



REVIEW ARTICLE




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# Examining the suitability of extant primates as models of hominin stone tool culture

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Extant primates, especially chimpanzees, are often used as models for pre-modern hominin (henceforth: hominin) behaviour, anatomy and cognition. In particular, as hominin behaviour cannot be inferred from archaeological remains and artefacts alone, extant primates (including modern humans) are used as a ‘time machine’ to reconstruct the technological repertoires of our early ancestors. Whilst many continue to use primates to approximate hominin tool behaviours, others have questioned the value of these comparisons. The aim of this review is to critically examine how previous studies have compared various primate species to hominins with regards to stone percussion and flaking, as well as to discuss the limitations and strengths of these comparisons. Evidence is presented to support the view that certain monkey species, alongside non-primate animal species, might provide important insights when reconstructing hominin stone tool culture, despite being phylogenetically further removed from our lineage. In conclusion, whilst some studies may inflate the value of primates as models for early hominins, data from extant primates, alongside the archaeological record and anthropological reports, can help create a more comprehensive picture of hominin stone tool culture.

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## Introduction

“We need some outside references, some living models for a dead past, to help us understand what the archaeological record might mean” (Schick and Toth, 1994, p. 74)

The second half of the 20th century saw a shift in archaeology from a cultural-historical perspective focused on describing assemblages to a behavioural or ethological perspective focused on interpreting the archaeological past using modern comparative models. Since some of the earliest scientific observations of primate tool use, researchers have emphasised the relevance of these findings for the study of early hominin material culture (e.g., Goodall, 1964), particularly lithic technologies (e.g., Teleki, 1974). Stone tools played a key role in human evolution by allowing individuals to efficiently gain access to highly caloric resources. For instance, unmodified stones were most likely used by early hominins as percussive tools to access encased nuts and bone marrow, whereas flaked, sharp stones may have been used as cutting tools to butcher large prey (Bunn, 1981; Goren-Inbar et al., 2002; Keeley and Toth, 1981; Potts and Shipman, 1981). The oldest potential stone tools date back to 3.3 Ma (Harmand et al., 2015; though see also Dominguez-Rodrigo and Alcalá, 2016), and possible evidence for butchery has been found on remains dating to 3.39 Ma (McPherron et al., 2010). Although stone tools recovered from the archaeological record provide some insight into hominin behaviour, there are some aspects of lithic technologies that cannot be derived from excavated artefacts alone. Information on the learning processes behind stone tool manufacture and use, the social context of these activities, the gender of stone tool users and the ontogeny of these skills can be better examined by studying living models. As some primate species use stone tools during foraging activities (encompassed by the term “lithic percussive behaviour”, Marchant and McGrew, 2005), comparisons between primate and hominin stone-related behaviours and artefacts are often made in the literature. Furthermore, primate tool repertoires represent a valuable resource for the reconstruction of tool behaviours preceding or complementing lithic technologies in our lineage. This is because whilst early hominins most likely also used organic tools observed in modern primate tool repertoires (such as wooden tools; Hernandez-Aguilar et al., 2007; Pruetz and Bertolani, 2007; Pascal-Garrido and Almeida-Warren, 2021), these types of objects are rarely preserved in the archaeological record.

Researchers across fields have embraced this comparative approach, and an ever-growing number of studies draw insights on the stone tool behaviour of early hominins from various species of extant primates including modern humans, chimpanzees, and, albeit to a lesser extent, macaques and capuchins (e.g., Schick and Toth, 1994; Proffitt et al., 2016; Gumert et al., 2019). Although this approach seems to be common practice in the comparative cognition literature, some authors have questioned the validity of primates as models of hominin stone tool repertoires. Sceptics of this research avenue cite the long time span between the last common ancestor (LCA) of early hominins and extant non-human primates (6–8 Ma in the case of the *Pan* genus); the different environments these species inhabited; discrepancies in the anatomy of fossil hominins and extant primates; and the possibility of convergent evolution and/or equifinality as evidence that living primates might not be the most reliable comparative models for early hominins (Sayers and Lovejoy, 2008; Whiten et al., 2009; Sayers et al., 2012). However, given the impossibility of investigating early hominin behaviour directly, and with the limited amount of information on behavioural processes that can be gleaned from the artefacts found in the archaeological record, simply dismissing the potential of extant primates as models is not a conductive scientific avenue (see also Whiten et al., 2009; Wynn et al., 2011; McGrew et al., 2019).

