd:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Formal analysis, Data curation. **T. Plummer:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **D. Biro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **T. Matsuzawa:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no competing interests in the publication of this work.

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Appendix A. Supplementary Online Material

Supplementary online material to this article can be found online at https://doi.org/10.1016/j.jhevol.2024.103625.

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