

Archaeology of the Perishable

Ecological Constraints and Cultural Variants in Chimpanzee Termite Fishing

Alejandra Pascual-Garrido and Katarina Almeida-Warren

Selection and transport of materials for tools is ubiquitous throughout our species' evolutionary history. Yet our understanding of early human material culture is heavily skewed toward lithic technology. This poses challenges when reconstructing our technical origins, as organic raw materials, especially plants, likely played a significant role despite their absence from the record until 300 kya. Studies of plant-tool use by living apes can serve as a proxy to reconstruct such aspects of human behavior. Employing archaeological methods, we investigated raw material procurement for termite-fishing tools by three chimpanzee (*Pan troglodytes schweinfurthii*) populations in Tanzania: Gombe, Issa, and Mahale. All communities exploited plant sources from the immediate vicinity of termite mounds, as well as farther away, and reused them. However, at Issa, more parts were sourced per plant, with the number of removals decreasing as distance from the mound increased. These disparities are likely caused by environmental differences. Issa apes might try to minimize transport costs in what is a comparably more open and drier habitat with fewer suitable sources available near mounds. Despite similar raw material types being available, Issa and Mahale chimpanzees exclusively used bark for tool manufacture, while at Gombe, various materials were employed; these differences may reflect cultural variants. Our study highlights how environmental and cultural factors shape chimpanzee technology and identifies similarities to raw material selection processes inferred for Oldowan tool users. The archaeology of the perishable, even if at its infancy, is providing a new framework for reconstructing archaeologically invisible aspects of early human behavior and our own technological origins.

Online enhancements: supplemental tables.

The selection of raw materials for tool manufacture is ubiquitous throughout our evolutionary history stretching back to the earliest stages of stone technology (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2012). This included the use of flexible procurement strategies involving the targeting of locally available material to keep the energy costs low (Kimura 1999) but that may also have encompassed extensive energy investment in long-distance transport as a result of selective raw material sourcing (Braun et al. 2008). Such strategies are considered key aspects of Plio-Pleistocene hominin adaptations and reflect awareness of technically desirable material, bipedal carrying abilities, and the technocultural traditions of the tool users (Kimura 1999; Schick 1987; Stout et al. 2005, 2010). Furthermore, their long-distance raw material transport indicates foresight, planning, and other cognitive abilities unseen in any technological nonhuman primate (Delagnes and Roche 2005; de la Torre et al. 2003; Schick 1987; Shea 2016; Stout et al. 2010). Yet it is possible that some of the characteristics attributed to the Oldowan were in place long before. All modern nonindustrialized human societies as well as non-

human primate species use plant materials for implements far more often than bones or stone (Carvalho and Almeida-Warren 2019; González-Ruibal, Hernando, and Politis 2011; Hoffecker and Hoffecker 2018). Thus, while plant-based artifacts are completely absent from the early archaeological record until 300 kya (Conard et al. 2015; Richter and Krbetschek 2015; Thieme 1997), it is unlikely that our early ancestors overlooked the potential value of this material as a tool (Conard et al. 2015; Dominguez-Rodrigo et al. 2001; Wynn and McGrew 1989). This suggests that current archaeological data are missing a substantial component of ancient technology (Panger et al. 2002).

The emerging discipline of primate archaeology compares material records across monkeys and apes and is enriching our understanding of human evolution (Carvalho and Almeida-Warren 2019; Carvalho and Beardmore-Herd 2019; Haslam et al. 2009, 2017; McGrew et al. 2019). For example, we now know that stone tool use and transport by monkeys and chimpanzees generate landscape patterns of raw material acquisition and artifact deposition similar to inferred (archaeologically invisible)

Alejandra Pascual-Garrido is a Postdoctoral Fellow in the Primate Models for Behavioural Evolution Lab of the School of Anthropology and Museum Ethnography of the University of Oxford (Oxford OX2 6PN, United Kingdom [alejandra.pascual-garrido@anthro.ox.ac.uk]). **Katarina Almeida-Warren** is a Doctoral Student in the Primate Models for Behavioural Evolution Lab of the School of Anthropology and Museum Ethnography of the University of Oxford (Oxford OX2 6PN, United Kingdom) and the Interdisciplinary Center for Archaeology and Evolution of Human Behaviour of the Universidade do Algarve (Faro, Portugal). This paper was submitted 14 I 19, accepted 10 II 20, and electronically published 30 IV 21.

aspects of early human behavior (Boesch and Boesch 1984; Carvalho et al. 2008; Luncz et al. 2016; McGrew et al. 2019; Mercader, Panger, and Boesch 2002; Mercader et al. 2007; Proffitt et al. 2016), including affinities to the Oldowan (Carvalho et al. 2008; McGrew et al. 2019; Toth and Schick 2009). Furthermore, as described for Oldowan technological behaviors (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2012; Kimura 1999; Stout et al. 2005, 2010), those of nonhuman primates are influenced not only by the local environment but also by their technocultural traditions (Carvalho et al. 2008; Koops, McGrew, and Matsuzawa 2013; Luncz, Mundry, and Boesch 2012; Luncz, Wittig, and Boesch 2015; Luncz et al. 2016; McGrew et al. 2019; van Schaik et al. 2003).

But, perhaps as expected, primate archaeology has largely focused on lithic technology, even when plant-based technology is the most common and arguably the most diverse and complex form of primate tool use, as well as the only form involving manufacture (Whiten et al. 1999; Wynn et al. 2011). The opportunity to focus on ephemeral records remains another important asset of studying primate technology, providing a unique framework for reconstructing invisible aspects of hominin behavior (Hernandez-Aguilar 2009; Hernandez-Aguilar, Moore, and Pickering 2007; Hicks et al. 2019; McBeath and McGrew 1982; Sanz et al. 2014; Sept 1992; Stewart, Piel, and McGrew 2011). These studies hold the key for obtaining a comprehensive understanding of primate technology as a whole (Carvalho and Almeida-Warren 2019).

Studies of chimpanzees (*Pan troglodytes*), with whom humans shared a last common ancestor 8–7 mya (Langergraber et al. 2012), are particularly promising. Their prolific use and manufacture of various types of tools (McGrew 1992; Whiten et al. 1999) make chimpanzees key living models for understanding the emergence of technology in our own lineage (Carvalho and Beardmore-Herd 2019; McGrew 1992, 2004; Rolian and Carvalho 2017; Teleki 1974; Toth and Schick 2009; Wynn and McGrew 1989; Wynn et al. 2011).

The first scientifically described mode of chimpanzee tool use was “termite fishing,” a skillful technique that makes use of slim and pliable plant probes to extract the nutritious insects from their mounds (Goodall 1964). This technology has gained considerable attention from the paleoanthropology community (Lesnik 2011, 2014) since Backwell and d’Errico (2001) published their paper suggesting the use of bone tools for termite foraging by *Paranthropus (Australopithecus) robustus*, followed by the discovery of 3.7-myia *Macrotermes* termite mounds at Laetoli in Tanzania (Darlington 2005), roughly synchronous in time and space with *Australopithecus afarensis* (Leakey and Hay 1979; Leakey et al. 1976). That the consumption of termites by chimpanzees and present-day modern humans is a well-documented phenomenon poses the hypothesis that early humans also made use of this resource (Lesnik 2014; Nonaka 1996; O’Malley and McGrew 2014).

The manufacture of termite-fishing tools by wild chimpanzees includes the use of a variety of plant parts and materials, such as bark, grass, leaves, twigs, vines, petioles, and palm fronds

(Fay and Carroll 1994; McGrew and Collins 1985; McGrew, Tutin, and Baldwin 1979; Sanz, Morgan, and Gulick 2004). Materials are usually obtained from near the termite mounds but also from farther away when they are locally unavailable. Distances of transport vary between a few meters and more than a kilometer (McGrew, Tutin, and Baldwin 1979; Sanz, Morgan, and Gulick 2004; Teleki 1974), and recovered assemblages indicate a preference for the materials and plant species employed (Bermejo and Illera 1999; Fay and Carroll 1994; Sanz, Morgan, and Gulick 2004; Sanz et al. 2014; Stewart and Piel 2014). However, without a detailed record of the raw material available, it is difficult to assert through artifacts alone whether plant species or materials were used (and thus selected) because of their physical characteristics or were simply used because they were more abundant in the environment (McBeath and McGrew 1982). Recent research has made a start in this respect, providing unequivocal evidence of tool material transport and selection for termite-fishing tools, including cultural preferences for material types used across groups (Almeida-Warren et al. 2017; Pascual-Garrido 2018, 2019; Sanz and Morgan 2007; Sanz, Morgan, and Gulick 2004). However, while a combination of ecological and social factors is known to shape primate material culture (Carvalho et al. 2008; Gruber et al. 2012; Hobaiter et al. 2014; Humle, Snowdon, and Matsuzawa 2009; Koops, Visalberghi, and van Schaik 2014; McGrew et al. 2019; Nishie 2011; Sanz and Morgan 2013; Schuppli and van Schaik 2019), including that of hominins (Andrefsky 1994; Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2012; Harmand 2009; Kimura 1999; Stout et al. 2005, 2010, 2019), the extent to which these factors dictate raw material use for termite-fishing tools by our closest living relatives still remains largely unexplored (Almeida-Warren et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982; Musgrave et al. 2016, 2020; Sanz and Morgan 2007; Sanz et al. 2014).

Chimpanzee termite fishing offers a unique opportunity to investigate raw material procurement for tools: First, unlike the nomadic characteristic of other social insects habitually harvested with implements by these apes (Pascual-Garrido et al. 2013), *Macrotermes* termites reside in the same conspicuous mounds for decades (Sanz and Morgan 2013) and possibly for much longer (Darlington 2005). This allows not only the easy recovery of artifacts at their place of discard (termite mounds; Jones and Sabater Pi 1969; McGrew and Collins 1985; Suzuki 1966) but also the systematic study of raw material availability and use near tool use sites (Almeida-Warren et al. 2017; McBeath and McGrew 1982; Pascual-Garrido 2019).

With the aim of more precisely defining the determinants that may influence raw material use for termite-fishing tools by wild chimpanzees (McBeath and McGrew 1982; Sanz et al. 2014), we extended our study conducted at the Issa Valley and compared it (Almeida-Warren et al. 2017) with two other genetically related termite-fishing communities living in different habitats in western Tanzania: Gombe and Mahale (Inoue et al. 2013; Piel et al. 2013). Previous studies indicate differences in

raw material use and transport among these sites (Almeida-Warren et al. 2017; Pascual-Garrido 2018). In this ethoarchaeological study, we evaluate the influence of environmental and cultural factors on raw material procurement for termite-fishing tools by chimpanzees by addressing the following questions: How are chimpanzees using sources of raw material for the manufacture of termite-fishing tools? Are sources used once or multiple times? How does this compare with the general abundance of the source species and its location (distance) in relation to the targeted mound?

Given that raw material availability and type, distance from the source, and cultural processes influence stone technology in chimpanzees (Carvalho et al. 2008; Luncz, Mundry, and Boesch 2012; Luncz, Wittig, and Boesch 2015; Luncz et al. 2016) and early humans (Andrefsky 1994; Braun et al. 2008, 2009; Kimura 1999; Stout et al. 2005, 2010), we expect these variables to also be determinants of chimpanzee termite-fishing technology. We also discuss implications for our understanding of the origins of human technology.

Background

Our study took place in three populations of *Pan troglodytes schweinfurthii* living in different habitats in western Tanzania (fig. 1). Study sites include (1) Gombe Stream National Park (S 4.67, E 29.65; 772–1,500 m in altitude), set on the eastern shore of Lake Tanganyika (fig. 1). The 35-km² national park is characterized by thicket woodland and vine tangle inter-

spersed with small patches of open woodland and deep valleys falling from the rift escarpment to the lake. A wet season (November–April) is followed by a dry one (May–October), with an average annual rainfall of 1,495 mm (Collins and McGrew 1988). (2) Issa Valley (S 5.50, E 30.56; 900–1,800 m in altitude) is one of the driest, most open, and most seasonal habitats where chimpanzees reside. It is located 81 km inland and east of Lake Tanganyika (fig. 1), and its vegetation is mainly miombo woodland, dominated by *Brachystegia* and *Julbernardia* (Fabaceae) and interspersed with swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest (Hernandez-Aguilar 2009). As in Gombe, a wet season (November–April) is followed by a dry one (May–October), with an average annual rainfall of 1,200 mm (Stewart and Piel 2014). (3) Mahale Mountains National Park (S 6.02, E 29.45; 772–2,462 m in altitude) is located on the eastern shore of Lake Tanganyika (fig. 1). Our study took place in Bilenge (Collins and McGrew 1987), located approximately 9 km to the north of the long-term Japanese research camp (Nakamura et al. 2013; Nishida and Uehara 1980). The terrain is mostly rugged and hilly and is dominated by the Mahale Mountains chain, which runs from the northwest to the southeast across the western part of the park. Bilenge is largely an open grassy forest woodland of *Brachystegia*, with narrow strips of vine tangle and forest along the valley. As at Gombe and Issa, a wet season (November–April) is followed by a dry period (May–October), with an average annual rainfall of 1,400 mm (Collins and McGrew 1988).

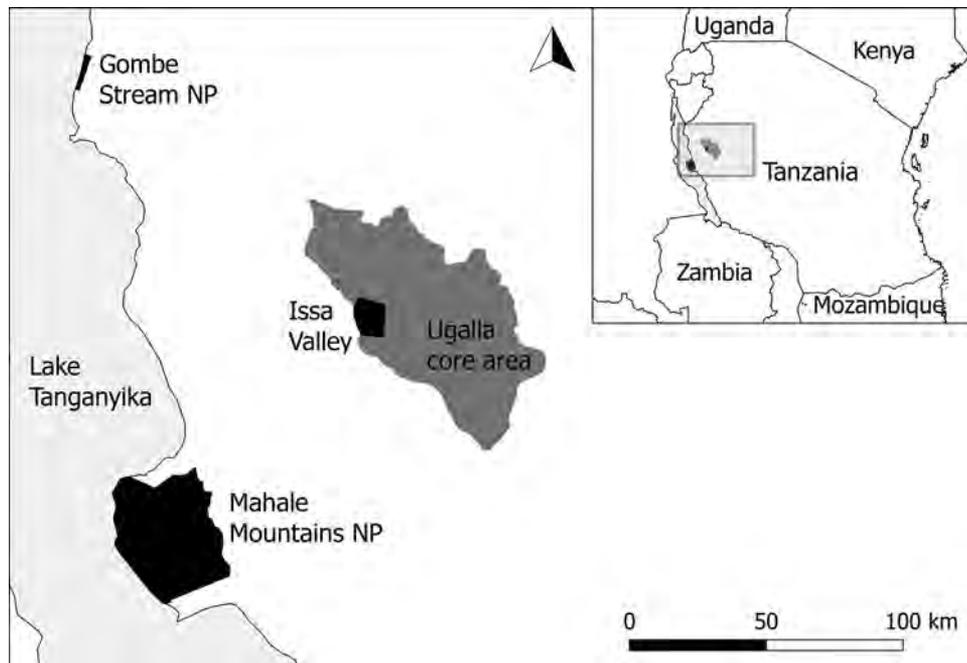


Figure 1. Map of western Tanzania indicating the three study sites. Map credit: Katarina Almeida-Warren. NP = National Park.

Study Communities

Study communities included the habituated community of Kasekela of Gombe Stream National Park (Goodall 1986), the partly habituated community of the Issa Valley (Stewart and Piel 2014), and the unhabituated Bilenge group of the Mahale Mountains National Park (McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982). While these three populations are currently, but possibly not entirely, isolated from each other because of habitat fragmentation, genetic evidence suggests a history of gene flow between the Issa and Mahale populations and possibly also with Gombe (Inoue et al. 2013; Piel et al. 2013).

Chimpanzees at the three sites habitually termite fish at *Macrotermes* mounds. While apes at Gombe and Mahale are known to employ a wide variety of materials obtained from different plant species to manufacture their implements (McGrew 1992; McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982), Issa chimpanzees specialize only in bark (Stewart and Piel 2014). Chimpanzees at Gombe termite fish year-round, though efforts are most frequent at the start of the rainy season from October to December (Goodall 1986). At Issa and Mahale, termite fishing is limited to the rainy months, with the most productive period being at the onset of the first rains (October–November; McGrew and Collins 1985; Stewart and Piel 2014; Uehara 1982). While direct observation of the behavior was possible only at Gombe (Lonsdorf 2005), at all study sites, research focused on the recovery of artifacts and other remnants left by chimpanzees as a result of their termite-fishing activities. This ensured a better standardization of the data collected and an unbiased cross-site comparison.

Methods

Data Collection

Data were collected by Alejandra Pascual-Garrido and Katarina Almeida-Warren, assisted by experienced Tanzanian research assistants, over 285 days from 2014 to 2016. This included a total of 117 days at Gombe (Pascual-Garrido: October 12–November 12, 2014; November 14–December 14, 2015; October 13–November 12, 2016; Almeida-Warren: April 16–May 12, 2015), 53 days at Mahale (Pascual-Garrido: November 25–December 14, 2014; October 20–November 8, 2015; November 21–December 8, 2016), and 115 days at Issa (Pascual-Garrido: January 9–February 9, 2015; Almeida-Warren: May 17–June 27, 2015; November 2–December 15, 2015).

Research focused on 29 *Macrotermes* termite mounds that had been targeted by chimpanzees for termite fishing: 7 at Gombe, 8 at Issa, and 14 at Mahale. Because of time constraints and the need to collect sufficient data for each mound, chosen mounds constitute a subset of mounds at which termite fishing occurred. A mound was considered to have been targeted if one or more of the following criteria applied: (1) apes were seen fishing, (2) artifacts, fragments, debris, or raw materials modified as a result of the manufacture process were present, and (3) plants from

which raw material was sourced were detected (source plants; Almeida-Warren et al. 2017; Pascual-Garrido 2018). At each of these mounds, a site datum was assigned to a nail placed on a tree near the center of the mound to allow measurements in a standardized coordinate system, to map the relative positions of sources, and to measure their distances to the targeted mound (Almeida-Warren et al. 2017; Carvalho et al. 2008). Mounds were visited every one to three days so that abandoned artifacts and sources could be recorded.

Raw Material Availability

The availability of raw material for termite-fishing tools (i.e., living plants) was recorded for each targeted mound once ($n = 29$). Employing cardinal orientations (north-south, east-west), we divided the mound vicinity into four quadrants and arbitrarily selected the northwest 90° quadrant of a 5-m circle around the mound for scrutiny (Almeida-Warren et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982). For each surveyed quadrant, we counted the number of plants suitable for tool making by species and material class (bark, twig, vine, grass). Material types were determined on the basis of previous research (McGrew and Collins 1985; McGrew, Tutin, and Baldwin 1979; Stewart and Piel 2014). Suitable sources were defined as plants that could provide long, thin, flexible pieces from which a functional termite-fishing implement could be made (Almeida-Warren et al. 2017).

Source Plants

Previous research at these sites indicates that chimpanzees obtain their tool material from plants close to targeted termite mounds but also from meters away (Almeida-Warren et al. 2017; Pascual-Garrido 2018). Thus, we surveyed for vegetation that chimpanzees had used for tool making (source plants) within a 20-m radius of the mound. Some materials may have occasionally been obtained from farther away (Pascual-Garrido 2018), but implementing a standardized search field allowed cross-site comparison and ensured data collection within a limited time frame.

We followed the criteria established by Pascual-Garrido (2018) for the identification of sources discernible by the following: (1) one or multiple removals (scars) were present as a result of apes removing material, (2) scars were located in specific parts of the specimen, (3) only a selected number of species showed signs of being sourced, (4) they were normally concentrated within the mound periphery, (5) they included species represented in the tool assemblage, and (6) chimpanzees were directly observed detaching the material. For each source identified, we recorded the distance from the targeted mound, the species, the type of material procured (i.e., twigs, bark), and the number of scars—the latter as an indicator of the intensity of use. Each source was marked and assigned a number to avoid recording it twice during repeated visits to the mounds. Samples from all plants recorded were collected and

curated in camp with a dryer for future identification by Frank Mbagi, Department of Botany, University of Dar es Salaam, Tanzania.