Previous studies have highlighted the value of individual species as behavioural and/or cognitive models of early hominin stone technologies (e.g., Wynn and McGrew, 1989; Schick and Toth, 1994; Marchant and McGrew, 2005; Carvalho et al., 2009; Carvalho and McGrew, 2012), plant technologies (e.g., van Schaik et al., 2003; Sanz et al., 2014) or both (Rolian and Carvalho, 2017). However, few have critically compared the potential contributions of multiple modern primate species and even fewer have considered the value of stone tool-using monkeys to better understand hominin technology (although see: Wynn et al., 2011; Haslam et al., 2017; McGrew et al., 2019). Thus, the aim of this paper is to jointly review, compare and critically evaluate the potential value of using different species of extant primates as behavioural models for early hominin behaviour, with a focus on the acquisition and expression of stone tool behaviours, in particular percussive and sharp stone production or flaking. For the sake of brevity, we will not discuss all the studies that have made these comparisons, but instead highlight case studies (if any) where each extant great ape species, as well as two genera of monkeys, have been used to draw inferences about early hominin stone tool repertoires. If no or few such studies exist, and contrary to previous reviews on the topic, we describe potential aspects of hominin biology besides behaviour which the different species could help reconstruct, such as social structure or anatomy. We also emphasize the role of monkeys (particularly long-tailed macaques (*Macaca fascicularis*) and capuchin monkeys (*Cebus* spp. and *Sapajus* spp.)) as valuable sources of information on early hominin stone tool repertoires (see also McGrew et al., 2019) while highlighting the limitations of these inferences. Overall, our aim is to discuss how great apes and stone tool-using monkeys, alongside other animals outside the primate taxa, may provide valuable information for researchers interested in the origins of material culture in our lineage. Although the focus of our review is on early hominin stone tool behaviours (both percussive and sharp stone production or flaking), we will also briefly discuss how some of these species can help us build more informed hypothesis about the organic tool repertoires present in our hominin ancestors.

## Primate models

**Chimpanzees.** Due to the close phylogenetic ties with our lineage (Langergraber et al., 2012) and their extensive tool use repertoires (Whiten et al., 1999), chimpanzees (*Pan troglodytes*) are the primate species most often used in studies assessing potential tool-related behavioural processes across hominin species (e.g., Carvalho et al., 2009; Arroyo et al., 2016). Furthermore, whilst a large (and ever-growing) number of animal species have now been observed using tools in the wild and in captivity, chimpanzees are one of the few species that include stones in their repertoires both as tools and proto-tools (i.e. objects involved in the achievement of an outcome that are not manipulated by the animal; Shumaker et al., 2011). For example, wild chimpanzees use stones to open hard-shelled fruits by hitting them repeatedly against a stone anvil at Gombe, Tanzania (McGrew et al., 1999). In Assirik, Senegal, chimpanzees crack open baobab fruits by smashing them against stationary stone anvils (Marchant and McGrew, 2005) and indirect evidence suggests that chimpanzees living in the Nimba mountains of Guinea open *Treculia* fruits by hitting them with clubs and stone cleavers, as well as by smashing the fruits against stationary anvils (Koops et al., 2010). Yet, among chimpanzee stone-related behaviours, nut-cracking with stone hammers and anvils is probably one of the most complex ones (Hayashi et al., 2005; Hirata et al., 2009).

Nut-cracking is practiced primarily by chimpanzee populations in West Africa (although see Morgan and Abwe, 2006 for a

possible, not yet confirmed, report of chimpanzee nut-cracking in Cameroon), and involves the use of stone or wooden hammers and anvils to crack nuts of various tree species in order to consume the nuts' highly caloric kernel (Boesch and Boesch, 1983, 1984; Biro et al., 2006; Carvalho et al., 2008, 2009). Here, we will focus on studies of stone hammer and anvil use in chimpanzees. Previous studies have proposed that chimpanzee nut-cracking shares affinities with hominin knapping. These are, for example, the selection of stone hammers based on physical properties such as size, weight, and raw material as well as the transport and reuse of stone hammers (Carvalho et al., 2008).

