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ORIGINAL PAPER

Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins?

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Abstract Recent etho-archaeological studies of stone-tool use by wild chimpanzees have contributed valuable data towards elucidating the variables that influenced the emergence and development of the first lithic industries among Plio-Pleistocene hominins. Such data help to identify potential behaviours entailed in the first percussive technologies that are invisible in archaeological records. The long-term research site of Bossou in Guinea features a unique chimpanzee community whose members systematically use portable stones as hammers and anvils to crack open nuts in natural as well as in field experimental settings. Here we present the first analysis of repeated reuse of the same tool-composites in wild chimpanzees. Data collected over 5 years of experimental nut-cracking sessions at an "outdoor laboratory" site were assessed for the existence of systematic patterns in the selection of tool-composites, at group and at individual levels. Chimpanzees combined certain stones as hammer and anvil more often than expected by chance, even when taking into account preferences for individual stones by themselves. This may reflect an ability to recognise the *nut-cracker* as a single tool (composed of two elements, but functional only as a whole), as well as discrimination of tool quality-effectiveness. Through repeatedly combining the same pairs of stones—whether due to preferences for particular composites or for the two elements independently—tool-users may amplify use-wear traces and increase the likelihood of fracturing the stones, and thus of detaching pieces by battering.

Keywords Stone-tool use · Tool-composites · Chimpanzee · Etho-archaeology · Technological evolution

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Introduction

Stone-tool use by wild chimpanzees and the etho-archaeological approach

Stone-tool use in nature has been much studied in non-human primates such as the chimpanzee (*Pan troglodytes*) (Sugiyama and Koman 1979; Sugiyama 1981; Boesch and Boesch 1983; Anderson et al. 1983; Whitesides 1985; Kortlandt 1986; Hannah and McGrew 1987; Morgan and Abwe 2006) and capuchin monkeys (*Cebus libidinosus*) (Fragaszy et al. 2004; Visalberghi et al. 2007). Depending on the definition of tool-use adopted, the behaviour has been said to represent an extension of the primate body (Goodall 1964), although it also occurs in various vertebrate and invertebrate taxa that use stones for subsistence purposes (McGrew 1992). Chimpanzees show an extensive cultural repertoire of tool-use (Whiten et al. 1999), with lithic tool use being one component of their elaborate and flexible cultural behaviour. Together with humans, great apes are the primates who show the most extensive ability to modify and to use a variety of tools for specific purposes (Whiten et al. 2001; McGrew 2004).

The behavioural repertoires of chimpanzees living in several West African countries include nut-cracking with stone or wooden tools (Boesch 1978; Nishida 1987; McGrew 1992, 2004; Matsuzawa 1994; Matsuzawa et al. 2001; Biro et al. 2003, 2006), while in East and Central Africa such percussive technology is absent despite evident availability of stones and nuts (McGrew et al. 1997). Since the 1970s, long-term research on stone-tool use by wild chimpanzees has focused on the Taï and Bossou forests (Matsuzawa 1994; Boesch and Boesch-Achermann 2000; Matsuzawa et al. 2001), providing consistent data indicative of a cultural origin for this behaviour (McGrew 1992, 2004; Matsuzawa et al. 2001; Biro et al. 2003; Humle and Matsuzawa 2004; Lycett et al. 2007). Evidence points to social transmission involving a "master-apprenticeship" system scaffolded by ontogenetic maturation (Matsuzawa et al. 2001; Biro et al. 2003, 2006).

Over the last 20 years, interdisciplinary approaches to chimpanzee tool-use have been steadily proliferating (Wynn and McGrew 1989; Schick et al. 1999; Toth and Schick 2006; Joulian 1996; Sept 1992; Mercader et al. 2002; Davidson and McGrew 2005; Matsuzawa 2009), providing not only new insights into the ethology and cognition of chimpanzees, but also raising new premises to understand evolutionary processes relating to the emergence of technology. The latter aim to fill gaps that result from the nature of the archaeological record, given that behaviour does not fossilise (Whiten et al. 2003; McGrew 2004). As *Pan* and *Homo* share ancestral traits, it is reasonable to assume that tool-use was one of these traits (Panger et al. 2002). Recent discussions among workers from different fields have given support to the importance of extending this novel approach further, and have led to the promotion of a new discipline: Primate archaeology (Ling et al. 2009; Haslam et al. 2009).

Recent archaeological excavations at chimpanzees' abandoned nut-cracking sites have given new insights into the similarities between chimpanzee and hominin lithic assemblages (Mercader et al. 2002, 2007). Innovative archaeological research methods at chimpanzee stone tool-use sites combine the classical archaeological approach with an ethological one. This combination shows that technological and typological diversity exists in contemporary stone assemblages among different chimpanzee communities (Carvalho et al. 2008; Biro et al., in press) as seems to have been the case with the tool-makers of the first Oldowan industries. For example, sites such as Lokalalei 1 and 2C (West Turkana, Kenya) dated around 2.3 Mya and separated by a distance of only 1 km, show both typological and technical diversity (Delagnes and Roche 2005). This ethoarchaeological research has identified variables (such as raw material availability and mobility) that may influence this regional diversity in chimpanzees (Carvalho et al. 2008). If we further extrapolate, it resembles patterning in the emergence of the first hominin lithic industries, e.g. the oldest findings from Gona, in Ethiopia, dated to 2.6 Mya (Semaw et al. 1997; Semaw 2000).