Statistical Analyses

Given that all data in this study had a nonnormal distribution ($P < .05$), nonparametric statistics were implemented. To investigate potential differences among materials used, their availability, and the differences between them (i.e., raw material classes, species) both within and between sites, we conducted tests for the equality of proportions using the `prop.test` function in R with Yates's continuity correction. To test whether pairs of proportions were different within and between sites, we calculated individual P values of paired groups via pairwise post hoc proportion tests with the "Bonferroni" adjustment method. Kruskal-Wallis tests were employed as a nonparametric version of one-way analysis of variance (ANOVA) to compare continuous variables (i.e., number of scars per individual source) between sites. To assess differences between pairs of sites, we employed post hoc pairwise Wilcoxon rank sum tests. To examine whether the distance of a source from the targeted mound and relative species abundance in the vicinity of the mound influenced the number of times a plant was procured and whether there were site-specific differences, we applied generalized linear mixed models (GLMMs; Zuur et al. 2009) with the number of parts removed per individual plant (scars) as the response variable. As predictor variables with fixed effects, we included the site, the distance from the source to target mound, and mound-specific sourced species abundance relative to known sourced species, as well as their possible interactions (three-way and two-way). To control for possible between-mound variation, we included mound ID as a random effect. Additionally, before fitting the model, we z transformed the distance from the mound (mean = 6.57 m, SD = 5.42) and species abundance (mean = 0.40, SD = 0.32). Because the response variable was zero-truncated (minimum value = 1) and there was evidence of moderate overdispersion (dispersion ratio = 3.2, $P < .01$), we applied a zero-truncated Poisson-lognormal model with the addition of plant ID as an observation-level random effect (Harrison 2014). This was achieved using the `glmmTMB` (ver. 0.2.3) package in R. To test whether the predictors had a collective effect on the number of removals, we first conducted full null model comparison using a likelihood ratio test (R function `ANOVA`); the null model excluded all fixed effects but was otherwise identical to the full model (Dobson 2002; Schielzeth and Forstmeier 2009). We tested the significance of three-way and two-way interactions by systematically dropping them from the model one at a time and comparing the resulting reduced models with the respective full model using the `drop1` function in R. Individual effects' P values were based on the likelihood ratio test results from the `drop1` function (Dobson 2002). Collinearity between predictor variables, calculated by applying the `vif` function of the R package `car` (Fox and Weisberg 2011) to a linear model lacking

the random effects and interactions, was not an issue (maximum variance inflation factor = 1.36). All analyses were performed in R (R Core Team 2017). All tests were two-tailed, and the level of significance for all statistical analyses was set at $P < .05$.

Ethical Note

No data were collected from chimpanzee individuals for the purpose of this study. Data were recorded when chimpanzees were absent from the study mounds, with no direct contact with any of the individuals. Research was conducted under the permits of Tanzania National Parks (TANAPA), Tanzania Wildlife Research Institute (TAWIRI), and Tanzania Commission for Science and Technology (COSTECH).

Results

Chimpanzees at Gombe, Issa, and Mahale behaved similarly in that they sourced raw material from the immediate vicinity of termite mounds and also from farther away, selected materials and plant species to make their implements (Pascual-Garrido 2018), and reused sources (fig. 2). However, chimpanzees in Issa exploited sources more intensively (i.e., more plant parts were extracted per individual), possibly to save transport distance costs in what is a comparably more open and drier habitat with less available raw material nearby. Despite similar raw material types available at all sites, Issa and Mahale chimpanzees exclusively used bark for tool manufacture, while at Gombe, various materials were employed—differences that potentially reflect cultural variants (i.e., behaviors present in at least one site and absent elsewhere without clear ecological differences; van Schaik et al. 2003; Whiten et al. 1999, 2001).

Abundance of Raw Material versus Use

Regarding the abundance of suitable sources per mound (plants that could provide at least one type of raw material), Gombe had the highest, followed by Mahale and Issa (table 1). At all sites, there was a significant difference between the proportion of raw material classes available near mounds, with twigs being the most abundant, followed by bark. Grass was rare at all sites, while vines were present only at Gombe (table 1). Differences were maintained when pairs of material types for each site were compared, except between vines and grasses at Issa, where they were equally rare (table A1; tables A1–A5, B1, C1, C2 are available online). There were also significant differences between sites regarding abundance by material type (table A2). These differences were maintained when pairs of sites were compared, except between Issa and Mahale, where grasses and vines were equally available or absent, respectively (table A3).

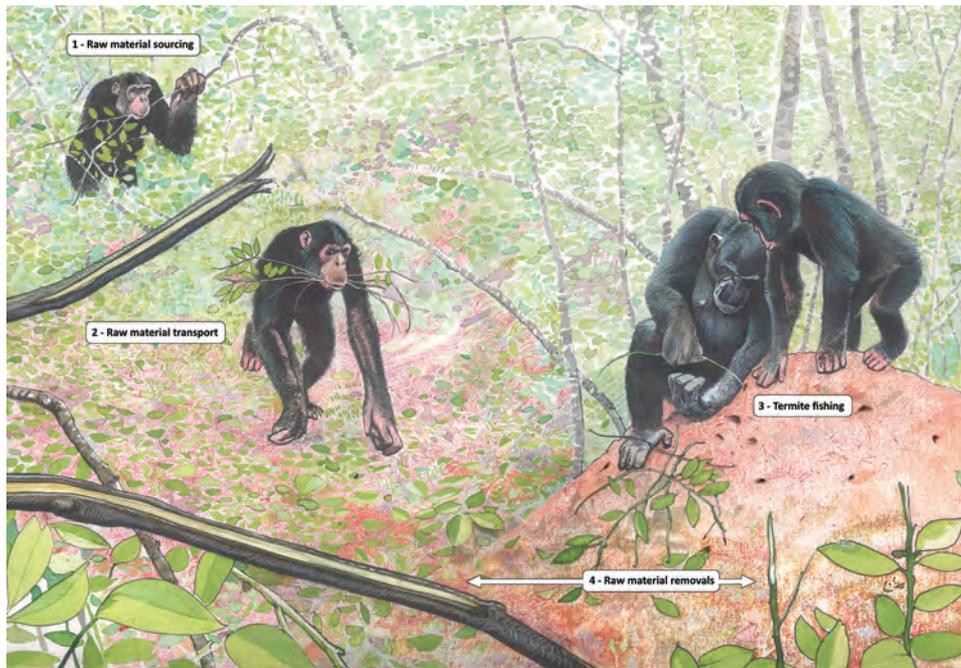


Figure 2. Raw material sourcing for termite-fishing tools by wild chimpanzees. 1, Tool material sourcing from the source plant. 2, Raw material transport to the tool use site (termite mound). 3, Tool manufacture and use. 4, Physical traces left on source plants as a result of chimpanzee tool material removal (*left*: bark removal; *right*: twig removal).

However, despite the availability of various materials at all sites, only Gombe chimpanzees procured different materials to make their implements (table 2). While Gombe chimpanzees used twig (44.0%) and bark (48.7%) in almost equal proportions, they manufactured only a small percentage of their utensils from vine (6.1%), while grass was used only rarely (1.2%). Only artifacts made from bark were recovered at Issa and Mahale (Pascual-Garrido 2018).

Suitable versus Sourced Plants

To test for species selection, we compared the proportion of plants from suitable versus sourced species. Results showed that chimpanzees at Gombe used 85.3% of the total suitable species available, while at Issa and Mahale, chimpanzees exploited only 12% (table A4). Pairwise tests between sites revealed significant differences in the proportion of plants of known source species used between Gombe and all sites ($P < .001$). This indicates that chimpanzees at Mahale and Issa were more selective regarding their tool species. There was no sig-

nificant difference in proportions between Mahale and Issa ($P = 1$; table A5).

Source Taxa

Species exploited for implements during this study included a total of 31 species from 15 families, with six species yielding more than one tool material type. Annonaceae and Tiliaceae were the most prevalent families, the latter represented exclusively by one genus: *Grewia* (table 3, adapted from Pascual-Garrido 2018). To test whether chimpanzees preferred some species over others, we compared for each source species the number of individuals exploited relative to their general abundance within the source species near mounds. Results showed that at Gombe, *Monanthonotaxis poggei*, *Grewia* spp., and *Uvaria angolensis* were preferentially used (table B1; fig. 3), while at Issa and Mahale, source species were selected equally (except for *Azanza garckeana* at Issa). Interestingly, *Dicyophlena lucida* at Gombe and *A. garckeana* at Issa revealed a significant but inverse difference, with more individuals available than sourced, suggesting that these species, even if exploited for tool manufacture, were not preferred.

Table 1. Abundance of raw material types for each site

Site	Total	Mean per mound	Bark	Twig	Vine	Grass	χ^2	P
Gombe	457	65.3	.486	.871	.013	.116	892.925	<.001
Issa	264	33	.182	.936	0	.023	756.47	<.001
Mahale	639	45.6	.801	.983	0	.017	2,057.557	<.001

Note. The total was calculated based on the plants that could provide suitable raw material. The χ^2 and P values are a result of an equality of proportions test between raw material types for each site total.

Table 2. Proportion of raw material types available versus proportion of tool materials

Site, type	Raw material	Tools	χ^2	<i>P</i>
Gombe:				
Bark	.486	.487	0	1
Grass	.116	.012	35.75	<.001
Twig	.871	.44	178.644	<.001
Vine	.013	.061	12.944	<.001
Total (<i>n</i>)	457	411		
Issa:				
Bark	.182	1	242.873	<.001
Grass	.023	0	1.863	172
Twig	.936	0	333.13	<.001
Vine	0	0		
Total (<i>n</i>)	264	140		
Mahale:				
Bark	.801	1	4.926	.026
Grass	.017	0	0	1
Twig	.983	0	434.21	<.001
Vine	0	0		
Total (<i>n</i>)	639	25		

Note. Raw material was calculated based on the number of plants that could provide suitable raw material. Adapted from Pascual-Garrido (2018).

Reuse of Source Plants

The number of scars left as a result of chimpanzees removing tool material from an individual plant (Pascual-Garrido 2018) can function as a proxy for determining sourcing intensity (i.e., how often a plant is procured; fig. 4). At all sites, chimpanzees exploited sources once and multiple times; however, the intensity of use differed among sites.

At Gombe, chimpanzees sourced individual plants once (56.4%) and multiple times (43.6%) in almost equal proportions ($\chi^2: \chi^2 = 2.3143, df = 1, P = .128, n = 140$). At Mahale, plants were mostly procured once (73.3%; $\chi^2 = 9.8, df = 1, P < .05, n = 45$), while at Issa, more than half (63.1%) of all recorded sources were used multiple times ($\chi^2 = 8.3934, df = 1, P < .05, n = 122$). Likewise, the average number of parts removed per plant differed significantly among sites (Kruskal-Wallis: $\chi^2 = 25.328, df = 2, P < .001$). The post hoc pairwise Wilcoxon rank sum test revealed that this difference was maintained among all sites (table A6). While Gombe chimpanzees removed, on average, 2.4 parts per individual plant (range = 1–22, SD = 2.85, *n* = 140), Mahale chimpanzees detached on average 1.3 parts (range = 1–3, SD = 0.55, *n* = 44), and at Issa, individual sources had the largest number of removals, with an average of 3.2 parts detached (range = 1–23, SD = 3.6, *n* = 122).

Use of Source Plants: Effects of Distance from Mound and Species Abundance on Number of Removals

If the number of removals per individual plant decreases the farther it is located from the targeted mound, it seems likely that a transport distance cost-benefit effect is at play, with apes

reducing the costs of transport by preferentially exploiting sources closer to the mound rather than turning to those located farther away.

Overall, distance from the mound, species abundance, and study site influenced the number of removals (GLMM, full null model comparison: $\chi^2 = 90.03, df = 11, P < .001$). In the full model, the three-way interaction among site, distance

Table 3. Families and species of plants sourced for tool material types at Gombe, Issa, and Mahale

Family, species	Gombe	Issa	Mahale
Annonaceae:			
<i>Artabotrys collinus</i>		B	
<i>Artabotrys monteiroae</i>		B	
<i>Annona senegalensis</i>	B	B	
<i>Monanthes buchananii</i>		B	B
<i>Monanthes poggei</i>	B, T		
<i>Uvaria angolensis</i>	B, T	B	B
<i>Uvaria</i> sp. A of FTEA		B	B
<i>Uvaria welwetschii</i>		B	
Apocynaceae:			
<i>Dicyophlena lucida</i>	B, T		
<i>Diplorhynchus condylocarpon</i>	B, T		
<i>Saba comorensis</i>	B	B	B
Asclepiadaceae:			
<i>Gymnema sylvestre</i>	T		
Capparidaceae:			
<i>Maerua holstii</i>			B
Combretaceae:			
<i>Combretum zeyheri</i>	T		
Connaraceae:			
<i>Byrsocarpus orientalis</i>	T		
Euphorbiaceae:			
<i>Cleistanthus polystachyus</i>		B	
Gramineae:			
Grass	G		
Guttiferae:			
<i>Garcinia buchananii</i>			B
Malvaceae:			
<i>Azanza garckeana</i>		B	
Rubiaceae:			
<i>Rothmannia urcelliformis</i>		B	
<i>Sabicea orientalis</i>	V		
Sapindaceae:			
<i>Allophylus congolanus</i>	B, T		B
<i>Paullinia pinnata</i>			B
Sapotaceae:			
<i>Mimusops kummel</i>			B
Sterculiaceae:			
<i>Dombeya burgessiae</i>		B	
Tiliaceae:			
<i>Grewia</i> sp.		B	
<i>G. forbesii</i>	B, T		
<i>G. platyclada</i>	B		
<i>G. mollis</i>	B		
<i>G. rugosifolia</i>		B	
<i>G. stolzii</i>			B

Note. Adapted from Pascual-Garrido (2018). B = bark; FTEA = Flora of Tropical East Africa; G = grass; T = twig; V = vine.

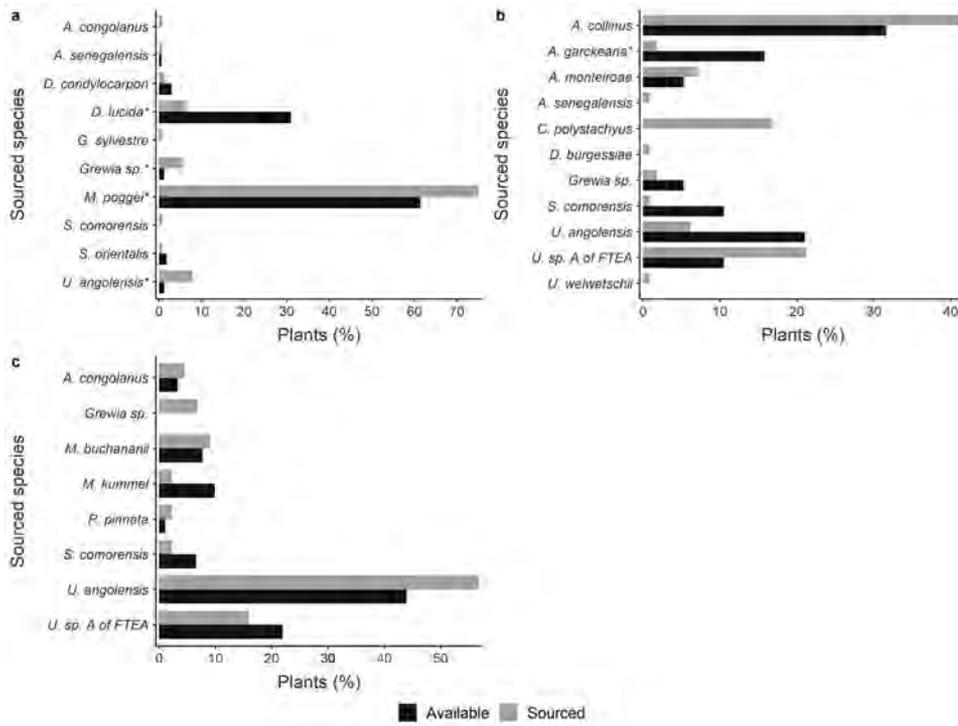


Figure 3. Percentage of plants sourced for tools by species (sourced; gray) compared with the species' general availability among exploited species (available; black). *a*, Gombe. *b*, Issa. *c*, Mahale. An asterisk indicates a significant difference between proportions where $P < .05$. Plants of the genus *Grewia* were combined into a *Grewia sp.* taxon, as it was not always possible to identify individual species.

from the mound, and species abundance appeared nonsignificant ($P = .208$; table C1), as did the two-way interaction between distance from the mound and species abundance ($P = .207$; table C2).

After the nonsignificant interactions were removed, the resulting reduced model revealed that the influence of distance from the mound and species abundance on the number of removals differed among the three study sites (table 4; fig. 5).



Figure 4. Examples of source plant locations at Issa where chimpanzees removed tool material, indicated by arrows (*a*, *b*) or orange tape (*c*). Photo credit: Katarina Almeida-Warren.

Distance from the mound has a clear negative effect on the number of removals at Issa, while at Gombe and Mahale, this effect shows positive and neutral trends, respectively. Conversely, species abundance has a clear negative effect on the number of removals at Gombe, while there is no evident trend for Issa or Mahale.

Discussion

The breadth and diversity of insectivory by modern nonindustrialized human societies (Allsop and Miller 1996; Berbesque and Marlowe 2009) and wild ape populations (Bogart and Pruett 2011; Deblauwe 2009; Hicks et al. 2019; Schöning et al. 2008) make it likely that early humans were also exploiting this resource (Backwell and d'Errico 2001; Lesnik 2014; O'Malley and McGrew 2014). Given the prevalence of perishable tools to harvest insects among chimpanzees (McGrew 1992), it seems likely that early humans also used similar technologies (McGrew 2014).

Our previous studies indicate differences across study sites in the material selection and transport of termite-fishing tools (Almeida-Warren et al. 2017; Pascual-Garrido 2018). In this study, we evaluate the extent to which raw material availability and thus the local environment dictate these differences. Our results show that chimpanzees living in a drier and more open habitat with less raw material available nearby exploited sources more intensively, with more parts detached per individual plant, and reused them more frequently. Independent of habitat, Issa and Mahale chimpanzees preferred bark to fish termites, while Gombe chimpanzees used various materials. Unless other environmental differences, such as the efficiency of different raw material types, influence this choice, this discrepancy may be socially driven. Our study shows that, as described for early humans (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Harmand 2009) and chim-

panzee stone technology (Carvalho et al. 2008; Luncz et al. 2016), raw material plays a major role in the variation of chimpanzee perishable technology. While part of this variation may be due to differences in the ecological context (i.e., raw material abundance), other aspects, such as material selection, could not be attributed to the same ecological reasons and thus, if socially learned and transmitted repeatedly across generations, as suggested by recent findings from Pascual-Garrido and Scheffrahn (2020), may be termed cultural (Koops, Schuppli, and van Schaik 2018; van Schaik et al. 2003; Whiten et al. 1999, 2001).

Raw Material Use and Selection

We would expect that if chimpanzees show no selectivity for the raw materials they use to manufacture tools, the distribution of artifacts would reflect the distribution of available material types around the mounds. However, when we compared the actual tool assemblage with an expected assemblage based on the percentage of raw material available around mounds, there were consistent differences. At all sites, twigs were the most abundant material, followed by bark and, in a much lower proportion, grass and vine (cf. table 2). Despite this, only Gombe chimpanzees employed different materials for tools, while Issa and Mahale chimpanzees used only bark. If chimpanzee technology were positively correlated to the availability of materials, we would expect chimpanzees at Issa and Mahale to also incorporate other materials and, more importantly, for all three communities to favor twigs. This is clearly not the case.

On the basis of the recovery of chimpanzee assemblages, preferences for materials have been described across sites (cf. Stewart and Piel 2014). In some cases, their use is linked to differences in tool functions (probe vs. puncture; Sanz and Morgan 2007). However, this cannot be applied to our studied communities given the presence of termite-fishing probes alone. While the lack of use of grass and vines at Issa may correspond

Table 4. Results from the final reduced model (generalized linear mixed model; lacking the nonsignificant three-way and two-way interactions) investigating potential predictors influencing number of removals

Term	Estimate	SE	Lower CI	Upper CI	χ^2	df	P^c
Intercept	.258	.244	-.220	.736			NI ^d
SiteIssa ^a	.417	.288	-.148	.982			NI ^d
SiteMahale ^a	-1.208	.435	-2.060	-.356			NI ^d
Distance ^b	.121	.287	-.442	.684			NI ^d
Abundance ^b	-.523	.106	-.732	-.315			NI ^d
SiteIssa × distance	-.740	.295	-1.318	-.162	7.747	2	.021
SiteMahale × distance	-.081	.517	-1.093	.932			
SiteIssa × abundance	.565	.129	.313	.817	2.538	2	<.001
SiteMahale × abundance	.636	.439	-.223	1.496			

Note. CI = confidence interval.

^a Site was dummy coded, with Gombe as the reference category.

^b Variables were z transformed to a mean of 0 and SD of 1.

^c Results from the likelihood ratio test using the drop1 function.

^d Not indicated (NI) because it has a limited interpretation.