An aspect of nut-cracking that has received particular attention (e.g., Mercader et al., 2007), is the fact that chimpanzees occasionally fracture the stones they use as hammers and anvils. Missed hits during nut-cracking events sometimes produce flake-like objects that present morphological characteristics (such as sharp-edges or bulb of percussion) also found in archaeological artefacts (e.g., Mercader et al., 2002; but see Proffitt et al., 2018a and below). However, although stone fracture during nut-cracking has been observed on several occasions, chimpanzees rarely use the detached stone pieces as tools themselves, likely because fractures change the tool dimensions, often making them ineffective (Carvalho et al., 2008). Analysing 1165 nut-cracking actions performed by chimpanzees at Bossou, Carvalho et al. (2008) observed the re-use of fractured stone tools on just nine occasions. Hence, these observations are extremely rare and, contrary to early hominin knapping, chimpanzees do not seem to intentionally or systematically detach stones to use them as tools.

The difference in intentionality between chimpanzee stone detachment (Carvalho et al., 2008) and hominin knapping is further reflected in the size of chimpanzee and early hominin stone tool assemblages. Mercader et al. (2002) excavated and analysed the first non-human archaeological site: a chimpanzee nut-cracking site (Panda 100) in the Taï forest (Côte d'Ivoire) including six anvils located around a nut tree. The authors recovered approximately 4.5 kg of fractured stone which they compared to hominin artefacts from archaeological sites dated to 2.5 Ma (Chavaillon, 1976; Merrick and Merrick, 1976; Isaac et al., 1997). The authors concluded that the fragmented stone recovered at Panda 100 fell within the dimensional and morphological range of some of the earliest hominin artefacts (Mercader et al., 2002), a conclusion challenged by later studies (de la Torre, 2004; Schick and Toth, 2006; Proffitt et al., 2018a). Proffitt et al. (2018a) conducted a morphological, refit, and microscopic re-analysis of the Panda 100 artefacts in order to assess the validity of the comparisons between stone artefacts found at the chimpanzee nut-cracking site and hominin assemblages. The authors argued that the rarity of conchoidal flakes in the Panda 100 assemblage (1 out of 473 pieces) pointed to a lack of intentionality during stone detachment, absence of structured exploitation strategies, and an inability to identify and rectify accidents in chimpanzees. Based on their re-analysis of the artefacts, Proffitt et al. (2018a) questioned the suitability of Panda 100 as a comparative sample to hominin knapped assemblages.

Some have argued that the lack of deliberate and systematic flaking in chimpanzees is not due to an absence of the necessary cognitive abilities to produce or use sharp tools (Wynn and McGrew et al., 1989; Mercader et al., 2002), but rather due to the fact that chimpanzee teeth are sharp enough to fulfill their needs in the wild (Wynn and McGrew, 1989; Pradhan et al., 2012). To test this hypothesis, and following the suggestion from Pradhan et al. (2012), Bandini et al. (2021) examined whether chimpanzees would make sharp stone tools if they could not use their teeth. The authors provided two groups of captive chimpanzees (in a sanctuary and a zoo,  $N_{total} = 11$ ) with the materials (hammer-stones and chert cores) and the motivation (two baited puzzle

boxes) to make flakes and use them as cutting tools to access a food reward. The chimpanzees could only access the reward by cutting a rope or an artificial 'hide' keeping the puzzle box closed which they could not cut with their teeth. The chimpanzees were tested in several experimental conditions in which different types of social information were provided, including human-made flakes. Despite ample opportunities, none of the captive chimpanzees made sharp stones or used the provided human-made flakes as cutting tools. Consequently, it is possible that the ability to intentionally produce sharp stones for their subsequent use as cutting tools is beyond the natural abilities of chimpanzees (Bandini et al., 2021).

Another difference between chimpanzee nut-cracking and hominin knapping is that while intentional knapping to make sharp flakes requires an assessment and adaptation of the stone core features following each strike, nut-cracking relies on a much lower level of striking precision (Bril et al., 2015). Furthermore, tool transport distances have also been shown to be fundamentally different between chimpanzee nut-cracking and hominin flaking. Whilst wild chimpanzees have been observed transporting their nut-cracking tools over some meters (Haslam, 2014; Luncz et al., 2016), it is likely that early hominins transported their tools over hundreds of kilometres (McBrearty and Brooks, 2000). However, it is still debated whether hominin tool transport occurred in single journeys or as a result of multiple shorter journeys, perhaps even completed by different individuals (McGrew et al., 2019), a possibility recently modelled by Reeves et al. (2021). Given these differences in form and product, we should be cautious when extrapolating findings from chimpanzee nut-cracking to early hominin knapping.