An archaeological re-examination of percussion tools from one of the most well-known Oldowan assemblages, Olduvai Beds I and II (Mora and de la Torre 2005), reviews Leakey's original typological classification (Leakey 1971) and reassesses the technological process of tool-making and use. This revision suggests that pounding tools had a more important role in the development of the first lithic industries in these hominin groups than was previously thought (de Beaune 2004; Mora and de la Torre 2005). Moreover, recognising that chimpanzee stone assemblages not only are a helpful indicator of possible functions of hominin pounding tools, but also are similar to these pounding tools in their typology and technology emphasises the need for an extensive comparison between ape and hominin lithic assemblages (Mora and de la Torre 2005; Haslam et al. 2009).

Several archaeological studies demonstrate that, in order to approximate more closely how early hominins may have acted, it is necessary to combine: (1) Techniques to identify technological processes, such as refitting (e.g. Delagnes and Roche 2005) and experimental exercises (e.g. Isaac 1981; Dibble 1997; Toth and Schick 2006); and (2) Techniques to identify tool functionality, such as microscopic or macroscopic use-wear analyses (e.g. Backwell and d`Errico 2001; Goren-Inbar et al. 2002) and residue analyses (e.g. Haslam 2004; Mercader et al. 2007).

One form of stone-tool use in wild chimpanzees, the systematic combination of *movable* hammer and anvil stones for the cracking of hard-shelled nuts, has so far been reported only for the chimpanzees of Bossou, Guinea (Matsuzawa 1994; Biro et al. 2003; Carvalho et al. 2008). Compared with other sites where anvils consist of fixed substrates, such as rock outcrops or tree roots, it seems reasonable to interpret this advanced percussive technology as a case of progressive problem-solving (Stokes and Byrne 2001). Such advancement may also be evident in the occasional use by Bossou chimpanzees of a wedge-stone to stabilise the anvil (Matsuzawa 1994), and may be comparable to techno-units of different levels of complexity (Oswalt 1976).

Archaeological research now in progress in Bossou shows that chimpanzees have a systematic *chaîne opératoire* (Mauss 1967; Boëda et al. 1990) of sequential behaviours. Here, the nut-cracker exemplifies a tool-composite defined as a *tool constructed through the purposeful association of two or more objects (transformed or not) that need to be used in combination in order to function and to* *achieve a specific goal* (Carvalho et al. 2008, p 159). In terms of the three tool categories laid out by Karlin and Pelegrin (1988): *outil*, *outil composite* and *instrument*, the *nut-cracker* tool shows close affinities with Karlin and Pelegrin's definitions of *outil composite*, a category also adopted by primatology, referring to the sequential and simultaneous use of several objects to attain one single goal (Sugiyama 1997). Hammers and anvils at Bossou show evidence of extensive reuse (use-wear traces, e.g. concentrated pitting and depressions) and of frequent transport, despite the availability of other potential tools in the nut-cracking areas. Moreover, this tool transport occurs not only at Bossou's outdoor laboratory (the site for our field experiments, see "Methods" section), where some variables are under easier control, but also in the completely natural nut-cracking sites of Bossou forest, indicating that the frequency of transport could not be explained only by the distribution of the natural resources. Recent studies identified attributes of stones that correlated with their frequency of use and function, such as size, weight, and material, suggesting that chimpanzees discriminate among available raw materials along these parameters (Sakura and Matsuzawa 1991; Biro et al. 2003; Carvalho et al. 2008). Such selectivity has been hypothesised to be an indicator of preferences for tools or possessiveness towards particular tools (Matsuzawa 1999).

Chimpanzees may also exhibit preferences for *combinations* of stones in nut-cracking, i.e. they may repeatedly combine the same two stones as hammer and anvil in repeated executions of the task. Such tool-composite reuse in nut-cracking by wild chimpanzees has not been recorded before, but it would have important implications for: (1) Recognising that chimpanzees may have the cognitive ability to select tools in combination; (2) Arguing that chimpanzees identify a nut-cracker as a single tool; (3) Highlighting such associative stone-tool use as a behaviour indicative of technological complexity; (4) Inferring that, for early hominin pounding tools, similar behavioural steps are likely to have occurred during the emergence of the first lithic industries.

We focus on testing the potential existence of tool-combination selection during the use of stone tools for nut-cracking by wild chimpanzees. We examine the composition of nut-crackers—the pairing of a hammer stone with an anvil stone—during direct observations of experimental nut-cracking sessions in an outdoor laboratory, in the forest of Bossou, Guinea.

Methods

Study site and population

Bossou offers an "outdoor laboratory" in the heart of the home range of a chimpanzee community that allows researchers to perform experiments on nut-cracking and to gather a direct, continuous, long-term, and detailed record of individuals' performance, tools, and behaviour (Fushimi et al. 1991; Matsuzawa 1994, 1996, 1999; Matsuzawa et al. 2001; Biro et al. 2003, 2006). The outdoor laboratory site is a rectangular natural clearing (7 m × 20 m), atop Mount Gban (07° 39′N; 008° 30′W), where raw materials for tool-use are provided by experimenters. After 2 decades of annual experimental sessions during the dry season (December to February), with 20–30 h of observation per year, this longitudinal study has revealed insights into the acquisition of tool-use behaviour and mechanisms of social transmission in wild chimpanzee communities (see Biro et al. 2006; Biro et al., in press, for extensive reviews). Currently, a newly introduced archaeological approach at Bossou allows direct observation of ape stone-tool use in experimental contexts and the creation of a non-human archaeological record. These studies seek to compare typologies and techniques at the outdoor laboratory with those at natural nut-cracking sites in the same and nearby forests (Carvalho et al. 2007, 2008).