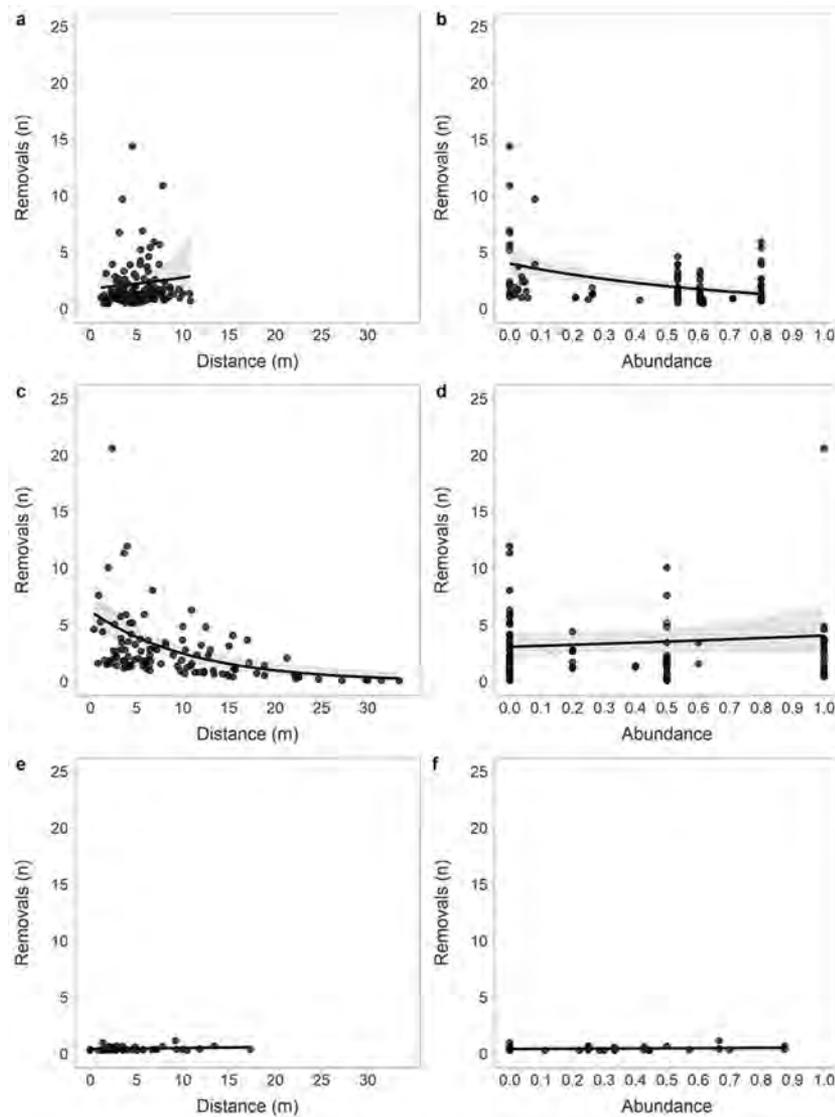


Figure 5. Comparison of the number of removals per sourced plant by study site in response to the distance from the mound (*a, c, e*) and species abundance (*b, d, f*). *a, b*, Gombe. *c, d*, Issa. *e, f*, Mahale. The circles represent individual sourced plants recorded at each study site (Gombe: $n = 141$; Issa: $n = 113$; Mahale: $n = 44$). The fitted generalized linear mixed model and confidence intervals are depicted by the line and the gray area, respectively.

to a lower abundance or absence of these materials at mounds, the absence of twigs cannot be explained by the same ecological reasons. That post hoc experiments with twigs showed that this material was also suitable for termite fishing (Almeida-Warren et al. 2017) further supports the lack of an environmental explanation for the absence of twigs in the Issa community. Lack of knowledge or familiarity is also falsified as a possible explanation given the use of other materials by these apes to access underground tubers and fish for *Camponotus* ants (Hernandez-Aguilar, Moore, and Pickering 2007; Wondra et al. 2016). Unless other environmental factors dictate the exclusive employment of bark by Issa chimpanzees (i.e., tool material efficiency, prey behavior), social learning, which plays a fundamental role in the acquisition of termite-fishing skills and is key for the development and maintenance of cultural

behaviors and traditions, particularly from mother (and older siblings) to offspring (Koops, Schuppli, and van Schaik 2018; Lonsdorf 2005, 2006; Lonsdorf, Eberly, and Pusey 2004; Musgrave et al. 2016, 2020; Sanz and Morgan 2013; Sanz et al. 2014; Schuppli and van Schaik 2019), may be responsible for this “specialty.”

At Mahale, while bark was also predominantly employed in the past, other types of materials were also used decades ago (McGrew and Collins 1985; Nishida and Uehara 1980; Uehara 1982). That only bark implements were recovered during this study (Pascual-Garrido 2017) may correspond to our low sample size ($n = 25$) compared with the total number of tools collected by McGrew and Collins (1985; $n = 290$) and Nishida and Uehara (1980; $n = 133$). A larger sample size is necessary to assess whether chimpanzees from Bilenge at Mahale

have become exclusive bark users in recent decades. Historical data from Gombe (McGrew, Tutin, and Baldwin 1979) also corroborate changes in the proportion of the class of material employed. At that time, almost half (48%) of the artifacts were made from grass, while bark (21%), vine (17%) and twigs (10%), and leaves of oil palms (4%) were less represented. This contrasts with the percentages reported in our study (bark, 48.7%; twig, 44.0%; vine, 6.0%; grass, 1.2%). Changes in the raw material available might explain these differences. For example, at Gombe, grass near mounds may have decreased during the past decades after the ending of annual burning, which allowed the natural regeneration of vegetation (Collins and McGrew 1988; Anthony Collins, personal communication). Alternatively, previous studies might have focused on mounds in areas where grass was more abundant (McGrew, Tutin, and Baldwin 1979). However, without a detailed description of the raw material available near mounds at that time, this is simply not possible to test. It could also be that changes in tool materials by Gombe chimpanzees occurred as a result of behavioral shifts toward greater material efficiency, as recently documented for drinking sponges (leaf vs. moss) manufactured by the Sonso community at the Budongo Forest, Uganda (Hobaiter et al. 2014; Lamon et al. 2018). Future field experiments should aim to explore the potential role of efficiency in tool material selection for termite fishing by chimpanzees.

Source Species

Plant species used for termite fishing have been recorded at various sites, including the current ones (Almeida-Warren et al. 2017; Pascual-Garrido 2018). Previous studies indicate a prevalence of plant species in tool assemblages (Bermejo and Illera 1999; Fay and Carroll 1994; McGrew and Collins 1985; McGrew, Pruettz, and Fulton 2005; Sanz and Morgan 2007; Sugiyama 1985; Suzuki, Kuroda, and Nishihara 1995). However, without a detailed record of the raw material available, these studies could not assess species selection empirically. McBeath and McGrew (1982) were the first to address the influence of plant variety on chimpanzee biodegradable technology. These authors found that chimpanzees at Mount Assirik, Senegal, concentrated their termite fishing at mounds close to abundant *Grewia lasciodiscus*, the species most represented in tool assemblages. Likewise, botanical surveys conducted at Goulougo, Republic of Congo (Sanz, Morgan, and Gulick 2004), and at Issa Valley (Almeida-Warren et al. 2017) indicate selection for plant species to make termite-fishing implements. Our study provides further evidence supporting this but also reveals differences across the study communities.

At Gombe, chimpanzees seemed to be more “generalist,” exploiting almost 90% of all suitable species available in the vicinity of mounds—while at Issa and Mahale, apes were more “specialist,” using only 12% of the total suitable species accessible (cf. table A4). These differences may likely correspond to the exclusive use of bark by Issa and Mahale chimpanzees,

further evidenced by the differential sourcing of materials from the same plant species (i.e., *Uvaria angolensis*, *Grewia* spp., and *Allophylus congolanus*) between the study communities (cf. table 3). Interestingly, *Monanthes poggei*, *U. angolensis*, and *Grewia forbesii*, three species preferentially used by Gombe chimpanzees, also provide termite-fishing material for apes living in West Africa (McBeath and McGrew 1982; McGrew, Pruettz, and Fulton 2005). Perhaps these taxa hold still-unexplored mechanical and physical characteristics that make them ideal for termite fishing.

But what makes a “good” material for termite-fishing tools remains largely unexplored and deserves further investigation. As McGrew, Tutin, and Baldwin (1979) pointed out decades ago, “The nature of the task defines the material to be used” (205). At Goulougo, for example, puncturing sticks are manufactured mostly from branches of *Thomandersia hensii*, a rigid and straight tree, while *Sarcophrynium* spp., a species with sufficiently flexible twigs, is mostly sourced for fishing probes (Sanz and Morgan 2007). The same holds true for chimpanzees at Bai Hokou and the Ndoki Forest, Republic of Congo: tool types are manufactured from plant species that offer specific physical characteristics (Fay and Carroll 1994; Suzuki, Kuroda, and Nishihara 1995). Most of the source species at our studied sites belong to the Annonaceae and Tiliaceae families (Pascual-Garrido 2018). These families may embody physical and mechanical characteristics ideal for termite fishing, although we still do not know what characteristics are being selected by chimpanzees or whether and how the selection criteria are passed on, for example, via tool transfers or peering observation of users (Biro et al. 2003; Musgrave et al. 2016, 2020; Schuppli and van Schaik 2019; Whiten 2019).

Still, within the set of optimal species for tool manufacturing, why should chimpanzees at Gombe use bark and twigs, while those at Issa specialize on bark when twigs are predominant at this site? While still-unexplored local ecological factors may shape preferences for tool material types (e.g., termite nest structure), we suspect that differences in the tool materials used among our study sites are socially influenced and thus reflect socially learned variants (i.e., population-specific socially transmitted behaviors within and across generations; Koops, Schuppli, and van Schaik 2018; Lonsdorf 2006; Musgrave et al. 2020, 2021; Whiten et al. 1999). Cultural differences as a driving factor in primate technology should not be overlooked (Boesch et al. 2020; Koops, Schöning, and Hashimoto 2015; Luncz, Wittig, and Boesch 2015; Möbius et al. 2008; Pascual-Garrido 2019; Schöning et al. 2008; Whiten 2019). In his pioneering studies at Gombe, Teleki (1974) concluded that selection proficiency for tool manufacture is a learned skill. This may be information acquired solely through repetitive individual trial and error but may also be accompanied through social learning via stimulus enhancement, peering behavior, or active facilitation, such as tool transfers (Hobaiter et al. 2014; Lonsdorf 2005; Lonsdorf, Eberly, and Pusey 2004; Musgrave et al. 2016, 2020; Sanz et al. 2014; Sanz and Morgan 2013; Schuppli and van Schaik 2019). Given that material selectivity often improves tool efficiency, it would be

advantageous to retain this information (Lamon et al. 2018; Musgrave et al. 2016, 2020; Sanz et al. 2014).

Reuse of Source Plants: Distance of Transport and Species Abundance

Reuse of stone tools to crack nuts by chimpanzees reduces the energetic costs associated with the procurement and transport of new material (Boesch and Boesch 1984; Carvalho et al. 2008; Luncz et al. 2016). While the lifetime of perishable implements is comparably short, the reuse of organic tools has been documented for types that require specific materials, not always readily available, and several modifications. This is the case for puncturing sticks at the Goualougo Triangle, Republic of Congo, that are cached for later use (Sanz and Morgan 2007). But perhaps because of their more delicate physical characteristics and thus quicker deterioration, carrying and reusing fishing probes by chimpanzees is less frequent and is reduced to only a few hours or, at most, a day (Davidson and McGrew 2005; Sanz and Morgan 2007; Teleki 1974). Likewise, the repetitive use of individual sources might help reduce the time invested in searching for a new source, especially for species that may not be abundant nearby. Such is the case for *Thomandersia* trees, which Goualougo chimpanzees repeatedly exploit for puncturing sticks. This genus of tree, though one of the most common in the study area, is not always located close to the tool use site (Sanz and Morgan 2007). In this study, we provide new evidence that chimpanzees reuse sources of raw material for the manufacture of termite-fishing tools, with differences emerging among sites.

At Issa, not only did the chimpanzees extract, on average, more parts per individual plant, but also the distance from the source to the mound was negatively correlated with the number of parts removed, with fewer parts detached from sources found farther away (cf. table 4; fig. 5). This may reflect a strategy to minimize the costs of transport from source to tool site (Blumenschine et al. 2008; Potts 1994) in an environment where suitable sources are not only less abundant (cf. table A2) but also farther away (Pascual-Garrido 2018). Such a strategy would enable Issa apes to maximize the procurement of tool material with the least investment of energy (Carvalho et al. 2008; Luncz et al. 2016). Abundance did not seem to affect the number of parts removed, perhaps because of the overall rarity of source species in the mound vicinity; Issa chimpanzees target all source species equally.

At Mahale, sources were exploited mostly once, and neither the distance of the source from the targeted mound nor the abundance of the source species seemed to have an effect on the number of parts taken per source. With abundant bark sources available nearby and approximately 80% of the plants around mounds providing suitable bark (cf. table A2), Mahale apes have abundant sources from which to choose, which they do, given that only 12% of all available species are used (cf. table A4). Similar findings have been described among chimpanzees at Mount Assirik, where 90% of all sources were lo-

cated in close proximity to the targeted mounds (McGrew, Tutin, and Baldwin 1979). At Gombe, where raw material was the most abundant among all study sites (cf. table 1), a slightly different picture emerged: even when apes obtained their material from a relatively close distance and at distances similar to those at Mahale (Pascual-Garrido 2018), a species' abundance showed a negative trend relative to the number of times it was sourced. Rare species were procured more often.

Use and reuse of tool materials provide valuable insights into hominoid technological patterns. Boesch and Boesch (1984) proposed that the transport of stone tools to *Panda* nut-cracking sites by chimpanzees living in the Tai Forest, Côte d'Ivoire, follows a least-distance strategy, with hammerstone weights decreasing with increasing distances from the nearest location of tool material sources (Luncz et al. 2016). The optimal use of resources with flexible, dynamic, opportunistic, and low-energy strategies to solve problems, which share affinities to the Oldowan, has also been described for nut-cracking chimpanzees in Bossou, Guinea (Carvalho et al. 2008). While perishable implements do not impose a weight constraint similar to that of stones ("A chimpanzee carrying a 3 kg stone walks on three limbs and carries the stone in one arm" [Boesch and Boesch 1984:164]) and so can be carried in the mouth, the distance traveled from a suitable source to the tool site could still demand extra energetic costs, especially for sources that are rare and at a considerable distance (Sanz and Morgan 2007). That chimpanzees at Gombe, Issa, and Mahale selected and transported different materials for termite-fishing tools and reused sources in ways that seemed to be influenced by the abundance of raw material available suggests that, as described for lithic technology (Carvalho et al. 2008), different resource exploitation strategies might also be at play for organic technology. Further investigations, including individual follows, are necessary to corroborate this.

Conclusion

Besides the human lineage, the selection and transport of materials for tool manufacture has been documented across many species. For example, New Caledonian crows (*Corvus moneduloides*) select and carry materials to fish for larvae at tree holes (Bluff et al. 2010; Klump, Cantat, and Rutz 2019; Rutz et al. 2007); woodpecker finches (*Cactospiza pallida*) employ twigs, cactus spines, or leaf petioles to probe for insects inside tree holes, sometimes carrying the tool from branch to branch (Hundley 1963); and orangutans (*Pongo abelii*) prefer certain lining materials, which they may carry for as far as 50 m from the nest site (leaf carrying), to construct their nests (Russon et al. 2007; van Casteren et al. 2012). This suggests that the selection and transport of materials are vital components of tool use or manufacture. However, what probably sets chimpanzees apart from the rest of the nonhuman tool manufacturers, including other apes, is their prolific and flexible use of materials for a diverse range of implements, more akin to

humans than to any other living nonhuman species (McGrew 1992; McGrew et al. 2019; Rolian and Carvalho 2017).

Stone tool use by Plio-Pleistocene hominins involved selectivity and transport behaviors dependent on the raw material available, with patterns of variation reflecting their cultural diversity (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Kimura 1999; Stout et al. 2005, 2010). In this study, we provide evidence that part of what archaeologists have reconstructed about the behaviors associated with the Oldowan can be accommodated within the perishable technology used by wild chimpanzees and thus likely was present in the last human-chimpanzee common ancestor (McGrew 2010), before the advent of the Oldowan (Carvalho and Beardmore-Herd 2019; Panger et al. 2002). These commonalities include selection and transport behaviors for tool manufacture (Braun et al. 2008, 2009; Goldman-Neuman and Hovers 2009, 2012; Schick 1987), tool-using strategies dependent on the raw material available (Kimura 1999), and technocultural diversity (Stout et al. 2005, 2010). Our studies continue to support Wynn and McGrew's (1989) and Wynn et al.'s (2011) assertions that everything archaeologists have reconstructed about the behavior of the Oldowan can be accommodated within the "ape adaptive grade" (more recently updated to the "simian adaptive grade"; McGrew et al. 2019), except for two specific behavioral patterns that still remain unknown among modern apes, one of which is relevant here: Oldowan hominins carried raw material and implements farther than any living ape, sometimes for up to tens of kilometers, and they competed with large carnivores for animal prey.

Future Directions

Given the predominance of biodegradable material in chimpanzees' (McGrew 1992) and hunter-gatherers' material culture (González-Ruibal, Hernando, and Politis 2011; Hoffeecker and Hoffeecker 2018), the prevalence of C_4 grassland since the late Miocene (Faith, Rowan, and Du 2019), and the possible exploitation of termite mounds early in our own lineage (Backwell and d'Errico 2001), it is likely that early humans also made use of this resource with a much richer and more diverse and varied tool kit (and associated technical behaviors) than is currently visible in the archaeological record (Backwell and d'Errico 2001; Carvalho and Almeida-Warren 2019; Dominguez-Rodrigo et al. 2001; Panger et al. 2002; Toth and Schick 2009). It is largely thought in the paleoanthropology community that the advent of flaked stone tool technology marked a qualitative leap in human evolution (Braun et al. 2019; Shea 2016). However, this and other studies, seeking to understand the Oldowan as being on a continuum of a way of life that might have been in place for millions of years, call for the placement of our early ancestors in their appropriate evolutionary context (Carvalho and Beardmore-Herd 2019; Panger et al. 2002; Wynn 1981; Wynn et al. 2011).

The archaeology of the perishable, even at its infancy, is providing a new framework for reconstructing archaeologi-

cally invisible aspects of early human behavior and our own technological origins (Almeida-Warren et al. 2017; Hernandez-Aguilar 2009; Hicks et al. 2019; Koops, Schöning, and Hashimoto 2015; Pascual-Garrido 2018; Sanz and Morgan 2007; Sept 1992; Stewart, Piel, and McGrew 2011). Future efforts should concentrate on providing information that will help contextualize the current archaeological record and aid investigations into potential, yet currently unknown, hominin sites (Carvalho and Almeida-Warren 2019). Current research in this direction includes mapping chimpanzee tool use sites to enable comparison with early archaeological sites (Almeida-Warren et al. 2018), using long-term records of chimpanzee perishable technology to model ranging patterns in early hominins (Hernandez-Aguilar 2009; Sept 1992; Stewart, Piel, and McGrew 2011), primate archaeological analysis of chimpanzee artifacts to enable comparisons with implements employed for similar purposes in the archaeological record (Backwell and d'Errico 2001; Heaton and Pickering 2006), and the identification of termite evidence at early human sites (Lesnik et al. 2019). The archaeology of the perishable, even within its limitations, may contribute to a comprehensive understanding of primate technology as a whole, including the origins of human technology. This study also emphasizes the importance of continuing to preserve culturally healthy wild chimpanzee populations, maintaining their ability to access the tool materials on which their traditions depend (Brakes et al. 2019).

Acknowledgments

We are grateful for permission to conduct research in Gombe Stream National Park, Mahale Mountains National Park, and Issa Valley by TANAPA, TAWIRI, and COSTECH; field assistance at Issa from Shedrack Lucas, Patrick Hassan, Godfrey Stephano, Mashaka Kalutwa, Busoti Juma, Mlema Juma, Msigwa Rashid, Sebastian Ramirez-Amaya, and Eden Wondra, at Mahale by Shaka and Singa Kabugonga, and at Gombe by Matendo Msafiri Katoto and Nasibu Zuberi Madumbi; logistical support from the Jane Goodall Institute, Greater Mahale Ecosystem Research and Conservation Project, and Mahale Mountains Chimpanzee Research Project; and plant identifications by Frank Mbago, Department of Botany, University of Dar es Salaam. Special thanks go to Anne Pusey, Anthony Collins, Deus Mjungu, Michio Nakamura, and Alex Piel for aiding logistics in the field; Edward Kohi, Pius Kavana, and Maria Mbogo for the safekeeping of Alejandra Pascual-Garrido's equipment in Kigoma town; and Alex Mielke and Thomas Püschel for assistance with data analysis. We are very grateful to Luis da Silva for providing the illustration of chimpanzees sourcing raw material for termite-fishing tools. William C. McGrew, Volker Sommer, two anonymous reviewers, and the editorial team at *Current Anthropology* provided much constructive critique and greatly improved the article. This research greatly benefited from discussions with Susana Carvalho, Anthony Collins, and William C. McGrew. Alejandra Pascual-Garrido was supported by a Leverhulme Trust Early Career Fellowship and

received further funding for fieldwork from the Boise Trust Fund, University of Oxford. During writing, Alejandra Pascual-Garrido was supported by the John Fell Fund, University of Oxford.