Indeed, chimpanzee nut-cracking could be most informative when investigating other hominin stone tool behaviours (see also Arroyo et al., 2016; Proffitt et al., 2018a; de la Torre, 2010). Analyses of percussive tools unrelated to knapping have highlighted the overlooked importance that percussive foraging likely had in early hominins' repertoires (Goren-Inbar et al., 2002). For example, Mora and de la Torre (2005) found that percussive tools (not used in knapping), rather than modified tools such as flakes, were predominant in certain sites of the Olduvai sequence (Olduvai Gorge, in Tanzania; Melka Junture, in Ethiopia). Furthermore, it is likely that early hominins also used stones to crack open nuts and seeds. Based on direct associations at the Acheulean site of Gesher Benot Ya'aqov in Israel between seven types of nuts and pitted stones (hammers and anvils), Goren-Inbar et al. (2002) traced the existence of nut-cracking behaviour as early as 780,000 years ago. Thus, given that nut-cracking is present in both modern chimpanzees and extinct hominins, chimpanzee nut-cracking sites could help characterise the signature that nut-cracking produces on stone artefacts and facilitate their identification. To investigate the parallels between hominin and chimpanzee nut-cracking, Arroyo et al. (2016) conducted an experimental study to directly compare the marks inflicted by chimpanzees when using raw material from Olduvai Gorge, Tanzania, with percussive objects from the Early Stone Age and experimental tools used by modern humans. The authors found that the use-wear patterns left on the chimpanzee tools after repeated nut-cracking bouts were similar to those observed on archaeological and modern human percussive objects (see also Carvalho et al., 2009).

Therefore, whilst the suitability of chimpanzees' nut-cracking tools and by-products as comparative samples for hominin knapping in particular may be limited (de la Torre, 2010; Proffitt et al., 2018a), chimpanzee nut-cracking tools may provide valuable comparative data to better understand early hominin percussive behaviours involving unmodified stones, such as nut-cracking itself (see also Mercader et al., 2002, 2007; Carvalho

et al., 2009). In addition, as Proffitt et al. (2018a) argue, chimpanzees' miss-hits and stone fractures during nut-cracking can be informative as references for archaeologists to identify unintentionally fractured stones during hominin nut-cracking. Going a step further, Davidson and McGrew (2005) even suggested that fractured stones detached as a consequence of missed hits during nut-cracking could have been important in the early stages of unintentional knapping as they might have exemplified how to make sharp stones.

*Chimpanzee conclusion.* The debate surrounding the utility of chimpanzees as models for early hominin material culture in the literature is vast and contentious (Carvalho et al., 2008; Sayers and Lovejoy, 2008; Sayers et al., 2012; Rolian and Carvalho, 2017). Taken at face-value, it is clear why chimpanzees are such a tempting species to use as a behavioural model of early hominin lithic behaviour. However, whilst we agree that their close phylogenetic ties with humans and the use of stone tools in some chimpanzee populations can provide insight into the evolution of some forms of material culture in our own lineage (particularly percussive foraging behaviours such as nut-cracking), there are also important differences between how and when chimpanzees use stone tools compared to the modified, sharp-edged stone tools found in the early hominin archaeological record. These differences suggest that chimpanzee stone behaviours (such as nut-cracking) may not be the most appropriate model for hominin intentional and systematic flaking (Bril et al., 2015). Instead, chimpanzee lithic percussive behaviours might be more useful as models for other early hominin foraging behaviours involving the use of stones such as nut-cracking itself (de Beaune, 2004), fruit processing, or bone smashing.

**Bonobos.** Despite bonobos (*Pan paniscus*) being just as closely related to humans as chimpanzees (Prüfer et al., 2012), this species is rarely included in comparative studies. This is likely due to their smaller population size compared to their sister species both in the wild and captivity (Gruber and Clay, 2016). In addition, bonobos are hardly ever the focus of technological studies as they possess a smaller and less varied tool repertoire than chimpanzees; so far only 13 tool use behaviours have been reported for wild bonobos (Furuichi et al., 2015; Samuni et al., 2021) and only one of these takes place in a foraging context (leaf sponging for water; Gruber and Clay, 2016). To date, no stone tool behaviours have been observed in this species in the wild. Possible explanations for the differences between chimpanzee and bonobo tool-using abilities are heavily debated. Some have argued that the reported differences between *Pan* species may be a biased result from the fact that wild habituated bonobo sites are rare and difficult to access, therefore limiting the amount of data we currently have for comparative studies (Gruber et al., 2010). Koops et al. (2015) further suggested that the differences in tool use frequencies and tool repertoire variability between wild bonobos and chimpanzees may be the product of an intrinsic variation in motivation towards object manipulation between the species, which might result in the observed difference in the extent of tool use. In addition, several hypotheses have been put forward highlighting different factors that could explain why certain species develop tool use and others do not. These hypotheses propose the abundance of foraging opportunities available ("opportunity hypothesis"; Koops et al., 2014), the degree of food scarcity (which would foment tool innovation, "the necessity hypothesis"; Fox et al., 1999) and/or the differing cost-benefit balance of using tools ("the relative profitability hypothesis", Rutz and St Clair, 2012) as possible factors leading to the innovation of tool use behaviours. These factors may interact to explain why