The chimpanzee community at Bossou has numbered about 20 individuals over the last 30 years, but recently this number has declined (Matsuzawa et al. 2004). In 2007 there were 13 individuals; during the study-period of 1999–2006, the number of individuals ranged from 12 to 19.

Apparatus and experimental sessions

Data presented here were collected during the field seasons (January to February) of 1999, 2000, 2002, 2005, and 2006, in 135 experimental sessions, with a total of 88 observational hours.

At the outdoor laboratory, nuts (mainly *Elaeis guineensis*, but also *Coula edulis* and *Panda oleosa*) were piled in seven spots, and the area was cleared of naturally available stones. Experimenters presented a specially selected set of stones of various shapes, sizes, and materials; each stone bore a unique ID number. The same set was available during each of the field seasons reported here, although numbers varied slightly (minimum 49 in 1999; maximum 57 in 2006) due to the loss of some stones and the fracturing of others into two or more pieces. The stones were placed in a rectangular formation (matrix) before each session—a process that was never observed directly by chimpanzees—arranged randomly at one spot in the clearing (1999–2005), or were divided between two spots and restored to the same position in the matrix at the end of each session (2006), offering the chimpanzees a choice of available raw materials [see Figs. 1, 2 for a view of the experimental site or Biro et al. (2006) and Carvalho et al. (2008), for details of the experimental procedures]. All the stones, whether presented in one matrix or two matrices, were within easy

Fig. 1 Two adult male chimpanzees [Yolo (*left*), and Foaf] of the Bossou community crack oil-palm nuts using tool-composites (comprised of one hammer and one anvil) in two spots where raw materials were provided in the outdoor laboratory. (Photo by S. Carvalho)

Fig. 2 View of the matrix of stones at the outdoor laboratory

arm's reach of the chimpanzees, and the matrices themselves could be approached from all directions, without any constraints. Chimpanzees could (and did) enter the outdoor laboratory itself from all directions, using terrestrial or arboreal locomotion, including the direction in which the experimenters were positioned. The maximum distance between stones (in any of the matrices) was approximately 1.60 m (length) and 1 m (width). For a chimpanzee to reach a stone positioned in the centre of the matrix, if approached from the side of the matrix the stone was closest to, the maximum distance was around 40 cm. Hence we had no reason to suppose that certain locations within the stone matrix were inherently easier to reach and thus biased choices made by the chimpanzees. An analysis examining the relationship between the location of stones and the frequency with which they were chosen by the subjects found no differences between three possible distance categories (0, 20, and 40 cm from the edge of the matrix, as a proxy for ease of access; ANOVA $F_{2,55} = 2.30$, $P = 0.110$; data from 2006 only). This suggests that the non-random positioning of stones in the matrix in 2006 was unlikely to have created systematic selection biases.

An experimental session began when the first chimpanzee entered the outdoor laboratory and ended 3 min after the last individual left the site. The timing of sessions depended entirely on the chimpanzees' decision to visit the outdoor laboratory, and the number of sessions within a day varied from 0 to 4. Following each session, all stones were again arranged in matrices, in readiness for the next visit. The chimpanzees' activities were recorded by two or three video cameras (Sony Digital Handycam, DCR-VX 1000; Sony Digital Handycam, DCR-PC 110) for subsequent analysis of fine details of stone-tool use, while researchers hidden behind a screen constructed from leaves concurrently observed and recorded behaviours directly.

We recorded each episode in which an individual selected and successfully combined two or more stones to crack open nuts, while at the same time noting the ID numbers of the tools (Figs. 1, 2). Chimpanzees initially selected stones by approaching a stone matrix and picking out two stones to be used as hammer and anvil for nut-cracking. One episode of using a given tool-composite refers to the successful use of a hammer–anvil combination for the cracking of one or more nuts, ending when the individual either abandoned both stones (and stopped nut-cracking) or changed one or both of the stones before cracking another nut (thus constructing a new composite).

To examine tool-composite reuse in our dataset, we used randomisation tests to compare individuals' tool choices to a null expectation based on (1) random tool choice, and (2) frequencies with which individual stones were used as either hammer or anvil (irrespective of the identity of the other stone in the pair). We compared the observed frequencies with which specific tool-composites were reused (by the same individual or by more than one individual) to frequencies expected by chance under the two different null assumptions, based on the number of stones presented [in (1)] or used [in (2)] and the size of our dataset. It should be noted that all the stones presented during our experiments were within the range of sizes and weights naturally utilised by the chimpanzees of Bossou, therefore one of the starting assumptions of our tests [in (1)] was that all stones presented *could* have been used by the subjects.

Because our methods for presenting stones varied slightly between two study periods (1999–2005 and 2006), we repeated the analysis separately for each. Since the results agreed between the two periods, we report only those for the combined dataset here (see also the argument above for why the one-matrix and two-matrix presentation methods were unlikely to have created differential—or indeed any—individual selection biases that would have influenced the results). In addition, to examine the effect of second and subsequent choices of tool-composites within a session being made from a reduced matrix (and hence not representing fully independent selections from *all* the available stones), we performed the analysis in two ways: (1) by including all our stone-utilisation data throughout all sessions and (2) limiting the dataset strictly to those instances where chimpanzees were forming tool-composites by choosing from among all the available stones (most commonly the very first selection in a session).