Comments

Susana Carvalho

Primate Models for Behavioural Evolution Lab, School of Anthropology and Museum Ethnography, University of Oxford, 51/53 Banbury Road, Oxford OX2 6PE, United Kingdom, and Primatology and Paleoanthropology, Gorongosa National Park, Sofala, Mozambique (susana.carvalho@anthro.ox.ac.uk). 26 X 20

No Country for Old Archaeology

Along came primate archaeology. At its inception, it targeted lithic technology, debunking myths about the exclusive “hominin country club” that accepted only members of our clade as makers of archaeological records. Because of it, we learned that non-humans leave behind assemblages that last thousands of years (Falótico et al. 2019; Mercader et al. 2007) and realized that there is intra- and interspecies variability in tools used for the same functions by contemporaneous communities of non-human primates (Carvalho et al. 2008; Luncz et al. 2019). We found that unintentional by-products of stone tool use by monkeys can mimic Oldowan morphotypes (Proffitt et al. 2016). Meanwhile, surveys commenced in older deposits, and we discovered that archaeology is older than the Oldowan and that *Homo* is most certainly not the first toolmaker (Harmand et al. 2015; McPherron et al. 2010; but see Carvalho and Beardmore-Herd 2019 for a review).

These discoveries were far-reaching, but the study by Pascual-Garrido and Almeida-Warren reminds us that we have barely scratched the surface of primate archaeology’s potential. Moreover, their work highlights how we overlooked what most likely was the majority of the hominin tool kit, thus missing the opportunity to understand behaviors that may depict a more complex scenario of our technological evolution. Perishable materials usually do not endure for as long as lithics do (but see Pante et al. 2020; Wadley et al. 2020). After all, we cannot find the older than the Oldowan until we survey deposits older than 2.6 Ma, and to find organic tools, we must search for them—both in the present and in the past.

The authors’ “archaeology of the perishable” shows that three communities (Mahale, Issa, Gombe) of the same subspecies of *Pan troglodytes* ranging in different ecological settings transport and reuse selected organic raw materials, exploiting resources near the tool use sites, albeit with differences at the most open site, Issa. Even more interesting are the plant removals at the source sites, which scarify and remain detectable. And the farther you move away from the site, the fewer plant removals found. So the number of removals could be used as an indicator of the distance from the tool source to the tool site. In reality, termite mounds can fossilize (Darlington 2005), and so could

some of the more robust woody vegetal sources from which these removals occur. Hence, if removal patterns are carefully recorded and the neo-taphonomy understood, it may be possible to identify this sourcing and transport in the fossil record.

Meanwhile, as the authors’ work reveals, there are important insights about behavioral evolution and technology—as well as some cautionary tales—from observing our closest living relatives using perishable tools to fish for insects. For example, the work presented reaffirms the importance of considering the ecology of culture (per Koops, Visalberghi, and van Schaik 2014). At Issa, the most open of the three sites, the lower density of resources may be altering the cost-benefit balance of this type of tool use and hence influencing how far and how often tools get transported. Why carry raw materials long distances if they are widely available? How do we truly know hominin tool transport distances if we are in the dark about nonlithic technology and assume that transport occurred in a single journey instead of in numerous short bouts? This piece prompts us to think of the importance of not using “one size fits all” when considering transport distances to infer species’ cognitive skills or complexity, especially if we are inferring skills from the absence of evidence.

Consider the example of the Bossou chimpanzees that use more than 20 different tool types, with only one being a lithic tool use (Matsuzawa 2011). At a forest location where stone tool use is customary, 1,200 hours of footage were collected over 30 years: they contain an individual average of 7.8% stone tool use time (Max Bain, Arsha Negrani, Daniel Schofield, Sophie Berdugo, Joana Bessa, Jake Owen, Kimberley J. Hockings, et al., unpublished). Now imagine carrying out an archaeological excavation of Bossou that recovered only lithic records and thus having less than 7.8% of the species’ technological activity budget to consider when reconstructing the group lifeways. You would never know about the pestle pound, ant dip, algae scoop, and so on or about the optimization of resource use, which might include transporting one stone 100 times over several years. What could this say about technological complexity, foresight, and strategies for the exploitation of resources? One cannot assume a species’ ability from studying one mode of tool use, or, better said, one cannot compare skill on the basis of comparing hominin lithics versus nonhominin lithics. Only a holistic understanding of the overall optimal foraging strategies can unveil such evolutionary pathways.

This piece carves a path that deserves further work. In the absence of early perishable archaeological records, deeper archaeological knowledge of the technological elements of modern species’ repertoires is fundamental. If we are to find earlier organic records, we must know first how to identify them, how such sites form, and what features may last and develop the analytical methods that will take us further than what we are classically trained to do. There are reasons for hope with the archaeology of the perishable. Just as with termite fishing, other chimpanzee behaviors, for example, tortoise smashing (Pika et al. 2019), crab processing (Koops et al. 2019), tree drumming (Babiszewska et al. 2015), accumulative stone throwing (Kühl

et al. 2016), or bark peeling (Lapunte et al. 2020), hold potential for expanding investigations.

Notably, in an era in which analyzing mega-data sets at the computer is commended, this piece speaks to the importance of carrying out systematic, robust fieldwork. The comparison of the three chimpanzee communities entailed remarkable efforts—and would not be possible to attain using only camera traps! We need more empirical studies that bring back natural history. It is urgent to look at technological and cultural evolution in broader taxonomic and ecological contexts, especially in highly endangered species and populations. Finally, to investigate technological evolution, we need to make use of . . . evolution. Not linear, not deterministic, but evolution in a mosaic fashion. The work by these archaeologists of the perishable is helping us to step away from the lithic mania and allowing the mosaic to take shape.

Wei Chu

Institute of Prehistoric Archaeology, University of Cologne, Weyertal 125, 50923 Cologne, Germany (wchu@uni-koeln.de). 23 X 20

This thought-provoking paper aims to provide insights into ephemeral technologies by using archaeological methods to compare termite mound fishing among different chimpanzee communities. The collected data show that the differences in tool selection, procurement, and management obtained from discarded tools may be partially explained by local environmental considerations but may also reflect socially transmitted behavior, in other words, ecology and culture. The authors suggest that understanding these patterns will help to contextualize the archaeological record and, in turn, provide insight into early human behavior.

Interdisciplinary collaboration between primatology and archaeology, astonishingly, is still quite novel despite being long identified as a need (Mason 1990). The authors respond to this need with an elegant, thoughtful, empirical approach for which they must be thoroughly congratulated. By using archaeological methods to study chimpanzee tool use, the paper shows the potential for future collaborative research and highlights how far we still are from true synthesis. I would like to comment on some of the archaeological aspects of this study, focusing on (1) the methodology, (2) the extent to which the data support the interpretations, and (3) issues surrounding the potential future applications of the methodology.

The authors use archaeological field techniques to analyze chimpanzee tool use patterns. This approach is one of the more difficult methods to apply to primate behavior—as opposed to more readily translatable analytical methods that may be used to understand perishable technology, such as *chaîne opératoire* or microwear (Carvalho et al. 2008; Marreiros et al. 2020). Some may bristle that the archaeological record is a reduced, biased, and static data set that is difficult to compare with the analyzed data here. Indeed, palimpsests and taphonomic alterations are the rule for archaeological sites, but they are al-

ways a question of scale, and many of the same issues are at stake when comparing archaeological sites (Bertran et al. 2019). By reducing archaeological field methods down to their simplest and focusing efforts on understanding behavioral patterns, this paper circumvents many complications. I imagine that, following this example, researchers may integrate other more targeted archaeological techniques to frame their work to strengthen their conclusions (Friesem 2016).

The role of seasonality was wisely minimized in this study. Given that chimpanzees have a range of physiological and behavioral responses to annual cycles suggests, however, that they may be an important factor in their tool provisioning as well. A range of different landscapes may also be similarly pertinent (van Leeuwen, Hill, and Korstjens 2020). Seasonal rhythms are an important factor in the archaeological interpretations, ones that may even be observable in the extant lithic record (Hosfield 2020; Richter et al. 2012). Understanding perennially controlled patterns of chimpanzee tool use may be one useful avenue to further synthesize the fields of primatology and archaeology in a meaningful way.

For ethical reasons, the chimpanzees' tool manufacture and use could not be recorded by live observation, though I wonder whether visual recordings could at some point alleviate this. A strength of primatology, ethnoarchaeology, and ethology more broadly is that they can incorporate aspects of intangible knowledge that archaeologists are unlikely to detect into research and material practices (Cazzella 2016). Given the complex social structure of chimpanzees, it would be valuable, for example, to integrate in the research even such simple categories as gender and age, which could be situated into the wider behavioral ecology and cultural transmission debates, which are currently anthropocentric. Such an approach would also give us a fuller understanding of the proximate and ultimate explanations of primate tool use and provide more robust context to the archaeological record (Tinbergen 1963).

The authors suggest that chimpanzee fishing patterns can be used to help explain ranging behavior among early hominins. I have no doubt that extant behaviors can reasonably be used to phylogenetically triangulate a point of origin. However, the extent to which entomophagy played a main role in the diet and evolution of hominoids is still unclear (Scott 2019), and suggesting an analogy between chimpanzees and early hominoids with regard to this form of subsistence may still be speculative, something for which future studies may provide further insight. We are reminded that the use of relational analogies, even within species, to infer past behavior has long stirred debate and undoubtedly will continue to do so (Cunningham and McGeough 2018; Gosselain 2016; Lyons and David 2019), a complication only further compounded by comparing behavior among genera that diverged long before major changes in locomotion and diet were in place.

The article promotes the application of the archaeology of the perishable to improve our models of early hominin ranging patterns, identify unknown sites, and augment our understanding of Paleolithic implements. These are important,

ambitious goals and ones for which expectations must surely be tempered: the fact that primate conspecific behavior is so variable only highlights the difficulties in understanding past hominoid actions, about which so little is known. The archaeological record provides little in terms of a solid framework, as time, climate change, and geological events have rendered landscapes and archaeological sites, particularly from the early African Plio-Pleistocene, difficult for direct comparison at comparable scales (Villaseñor, Bobe, and Behrensmeyer 2020). Similar efforts to apply primate archaeology to explain early hominin dwelling behavior have underscored the difficulties in such approaches, and the lack of substantial progress since then should at least be a sobering reminder that real advances, at least on the part of archaeology, are slow going (Chu 2009; Sept 1992, 1998; Stewart, Piel, and McGrew 2011).

Still, this study and primate archaeology at large aim to augment our understanding of early human evolution and provide compelling evidence that interdisciplinary approaches can only add to the sparse archaeological record. Archaeology often plays a dominant role in explaining human evolution and, by integrating a range of different disciplinary branches, provides, at the very least, a cross-check to prevalent models of early hominin evolution.

Francesco d'Errico and Lucinda R. Backwell

Préhistoire à l'Actuel: Culture, Environnement et Anthropologie, Unité Mixte de Recherche 5199, Centre National de la Recherche Scientifique, Université de Bordeaux, Bâtiment B2, Allée Geoffroy Saint Hilaire, CS 50023 F, 33615 Pessac CEDEX, France, and Centre for Early Sapiens Behaviour, Department of Archaeology, History, Cultural Studies and Religion, University of Bergen, Øysteinsgate 3, 5020 Bergen, Norway (francesco.derrico@u-bordeaux.fr)/Evolutionary Studies Institute, University of the Witwatersrand, 1 Jan Smuts Avenue, Braamfontein 2001, Johannesburg, South Africa, and Instituto Superior de Estudios Sociales, Consejo Nacional de Investigaciones Científicas y Técnicas, San Lorenzo 429, San Miguel de Tucumán, CP4000, Tucumán, Argentina (lucinda.backwell@wits.ac.za). 1 X 20

The contribution of Pascual-Garrido and Almeida-Warren is paradigmatic of how a comparative analysis of plant tools manufactured and used by different chimpanzee groups can distinguish, if conducted with the intellectual and methodological acuity demonstrated by the authors, factors related to cultural preferences learned socially from those dependent on environmental constraints. A more problematic endeavor, however, is verifying to what extent the model that emerges from these results is relevant to understanding the cultural adaptations of the first hominins. Ideally, the model would require establishing parallels between comparable tasks in terms of neuromotor, cognitive, and learning constraints, localization, and the type of resources exploited. Without a pertinent frame of reference, the danger is that the chimpanzee model remains just a model or that we compare apples and oranges. Knapped lithics do not lend themselves well to such a comparison because they are overly dependent on the presence of suitable rocks for knapping

in the geological environment, which may have involved longer transport distances than those required for the subsistence activities of today's chimpanzees. Lithics are also ill suited for comparison because knapping requires training and ensuing long-term selection that must continue for hundreds of generations, activities in which chimpanzees have not engaged in their evolutionary history. Stone is also unsuitable for comparison because the tasks in which the knapped tools were involved were either multiple or devoted to the exploitation of large animal carcasses, behaviors absent in chimpanzees. The same problem is posed by the rare knapped bone tools discovered at Olduvai Gorge in Tanzania (Backwell and d'Errico 2003; Leakey 1971). A comparison based on percussion tools would be best (Arroyo and de la Torre 2016, 2018; Arroyo et al. 2016; Mora and de la Torre 2005), but it is hampered by the fact that an intersite approach, such as that followed by Pascual-Garrido and Almeida-Warren, is made difficult by the fact that such tools are found at only one site, Olduvai, sporadically at more recent sites, or too far away from this key site (Goren-Inbar et al. 2002) to make meaningful comparisons.

The bone tools used by hominins in southern Africa (Brain and Shipman 1993; Robinson 1959) are much better suited to test the relevance of the chimpanzee model but have not been used to any great extent to date. Many ethologists working on chimpanzee cultures have limited their reading of our paper on termite foraging by early hominins (Backwell and d'Errico 2001) by not examining in detail the data that accompanied that paper and those that followed (Backwell and d'Errico 2003, 2004, 2008, 2009; Caruana, d'Errico, and Backwell 2013; d'Errico and Backwell 2003, 2009; d'Errico, Backwell, and Berger 2001; Hanon 2019; Stammers, Caruana, and Herries 2018) or the potential of this material for intersite comparisons. The advantage of these tools is that they were certainly used as digging sticks in termite mounds and perhaps other environments. They therefore reflect, like the activities described by Pascual-Garrido and Almeida-Warren, the practice of a repetitive task carried out locally by distinct groups, learned mostly by observation, and not requiring, like knapped lithics, the long-term implementation of specialized neuromotor skills. These bone tools are now known from five geographically close sites: Swartkrans, Sterkfontein, Drimolen, Kromdraai, and Cooper's, which shared comparable paleoenvironmental conditions (de Ruiter, Sponheimer, and Lee-Thorp 2008; Peterson et al. 2018; Reynolds and Kibii 2011). Like Pascual-Garrido and Almeida-Warren, we have endeavored to document different aspects of the *chaîne opératoire*, in particular those related to the choice of bone used as tools in comparison with the taxonomic composition, size, and thickness of the bones making up the faunal assemblages stratigraphically associated with them. In addition to elements common to all sites, such as the use of elongated, highly weathered fragments of the diaphysis of large animals, we have been able to highlight behaviors that are found only at certain sites, such as the rare use at Swartkrans of fresh bone or horn-cores sharpened by abrasion to compensate for the rapid wear of the tool tip due to the less robust nature of this bone

type. The number of tools found at some sites is too small to reach statistically valid conclusions when comparing sites, but many tools found in recent excavations are still waiting for detailed analysis. The possibility of verifying, in a relevant way, to what extent the cultural behaviors of the first hominins or of some of them correspond to those brilliantly documented by Pascual-Garrido and Almeida-Warren is therefore open, all the more so since the methods to make these objects speak are in place.

Thurston Cleveland Hicks

Faculty of "Artes Liberales," University of Warsaw, Pałac Zamoykskich, Ulicy Nowy Świat 69, 200 m od Kampusu Głównego UW, Poland (clevehicks@hotmail.com). 18 X 20

This important and well-crafted study expands our understanding not only of the behavior of our extant panin cousins but also of the vanished vegetal technologies we presume our own hominin ancestors must have used. Those ancient wands, probes, and clubs are, unlike stone tools, invisible in the hominin fossil record before about 300,000 years ago. Studying the behavior of nonhuman great apes offers us insight into what those lost tool traditions might have been like. In this paper, the authors make effective use of archaeological evidence from three chimpanzee communities inhabiting nearby Tanzanian forests and woodlands that all happen to use vegetal tools to fish for termites (this is fortuitous, as a number of chimpanzee populations ignore this nutritious resource even where it is abundant, such as in my study region in northern Democratic Republic of the Congo [DRC]; Hicks et al. 2019). In our efforts to understand the full diversity of chimpanzee behavior across Africa under a range of habitats and circumstances, we are faced with the limitation that only a tiny proportion of communities have been habituated for observation. The authors' work significantly advances the methodology for reconstructing and comparing nonhuman great ape behaviors on the basis of indirect evidence.

Only recently have enough populations of African great apes been studied to give us a hint of their behavioral diversity, some of which likely reflects culture or socially transmitted population-specific behaviors. Hobaiter et al. (2017) demonstrated that neighboring chimpanzee communities in the Budongo Forest favor different prey species despite comparable prey abundance, and Samuni, Wegdell, and Surbeck (2020) revealed similar dietary diversity among neighboring bonobo communities (for another example involving chimpanzee plant foods, see Nishida et al. 1983). Gorillas, which, like bonobos, have little to show in terms of material culture, nevertheless display a number of potential cultural variants across their range (Robbins et al. 2016). Where direct observation of behavior is impossible, which is the case for the majority of nonhuman great ape populations, indirect remains of material culture as well as camera trap data are now being used to investigate potentially divergent traditions (Hicks et al. 2020; Luncz, Wittig, and Boesch 2015).

A frequent bugbear of such efforts to claim cultural differences is the fact that ecological factors (reviewed in McGrew 1992) and possibly even genetic ones (Langergraber et al. 2011) also impact great ape behavior. By focusing exclusively on Tanzanian chimpanzees, Pascual-Garrido and Almeida-Warren have minimized the potential influence of any major genetic differences among the populations. The authors carefully compared termite-fishing sites at three localities, recording the materials used in tool construction as well as plant availability for tool making. They discovered that, although all of the chimpanzees used and reused sources both close to and farther away from the termite mounds, the more open country Issa chimpanzees used more parts of each plant and focused more on plant sources closer to the mounds. This is likely due to increased transportation costs in a more open habitat (might the danger of encountering a predator with increasing distance traveled also play a part?).

Another of the key findings of this study is that two of the three chimpanzee communities (Issa and Mahale) used only bark to make their tools, whereas at Gombe, the apes used a diverse mix of materials, including twigs as often as bark. Because of the authors' careful attention to detail and context, we can be certain that the preference of Issa and Mahale chimpanzees for bark as a tool material is not due to differences in the availability of bark or twigs. This makes it much more plausible that these group differences might be cultural (we are duly cautioned, however, about the authors' small sample size for tool sites at Mahale). In addition, they are even able to point to possible changes in tool source preference over time: at Mahale approximately 40 years ago, the chimpanzees used a variety of source types, not just bark. Similarly, the Gombe chimpanzees once used more grass to fashion their tools than they do today. It would be interesting to know how such changes might come about: a transfer in of traditions from neighboring communities? In the case of Gombe, the authors speculate that (among other theories) the reduction in the use of grass to make tools may be related to ecological change due to human activities, in this case, the cessation of annual burning, which has allowed forests to regenerate and replace grass. Here we see an excellent possible example of the tight intertwining of ecology and culture.

Ever since William McGrew and Caroline Tutin left Gombe to visit Mahale and, through their observations and conversations with Junichiro Itani, realized that Gombe and Mahale chimpanzees had developed different grooming traditions (McGrew 2004; McGrew and Tutin 1978), a realization has been forming that humans are not alone in our propensity for the socially transmitted diversification of traditions among populations. As the years have passed, primatologists have developed an increasingly sophisticated approach to handling the difficult task of disentangling cultural explanations from those based on ecology or genetics (made even more difficult by the likelihood that these three factors are entangled). With this paper, Pascual-Garrido and Almeida-Warren have advanced the comparative approach further with their careful attention to

the ecological context in which similar tools are used for the same type of food at three nearby sites. This study will serve as a model for future efforts to understand the context in which great ape tool traditions have evolved in areas such as the vast and interconnected chimpanzee “behavioral realm” I study in northern DRC.

One thing that I appreciate about this paper is that the results are not the end of it. In the lengthy and insightful discussion, the authors are unafraid to speculate and explore the bigger picture, always careful to delineate between what is known and what remains uncertain. This approach is essential for designing new studies to fill the vexing gaps in our knowledge and for inspiring more researchers to add their findings to our steadily increasing data set on behavioral diversity in our nonhuman great ape cousins.

William C. McGrew

School of Psychology and Neuroscience, University of St Andrews, Fife KY16 9JP, United Kingdom, and Evolutionary Primatology, University of Cambridge, Cambridge, United Kingdom (wcm2@st-andrews.ac.uk, wcm21@cam.ac.uk). 22 X 20

Modeling Past Technological Evolution with Ethoarchaeology

Most of the biodegradable material culture of our long gone evolutionary predecessors is absent, along with their behavior. The challenge presented by these missing organic materials has been tackled ingeniously and assiduously by paleoarchaeologists, but, lacking behavior and artifacts, their conclusions are limited to inferences. Even when precious organic remnants of prehistoric material culture survive and are recovered, interpretation of their function remains inferential (e.g., Hardy et al. 2020). Even more tenuous is the intuitive attribution of unobservable cognitive processes underlying the “missing majority” of artifacts (Hurcombe 2008). So, what to do?