chimpanzees, but not bonobos, exhibit tool use behaviours in the wild.

However, in contrast to their wild counterparts, captive bonobos have been observed practicing several tool use behaviours comparable to those present in chimpanzees. Gruber and colleagues conducted a comparative study on the tool use behaviours of captive bonobos and chimpanzees, and found that the two species presented comparably diverse tool use repertoires (Gruber et al., 2010). Out of the 52 different tool use behaviours observed across both species, the authors only identified seven that differed between *Pan* species. Therefore, it seems that bonobos possess the cognitive abilities required to produce and use tools for extractive foraging, despite these behaviours not being expressed in the wild, possibly because they are not required or because they do not pose a significant improvement compared to non-tool foraging strategies (Rutz and St Clair, 2012; Grund et al., 2019). Examples of stone tool use have been described in several captive bonobo studies. At the Lola ya Bonobo sanctuary, DRC, bonobos have been observed using hammerstones and anvils to crack oil-palm nuts (*Elaeis guineensis*) for more than 20 years, using similar methods to those employed by chimpanzees to crack nuts (Neufuss et al., 2017). These findings provide further evidence for the view that no cognitive or physiological differences exist between bonobos and chimpanzees that limit bonobos' tool-using abilities.

Interestingly, the most famous knapping experiments with a non-human animal as a model of early hominin stone tool behaviour were conducted with the adult male bonobo known as 'Kanzi' (Toth et al., 1993). In an experimental paradigm that was later used by Bandini et al. (2021) and Motes-Rodrigo et al. (2022) to study chimpanzee and orangutan knapping in captivity, Toth et al. (1993) provided Kanzi with all the materials necessary to make flake-like objects and the motivation to do so in the form of a baited puzzle box. Contrary to the later studies however, Kanzi was provided with repeated demonstrations from the start, as well as verbal and physical encouragement to make and use stone tools. After multiple demonstrations and guidance, Kanzi used several techniques to make his own sharp stones, which he continued to use almost 10 years after the original experiment (Roffman et al., 2012). Further research with Kanzi (Schick et al., 1999) found that whilst his knapping abilities improved over time, Kanzi never developed the technique of knapping at an acute angle to create flakes more efficiently, something that distinguished his flake production from that of early hominin tool-makers (Schick and Toth, 1994). Furthermore, Kanzi never modified or sharpened the flakes he made, a regular practice among early hominins (Andrejsky, 2009).

In addition to producing flake-like objects using the knapping technique that had been demonstrated to him (namely freehand percussion), Kanzi innovated several knapping techniques that had not been modelled for him. These techniques involved throwing cores against a hard tiled surface in his indoor enclosure (direct throwing technique) and throwing one stone against another on the ground (indirect throwing technique) when hard surfaces were not available (Toth et al., 1993; Schick et al., 1999). A later experimental study with human participants demonstrated that projectile or throwing techniques such as the ones shown by Kanzi are actually more expedient and energetically efficient than freehand knapping for novices (Putt, 2015). Thus, the techniques innovated by Kanzi seem to have been the "path of least resistance" to produce sharp-edge stones, and may have played an important role in the initial stages of lithic technologies in our lineage (Putt, 2015). In later years, Kanzi's half-sister Panbanisha and her two offspring also developed knapping abilities (Savage-Rumbaugh and Fields, 2006) although how these skills were acquired is unclear.