Finally, specific episodes of reusing a tool-composite (or one of its elements) that was previously selected by a different individual, during the same session, were initially considered as independent selections of that tool or tool-composite, since they typically occurred at times when there were already several other used tool-composites dispersed through the area, implying selection from among a number of available composites and/or the assortment of stones in the matrix. Nevertheless, the first-choice only dataset by definition excludes these cases.

A program written in Matlab (Mathworks, Natick, MA) generated the randomised distributions.

Table 1 Individuals attending the outdoor laboratory and the total number of tool-composites constructed by each individual in each year of the experiment

Individual	1999	2000	2002	2005	2006	Total
Tua	1	4	6	12	6	29
Yo	0	23	9	12	15	59
Foaf	6	16	8	11	19	60
Yolo	1	36	24	15	44	120
Fana	12	9	7	9	8	45
Fanle	×	×	10	19	17	46
Peley	×	×	1	22	22	45
Jire	3	16	20	20	19	78
Velu	0	6	11	4	4	25
Jeje	×	×	×	29	38	67
Kai	2	11	17	–	–	30
Vuavua	5	23	20	–	–	48
Fotayu	6	15	5	–	–	26
Poni	0	0	10	–	–	10
Nto	3	10	–	–	–	13
Pili	0	4	–	–	–	4
Vui	4	–	–	–	–	4
Unknown	19	23	29	9	0	80
Total	64	196	177	162	192	789

Only chimpanzees capable of cracking nuts during the study period are included. × Denotes individual not yet able to nut-crack, – denotes individual no longer present at Bossou

Results

In 135 experimental sessions, we observed the formation of 789 tool-composites from 17 individuals who cracked open nuts and visited the outdoor laboratory during the study period. These comprised 349 (ca. 11%) of over 3,000 possible unique combinations (based on the maximum number of stones available in the outdoor laboratory, and on assuming that each stone potentially could be paired with every other stone to make a hammer–anvil composite). Table 1 shows the number of tool-composites formed by each individual; these frequencies ranged from 4 (Vui and Pili) to 120 (Yolo). The number of composites recorded per year ranged from 62 in 1999 to 196 in 2000. In 80 cases tool-composites could not be assigned to individuals (they were recorded only after chimpanzees had departed from the outdoor laboratory, and the identity of the user could not be verified at the time, nor subsequently from video records, and were coded as "user unknown").

Of the 349 unique tool-composites recorded, 162 were used more than once. Figure 3a shows the frequencies of reuse: Most (46%) were used twice, while at the other extreme one set was used 23 times and another 29 times. The latter composite (hammer 56 + anvil 57; Fig. 4) was used by six chimpanzees.

Limiting our dataset to "first-choice-only" composites (i.e. dealing only with those composites that were formed at the beginning of a session, drawn from the full complement of stones), we have 148 such composites, encompassing 106 different hammer–anvil combinations. The discrepancy between the number of sessions (135) and the number in this dataset (148) is due to the inclusion of a small number of cases where a chimpanzee, after having chosen a composite from an intact matrix, later made a second choice within the same session—so long as no other chimpanzee had touched any of the stones in the meantime, we still considered these to be independent choices on the part of the individual from the full assortment of raw materials. Twenty-two of the 106 different composites were used more than once, with a maximum of seven reuses in the case of two composites (Fig. 3b): hammer 47 + anvil 35, and hammer 130 + anvil 53 (stone 130 was fractured into two stones in 2006).

Do these data demonstrate that Bossou chimpanzees repeatedly reuse the same tool-composites or that they show significant selectivity in choosing particular pairs of stones as hammer and anvil? First, based on the null assumption of random choice of hammer and anvil from the full assortment of stones available, we calculated a test distribution of expected frequencies for observing reuse of the same pair of stones. The expected values were calculated for each reuse frequency (i.e. for double, treble, etc, reuse)