On the basis of organic remnants or their mineralized counterparts, archaeologists turn to actualistic studies, which usually entail experimental replications. Vanhaeren et al. (2013) used modern snail shells to stand in for Middle Stone Age equivalents in experiments on use wear. Seeking to learn how these “beads” had been strung, they put the modern shells to laboratory wear with different stringing patterns. They found matches that indicated the functional patterns of the missing strings, with changes in style over time. Wadley (2005) noted evidence that flaked stone tools from the Middle Stone Age had been hafted by some adhesive mixed with ocher. The adhesive component turned out to be *Acacia* gum, but the combination worked only if heated precisely in terms of time and temperature.

Primatologists *can* observe the behavior of our nearest living relations and study their artifacts, organic and inorganic, in action as the next best approximation for modeling what is missing in prehistory. The luxury of having access to the apes’

actions allows the full *chaîne opératoire* to be recorded and analyzed (Carvalho et al. 2008). Even if behavioral observations are incomplete or absent (for unhabituated or only partly habituated subjects) or are constrained (by the limits of camera trapping), they provide fragments that can be knitted together. For example, partly habituated chimpanzees (*Pan troglodytes schweinfurthii*) at Semliki, Uganda, dig holes in sandy riverbeds to access drinking water in the dry season; even before the apes were seen to use these wells, their extractive (“sponge”) tools and evidence of the sequence of their production were available (see fig. 6).

Organic raw material, especially nonwoody vegetation, can be fragile and ephemeral. Wood can last for hundreds of thousands of years in certain (usually anoxic) conditions (Goren-Inbar, Werker, and Feibel 2002). Resins mixed with ocher last tens of thousands of years, still adhering to stone tools. Other residues persisting as by-products on inorganic tools, such as cashew nuts cracked by capuchin monkeys, can last for tens of years (Falótico et al. 2019). Most chimpanzee tools made of vegetation endure for much less time; the longest known so far are still-living twigs and branches in chimpanzee nests, which last for a few years (Stewart, Piel, and McGrew 2011). Artifacts such as termite-fishing tools may last only a few days or weeks but still are available to be reused and so may contribute to a palimpsest assemblage to be unraveled.

Pascual-Garrido and Almeida-Warren have taken the analytic process further than any other study of primate nonlithic technology, especially in tackling the early, more difficult stages of the *chaîne*, such as sourcing the origins of the raw materials. It is easy to collect tools abandoned at a termite mound but harder to learn where they came from! They also have led the way by indirectly but empirically tackling the distances traveled as raw materials were transported to the mound; previous studies dealt only with nearby sources a few meters away. Most importantly, they have pursued the puzzle of the types of raw materials used, in which some populations use only a single type but others a wide variety. These findings tend to concentrate at the beginning and end of the *chaîne*, but there is much more to be done following archaeological precedents.

Waiting to be studied are debitage, especially if it can be refitted; what to make of unused tools; the characteristics of abandoned tools; the enigma of some probes being used at both ends but others only at one end; the limits of various raw material types, for example, whether their cross-sectional shape reflects the “attachability” of termite prey; the physical characteristics of plant materials, presuming some optimality between too rigid and too floppy; aspects of wear at the inserted end of a tool; possible seasonal differences in the raw materials, for example, seasonal shoots, chosen on the basis of their vegetational state; which woody plants, for example, those with robust bast, make good sources of bark; and so on. Many of these questions can be tackled systematically via actualistic attempts by the researchers to replicate what the apes are doing.

All the above and much more can be tested against the observational data from watching chimpanzees in action, that is,



Figure 6. Tools used by chimpanzees to extract drinking water from wells dug in sand, Semliki, Uganda. *Top*, three leaves taken from a source plant but left unused beside a well. *Middle*, processed leaves, with softer portions between the leaf veins removed. *Bottom*, “sponges” made from combined processed portions, still wet from use (McGrew, Marchant, and Hunt 2007).

by applying the etho- part of ethoarchaeology (McGrew et al. 2003). For example, by retrieving the artifacts of known individuals left behind after a fishing session, the observers can start to tackle the perennial problem of who contributes to the palimpsest. Furthermore, they can see whether practices from the start to the finish of the *chaîne* show individual differences; for example, do maternal kin show more similarities in technique than others?

Finally, ethnographic scrutiny of the technology of living foraging societies may yield key differences and similarities in termite acquisition. Isoptera, especially the fungus-growing, mound-building Macrotermitinae favored by chimpanzees, commonly figure in human entomophagy. Pioneering work by Wendell Oswalt (1976) still provides a systematic methodology for studying the techniques and tools of the elementary technology of termitivory. There is so much more to do, and the authors seem set to be the ones to do it!

Stephanie Musgrave and Crickette Sanz

Department of Anthropology, University of Miami, PO Box 248106, Coral Gables, Florida 33124-2005, USA (smusgrave@miami.edu)/ Department of Anthropology, Washington University, 1 Brookings Drive, St. Louis, Missouri 63130, USA, and Congo Program, Wildlife Conservation Society, Brazzaville, Republic of Congo. 30 X 20

Examining tool raw material procurement is fundamental to our attempts to reconstruct the technologies of early hominins.

The authors bring unique expertise on tool variation within *Pan* to this endeavor, and they have pioneered interdisciplinary approaches that incorporate archaeological methods into the study of chimpanzee perishable tool behaviors. These advances have significantly enriched our understanding of primate technology and intraspecific behavioral variation. We commend their extension of this approach in the present study, as applying standardized methods across study sites affords fascinating insights into the ecological correlates of tool-assisted foraging. However, there are also myriad opportunities to link such archaeological data with long-term records and behavioral observations from these field sites. Such an integrated approach would foster a more comprehensive understanding of nonhuman primate material culture and improve our ability to reconstruct the invisible aspects of hominin technologies.

As the authors recognize, the ecological context of tool material procurement can elucidate both the cognitive underpinnings of tool behavior and broader landscape-scale patterns of technology. Among the most striking findings of this study are the population differences in raw material sourcing, specifically that only bark tools were recovered from Mahale and Issa, while variable material sourcing was documented for Gombe chimpanzees. Given that *Macrotermes* exhibits substantial inter- and intraspecific variation in response to both biotic and abiotic factors (Korb 2013), it will be illuminating to investigate whether prey species or termite mound characteristics influence the choice of tool materials (e.g., Sanz et al. 2014). Analyzing the mechanical and textural properties of raw

material types will also help to clarify to what extent chimpanzees select for particular characteristics that crosscut material categories. In addition, populations might use different postures or techniques (Boesch et al. 2020) that could make a particular plant material or species more effective. Differences in prey behavior (e.g., for army ants, Schöning et al. 2008) may also influence what strategies are energetically profitable.

Assessing the energetic requirements of termite gathering, including procurement, could also illuminate how patterns of raw material selection relate to foraging efficiency more broadly, as has been documented for lithic tool use in nonhuman primates (e.g., Luncz et al. 2016, 2018; Sirianni, Mundry, and Boesch 2015; Visalberghi et al. 2015) and suggested for hominin tool users (e.g., Blumenshine et al. 2008). Specifically, integrating data on the spatial distribution of termite nests and individual source plants, as well as chimpanzee home ranges, population density, and community boundaries, could further elucidate the ecological and social dynamics contributing to landscape-scale patterns of material sourcing and tool use. This information could also reveal whether communities spatially overlap at termite nests, which could facilitate information exchange between communities.

Ecological influences are compatible with a significant role for social learning in generating intraspecific behavioral variation (Byrne 2007; Koops, Visalberghi, and van Schaik 2014), and we agree with the authors that social learning likely influences tool raw material selection. In comparing the tool transfer behavior of chimpanzees of the Goualougo Triangle, Republic of Congo, with that of the Kasakela community at Gombe, we found that infants at both sites reuse discarded tools and are allowed to take tools from others, though mothers at Goualougo transfer tools to offspring more frequently and more actively (Musgrave et al. 2020). At Gombe, female compared with male offspring watch their mothers more and are more similar to their mothers with respect to the length of the tools inserted into termite nests (Lonsdorf, Eberly, and Pusey 2004). Together, these observations indicate that multiple social learning mechanisms occur in this context. It is also possible that abundant suitable raw material near termite mounds, as documented at Gombe, rewards frequent individual experimentation with diverse materials. This could promote more variable sourcing of plants by Gombe chimpanzees, even while termite fishing is maintained over generations by social learning.

Linking the plant sourcing and tool data to individual chimpanzees via direct observations will help to illuminate what contributes to variation in raw material sourcing within and between populations, for example, whether individuals or groups specialize in particular tool materials (e.g., Fujii, Ralls, and Tinker 2017) and whether preferences are transmitted within matrilineal (e.g., Lamon et al. 2017) or adopted by immigrants (e.g., Luncz, Wittig, and Boesch 2015). This will also clarify whether population variation in social interactions in these contexts (e.g., in the quality or quantity of tool transfers) mediates the fidelity of intergenerational transmission. Further, individual follows could reveal whether population differences in how youngsters pro-

cure tools are associated with different patterns of raw material sourcing and discard.

The present work should also inspire further investigation of the cognitive underpinnings of tool behavior, particularly regarding the planning and memory capacities (Krause and Sanz 2019) that chimpanzees rely on for efficient foraging (Rosati 2017) yet that remain understudied in wild populations (Janmaat 2019). For example, integrating spatial data (on termite nests, source plants, and home ranges) with direct observations of tool use and of visitation to other food sources (e.g., fruiting trees) could provide novel insights into the factors governing when and where to gather termites and with what raw materials and the time depth over which chimpanzees plan these activities. Individual follows will also help to illuminate how tool complexity relates to the acquisition of mental templates of tool form (Jelbert et al. 2018) and the social scaffolding of tool skills (Musgrave et al. 2020). For example, at Gombe, infants learn to make fishing probes before or at the same time that they learn to use them (Lonsdorf 2005). At Goualougo, where chimpanzees manufacture probes predominantly from just one or two herb species of the Marantaceae family (Sanz and Morgan 2007) and modify these herb probes into a more efficient brush-tipped design (Sanz, Call, and Morgan 2009), youngsters learn to termite fish significantly earlier than they learn to make brush-tipped probes (Musgrave et al. 2021).

While the many important contributions of the current work are to be recognized, we do hope that they inspire further research to integrate the authors' findings with long-term data from these sites. Such a holistic approach would enhance comparative studies of primate technology and strengthen models of hominin behavior and cognition.

Michio Nakamura

Graduate School of Science, Kyoto University, Kitashirakawa Oiwake-cho, Sakyo, Kyoto 606-8502, Japan (nakamura@jinrui.zool.kyoto-u.ac.jp). 22 X 20

In this study, Pascual-Garrido and Almeida-Warren investigated the “availability” of different types of raw material (viz. bark, twig, vine, and grass) for termite-fishing tools used by chimpanzees. The strong point of this study was that they made direct comparisons among three different sites in Tanzania. Although this paper is about more than just availability, I would like to focus my comments on this issue. This is because the novel and fundamental data presented here were on this availability, whereas other data used in further analyses were applied from already published papers.

To measure availability, Pascual-Garrido and Almeida-Warren set “a 5-m circle” (I am not sure whether this 5 m means radius, diameter, or circumference) around a target termite mound and counted the number of “living plants” (perhaps individual plants) in one-fourth of the circle (a quadrant).

The decimals shown in the columns of material types in table 1 appear to be proportions. Although they did not explain the way in which they did the calculation, I understood the figures to be referring to simple divisions of the numbers of plants (e.g., “.486” in the Gombe Bark cell means that there were 222 plants that could potentially produce bark tools, and thus $222/457 = 0.486$). If this is correct, then I wonder whether such numbers alone are good proxies of the availability of raw material types.

For instance, the sizes of plants as a source of tools also seem to matter because a large plant individual can provide more tools than a small one. For simplicity, in an extreme case, only one individual plant might inhabit the quadrant. If this is a large plant, say, a large tree, chimpanzees could make many tools from it. Thus, the raw material required is sufficiently available for them. On the other hand, if this is a small grass, only one tool could be procured from the quadrant, and thus raw material availability would be very low. Therefore, even when the number of individual plants (and thus the proportion) is equal, the availability of raw materials may be different.

Equally important is how plants (both individuals and species) are distributed in the quadrants. For example, if there are some individual plants very close to the mound that could provide a lot of tools, chimpanzees may not dare to search for tools in the outer quadrant area. Thus, in such a case, the weights of the number of plants in the center and at the periphery of each quadrant may be different.

The density of plants that are not suitable for making tools may also matter. When we see mean numbers of 65.3 in Gombe and 33 in Issa in table 1, we are tempted to think that raw materials are more easily obtained in Gombe. However, things are not that simple. Suppose that there are 1,000 and 33 individual plants (including nonmaterial plants) in the Gombe and Issa quadrants, respectively. Then Gombe chimpanzees must find 65.3 plants of 1,000 plants, whereas Issa chimpanzees can choose whichever plants to make a tool. In that scenario, despite the larger mean number of raw material plants, Gombe chimpanzees must expend more effort finding suitable material for tools. As such, the obtainability of tools is measured not only by the absolute number of suitable plants. In other words, in denser vegetation, chimpanzees may have more difficulty finding certain plants than in sparser vegetation.

In the discussion, Pascual-Garrido and Almeida-Warren argued that social learning may be responsible for the selection of tools because of “the lack of an environmental explanation for the absence of twigs in the Issa community.” Although I agree that we need to think of cultural variants, I wonder whether they really scrutinized every environmental explanation before concluding what was lacking. For example, assume that plant species whose twigs are suitable as tools are often distributed in the center of quadrants in Gombe, whereas they are distributed at the periphery of quadrants in Issa (such a skewed distribution of plants is possible across different vegetation types). Then, although the absolute numbers of twig plants in the quadrants do not differ, Gombe chimpanzees may use more twig tools

than their Issa counterparts (only because twigs can easily be obtained closer to the mound). Similarly, if there is a conspicuous species suitable for bark tools (such as a large tree) within a quadrant in Issa (this is possible if the plant species is the dominant one there), Issa chimpanzees may frequently obtain bark tools from this conspicuous tree (just because it is easy to find that tree). Therefore, before concluding “the lack of an environmental explanation,” we may need further descriptions of the prevailing environmental conditions. I think so because Pascual-Garrido and Almeida-Warren have been working on material evidence in the environment rather than observing chimpanzee tool behavior itself. As written above, the distribution of plants in the quadrant and perhaps information about plant sizes could be used to evaluate whether such ecological explanations can be ruled out, as the authors have currently concluded. The fact that only a limited number of plant species are used for bark tools at Issa and Mahale may also be explained by the specific distributions and sizes of such plant species.

Finally, I offer two other miscellaneous comments. First, I was slightly confused because the result on the “reuse of source plants” seemed to have become muddled with the discussion of the “reuse of tools.” The former refers to the multiple scars left on plants (these scars may be made at one time), and the latter is about the use of the same stone or stick tool again on a different day. These seem to be slightly different issues. Second, although Pascual-Garrido and Almeida-Warren state that competition with large carnivores for animal prey remains unknown for apes, some observations have suggested that such competition exists (Nakamura et al. 2019). However, the latter is not related to the use of tools.

Fiona A. Stewart

Department of Biological and Environmental Sciences, Liverpool John Moores University, Parsons Building, Byrom Street, Liverpool L3 3AF, United Kingdom, and Department of Anthropology, University College London, London, United Kingdom (f.a.stewart@ljmu.ac.uk). 22 X 20

In 2009, primate archaeology catapulted itself into a new domain as a means of understanding the unseen (Haslam et al. 2009). And whereas revealing work in the archaeological record of extant primates remains an active domain, for obvious reasons, much work has focused on the lithic record (reviewed in Carvalho and Almeida-Warren 2019). Application of archaeological techniques to the study of primate stone tool use has reshaped our view of the Plio-Pleistocene, suggesting that material culture was produced by a number of species across the landscape, and will ultimately help to identify the evolutionary origins of hominin tool use (Carvalho and Almeida-Warren 2019). More recently, Pascual-Garrido, Almeida-Warren, and colleagues have forged their own branch of research with the burgeoning subdiscipline of “the archaeology of the perishable”; they have applied archaeological techniques

to the study of chimpanzee termite fishing, a behavior that does not fossilize but was likely part of several hominin species' behavioral repertoire.

In the current study, Pascual-Garrido and Almeida-Warren build on their previous research to demonstrate that our reconstructed understanding of tool use behavior in the Oldowan is reflected in chimpanzee termite-fishing behavior, including selectivity and the reuse of tool sources that vary depending on raw material availability but also as a reflection of cultural diversity. Only by such comprehensive and careful identification of tool sources and the availability of suitable sources have they been able to identify these features across multiple communities of chimpanzees in Tanzania.

Cultural variation across chimpanzee communities is well documented (McGrew 2004; Whiten et al. 1999), and termite fishing was one of the first cultural behaviors recorded and studied. In fact, a 2020 study that analyzed behavioral observations from camera traps across 10 termite-fishing chimpanzee communities revealed exceptional cultural diversity—or termite-fishing “etiquette” (Boesch et al. 2020). Behaviors unconstrained by environmental conditions were investigated as culture. Pascual-Garrido and Almeida-Warren's study not only describes likely cultural variation in tool selection among communities by controlling for available material but also raises the possibility of cultural change within communities over time. Availability alone, though, does not explain tool material selection across these populations, and future work could further incorporate the interplay between environmental and social influences in shaping termite-fishing culture (*sensu* Koops, Visalberghi, and van Schaik 2014). Combining these archaeological techniques with direct behavioral observations of the ontology of tool use and individual follows is a necessary next step and a powerful method to tease apart the environmental and social influences on the development of tool use patterns across populations. Likewise, investigating the environmental influences on termite fishing within these populations is informative. Is there a difference in mound structure among these populations that makes flexible bark—used exclusively in the Issa community—more efficient tool material? Or does termite behavior differ in drier, more open miombo woodland habitats, where twigs could lack the flexibility needed to access deeply enough into the mound at certain times of the fishing season?

Issa is a comparatively dry and open habitat compared with other chimpanzee habitats and emerges as an outlier in this comparison of tool source reuse intensity in relation to availability and proximity to the mounds. Pascual-Garrido and Almeida-Warren's findings that Issa chimpanzees used sources more intensely closer to mounds while Gombe chimpanzees targeted rare species suggest different strategies influenced by culture, environment, and the availability of resources. Chimpanzees in dry habitats like Issa have been proposed as models for understanding how similar environments may have shaped the behavior of early hominins (Moore 1996). At Issa, suitable material availability is almost half of that at Mahale and Gombe,

which, in combination with selectivity for bark, could explain greater tool source use intensity. But whether the extra energetic costs of sourcing tools farther away shape the observed pattern deserves further scrutiny. Physiological measures of the energy balance of chimpanzees in West Africa suggest that forest-dwelling chimpanzees can experience periods of energy imbalance more than savanna woodland populations (Wessling et al. 2018). Similar physiological data on energy expenditure and intake across multiple populations are needed to better understand whether a need for energy conservation could influence tool-sourcing patterns. Pascual-Garrido and Almeida-Warren also suggest that tools may be sourced en route to the mounds with forward planning for fishing. It is equally possible that opportunistic tool sourcing as individuals approach a mound would result in more tools sourced in sight of the mound to influence use intensity. With Issa chimpanzees now habituated, there is scope for comparisons of individual follows of termite fishers between Gombe and Issa to further elucidate the mechanisms creating the pattern of perishable archaeology.

Issa chimpanzees also reuse nesting spots within trees that show similar scarring from prior nest-building events (Stewart, Piel, and McGrew 2011). I proposed that this might occur if nest building itself creates a suitable location for building again in the future through the shaping of branches continuing to grow in their new position and a coppicing effect on the trees sprouting new growth where branches were broken. A fruitful next step would be to explore a similar effect in tool sourcing and its potential influence on tool availability. The opposite effect could also result, with tool sources gradually being depleted over time, leading to individuals searching farther afield as closer resources are exhausted.

Irrespective of the mechanisms by which the pattern of tool source reuse occurs across these chimpanzee communities, there is a clear relationship between the availability of material and tool sourcing intensity that resembles that described in the archaeological record. Future work linking the (extant) archaeological signatures with direct behavioral observations and additional environmental and social influences can further elucidate the patterns observed in early archaeological sites and archaeologically invisible behaviors. As the archaeology of the perishable expands together with primate archaeology, such tools will continue to reveal more about our hominin ancestors and the evolution of technology.

Reply

We thank the commentators for the constructive and supportive responses to our paper. We are encouraged by the positivity with which our work was received by leading scholars in the fields of primate archaeology, primatology, and archaeology. Even in the infancy of primate archaeology and with the

limitations of working with ephemeral records, it is gratifying to see that there is a promising future for the archaeology of the perishable. Various suggestions made for future avenues of research match those that we are currently undertaking, which is encouraging.