Similar to the comparisons made by Mercader et al. (2002) between chimpanzee stone artefacts and hominin stone tools, Toth et al. (2006) compared the flake-like objects produced by Kanzi and Panbanisha to flakes made by experienced modern humans and to 2.6-million-year-old flakes found in the archaeological record (presumably made by *Australopithecus garhi*) at Gona (Ethiopia). Quantitative and qualitative analyses revealed that the Gona flakes had an intermediate morphology between those produced by bonobos and modern humans on a variety of measures, including the ratio of split to whole flakes (indicative of hammerstone velocity), the quality of flaking, and the amount of edge battering (indicative of less skilled flaking, Toth et al., 2006). Thus, in terms of motor skill, bonobos may represent a behavioural model of early hominin species that did not customarily or habitually engage in knapping, but that had the cognitive and motor abilities to produce sharp stones if required.

Whilst the studies using Kanzi as a behavioural model provide some interesting insight into the development of knapping skills in a non-human primate, an important limitation of these studies is Kanzi's validity as a wild-representative bonobo. Kanzi and the rest of the bonobos previously housed at the Language Research Center (Georgia, USA) are language trained individuals who were raised in a human cultural environment exposed to extensive human artefacts, directed teaching, and socio/communicative interactions (Furlong et al., 2008). This particular rearing environment generally leads to enculturation, extreme socialisation with humans, and elevated levels of attention towards human actions. This type of rearing environment can not only enhance the social and physical cognitive skills of the subjects (including their social learning abilities, Furlong et al., 2008), but also result in cognitive and physical abilities absent in naturally reared counterparts (Tennie, 2019). Consequently, it is likely that the tool manufacture and use abilities (as well as the social learning abilities) demonstrated by Kanzi are not representative of all bonobos (Bandini et al., 2021). However, studies with enculturated individuals such as those described above might provide relevant insights into the upper limits of certain motor and cognitive abilities available to a species after extensive human interaction.

One advantage of considering wild-representative bonobos as models to infer the behaviour of the last common ancestor between *Homo* and *Pan* is the possibility of using what Gruber and Clay (2016) refer to as the 'dual-Pan' model; in other words, comparing the behaviour of bonobos, chimpanzees, and modern humans under the assumption that behavioural similarities between all three are more likely to have been shared by a common ancestor. Similarly, Haslam (2014) conducted a theoretical reconstruction of the tool repertoire of the last common ancestor between bonobos and chimpanzees 1–2 Ma. Using data from unenculturated bonobos, Haslam (2014) suggested that the last common ancestor of living *Pan* species used a variety of plant tools for probing, sponging, and displaying (despite wild bonobos not presenting some of these skills) but did not possess stone tool using abilities. According to Haslam (2014), the ability to use stones as tools appeared independently in chimpanzees (around 200,000 years ago) and in hominins (during the Pliocene). This conclusion is in contrast to the evolutionary scenario proposed by Rolian and Carvalho (2017), who instead argue that the last common ancestor of *Pan* and *Homo* could have used stone tools. Rolian and Carvalho (2017) base their argument on the evidence that stone tool use is present in captive untrained bonobos (Neufuss et al., 2017), wild chimpanzees, and modern humans and thus is likely to have been present in the last common ancestor of these species.

**Bonobo conclusion.** Given that bonobos have not been reported to use stone tools in the wild, this species has limited value as a

direct model of early hominin stone technology. However, the controversy around the stone tool use abilities of hominins 6–8 Ma highlights the important role that bonobos play in providing a different perspective from that of chimpanzees on the material culture of the last common ancestors between *Pan* species (1–2 Ma) and between *Pan* and *Homo*. The fact that not all extant *Pan* species use stone tools in the wild presents the interesting possibility that despite having the ability to do so, not all hominin species might have used stone tools. Hominin species that shared environmental conditions or social structures with modern bonobos might not have relied on stone tools to obtain highly caloric food items. Thus, rather than debating whether chimpanzee or bonobo behaviour is more representative of hominin behaviour 7 Ma, open reconstructions including both *Pan* species as alternative technological models may prove more fruitful. However, whilst this approach may provide some insight into the ecological and social factors underlying stone tool use, it would still be limited by the fact that it involves only two species, making it impossible to determine which of the many ecological and social factors which differ between them are vital for stone tool use. Currently, the literature is strongly biased towards studies investigating the stone tool abilities of chimpanzees rather than bonobos. Further studies on the technological competency of captive bonobos would provide valuable data to create more informed hypotheses regarding the potential stone tool repertoires of extinct hominoid species. For instance, future studies could investigate how nut-cracking using stone hammers and anvils differs between *Pan* species in captivity when tested with the same methodology.