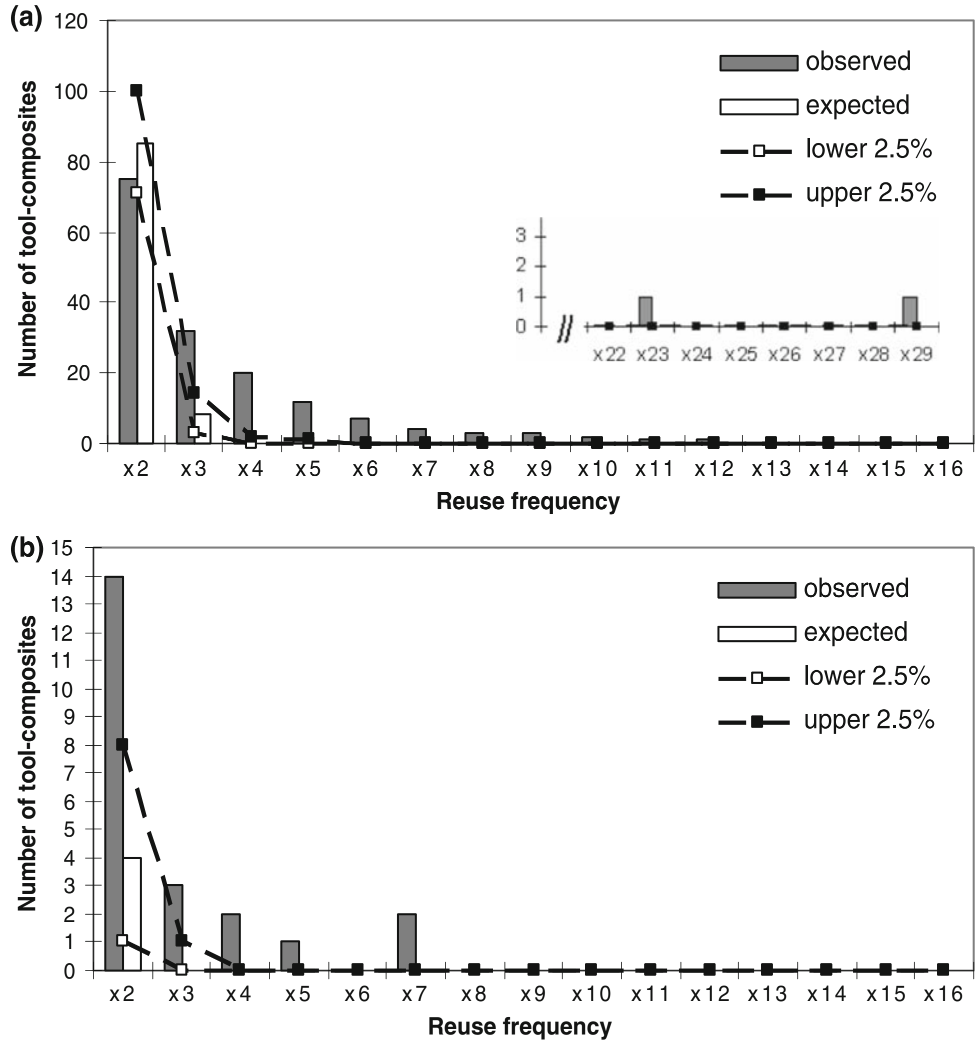

Fig. 3 Number of tool-composites reused at various rates. *Solid bars* show values observed during the study, *open bars* correspond to expected values based on random choice of stones. At each reuse frequency, *black squares* show the upper and lower 2.5 percentiles of a test distribution (1,000 iterations) based on random choice of *N* tool-composites from among 53 stones (the average number of stones across the 5 years when the experiment was conducted). Observed values outside this range indicate significant departure from randomness. **a** Analysis based on the full dataset (including all selections made by chimpanzees during any given session), *N* = 789; **b** analysis based on the first-choice-only dataset (taking into account only those instances where a single chimpanzee was selecting tools at a time when no other chimpanzee had utilised any of the stones in the given session), *N* = 148

Fig. 4 Hammer 56 + Anvil 57: the most frequently reused tool-set. Six individuals used this combination a total of 29 times (Photo by S. Carvalho)

and compared to those observed: If the observed frequency lay outside the central 95% of the test distribution, then we concluded a significant departure from randomness.

To generate the test distribution, we created mock data-sets (by 1,000 iterations) with the following parameters: Number of stones available was set at 53 (the mean across the 5 years of the study), and the number of tool-composites drawn independently from these was 789 (the size of our complete dataset) in our first analysis, and 148 (the size of the first-choice-only dataset) in the second. Since we had no a priori reason at this stage to specify precisely which stones chimpanzees would select as hammers and which as anvils, and with what probability, our initial analyses treated each stone as having equal probability of being selected as either hammer or anvil. The frequencies of reuse of particular hammer–anvil sets within each of the 1,000 mock data-sets formed the test distribution. Figure 3a shows that significant differences between observed and expected values existed in all but the double-reuse category of the full dataset, with observed values lying above the upper 2.5 percentile, signifying higher-than-expected frequencies. The pattern was essentially the same in the first-choice-only dataset, with significantly higher-than-expected occurrence of reuse in all categories for which data existed (Fig. 3b). Hence, Bossou chimpanzees reused the same tool-composites more often than would be expected by chance, if tools were selected randomly from among all suitable stones available.

These results suggest that chimpanzees do in fact select tools non-randomly—an observation already reported, albeit for different datasets, in previous work (see Sakura and Matsuzawa 1991; Biro et al. 2003; Carvalho et al. 2008). But other than selectivity for certain stones as hammers and others as anvils, do Bossou chimpanzees also display a selectivity in choosing particular tool-composites? In other words, do episodes of composite reuse reflect individuals' preferences for those specific tool-composites, or do they arise, incidentally, out of preferences for individual stones and not their combinations per se? To distinguish between these two scenarios, we repeated our analysis with a modified null-hypothesis: instead of fully random tool selection, mock datasets were created using probabilities based on the actual frequencies with which each stone was observed to have been used as hammer or anvil. The rationale was thus that if certain stones are preferred as hammers or as anvils, then reuse may arise simply as a consequence of such preferences, rather than a recognition that a specific pairing of stones works particularly well in combination.

Figure 5a, b (based on the full dataset, and the first-choice-only dataset, respectively) shows the results of the analysis using actual use frequencies of individual stones to generate mock datasets for the randomisation test. These suggest that much of the reuse we observed can be explained on the basis of preferences for individual stones—by choosing certain stones preferentially as hammers or anvils, chimpanzees come to reuse them repeatedly in combination. However, a small number of composites (those used 23 and 29 times in the full dataset, and those used seven times each in the first-choice-only dataset) cannot be predicted even under this modified null-hypothesis, demonstrating that chimpanzees are indeed capable of the systematic selection of tool-composites, rather than only of their separate elements independently.