As one of the main founders of the field of primate archaeology, Carvalho brings the bigger picture to our study. She reminds us that at the beginning of the twenty-first century, we possessed an archaeological record for one single lineage: our own. Now, only two decades later, we can add apes, Old World monkeys, and New World monkeys into what was previously an exclusively human “lithics” club. Like Carvalho, we hope that our work will help researchers realize that it is time to step away from lithic fixation and push the boundaries of the field further. Our study focused on one of many chimpanzee behaviors that could leave an archaeological signature. Carvalho goes further and suggests expanding this work to other chimpanzee behaviors that may also leave recognizable signatures, as not to do so will continue to offer partial and biased perspectives on technological evolution. We are particularly excited about the archaeological potential of tree drumming (Babiszewska et al. 2015) and bark peeling (Lapuente et al. 2020) as extensions of our methods to other chimpanzee behaviors. We agree with Carvalho that without knowing what features or traces to look for in the archaeological record, we will continue to be blinkered by the lithic bias. After all, plant-based technology is the most common, diverse, and complex form of non-human primate tool use, as well as the only form involving manufacture. Carvalho’s ingenious example provides a cautionary analogy of how much would be missed if we reconstructed the tool repertoire of Bossou chimpanzees from archaeological excavations that recovered only their lithic tools: lithics constitute just one of the 22 different tool types that they are known to use (Matsuzawa 2011). Plant-based technologies likely dominated the hominin technological repertoire, but they will remain eclipsed unless we develop novel analytical methods to enable their identification in archaeological records (Hardy 2018).

Chu questions the relevance of termite-fishing chimpanzees as models for the practice of entomophagy in early hominins given that the extent to which this type of subsistence influenced the hominin diet is still unclear (Scott 2019). The role of invertebrates has been largely understudied in the evolution of the human diet (McGrew 2014). Only recently has the paleoanthropology community started to pay attention to the role that insects might have had in hominin diets, in particular after the discovery of bone artifacts that might have been used to dig up termite mounds by *Paranthropus* (cf. McGrew 2021 for an alternative view of the use of these tools). This, together with isotopic evidence of significant amounts of C_4 resources in the *Paranthropus* diet, suggests insects, in particular grass-eating termites, as a possible source of the hominin’s C_4 signature (Lesnik 2014). Furthermore, insects and insect resources probably have been exploited by the order Primates since its origins; all living primates are probably to some degree insect-

tivorous. Insects are relatively high in energy, fat, and high-quality protein and may contain vitamins and minerals that are limited in common plants and fruits (O’Malley and McGrew 2014). Among long-term study populations of chimpanzees, invertebrates make up a larger proportion of the diet than vertebrate prey (Pruetz 2006). Furthermore, worldwide, insects (and some insect products, such as honey) are avidly consumed by many human societies (Bodenheimer 1951). Therefore, it is likely that early humans also made use of this resource and probably used a much richer and more diverse tool kit, including perishable tools, than is seen in the archaeological record (Lesnik 2018). Of course, we do not propose chimpanzees as living fossils of early humans, but they are our closest living relatives. Linking their behavior and artifacts to hominins, when done carefully, can be useful for identifying the common characteristics that were likely present after the divergence of the two clades (Rolian and Carvalho 2017).

Backwell and d’Errico suggest that bone tools may have been used for termite foraging by hominins in South Africa (Backwell and d’Errico 2001, 2008). Like Chu, Backwell and d’Errico question the use of termite-fishing chimpanzees as hominin models as a point of comparison for early hominin stone tool technology in this instance. Instead, Backwell and d’Errico encourage ethologists working on chimpanzee cultures to consider bone tools as the hominin technological evidence for which modern chimpanzees could be suitable models. We welcome Backwell and d’Errico’s suggestion to consider bone tool technologies when modeling hominin behavior in the future, but their model has limitations: First, chimpanzees have yet to be seen using bone tools either in captivity or in the wild. Second, chimpanzees do not dig up termite mounds, although some populations may use perforating and puncturing tools to gain access to termites in their earthen nests. Third, *Trinervitermes*, the termite genus chosen by d’Errico, Backwell, and Berger (2001) for their experimental digging into termite mounds, has not been reported to be consumed by any population of chimpanzees either with or without the use of tools (McGrew 2021). Like Backwell and d’Errico, we aim to help address similarities and differences between modern chimpanzee behavior and that inferred from early hominin artifacts.

Hicks reaffirms the importance of considering the ecology of culture (per Koops, Visalberghi, and van Schaik 2014) when studying great ape traditions. This focus requires a level of detail not attainable using camera traps but only through natural history studies. Hicks describes the time when William McGrew and Caroline Tutin left Gombe to visit Mahale and discovered, through their observations and conversations with Junichiro Itani, that Gombe and Mahale chimpanzees had developed different grooming traditions. His description resonates with Carvalho’s previous advice of not using “one size fits all” to infer species’ cognitive skills or complexity, especially if we are making inferences from the absence of evidence. Tool use variation across groups within the same population may result from different environmental affordances (e.g., Uehara 1982) or different cultural knowledge (O’Malley et al. 2012). Variation across

individuals within a population may result from differing experiences in ontogeny, in particular from mother (and older siblings) to offspring (Lonsdorf 2006; Musgrave et al. 2020). Disentangling how much each of these factors contributes to the patterns of tool use variation seen in chimpanzee populations across Africa is perhaps one of the biggest challenges that remains ahead.

McGrew provides examples of archaeologists using actualistic studies, which usually require experimental replication, for the study of organic or mineralized materials. We agree with him in that implementing a similar approach with the study of chimpanzee perishable tools, that is, by the researchers replicating what apes are doing, will help to pinpoint the questions that remain to be investigated. For example, do certain physical properties of the tools (e.g., cross-sectional shape) increase termite-fishing efficiency, and is this in turn influenced by the physical characteristics of the termite prey? Studies mimicking the use of tools by chimpanzees at army ant nests have provided insights not only into the cognitive abilities of the tool users but also into the behavior of the insect prey and their influence on tool design (Möbius et al. 2008). Comparable studies for termite fishing are still lacking.

Also worthy of further investigation are wear patterns on tool ends, which, in the absence of direct behavioral observation, can help to clarify the diagnostic features of a tool and help to distinguish materials that have been used as tools from those that have not (Carvalho and Almeida-Warren 2019). McGrew (and Chu, Musgrave and Sanz, and Stewart) emphasizes the urgent need to pursue the etho- part of ethoarchaeology, in which indirect data can be tested by observation of the chimpanzees in action. We agree with McGrew that retrieving the artifacts left by known individuals after a fishing session offers the observers the unique opportunity to study the creation of palimpsests in real time—an opportunity that archaeologists will never have.

Musgrave and Sanz highlight that integrating behavioral observations helps to elucidate what contributes to variation within and between populations, whether from individual or group preferences for tool material types, matriline, or immigrants. We endorse Chu's proposal that such inquiries should include variables such as gender and age. These foci are particularly relevant for tools used for foraging, where sex differences exist and in which technical skills are acquired at a certain age (Boesch and Boesch 1984; de A. Moura and Lee 2010; Falótico and Ottoni 2014; Fox et al. 2004; Gumert, Hoong, and Malaivijitnond 2011; Lonsdorf 2005; Musgrave et al. 2021). This could be straightforwardly done in the habituated communities of Gombe or Issa. For nonhabituated subjects, such as the Bilege apes of Mahale, the use of camera traps could assist (Lapuente, Hicks, and Linsenmair 2017). But even when behavioral observations are incomplete, they provide fragments that can be tied together, as McGrew exemplifies with a photograph showing the sequence of production and use of sponge tools by partly habituated chimpanzees (*Pan troglodytes schweinfurthii*) at Semliki, Uganda.

Assessing the energetic requirements of termite gathering by integrating data on the spatial distribution of termite nests and the individual source plants, as proposed by Musgrave and Sanz, is another crucial step in developing this research further and will help us fully understand how the different patterns of raw material selection relate to forage efficiency more broadly. Given that empirical data on the adaptive significance of tool use are surprisingly scarce (Biro, Haslam, and Rutz 2013), these investigations should be accompanied by studies that analyze the energetic payoffs of tool use behaviors. Even among the long-studied chimpanzee populations of Gombe and Mahale in Tanzania and Bossou in Guinea, which have yielded studies of the energetic and nutritional yields of insectivory (O'Malley and Power 2014), it is surprising that only one study has investigated the link between tool-assisted extractive foraging and fitness (Mackworth-Young and McGrew 2014) and none have investigated the potential variation in dietary payoffs among chimpanzee communities with different tool use behaviors (Musgrave et al. 2021). Such research would help answer questions such as: Do certain types of materials and techniques used offer better fitness returns than others? We agree with Musgrave and Sanz on the need to expand studies to a landscape scale (which we are undertaking) by including a spatial analysis of termite mounds, source plants, and other food sources. We particularly need to investigate the ecological and social drivers of the selection, reuse, and abandonment of tool use sites. Such studies will allow the identification of chimpanzee-like patterns of landscape use and provide a model that may enable us to answer one of the longest-standing questions in the archaeology of human origins: How did our earliest technological ancestors interact with their environment?

We welcome Nakamura's thoughtful critique of the methods we have employed, particularly the traditional method used to measure the availability of raw material for termite-fishing tools, which consists of counting the number of suitable plants near mounds (Almeida-Warren et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982; McGrew et al. 2007). Nakamura suggests that the size of the plant also matters, simply because a large plant can provide more tools than a small one. We have collected these data, including the source plants' height and the number of branches available per source plant, but it will require further studies of the physical and mechanical characteristics of the source plants for us to examine these relationships. Furthermore, it seems likely that there is a variation in the vegetative parts of each source plant, and so not all plant elements will constitute good sources for tools: branches of specific diameters located at certain heights are used by chimpanzees (Almeida-Warren et al. 2017; Pascual-Garrido 2017). Nakamura's comment on the spatial distributions and sizes of bark- versus twig-providing plants may explain the exclusive use of bark tools by Issa chimpanzees, as this may constitute one of the "other ecological factors," together with tool material efficiency and prey behavior. Raw material studies of termite-fishing tools are limited, as they are normally conducted within 5 m of the termite mound (Almeida-Warren

et al. 2017; Koops, McGrew, and Matsuzawa 2013; McBeath and McGrew 1982; McGrew et al. 2007). Chimpanzees sometimes get their raw materials from farther away (Pascual-Garrido 2018). Thus, it may be time to reexamine and expand on these long-established methods to better address the more nuanced and complex questions arising in this field.

Stewart's proposal motivates us to test a "scaffolding effect" for the reuse of raw material sources similar to that described for the reuse of chimpanzee nests, where nest building itself creates a suitable root location for future rebuilding (Stewart, Piel, and McGrew 2011). Future studies should also investigate whether scars left on source plants as a result of chimpanzees removing material for tools (Pascual-Garrido 2018) are used as an associative (learning) cue for identifying suitable raw material. When sourcing raw material for hooked stick tool manufacture, New Caledonian crows (*Corvus moneduloides*) identify their source material by its stem and possibly also by its leaves (Klump, Cantat, and Rutz 2019). We still do not know what features help chimpanzees identify their raw materials, but we hope that future experiments will investigate this. Stewart's suggestion of the opposite effect is also possible; that is, if closer tool sources are gradually being depleted, this may lead to individuals using sources located farther away. In Gashaka-Gumti National Park in Nigeria, Pascual-Garrido et al. (2012) found that the sourcing of raw material for tools used to harvest ants and bee products by chimpanzees follows such a depletion effect. We also take on board Stewart's suggestion of conducting a thorough investigation of the structure of termite mounds and the behavior of the termite prey. These foci should reveal whether prey species or termite mound characteristics influence chimpanzee termite-fishing cultures across populations (Sanz et al. 2014), as has been described for chimpanzee army ant dipping (Schöning et al. 2008).

We must express our gratitude to the chimpanzees for continuing to offer us clues about our origins and ourselves. In the Anthropocene, it is up to us to ensure the survival of our closest living relatives and the traditions on which their well-being and survival depend.

—Alejandra Pascual-Garrido and Katarina Almeida-Warren

References Cited

- Allsop, Karen A., and Jennie B. Miller. 1996. Honey revisited: a reappraisal of honey in pre-industrial diets. *British Journal of Nutrition* 75(4):513–520.
- Almeida-Warren, Katarina, David R. Braun, Tetsuro Matsuzawa, and Susana Carvalho. 2018. Mapping primate archaeology: new tools for standardizing spatial data collection across the primate order. Poster presented at the XXVII International Primatological Society Congress, Nairobi, August 19–25.
- Almeida-Warren, Katarina, Volker Sommer, Alexander K. Piel, and Alejandra Pascual-Garrido. 2017. Raw material procurement for termite fishing tools by wild chimpanzees in the Issa Valley, western Tanzania. *American Journal of Physical Anthropology* 164(2):292–304, <https://doi.org/10.1002/ajpa.23269>.
- Andrefsky, William. 1994. Raw-material availability and the organization of technology. *American Antiquity* 59(1):21–34.
- Arroyo, Adrián, and Ignacio de la Torre. 2016. Assessing the function of pounding tools in the Early Stone Age: a microscopic approach to the analysis of percussive artefacts from Beds I and II, Olduvai Gorge (Tanzania). *Journal of Archaeological Science* 74:23–34. [Fd'E/LRB]
- . 2018. Pounding tools in HWK EE and EF-HR (Olduvai Gorge, Tanzania): percussive activities in the Oldowan-Acheulean transition. *Journal of Human Evolution* 120:402–421. [Fd'E/LRB]
- Arroyo, Adrián, Satoshi Hirata, Tetsuro Matsuzawa, and Ignacio de la Torre. 2016. Nut cracking tools used by captive chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age percussive artefacts from Olduvai Gorge. *PLoS ONE* 11(11):e0166788. [Fd'E/LRB]
- Babiszewska, Magdalena, Anne Marijke Schel, Claudia Wilke, and Katie E. Slocombe. 2015. Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology* 156(1):125–134.
- Backwell, Lucinda R., and Francesco d'Errico. 2001. Evidence of termite foraging by Swartkrans early hominids. *Proceedings of the National Academy of Sciences of the USA* 98(4):1358–1363.
- . 2003. Additional evidence on the early hominid bone tools from Swartkrans with reference to spatial distribution of lithic and organic artefacts: research articles: human origins research in South Africa. *South African Journal of Science* 99(5/6):259–267. [Fd'E/LRB]
- . 2004. New bone tools from Swartkrans. In *Swartkrans: a cave's chronicle of early man*. Charles K. Brain, ed. Pp. 279–295. Pretoria: Transvaal Museum Monographs. [Fd'E/LRB]
- . 2008. Early hominid bone tools from Drimolen, South Africa. *Journal of Archaeological Science* 35(11):2880–2894, <https://doi.org/10.1016/j.jas.2008.05.017>.
- . 2009. Additional evidence of early hominid bone tools from South Africa: first attempt at exploring inter-site variability. *Palaeontologia Africana* 44:91–94. [Fd'E/LRB]
- Berbesque, Julia Colette, and Frank W. Marlowe. 2009. Sex differences in food preferences of Hadza hunter-gatherers. *Evolutionary Psychology* 7(4):601–616.
- Bermejo, Magdalena, and German Illera. 1999. Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates* 40(4):619–627.
- Bertran, Pascal, Dominique Todisco, Jean-Guillaume Bordes, Emmanuel Discamps, and Luc Vallin. 2019. Perturbation assessment in archaeological sites as part of the taphonomic study: a review of methods used to document the impact of natural processes on site formation and archaeological interpretations. *PALEO: Revue d'Archéologie Préhistorique* 30(1):52–75, <https://doi.org/10.4000/paleo.4378>. [WC]
- Biro, Dora, Michael Haslam, and Christian Rutz. 2013. Tool use as adaptation. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences* 368(1630):20120408, <https://doi.org/10.1098/rstb.2012.0408>.
- Biro, Dora, Noriko Inoue-Nakamura, Rikako Tonooka, Gen Yamakoshi, Claudia Sousa, and Tetsuro Matsuzawa. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition* 6(4):213–223.
- Bluff, Lucas A., Jolyon Troscianko, Alex A. S. Weir, Alex Kacelnik, and Christian Rutz. 2010. Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society B: Biological Sciences* 277(1686):1377–1385.
- Blumenschine, Robert J., Fidelis T. Masao, Joanne C. Tactikos, and James I. Ebert. 2008. Effects of distance from stone source on landscape-scale variation in Oldowan artefact assemblages in the Paleo-Olduvai Basin, Tanzania. *Journal of Archaeological Science* 35(1):76–86.
- Bodenheimer, Friedrich S. 1951. *Insects as human food: a chapter of the ecology of man*. London: W. Junk.
- Boesch, Christophe, and Hedwige Boesch. 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates* 25(2):160–170.
- Boesch, Christophe, Ammie K. Kalan, Roger Mundry, Mimi Arandjelovic, Simone Pika, Paula Dieguez, Emmanuel Ayuk Ayimisin, et al. 2020. Chimpanzee ethnography reveals unexpected cultural diversity. *Nature Human Behaviour* 4(9):910–916, <https://doi.org/10.1038/s41562-020-0890-1>.
- Bogart, Stephanie L., and Jill D. Pruett. 2011. Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology* 145(1):11–20.
- Brain, Charles K., and Pat Shipman. 1993. The Swartkrans bone tools. In *Swartkrans: a cave's chronicle of early man*. Charles K. Brain, ed. Pp. 195–215. Cape Town: C. T. P. Book Printers. [Fd'E/LRB]
- Brakes, Philippa, Sasha R. X. Dall, Lucy M. Aplin, Stuart Bearhop, Emma L. Carroll, Paolo Ciucci, Vicki Fishlock, et al. 2019. Animal cultures matter for conservation. *Science* 363(6431):1032–1034, <https://doi.org/10.1126/science.aaw3557>.
- Braun, David R., Vera Aldeias, Will Archer, J. Ramon Arrowsmith, Niguss Baraki, Christopher J. Campisano, Alan L. Deino, et al. 2019. Earliest known