**Orangutans.** Despite their broad tool use repertoires (van Schaik et al., 2009), orangutans (*Pongo* spp.) have rarely been used as models for early hominin tool use compared to the *Pan* species (especially chimpanzees). One possible reason is that orangutans share the oldest common ancestor between hominins and great apes ~13 Ma; that is, their phylogenetic relationship with early hominins is weaker than that of the *Pan* species (Glazco and Nei, 2003). A second possible explanation is the rarity of percussive behaviours and the absence of stone tool use in wild orangutans. Wild orangutans have been reported to "hammer" with wooden sticks to access termite or bee nests (Fox et al., 1999), but not to use stones as hammers. This absence of stone tool use is not derived from a lack of encased food sources in their diet or a general inability to use tools. For example, orangutans use plant tools to extract the seeds of the hard-shelled *Neesia* fruit by leveraging open its shell (van Schaik and Knott, 2001) and often extract water, honey, and insects from tree holes using tools (van Schaik et al., 2003).

Instead, the lack of stone tool behaviours in wild orangutans has been suggested to be associated to their high degree of arboreality. Taking into account that it takes several years of exposure (to conspecifics, the materials and/or the products of the behaviour) within a specific sensitive learning window for young chimpanzees to use stones as tools to successfully crack encased nuts (Biro et al., 2003), it is possible that the lack of exposure to stones in their immediate environment hinders orangutans' ability (and need) to use stone tools (see the "opportunity hypothesis" and "necessity hypothesis" above). As orangutans rarely go down to the ground (Fox et al., 1999), they also have limited learning and innovating opportunities for stone tool use in the wild (Meulman and van Schaik, 2013). van Schaik et al. (2003) found that variation in tool use specialisation in different populations of orangutans was related to female party size, which was taken as a proxy of socially mediated learning opportunities in a foraging context. Therefore, it is possible that the absence of

stone tool behaviours observed in wild orangutans is also related to their social organisation.

Despite the absence of stone tool use in wild orangutans, the first study on the abilities of non-human great apes to make and use stone tools was carried out with a juvenile male orangutan named Abang, housed at Bristol Zoo, UK (Wright, 1972). Abang was probably enculturated to a certain degree as he was often taken for walks by the zoo keepers and frequently interacted with humans within his enclosure (e.g., Wright conducted his experiments inside Abang's enclosure). In his study, Wright (1972) gave Abang a baited testing box which could only be opened by cutting the nylon cord fastening the boxes' lid to the floor. A flint nodule fixed on a platform and a hammerstone were also placed inside Abang's enclosure. In the first stage of the study, Wright demonstrated how to cut the rope of the box using a pre-made flake produced out of sight of the orangutan. These demonstrations included an instance of physical moulding, in which Abang's keeper took his hands and guided him on how to cut the rope. After nine demonstrations and twelve trial sessions in which Abang could manipulate the flakes and the box, Abang started using the human-made flakes to cut the rope of the box. The second phase of the study involved providing Abang with human demonstrations of how to make flakes using freehand percussion. Once more, Abang learned the target behaviour (sharp stone production) after seven demonstrations and eleven trial sessions. In the 12th trial session, Abang struck the fixed flint nodule with the hammerstone and detached three flake-like objects which he then immediately used to cut the string of the testing box (Wright, 1972). Although Wright ended the study soon after this successful trial, he interpreted his findings as evidence that, contrary to the opinion of many of Wright's contemporaries (e.g., Inskip, 1969), Australopithecines likely possessed sufficient cognitive and manipulative skills to develop stone flaking abilities (Wright, 1972).

A recent follow-up study was carried out by Motes-Rodrigo et al. (2022) who tested orangutans' capacity to individually and socially learn how to make and use sharp stone tools. Following a similar experimental paradigm as the previous ape knapping studies, two captive orangutans (a juvenile and an adult) were provided with all the materials necessary to make and use sharp stones as cutting tools (i.e. fixed chert core and hammers) as well as a task designed to motivate orangutans to use cutting tools (baited puzzled boxes). When tested in a baseline condition, neither of the orangutans made flakes, although both engaged in percussive behaviour, striking the hammers provided against the hard surfaces of the testing room. When provided with a human-made flake, the juvenile orangutan innovated its use as a cutting tool to open a puzzle box. In a second experiment, the authors attempted to elicit knapping by engaging the orangutans in a series of token exchanges of human-made flakes for food rewards in order to increase the value of the flakes and encourage the orangutans to produce their own to use in further exchanges. In this experiment, the juvenile orangutan detached three sharp stone pieces (which he did not exchange) as a by-product of percussive actions. These percussive actions involved striking the core against the hard concrete floor of the testing room. In a final experiment, the authors conducted a partial replication of Wright (1972) by testing the abilities of three female orangutans from a different captive population to socially learn how to make and use sharp stones after being exposed to human demonstrations. Contrary to the previous experiments, one female in this experiment engaged in lithic percussion targeted towards the fixed core, although no stone detachment took place.