To examine selectivity at the individual level, we utilised our full dataset (the first-choice-only dataset did not have sufficient sample sizes for many individuals to allow a meaningful analysis). All but three of the 17 chimpanzees

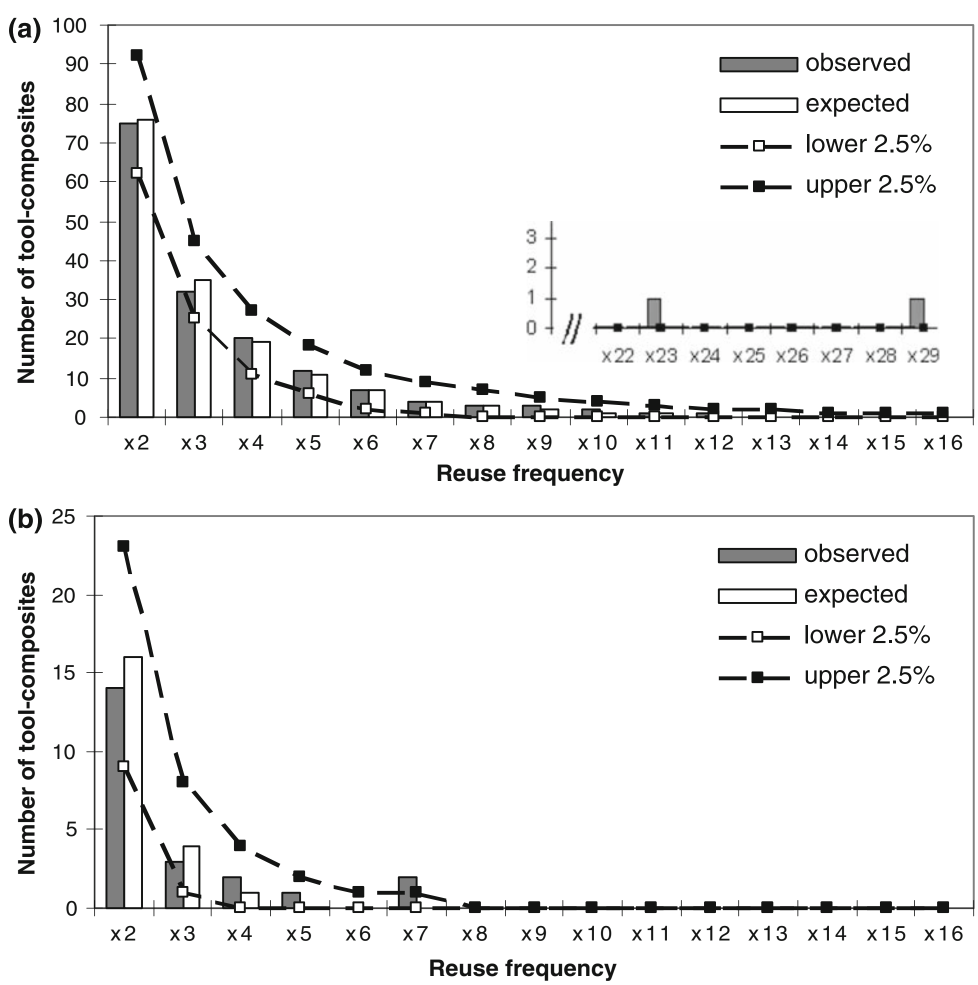

Fig. 5 Results of randomisation tests using actual use frequencies for individual stones to generate expected values and test distributions. **a** Analysis based on the full dataset, $N = 789$; **b** analysis based on the first-choice-only dataset, $N = 148$. See caption to Fig. 3 for further detail

reused tool-composites. The three who did not—Nto, Vui, and Pili—had very few observations. To control for different sample sizes across individuals, we calculated reuse proportion as the number of composites for which we observed double, treble, etc, reuse divided by the total number of observations for that individual. Figure 5 compares these proportions at different reuse frequencies across individuals. Randomisation tests were conducted as above, but instead of generating 1,000 datasets with $N = 789$, we used the minimum and maximum N of the individual data. As the minimum, we arbitrarily chose $N = 10$ and so discarded the two individuals with four observations each from the analysis, and $N = 120$ as the maximum: Using a larger sample size created a more conservative estimate for the threshold (of the 2.5 percentiles).

Figure 5 shows the locations of the upper 2.5 percentiles at each reuse frequency as thick horizontal bars. Observed values projecting above these boundaries signify significant departure from random selection of stones at the individual level. Thus, for the proportion of twice-used composites, for example, 11 of 15 chimpanzees exceeded values expected by chance based on random tool selection. While the expected probability of tool-composite reuse approaches 0 as the rate of repetitions increases beyond 2, nine chimpanzees reused composites at frequencies greater than that. Two of the four individuals who did not exceed chance level at double-reuse, exceeded it in the treble-reuse category; one individual (Yolo) reused the same set 10 times. Thus, reuse rates differed significantly from chance in all but two subjects, indicating individual- as well as group-level selectivity for tools. Furthermore, when taking into account actual use frequencies of stones separately for each individual, in a number of cases reuse frequencies exceeded chance level (indicated in Fig. 6 by asterisks). This suggests, similarly to the group data, that while most reuse could be explained by subjects' preferences for individual tools, preferences for specific tool-composites were also evident at the individual level.