- Oldowan artifacts at >2.58 ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *Proceedings of the National Academy of Sciences of the USA* 116(24):11712–11717, <https://doi.org/10.1073/pnas.1820177116>.
- Braun, David R., Thomas Plummer, Peter Ditchfield, Joseph V. Ferraro, David Maina, Laura C. Bishop, and Richard Potts. 2008. Oldowan behavior and raw material transport: perspectives from the Kanjera Formation. *Journal of Archaeological Science* 35(8):2329–2345.
- Braun, David R., Thomas Plummer, Joseph V. Ferraro, Peter Ditchfield, and Laura C. Bishop. 2009. Raw material quality and Oldowan hominin tool-stone preferences: evidence from Kanjera South, Kenya. *Journal of Archaeological Science* 36(7):1605–1614.
- Byrne, Richard. 2007. Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences* 362(1480):577–585. [SM/CS]
- Caruana, Matthew V., Francesco d'Errico, and Lucinda R. Backwell. 2013. Early hominin social learning strategies underlying the use and production of bone and stone tools. In *Tool use in animals: cognition and ecology*. Crickette M. Sanz, Josep Call, and Christophe Boesch, eds. Pp. 242–285. Cambridge: Cambridge University Press. [Fd'E/LRB]
- Carvalho, Susana, and Katarina Almeida-Warren. 2019. Primate archaeology. In *Encyclopedia of animal behavior*. 2nd edition. Jae Chun Choe, ed. Pp. 397–407. London: Elsevier.
- Carvalho, Susana, and Megan Beardmore-Herd. 2019. Technological origins: primate perspectives and early hominin tool use in Africa. In *Oxford research encyclopedia of African history*. Thomas Spear, ed. Oxford: Oxford University Press.
- Carvalho, Susana, Eugénia Cunha, Cláudia Sousa, and Tetsuro Matsuzawa. 2008. *Châmes opératoires* and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution* 55(1):148–163.
- Cazzella, Alberto. 2016. Ethnoarchaeology of the intangible culture: a trajectory towards paleoethnology as a global discipline? In *The intangible elements of culture in ethnoarchaeological research*. Stefano Biagetti and Francesca Lugli, eds. Pp. 37–46. Cham, Switzerland: Springer, https://doi.org/10.1007/978-3-319-23153-2_2. [WC]
- Chu, Wei. 2009. A functional approach to Paleolithic open-air habitation structures. *World Archaeology* 41:348–362. [WC]
- Collins, D. Anthony, and William C. McGrew. 1987. Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates* 28(4):457–471, <https://doi.org/10.1007/BF02380861>.
- . 1988. Habitats of three groups of chimpanzees (*Pan troglodytes*) in western Tanzania compared. *Journal of Human Evolution* 17(66):553–574.
- Conard, Nicholas J., Jordi Serangeli, Utz Böhner, Britt M. Starkovich, Christopher E. Miller, Brigitte Urban, and Thijs Van Kolfshoten. 2015. Excavations at Schöningen and paradigm shifts in human evolution. *Journal of Human Evolution* 89:1–17.
- Cunningham, Jeremy J., and Kevin M. McGeough. 2018. The perils of ethnographic analogy: parallel logics in ethnoarchaeology and Victorian Bible customs books. *Archaeological Dialogues* 25(2):161–189, <https://doi.org/10.1017/S1380203818000181>. [WC]
- Darlington, Jo P. E. C. 2005. Distinctive fossilised termite nests at Laetoli, Tanzania. *Insectes Sociaux* 52(4):408–409.
- Davidson, Iain, and William C. McGrew. 2005. Stone tools and the uniqueness of human culture. *Journal of the Royal Anthropological Institute* 11(4):793–817.
- de A. Moura, Antonio, and Phyllis Lee. 2010. Wild capuchins show male-biased feeding tool use. *International Journal of Primatology* 31(3):457–470, <https://doi.org/10.1007/s10764-010-9406-6>.
- Deblauwe, Isra. 2009. Temporal variation in insect-eating by chimpanzees and gorillas in southeast Cameroon: extension of niche differentiation. *International Journal of Primatology* 30(2):229–252.
- Delagnes, Anne, and Hélène Roche. 2005. Late Pliocene hominid knapping skills: the case of Lokalelei 2C, West Turkana, Kenya. *Journal of Human Evolution* 48(5):435–472.
- de la Torre, Ignacio, Rafael Mora, Manuel Dominguez-Rodrigo, Luis de Luque, and Luis Alcalá. 2003. The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of Lower Pleistocene hominids. *Journal of Human Evolution* 44(2):203–224.
- d'Errico, Francesco, and Lucinda R. Backwell. 2003. Possible evidence of bone tool shaping from the early hominid site of Swartkrans, South Africa. *Journal of Archaeological Science* 30:1559–1576. [Fd'E/LRB]
- . 2009. Assessing the function of early hominin bone tools. *Journal of Archaeological Science* 36(8):1764–1773. [Fd'E/LRB]
- d'Errico, Francesco, Lucinda R. Backwell, and Lee R. Berger. 2001. Bone tool use in termite foraging by early hominids and its impact on our understanding of early hominid behaviour. *South African Journal of Science* 97(3/4):71–75.
- de Ruiter, Darryl J., Matt Sponheimer, and Julia A. Lee-Thorp. 2008. Indications of habitat association of *Australopithecus robustus* in the Bloubaan Valley, South Africa. *Journal of Human Evolution* 55(6):1015–1030. [Fd'E/LRB]
- Dobson, Annette J. 2002. *An introduction to generalized linear models*. New York: Chapman & Hall.
- Dominguez-Rodrigo, Manuel, Jordi Serralonga, Jordi Juan-Tresserras, Luis Alcalá, and Luis Luque. 2001. Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). *Journal of Human Evolution* 40(4):289–299.
- Faith, Tyler, John Rowan, and Andrew Du. 2019. Early hominins evolved within non-analog ecosystems. *Proceedings of the National Academy of Sciences of the USA* 116(43):21478–21483.
- Falótico, Tiago, and Eduardo B. Ottoni. 2014. Sexual bias in probe tool manufacture and use by wild bearded capuchin monkeys. *Behavioural Processes* 108:117–122, <https://doi.org/10.1016/j.beproc.2014.09.036>.
- Falótico, Tiago, Tomos Proffitt, Eduardo B. Ottoni, Richard A. Staff, and Michael Haslam. 2019. Three thousand years of wild capuchin stone tool use. *Nature Ecology and Evolution* 3(7):1034–1038, <https://doi.org/10.1038/s41559-019-0904-4>. [SC, WCM]
- Fay, Michael C., and Richard W. Carroll. 1994. Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology* 34(4):309–317.
- Fox, Elizabeth A., Carel P. van Schaik, Arnold Sitompul, and Donielle N. Wright. 2004. Intra- and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology* 125(2):162–174, <https://doi.org/10.1002/ajpa.10386>.
- Fox, Jon, and Sanford Weisberg. 2011. *An R companion to applied regression*. 2nd edition. New York: Sage.
- Friesem, David E. 2016. Geo-ethnoarchaeology in action. *Journal of Archaeological Science* 70:145–157, <https://doi.org/10.1016/j.jas.2016.05.004>. [WC]
- Fujii, Jessica A., Katherine Ralls, and M. Tim Tinker. 2017. Food abundance, prey morphology, and diet specialization influence individual sea otter tool use. *Behavioral Ecology* 28(5):1206–1216. [SM/CS]
- Goldman-Neuman, Talia, and Erella Hovers. 2009. Methodological considerations in the study of Oldowan raw material selectivity: insights from A. L. 894 (Hadar, Ethiopia). In *Interdisciplinary approaches to the Oldowan*. Erella Hovers and David R. Braun, eds. Pp. 71–84. Dordrecht, Germany: Springer.
- . 2012. Raw material selectivity in Late Pliocene Oldowan sites in the Makaamitalu Basin, Hadar, Ethiopia. *Journal of Human Evolution* 62(3):353–366.
- González-Ruibal, Alfredo, Almudena Hernando, and Gustavo Politis. 2011. Ontology of the self and material culture: arrow-making among the Awá hunter-gatherers (Brazil). *Journal of Anthropological Archaeology* 30(1):1–16.
- Goodall, Jane. 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* 201:1264–1266.
- . 1986. *The chimpanzees of Gombe: patterns of behaviour*. Cambridge, MA: Harvard University Press.
- Goren-Inbar, Naama, Gonen Sharon, Yoel Melamed, and Mordechai Kislev. 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. *Proceedings of the National Academy of Sciences of the USA* 99(4):2455–2460.
- Goren-Inbar, Naama, Ella Werker, and Craig Feibel. 2002. *The Acheulian site of Gesher Benot Ya'aqov, Israel: the wood assemblage*. Oxford: Oxbow. [WCM]
- Gosselain, Olivier P. 2016. To hell with ethnoarchaeology! *Archaeological Dialogues* 23(2):215–228, <https://doi.org/10.1017/S1380203816000234>. [WC]
- Gruber, Thibaud, Kevin B. Potts, Christopher Krupenye, Maisie Rose Byrne, Constance Mackworth-Young, William C. McGrew, Vernon Reynolds, and Klaus Zuberbühler. 2012. The influence of ecology on chimpanzee (*Pan troglodytes*) cultural behavior: a case study of five Ugandan chimpanzee communities. *Journal of Comparative Psychology* 126(4):446–457.
- Gumert, Michael D., Low Kuan Hoong, and Suchinda Malaivijitnond. 2011. Sex differences in the stone tool-use behavior of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). *American Journal of Primatology* 73(12):1239–1249, <https://doi.org/10.1002/ajp.20996>.

- Hanon, Raphael. 2019. Les comportements de subsistance des hominines du Pléistocène inférieur d'Afrique du Sud: étude zooarchéologique du site de Cooper's D (Bloubaan Valley). PhD thesis, National History Museum, Paris. [Fd'E/LRB]
- Hardy, Bruce L., M.-H. Moncel, Celine Kerfant, Matthieu Lebon, Ludovic Bellot-Gurlet, and Nicolas Melard. 2020. Direct evidence of Neanderthal fibre technology and its cognitive and behavioural implications. *Scientific Reports* 10:4889. [WCM]
- Hardy, Karen. 2018. Plant use in the Lower and Middle Palaeolithic: food, medicine and raw materials. *Quaternary Science Reviews* 191:393–405. <https://doi.org/10.1016/j.quascirev.2018.04.028>.
- Harmand, Sonia. 2009. Variability in raw material selection at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In *Interdisciplinary approaches to the Oldowan*. Erella Hovers and David R. Braun, eds. Pp. 85–99. Dordrecht, Germany: Springer.
- Harmand, Sonia, Jason E. Lewis, Craig S. Feibel, Christopher J. Lepre, Sandrine Prat, Arnaud Lenoble, Xavier Boes, et al. 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521(7552):310–315. [SC]
- Harrison, Xavier A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2:e616, <https://peerj.com/articles/616>.
- Haslam, Michael, Adriana Hernandez-Aguilar, Victoria Ling, Susana Carvalho, Ignacio de la Torre, April Destefano, Andrew Du, et al. 2009. Primate archaeology. *Nature* 460(7253):339–344.
- Haslam, Michael, Adriana Hernandez-Aguilar, Tomos Proffitt, Adrian Arroyo, Tiago Falótico, Dorothy Frigaszy, Michael Gumert, et al. 2017. Primate archaeology evolves. *Nature Ecology and Evolution* 1:1431–1437.
- Heaton, Jason L., and Travis R. Pickering. 2006. Archaeological analysis does not support intentionality in the production of brushed ends on chimpanzee termiting tools. *International Journal of Primatology* 27(6):1619–1633.
- Hernandez-Aguilar, R. Adriana. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *Journal of Human Evolution* 57(4):350–364.
- Hernandez-Aguilar, R. Adriana, Jim Moore, and Travis R. Pickering. 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceedings of the National Academy of Sciences of the USA* 104(49):19210–19213.
- Hicks, Thurston C., Hjalmar S. Kühl, Christophe Boesch, Paula Dieguez, Ayuk Emmanuel Ayimisin, Rumen Martin Fernandez, Donatienne Barubiyo Zungawa, et al. 2019. Bili-Uére: a chimpanzee behavioural realm in northern Democratic Republic of Congo. *Folia Primatologica* 90(1):3–64.
- Hicks, Thurston C., Hjalmar S. Kühl, Christophe Boesch, Steph B. J. Menken, John Hart, Peter Roessingh, Corneille Ewango, and Roger Mundry. 2020. The relationship between tool use and prey availability in chimpanzees (*Pan troglodytes schweinfurthii*) of northern Democratic Republic of Congo. *International Journal of Primatology* 41:936–959. [TCH]
- Hobaiter, Catherine, Timothée Poisot, Klaus Zuberbühler, William Hoppitt, and Thibaud Gruber. 2014. Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology* 12(9):e1001960, <https://dx.plos.org/10.1371/journal.pbio.1001960>.
- Hobaiter, Catherine, Liran Samuni, Caroline Mullins, Walter John Akankwasa, and Klaus Zuberbühler. 2017. Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo Forest, Uganda. *PLoS ONE* 12(6):e0178065. [TCH]
- Hoffecker, John F., and Ian T. Hoffecker. 2018. The structural and functional complexity of hunter-gatherer technology. *Journal of Archaeological Method and Theory* 25:202–225.
- Hosfield, Robert. 2020. *The earliest Europeans: a year in the life: survival strategies in the lower Palaeolithic*. Oxford: Oxbow. [WC]
- Humle, Tatyana, Charles T. Snowdon, and Tetsuro Matsuzawa. 2009. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition* 12(suppl. 1):S37–S48.
- Hundley, Margaret H. 1963. Notes on methods of feeding and the use of tools in the Geospizinae. *The Auk* 80(2):372–373.
- Hurcombe, Linda. 2008. Organics from inorganics: using experimental archaeology as a research tool for studying perishable material culture. *World Archaeology* 40(1):83–115. [WCM]
- Inoue, Eiji, Yasuko Tashiro, Hideshi Ogawa, Miho Inoue-Murayama, Toshisada Nishida, and Osamu Takenaka. 2013. Gene flow and genetic diversity of chimpanzees in Tanzanian habitats. *Primate Conservation* 26(1):67–74.
- Janmaat, Karlina R. L. 2019. What animals do not do or fail to find: a novel observational approach for studying cognition in the wild. *Evolutionary Anthropology: Issues, News, and Reviews* 28(6):303–320. [SM/CS]
- Jelbert, Sarah A., Roger J. Hosking, Adrian H. Taylor, and Russell D. Gray. 2018. Mental template matching is a potential cultural transmission mechanism for New Caledonian crow tool manufacturing traditions. *Scientific Reports* 8(1):1–8. [SM/CS]
- Jones, Clyde, and Jorge Sabater Pi. 1969. Sticks used by chimpanzees in Rio Muni, West Africa. *Nature* 223:100–101.
- Kimura, Yuki. 1999. Tool-using strategies by early hominids at Bed II, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 36(6):807–831.
- Klump, Barbara, Mathieu Cantat, and Christian Rutz. 2019. Raw material selectivity in hook-tool-crafting New Caledonian crows. *Biology Letters* 15(2):20180836, <https://royalsocietypublishing.org/doi/10.1098/rsbl.2018.0836>.
- Koops, Kathelijne, William C. McGrew, and Tetsuro Matsuzawa. 2013. Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Animal Behaviour* 85(1):175–185, <https://doi.org/10.1016/j.anbehav.2012.10.022>.
- Koops, Kathelijne, Caspar Schöning, and Chie Hashimoto. 2015. Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. *Scientific Reports* 5:12456, <http://www.nature.com/articles/srep12456>.
- Koops, Kathelijne, Caroline Schuppli, and Carel P. van Schaik. 2018. Cultural primatology. In *The international encyclopedia of biological anthropology*. Wenda Trevathan, Matt Cartmill, Darna L. Dufour, Carl Spencer Larsen, Dennis H. O'Rourke, Karen Rosenberg, and Karen B. Strier, eds. Hoboken, NJ: Wiley & Sons.
- Koops, Kathelijne, Elisabetta Visalberghi, and Carel P. van Schaik. 2014. The ecology of primate material culture. *Biology Letters* 10(11):20140508, <https://doi.org/10.1098/rsbl.2014.0508>.
- Koops, Kathelijne, Richard W. Wrangham, Neil Cumberlidge, Maegan A. Fitzgerald, Kelly L. van Leeuwen, Jessica M. Rothman, and Tetsuro Matsuzawa. 2019. Crab-fishing by chimpanzees in the Nimba Mountains, Guinea. *Journal of Human Evolution* 133:230–241. [SC]
- Korb, Judith. 2013. Termite mound architecture, from function to construction. In *Biology of termites: a modern synthesis*. David Edward Bignell, Yves Roisin, and Nathan Lo, eds. Pp. 349–373. Dordrecht, Germany: Springer. [SM/CS]
- Krause, Mark A., and Crickette M. Sanz. 2019. The evolution of learning and memory in humans: comparative perspectives on testing adaptive hypotheses. In *Handbook of cognitive archaeology*. Tracy B. Henley, Matt J. Rossano, and Edward P. Kardas, eds. Pp. 174–195. New York: Routledge. [SM/CS]
- Kühl, Hjalmar S., Ammie K. Kalan, Mimi Arandjelovic, Floris Aubert, Lucy D'Auvergne, Annemarie Goedmakers, Sorrel Jones, et al. 2016. Chimpanzee accumulative stone throwing. *Scientific Reports* 6:22219. [SC]
- Lamon, Noemie, Christof Neumann, Jennifer Gier, Klaus Zuberbühler, and Thibaud Gruber. 2018. Wild chimpanzees select tool material based on efficiency and knowledge. *Proceedings of the Royal Society B: Biological Sciences* 285(1888):20181715, <https://royalsocietypublishing.org/doi/10.1098/rspb.2018.1715>.
- Lamon, Noemie, Christof Neumann, Thibaud Gruber, and Klaus Zuberbühler. 2017. Kin-based cultural transmission of tool use in wild chimpanzees. *Science Advances* 3(4):e1602750. [SM/CS]
- Langergraber, Kevin E., Christophe Boesch, Eiji Inoue, Miho Inoue-Murayama, John C. Mitani, Toshisada Nishida, Anne Pusey, et al. 2011. Genetic and “cultural” similarity in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 278(1704):408–416. [TCH]
- Langergraber, Kevin E., Kay Prüfer, Caroline Rowney, Christophe Boesch, Catherine Crockford, Katie Fawcett, Eiji Inoue, et al. 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences of the USA* 109(39):15716–15721.
- Lapuente, Juan, Mimi Arandjelovic, Hjalmar Kühl, Paula Dieguez, Christophe Boesch, and K. Eduard Linsenmair. 2020. Sustainable peeling of Kapok Tree (*Ceiba pentandra*) bark by the chimpanzees (*Pan troglodytes verus*) of Comoé National Park, Ivory Coast. *International Journal of Primatology* 41:962–988. [SC]
- Lapuente, Juan, Thurston C. Hicks, and K. Eduard Linsenmair. 2017. Fluid dipping technology of chimpanzees in Comoé National Park, Ivory Coast. *American Journal of Primatology* 79(5):e22628, <https://doi.org/10.1002/ajp.22628>.
- Leakey, M. D. 1971. *Excavations in beds I and II, 1960–1963*, vol. 3 of *Olduvai Gorge*. Cambridge: Cambridge University Press. [Fd'E/LRB]
- Leakey, M. D., and R. L. Hay. 1979. Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania. *Nature* 278:317–323.
- Leakey, M. D., R. L. Hay, G. H. Curtis, R. E. Drake, M. K. Jackes, and T. D. White. 1976. Fossil hominids from Laetoli beds. *Nature* 262:460–466.