We next examined patterns of within- vs. between-individual reuse by focusing on composites that were repeatedly constructed either by a single subject, or by multiple subjects. Figure 7 shows that the majority (78%) of such composites (i.e. those that were used at least twice by at least one subject; $N = 58$) were unique to single individuals. At the other extreme, two composites were reused by six different chimpanzees. It therefore seems that individuals are to a large extent idiosyncratic in their choice of tools and composites, although at least in some cases the same composites are reused by several subjects.

Discussion

Wild chimpanzees select and use stone hammers and anvils for cracking hard-shelled nuts based on several variables: (1) Type of raw material; (2) Stone tool characteristics; (3) Tool portability; (4) Type of nut (Sakura and Matsuzawa 1991; Carvalho et al. 2008). Our present results again confirm the existence of non-random tool choice among suitable raw materials available, and illustrate further that such

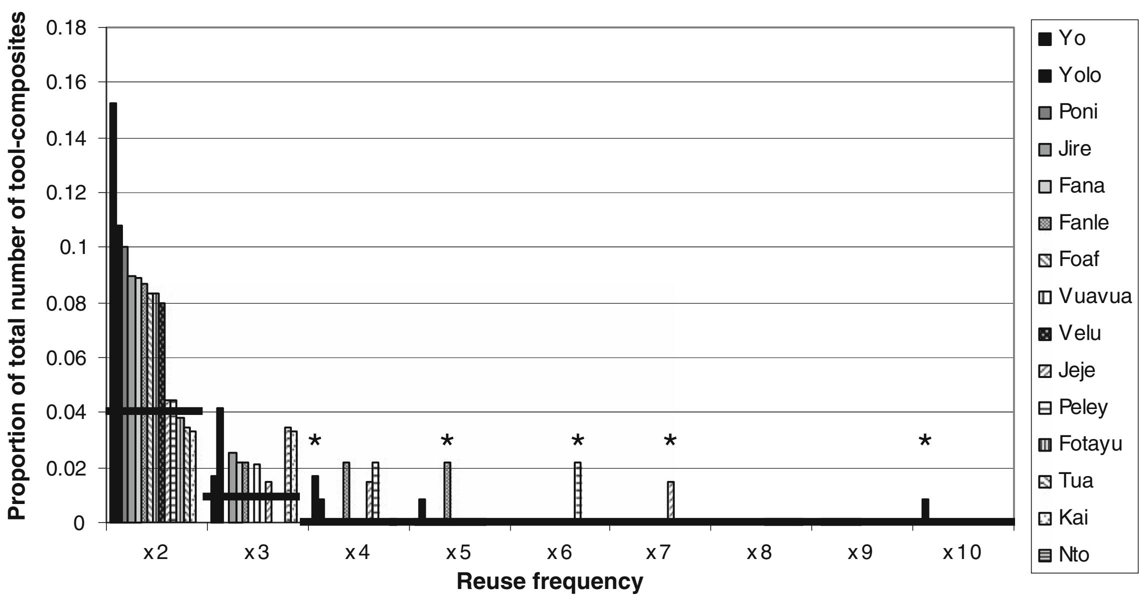

Fig. 6 Proportion of tool-composites within each individual's dataset as a function of reuse frequency. Only individuals with at least 10 observations are included. *Horizontal black lines* indicate the location of the upper 2.5 percentile of a test distribution based on random choice of stones and the maximum sample size for any individual ($N = 120$); *asterisks* indicate *bars* which show higher-than-chance reuse once actual use frequencies of individual stones by that subject are taken into account (see text for further detail)

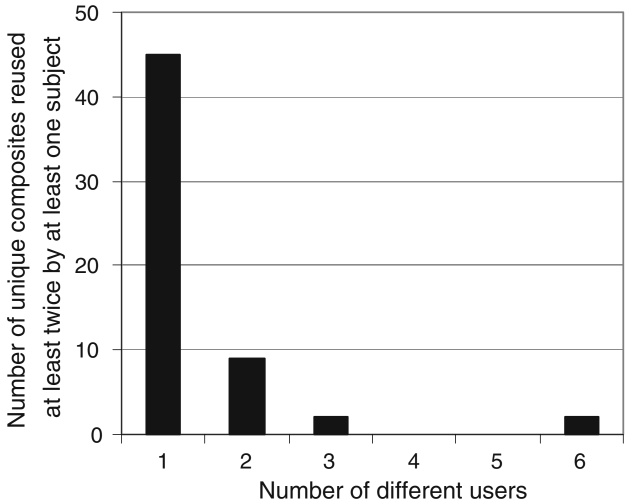

Fig. 7 Number of composites used at least twice as a function of the number of different individuals who used them. Only those unique composites are included which were used on more than one occasion by any single individual

selectivity can lead to the repeated use not only of particular stones, but also of particular hammer–anvil combinations ("tool-composites"). Whether the reuse of composites arises incidentally out of chimpanzees' preferences for particular stones, or is due to preferences for specific composites based on their effectiveness as a single tool, is a central question of our study. Our analyses suggested that although most instances of reuse cannot be distinguished from independent preferences for the separate elements of a composite, at least in some cases the nut-cracker does seem to be preferentially selected as a whole. Nevertheless, both processes can lead to the repeated combination of the same tools, and thus to the reuse of the same nut-crackers, with important implications for understanding the evolution of technology across all the "pounding tool-users" of the primate order and for discussing the origins of intentionality in tool-use and tool production (see below). The observation that the identity of reused nut-crackers differs across individuals further suggests that chimpanzees may have idiosyncratically preferred tool-composites. Matsuzawa (1999) argued that such idiosyncrasies may underlie the evolutionary emergence of possessiveness, although this remains open to interpretation.

Repeated use of the same tool-composites, if achieved through selection for the nut-cracker as a whole rather than for its elements separately, may suggest that chimpanzees are able to discriminate functional tool features such as the quality-efficacy of a nut-cracker as a whole. They may therefore reuse those tool-composites that are most effective for cracking open nuts, suggesting optimisation. Further studies are needed to test hypotheses related to optimal features, such as the working area of an anvil surface. Nevertheless, the fact that our analysis examining the link between location of stones and the frequency with which they were used found no significant relationship (stones most accessible were not used significantly more often than less accessible ones) suggests that neither location per se nor location optimal in terms of access to tools may be a decisive variable when chimpanzees select nut-crackers. This also corroborates results concerning the frequency of transport of stone items by chimpanzees, even in cases when transport would be unnecessary due to the alternative offer of raw materials at the nut-cracking site. The present analysis, together with previous studies on tool transportation (Boesch and Boesch 1984; Carvalho et al. 2008), highlights the point that selection of tools by chimpanzees is likely to be linked with their ability to discriminate among more or less efficient tools for performing the pounding activity.

Moreover, the *mobility* that characterizes stone technology at Bossou (where, uniquely among nut-cracking chimpanzee communities, both hammer and anvil are movable items) offers an especially close similarity with the corresponding hominin pounding tools found in archaeological contexts, in which anvils are considered to be only one component of a pair (Leakey and Roe 1994). From this functional perspective, the nut-cracker is seen as a single tool since, when separated, neither hammer nor anvil can achieve the goal of the task. Along the same lines, we may argue that since only pairs of stones will ever produce results, it is questionable whether evaluating the quality-effectiveness of any single tool in isolation is in fact a realistic possibility.

It is also important to note that nut-cracking is part of a complex social learning process, extensively studied at Bossou (see, for example, Matsuzawa et al. 2001), which may also help to explain particular preferences for tools or tool-composites: For example, it has been shown that juveniles show higher frequencies of reusing tools previously chosen by adults (Carvalho et al. 2008), and this could be seen as an indicator of juveniles' lack of efficiency in selecting and using tool-composites, during the long process of skill acquisition.

The present research also highlights the insufficiency of investigating chimpanzee stone tool typologies and technologies with a conventional archaeological approach. The same temporal gaps that exist in prehistory implying an irrecoverable loss of essential information exist when looking for chimpanzee material culture based on indirect evidence only. However, an etho-archaeological approach—which has already shown in previous studies the existence of regional diversity in typologies and technologies of chimpanzee stone tools (Marchant and McGrew 2005; Carvalho et al. 2008; Biro et al., in press)—permits the recognition of precise technical behaviour that can be applied to understanding the evolution of technological complexity in non-human primates and hominins.

In seeking to reconstruct the extractive technology of Plio-Pleistocene hominins, the challenge is to identify ape behaviour that illuminates the first percussive technologies that are invisible in the archaeological record, as the earliest hominin technology remains poorly understood (Delagnes and Roche 2005). The emergence and evolution of technology probably happened through small behavioural steps, during micro-temporal frames that cannot be inferred from the conventional archaeological record (Dibble 1997). Percussive technologies (pounding tools) probably were hugely important in the Plio-Pleistocene for the emergence and development of the first hominin lithic industries and for hominin subsistence (McGrew 1992; de Beaune 2004; Mora and de la Torre 2005).

Recent archaeological findings suggest similarities between *Pan* nut-cracking site assemblages and Plio-Pleistocene hominin pounding tool site assemblages: (1) Functional nut-cracking (Goren-Inbar et al. 2002; Mercader et al. 2002, 2007); (2) Use-wear traces that circumscribe clearly impact zone areas as a result of bashing activities (Delagnes and Roche 2005); (3) Lack of correlation between the function and shape of tools, although for chimpanzees a relation was found between function and size (Semaw 2000; Marchant and McGrew 2005; Carvalho et al. 2008); (4) Typological and technological diversity between assemblages from contemporary sites, thus multi-diversity and multiregional focus of the emergence of culture (Delagnes and Roche 2005; Carvalho et al. 2008); (5) Flexible and adaptive strategies of resource exploitation (Kimura 1999; Carvalho et al. 2008).

We suggest that the repeated combination and use of the same elements to process the same type of food items may combine to amplify specific use-wear traces (such as pitting and bruising marks) and should increase the possibility of fracturing the stones and detaching positives. Following this perspective, three points should be added to the innovative approach on percussive technology that analysed the capacities needed for knapping (Marchant and McGrew 2005): (1) the capacity for combining elements, which demands a complex cognitive capacity (Matsuzawa 1996); (2) the capacity to anticipate tasks (Stokes and Byrne 2001); and (3) the capacity to recognise tool function-effectiveness and elements that depend on each other in order to function.

In addition, the recent re-classification of several Oldowan pieces previously categorised as subspheroids or spheroids (Leakey 1971) as objects detached by battering, or of a group of flakes now claimed only to be positives detached from anvils (Mora and de la Torre 2005), hint that Plio-Pleistocene hominins also reused pounding tool-kits that may have yielded the first unintentional flaking episodes. These provocative similarities between chimpanzee and hominin pounding stone-tools suggest the possibility of a phase of technology prior to the Oldowan that calls for further investigation.

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