- Lesnik, Julie J. 2011. Bone tool texture analysis and the role of termites in the diet of South African hominids. *PaleoAnthropology* 2011:268–281, <https://doi.org/10.4207/PA.2011.ART57>.
- . 2014. Termites in the hominin diet: a meta-analysis of termite genera, species and caste as a dietary supplement for South African robust australopithecines. *Journal of Human Evolution* 71:94–104, <https://doi.org/10.1016/j.jhevol.2013.07.015>.
- . 2018. *Edible insects and human evolution*. Gainesville: University Press of Florida.
- Lesnik, Julie J., Robert O'Malley, Audax Mabulla, Enrique Baquedano, Manuel Dominguez-Rodrigo, and Clayton Magill. 2019. Evidence of *Macrotermes* termites within the *Zinjanthropus* horizon at Olduvai Gorge, Tanzania. Paper presented at the 88th Annual Meeting of the American Association of Physical Anthropologists, Cleveland, OH, March 27–30.
- Lonsdorf, Elizabeth V. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour* 70(3):673–683, <https://doi.org/10.1016/j.anbehav.2004.12.014>.
- . 2006. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition* 9(1):36–46, <https://doi.org/10.1007/s10071-005-0002-7>.
- Lonsdorf, Elizabeth V., Lynn E. Eberly, and Anne E. Pusey. 2004. Sex differences in learning in chimpanzees. *Nature* 428(6984):715–716.
- Luncz, Lydia V., Mike Gill, Tomos Proffitt, Magdalena S. Svensson, Lars Kulik, and Suchinda Malaivijitnond. 2019. Group-specific archaeological signatures of stone tool use in wild macaques. *eLife* 8:e46961. [SC]
- Luncz, Lydia V., Roger Mundry, and Christophe Boesch. 2012. Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology* 22(10):922–926.
- Luncz, Lydia V., Tomos Proffitt, Lars Kulik, Michael Haslam, and Roman M. Wittig. 2016. Distance-decay effect in stone tool transport by wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 283(1845):20161607, <https://royalsocietypublishing.org/doi/10.1098/rspb.2016.1607>.
- Luncz, Lydia V., Gilia Sirianni, Roger Mundry, and Christophe Boesch. 2018. Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. *Animal Behaviour* 137:63–73. [SM/CS]
- Luncz, Lydia V., Roman M. Wittig, and Christophe Boesch. 2015. Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). *Philosophical Transactions of the Royal Society B: Biological Sciences* 370(1682):20140348, <https://royalsocietypublishing.org/doi/10.1098/rstb.2014.0348>.
- Lyons, Diane, and Nicholas David. 2019. To hell with ethnoarchaeology . . . and back! *Ethnoarchaeology* 11(2):99–133, <https://doi.org/10.1080/19442890.2019.1642557>. [WC]
- Mackworth-Young, Constance, and William C. McGrew. 2014. Elementary technology correlates with lifetime reproductive success in wild chimpanzees, but why? *Pan Africa News* 21(2):12–15.
- Marreiros, João, Ivan Calandra, Walter Gneisinger, Eduardo Paixão, Antonella Pedergnana, and Lisa Schunk. 2020. Rethinking use-wear analysis and experimentation as applied to the study of past hominin tool use. *Journal of Paleolithic Archaeology* 3:475–502, <https://doi.org/10.1007/s41982-020-00058-1>. [WC]
- Mason, William A. 1990. Premises, promises, and problems of primatology. *American Journal of Primatology* 22(2):123–138, <https://doi.org/10.1002/ajp.1350220206>. [WC]
- Matsuzawa, Tetsuro. 2011. Field experiments of tool use. In *The chimpanzees of Bossou and Nimba*. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 157–164. Tokyo: Springer.
- McBeath, Norman M., and William C. McGrew. 1982. Tools used by wild chimpanzees to obtain termites at Mt Assirik, Senegal: the influence of habitat. *Journal of Human Evolution* 11(1):65–72, [https://doi.org/10.1016/S0047-2484\(82\)80032-8](https://doi.org/10.1016/S0047-2484(82)80032-8).
- McGrew, William C. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.
- . 2004. *The cultured chimpanzee: reflection on cultural primatology*. Cambridge: Cambridge University Press.
- . 2010. In search of the last common ancestor: new findings on wild chimpanzees. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1556):3267–3276.
- . 2014. The “other faunivory” revisited: insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution* 71:4–11, <https://doi.org/10.1016/j.jhevol.2013.07.016>.
- . 2021. Chimpanzees digging up termites: a problematic but persisting issue. *Pan Africa News*.
- McGrew, William C., Pamela J. Baldwin, Linda F. Marchant, Jill D. Pruett, Sarah Scott, and Caroline E. G. Tutin. 2003. Ethoarchaeology and elementary technology of unhabituated wild chimpanzees at Assirik, Senegal, West Africa. *PaleoAnthropology* 2003:1–20. [WCM]
- McGrew, William C., and D. Anthony Collins. 1985. Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology* 9(1):47–62.
- McGrew, William C., Tiago Falótico, Michael D. Gumert, and Eduardo B. Ottoni. 2019. A simian view of the Oldowan. In *Squeezing minds from stones*. Karenleigh A. Overmann and Frederick L. Coolidge, eds. Pp. 13–41. Oxford: Oxford University Press.
- McGrew, William C., Linda Marchant, Melanie Beuerlein, Deirdre Vrancken, Barbara Fruth, and Gottfried Hohmann. 2007. Prospects for bonobo insectivory: Lui Kotal, Democratic Republic of Congo. *International Journal of Primatology* 28(6):1237–1252, <https://doi.org/10.1007/s10764-007-9215-8>.
- McGrew, William C., Linda F. Marchant, and Kevin D. Hunt. 2007. Ethoarchaeology of manual laterality: well-digging by wild chimpanzees. *Folia Primatologica* 78(4):240–244. [WCM]
- McGrew, William C., Jill D. Pruett, and S. J. Fulton. 2005. Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatologica* 76(4):222–226.
- McGrew, William C., and Caroline E. G. Tutin. 1978. Evidence for a social custom in wild chimpanzees? *Man* 13(2):234–251. [TCH]
- McGrew, William C., Caroline E. G. Tutin, and Pamela J. Baldwin. 1979. Chimpanzees, tools and termites: cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man*, n.s., 14(2):185–214.
- McPherron, Shannon P., Zeresenay Alemseged, Curtis W. Marean, Jonathan G. Wynn, Denné Reed, Denis Geraads, René Bobe, and Hamdallah A. Béarat. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466(7308):857–860. [SC]
- Mercader, Julio, Huw Barton, Jason Gillespie, Jack Harris, Steven Kuhn, Robert Tyler, and Christophe Boesch. 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences of the USA* 104(9):3043–3048.
- Mercader, Julio, Melissa A. Panger, and Christophe Boesch. 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296(5572):1452–1455.
- Möbius, Yasmin, Christophe Boesch, Kathelijne Koops, Tetsuro Matsuzawa, and Tatyana Humle. 2008. Cultural differences in army ant predation by West African chimpanzees? a comparative study of microecological variables. *Animal Behaviour* 76(1):37–45, <https://doi.org/10.1016/j.anbehav.2008.01.008>.
- Moore, Jim. 1996. Savanna chimpanzees, referential models and the last common ancestor. In *Great ape societies*. William C. McGrew, Linda F. Marchant, and Toshisada Nishida, eds. Pp. 275–292. Cambridge: Cambridge University Press. [FAS]
- Mora, Rafael, and Ignacio de la Torre. 2005. Percussion tools in Olduvai Beds I and II (Tanzania): implications for early human activities. *Journal of Anthropological Archaeology* 24(2):179–192. [F'dE/LRB]
- Musgrave, Stephanie, Elizabeth Lonsdorf, David Morgan, Madison Prestipino, Laura Bernstein-Kurtycz, Roger Mundry, and Crickette M. Sanz. 2020. Teaching varies with task complexity in wild chimpanzees. *Proceedings of the National Academy of Sciences of the USA* 117(2):969–976.
- Musgrave, Stephanie, Elizabeth Lonsdorf, David Morgan, and Crickette M. Sanz. 2021. The ontogeny of termite gathering among chimpanzees in the Goualougo Triangle, Republic of Congo. *American Journal of Physical Anthropology* 174(2):187–200, <https://doi.org/10.1002/ajpa.24125>.
- Musgrave, Stephanie, David Morgan, Elizabeth Lonsdorf, Roger Mundry, and Crickette M. Sanz. 2016. Tool transfers are a form of teaching among chimpanzees. *Scientific Reports* 6:34783, <http://www.nature.com/articles/srep34783>.
- Nakamura, Michio, Nadia Corp, Mariko Fujimoto, Shihō Fujita, Shunkichi Hanamura, Hitoshige Hayaki, Kazuhiko Hosaka, et al. 2013. Ranging behavior of Mahale chimpanzees: a 16-year study. *Primates* 54(2):171–182.
- Nakamura, Michio, Kazuhiko Hosaka, Noriko Itoh, Takuya Matsumoto, Takahisa Matsusaka, Nobuko Nakazawa, Hitonaru Nishie, et al. 2019. Wild chimpanzees deprived a leopard of its kill: implications for the origin of hominin confrontational scavenging. *Journal of Human Evolution* 131:129–138. [MN]
- Nishida, Toshisada, and Shigeo Uehara. 1980. Chimpanzees, tools and termites: another example from Tanzania. *Current Anthropology* 21(5):671–672.
- Nishida, Toshisada, Richard W. Wrangham, Jane Goodall, and Shigeo Uehara. 1983. Local differences in plant-feeding habits of chimpanzees between the

- Mahale Mountains and Gombe National Park, Tanzania. *Journal of Human Evolution* 12(5):467–480. [TCH]
- Nishie, Hitonaru. 2011. Natural history of *Camponotus* ant-fishing by the M group chimpanzees at the Mahale Mountains National Park, Tanzania. *Primates* 52:329–342.
- Nonaka, Kenichi. 1996. Ethnoentomology of the Central Kalahari San. *African Study Monographs* 22(suppl.):S29–S46.
- O'Malley, Robert C., and William C. McGrew. 2014. Primates, insects and insect resources. *Journal of Human Evolution* 71:1–3, <https://doi.org/10.1016/j.jhevol.2014.02.010>.
- O'Malley, Robert C., and Michael L. Power. 2014. The energetic and nutritional yields from insectivory for Kasekela chimpanzees. *Journal of Human Evolution* 71:46–58, <https://doi.org/10.1016/j.jhevol.2013.09.014>.
- O'Malley, Robert C., William Wallauer, Carson M. Murray, and Jane Goodall. 2012. The appearance and spread of ant fishing among the Kasekela chimpanzees of Gombe: a possible case of intercommunity cultural transmission. *Current Anthropology* 53(5):650–663, <https://doi.org/10.1086/666943>.
- Oswalt, Wendell H. 1976. *An anthropological analysis of food-getting technology*. London: John Wiley & Sons. [WCM]
- Panger, Melissa A., Alison S. Brooks, Brian G. Richmond, and Bernard Wood. 2002. Older than the Oldowan? rethinking the emergence of hominin tool use. *Evolutionary Anthropology* 11(6):235–245.
- Pante, Michael, Ignacio de la Torre, Francesco d'Errico, Jackson Njau, and Robert Blumenshine. 2020. Bone tools from Beds II–IV, Olduvai Gorge, Tanzania, and implications for the origins and evolution of bone technology. *Journal of Human Evolution* 148:102885. [SC]
- Pascual-Garrido, Alejandra. 2017. Termite fishing by Mahale chimpanzees: revisited, decades later. *Pan Africa News* 24(2):15–19, <https://doi.org/10.5134/228897>.
- . 2018. Scars on plants sourced for termite fishing tools by chimpanzees: towards an archaeology of the perishable. *American Journal of Primatology* 80(9):e22921. <http://doi.wiley.com/10.1002/ajp.22921>.
- . 2019. Cultural variation between neighbouring communities of chimpanzees at Gombe, Tanzania. *Scientific Reports* 9:8260, <http://www.nature.com/articles/s41598-019-44703-4>.
- Pascual-Garrido, Alejandra, and Rudolf H. Scheffrahn. 2020. Cultural dietary stasis? four decades on, Mahale chimpanzees still favour *Macrotermes*. *Pan Africa News* 27(1):6–9.
- Pascual-Garrido, Alejandra, Buba Umaru, Oliver Allon, and Volker Sommer. 2013. Apes finding ants: predator-prey dynamics in a chimpanzee habitat in Nigeria. *American Journal of Primatology* 75(12):1231–1244.
- Pascual-Garrido, Alejandra, Buba Umaru, George Nodza, and Volker Sommer. 2012. Obtaining raw material: plants as tool sources for Nigerian chimpanzees. *Folia Primatologica* 83(1):24–44, <https://doi.org/10.1159/000338898>.
- Peterson, Alexandria, Elicia F. Abella, Frederick E. Grine, Mark F. Teaford, and Peter S. Ungar. 2018. Microwear textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to paleoenvironment and diet. *Journal of Human Evolution* 119:42–63. [Fd'E/LRB]
- Piel, Alexander K., Fiona A. Stewart, Lilian Pintea, Yingying Li, Miguel A. Ramirez, Dorothy E. Loy, Patricia A. Crystal, et al. 2013. The Malagarasi River does not form an absolute barrier to chimpanzee movement in western Tanzania. *PLoS ONE* 8(3):e58965, <https://dx.plos.org/10.1371/journal.pone.0058965>.
- Pika, Simone, Harmonie Klein, Sarah Bunel, Pauline Baas, Erwan Théleste, and Tobias Deschner. 2019. Wild chimpanzees (*Pan troglodytes troglodytes*) exploit tortoises (*Kinixys erosa*) via percussive technology. *Scientific Reports* 9(1):7661. [SC]
- Potts, Richard. 1994. Variables versus models of early Pleistocene hominin land use. *Journal of Human Evolution* 27(1/3):7–24.
- Proffit, Tomos, Lydia V. Luncz, Tiago Falótico, Eduardo B. Ottoni, Ignacio de la Torre, and Michael Haslam. 2016. Wild monkeys flake stone tools. *Nature* 539:85–88.
- Pruetz, Jill D. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In *Feeding ecology in apes and other primates: ecological, physical and behavioral aspects*. Gottfried Hohmann, Martha M. Robbins, and Christophe Boesch, eds. Pp. 161–182. Cambridge: Cambridge University Press.
- R Core Team. 2017. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Reynolds, Sally, and Job M. Kibii. 2011. Sterkfontein at 75: review of paleoenvironments, fauna, dating and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa). *Palaeontologia Africana* 46:59–88. [Fd'E/LRB]
- Richter, Daniel, and Matthias Krbetschek. 2015. The age of the Lower Palaeolithic occupation. *Journal of Human Evolution* 89:46–56.
- Richter, Jürgen, Thomas Hauck, Ralf Vogelsang, Thomas Widlok, Jean-Marie Le Tensorer, and Peter Schmid. 2012. “Contextual areas” of early *Homo sapiens* and their significance for human dispersal from Africa into Eurasia between 200 Ka and 70 Ka. In *Temporal and spatial corridors of Homo sapiens sapiens population dynamics during the Late Pleistocene and Early Holocene*. Special issue, *Quaternary International* 274:5–24, <https://doi.org/10.1016/j.quaint.2012.04.017>. [WC]
- Robbins, Martha M., Chieko Ando, Katherine A. Fawcett, Cyril C. Grueter, Daniela Hedwig, Yuji Iwata, Jessica L. Lodwick, et al. 2016. Behavioral variation in gorillas: evidence of potential cultural traits. *PLoS ONE* 11(9):p.e0160483. [TCH]
- Robinson, John T. 1959. A bone implement from Sterkfontein. *Nature* 184:583–585. [Fd'E/LRB]
- Rolian, Campbell, and Susana Carvalho. 2017. Tool use and manufacture in the last common ancestor of *Pan* and *Homo*. In *Chimpanzees and human evolution*. Martin Muller, Richard Wrangham, and David Pilbeam, eds. Pp. 602–644. Cambridge, MA: Harvard University Press.
- Rosati, Alexandra G. 2017. Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in Cognitive Sciences* 21(9):691–702. [SM/CS]
- Russon, Anne E., Dwi Putri Handayani, Purwo Kuncoro, and Agnes Ferisa. 2007. Orangutan leaf-carrying for nest building: toward unravelling cultural processes. *Animal Cognition* 10(2):189–202.
- Rutz, Christian, Lucas A. Bluff, Alex A. S. Weir, and Alex Kacelnik. 2007. Video cameras on wild birds. *Science* 318(5851):765, <http://www.sciencemag.org/cgi/doi/10.1126/science.1146788>.
- Samuni, Liran, Franziska Wedgell, and Martin Surbeck. 2020. Behavioural diversity of bonobo preference as a potential cultural trait. *eLife* 9:e59191. [TCH]
- Sanz, Crickette M., Josep Call, and David B. Morgan. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters* 5(3):293–296. [SM/CS]
- Sanz, Crickette M., Isra Deblauwe, Nikki Tagg, and David B. Morgan. 2014. Insect prey characteristics affecting regional variation in chimpanzee tool use. *Journal of Human Evolution* 71:28–37, <https://doi.org/10.1016/j.jhevol.2013.07.017>.
- Sanz, Crickette M., and David B. Morgan. 2007. Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *Journal of Human Evolution* 52(4):420–433, <https://doi.org/10.1016/j.jhevol.2006.11.001>.
- . 2013. Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1630):20120416, <https://royalsocietypublishing.org/doi/10.1098/rstb.2012.0416>.
- Sanz, Crickette M., David B. Morgan, and Steve Gulick. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *American Naturalist* 164(5):567–581.
- Schick, Kathy D. 1987. Modelling the formation of Early Stone Age artefact concentrations. *Journal of Human Evolution* 16(7/8):789–807.
- Schielzeth, Holger, and Wolfgang Forstmeier. 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology* 20(2):416–420.
- Schöningh, Caspar, Tatyana Humle, Yasmin Möbius, and William C. McGrew. 2008. The nature of culture: technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution* 55(1):48–59, <https://doi.org/10.1016/j.jhevol.2007.12.002>.
- Schuppli, Caroline, and Carel P. van Schaik. 2019. Animal cultures: how we've only seen the tip of the iceberg. *Evolutionary Human Sciences* 1:E2, <https://doi.org/10.1017/ehs.2019.1>.
- Scott, Jeremiah E. 2019. Macroevolutionary effects on primate trophic evolution and their implications for reconstructing primate origins. *Journal of Human Evolution* 133:1–12, <https://doi.org/10.1016/j.jhevol.2019.05.001>. [WC]
- Seft, Jeanne M. 1992. Was there no place like home? a new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. *Current Anthropology* 33(2):187–207.
- . 1998. Shadows on a changing landscape: comparing nesting patterns of hominids and chimpanzees since their last common ancestor. *American Journal of Primatology* 46(1):85–101. [WC]
- Shea, John J. 2016. *Stone tools in human evolution: behavioral differences among technological primates*. New York: Cambridge University Press.
- Sirianni, Giulia, Roger Mundry, and Christophe Boesch. 2015. When to choose which tool: multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. *Animal Behaviour* 100:152–165. [SM/CS]
- Stammers, Rhiannon C., Matthew V. Caruana, and Andy I. Herries. 2018. The first bone tools from Kromdraai and stone tools from Drimolen, and the

- place of bone tools in the South African Earlier Stone Age. *Quaternary International* 495:87–101. [Fd'E/LRB]
- Stewart, Fiona A., and Alexander K. Piel. 2014. Termite fishing by wild chimpanzees: new data from Ugalla, western Tanzania. *Primates* 55:35–40.
- Stewart, Fiona A., Alexander K. Piel, and William C. McGrew. 2011. Living archaeology: artefacts of specific nest site fidelity in chimpanzees. *Journal of Human Evolution* 61(4):388–395.
- Stout, Dietrich, Jay Quade, Sileshi Semaw, Michael J. Rogers, and Naomi E. Levin. 2005. Raw material selectivity of the early stone toolmakers at Gona, Afar, Ethiopia. *Journal of Human Evolution* 48(4):365–380.
- Stout, Dietrich, Michael J. Rogers, Adrian V. Jaeggi, and Sileshi Semaw. 2019. Archaeology and the origins of human cumulative culture. *Current Anthropology* 60(3):309–340.
- Stout, Dietrich, Sileshi Semaw, Michael J. Rogers, and Dominique Cauche. 2010. Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution* 58(6):474–491.
- Sugiyama, Yukimaru. 1985. The brush-stick of chimpanzees found in southwest Cameroon and their cultural characteristics. *Primates* 26:361–374.
- Suzuki, Akira. 1966. On the insect eating habits among wild chimpanzees living in the savanna woodland of western Tanzania. *Primates* 7:481–487.
- Suzuki, Shigeru, Suehisa Kuroda, and Tomoaki Nishihara. 1995. Tool-set for termite fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour* 132(3): 219–235.
- Teleki, Geza. 1974. Chimpanzee subsistence technology: materials and skills. *Journal of Human Evolution* 3(6):575–594.
- Thieme, Hartmut. 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385:807–809.
- Tinbergen, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20(4):410–433, <https://doi.org/10.1111/j.1439-0310.1963.tb01161.x>. [WC]
- Toth, Nicholas, and Kathy Schick. 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology* 38:289–305.
- Uehara, Shigeo. 1982. Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). *Folia Primatologica* 37(1/2):44–76, <https://doi.org/10.1159/000156020>.
- van Casteren, Adam, William I. Sellers, Susannah K. S. Thorpe, Sam Coward, Robin H. Crompton, Julia P. Myatt, and A. Roland Ennos. 2012. Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proceedings of the National Academy of Sciences of the USA* 109(18):6873–6877.
- Vanhaeren, Marian, Francesco d'Errico, Karen van Niekerk, Christopher Henshilwood, and Rudolph Erasmus. 2013. Thinking strings: additional evidence for personal ornament use in the Middle Stone Age at Blombos Cave, South Africa. *Journal of Human Evolution* 64(6):500–517. [WCM]
- van Leeuwen, Kelly L., Ross A. Hill, and Amanda H. Korstjens. 2020. Classifying chimpanzee (*Pan troglodytes*) landscapes across large-scale environmental gradients in Africa. *International Journal of Primatology* 41:800–821, <https://doi.org/10.1007/s10764-020-00164-5>. [WC]
- van Schaik, Carel P., Marc Ancrenaz, Gwendolyn Borgen, Birute Galdikas, Cheryl D. Knott, Ian Singleton, Akira Suzuki, Sri Suci Utami, and Michelle Merrill. 2003. Orangutan cultures and the evolution of material culture. *Science* 299(5603):102–105.
- Villaseñor, Amelia, René Bobe, and Anna K. Behrensmeyer. 2020. Middle Pliocene hominin distribution patterns in eastern Africa. *Journal of Human Evolution* 147:102856, <https://doi.org/10.1016/j.jhevol.2020.102856>. [WC]
- Visalberghi, Elisabetta, Giulia Sirianni, Dorothy Fragaszy, and Christophe Boesch. 2015. Percussive tool use by Tai Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370(1682):20140351. [SM/CS]
- Wadley, Lyn. 2005. Putting ochre to the test: replication studies and adhesives that may have been used for hafting tools in the Middle Stone Age. *Journal of Human Evolution* 49(5):587–601. [WCM]
- Wadley, Lyn, Irene Esteban, Paloma de la Peña, Marine Wojcieszak, Dominic Stratford, Sandra Lennox, Francesco d'Errico, et al. 2020. Fire and grass-bedding construction 200 thousand years ago at Border Cave, South Africa. *Science* 369(6505):863. [SC]
- Wessling, E. G., Tobias Deschner, Roger Mundry, Jill D. Pruett, Roman M. Wittig, and Hjalmar S. Kühl. 2018. Seasonal variation in physiology challenges the notion of chimpanzees (*Pan troglodytes verus*) as a forest-adapted species. *Frontiers in Ecology and Evolution* 6:60. [FAS]
- Whiten, Andrew. 2019. Social learning: peering deeper into ape culture. *Current Biology* 29(17):829–850.
- Whiten, Andrew, Jane Goodall, William C. McGrew, Toshisada Nishida, Vernon Reynolds, Yukimaru Sugiyama, Caroline E. G. Tutin, Richard W. Wrangham, and Christophe Boesch. 1999. Cultures in chimpanzees. *Nature* 399:682–685.
- . 2001. Charting cultural variation in chimpanzees. *Behaviour* 138(11/12): 1481–1516.
- Wondra, Eden M., Adam van Casteren, Alejandra Pascual-Garrido, Fiona A. Stewart, and Alexander K. Piel. 2016. A new report of chimpanzee ant-fishing from the Issa Valley, Tanzania. *African Primates* 11:1–18.
- Wynn, Thomas. 1981. The intelligence of Oldowan hominids. *Journal of Human Evolution* 10(7):529–541.
- Wynn, Thomas, Adriana Hernandez-Aguilar, Linda F. Marchant, and William C. McGrew. 2011. “An ape’s view of the Oldowan” revisited. *Evolutionary Anthropology* 20(5):181–197.
- Wynn, Thomas, and William C. McGrew. 1989. An ape’s view of the Oldowan. *Man* 24(3):383–398.
- Zuur, Alain F., Elena N. Ieno, Neil J. Walker, Anatoly A. Saveliev, and Graham M. Smith. 2009. GLMM and GAMM. In *Mixed effects models and extensions in ecology with R*. Pp. 323–341. New York: Springer.