In light of these results, Motes-Rodrigo and colleagues concluded that orangutans possess two pre-requisites necessary for the development of lithic technologies, namely the capacity

for lithic percussion and the recognition and use of sharp stones as cutting tools. However, the orangutans tested by Motes-Rodrigo et al. (2022) did not perform the entire sequence of sharp stone tool production and use even when demonstrations were provided, suggesting that this sequence is outside the natural repertoire of unenculturated individuals of this species.

The observation of lithic percussion in orangutans by Motes-Rodrigo et al. (2022) is in contrast to Bandini et al. (2021) who did not observe percussive actions when the same materials were provided to captive chimpanzees in a zoo and a sanctuary. The differences between species may suggest that orangutans have stronger predispositions for percussive actions than chimpanzees and/or that orangutans are less neophobic than chimpanzees towards novel materials (Forss et al., 2019). Indeed, although these were not the target of experimental investigations, anecdotal reports of captive orangutans engaging in stone percussive behaviours can also be found in the literature. Shumaker et al. (2011) described multiple observations of individuals at different zoological institutions using stones to "force locks, presumably by pounding on them", "pounding one stone with another" and "pounding on the glass with stones" (p. 114). Furthermore, orangutans in captivity have been reported to spontaneously acquire nut-cracking with wooden hammers, showing that this species can also engage in percussive extractive foraging (Bandini et al., 2021).

*Orangutan conclusion.* Orangutans may have limited value as models to reconstruct the stone tool repertoire of early hominins mainly because this species has not been reported to engage in stone tool use in the wild. Previous reports of captive orangutan stone tool use also had limitations as they were either anecdotal (Shumaker et al., 2011) or involved partly enculturated individuals (Wright, 1972). As mentioned above, studies on (partially) enculturated individuals provide limited insight into the natural abilities of their wild conspecifics as they might identify behaviours installed during the enculturation process rather than behaviours present (expressed or latent) in the species' natural repertoire. However, for researchers interested in the hypothetical tool use abilities of primates after human intervention, enculturated subjects can provide valuable insight. Although recent studies have avoided some of these issues by testing unenculturated individuals (Motes-Rodrigo et al., 2022), other limitations should be taken into consideration when drawing inferences about early hominin stone repertoires, such as the fact that orangutans have undergone 13 Ma of independent evolution after their split from our LCA. Yet, orangutans are the only extant great ape species that can provide some insight into the potential stone-tool using abilities of the LCA between *Pongo* and *Homo*. The data presented by Motes-Rodrigo et al. (2022) demonstrate that lithic percussion and the recognition and use of sharp stones as cutting tools might be more widespread among primates than previously thought. To further our knowledge in this regard, future knapping experiments should include a broader sample of orangutans of different ages to investigate the generalisability of these observations as well as the ontogeny of the behaviours. In addition, the fact that orangutans used stones as percussive tools in experimental conditions suggests that the availability of materials and the increased terrestriality of orangutans in captive settings may be important factors mediating the expression of stone-related behaviours in this species.

Given that they are the most arboreal ape species, orangutans might also be valuable models for building hypotheses regarding the plant-based repertoires of early hominins with higher degrees of arboreality, such as *A. sediba* (Dunmore et al., 2020) and *A. afarensis* (Green and Alemseged, 2012). Studies on wild orangutan behaviour suggest that if hominin or hominoid species

were (at least partially) arboreal, they might not have expressed stone tool using abilities (although note reports of arboreal nut cracking in chimpanzees reviewed by Carvalho et al., 2013). Therefore, orangutans might represent the best available model species to infer the material culture of arboreal or partially arboreal hominins (and hominoids).

**Gorillas.** In comparison to the other great apes, gorilla (*Gorilla* spp.) tool use is relatively rare both in the wild and in captivity, and gorillas have never been reported to use stones as tools. It has been hypothesized that wild gorillas do not engage in tool use due to their relative dietary specialisation (van Schaik et al., 1999). Gorillas are mostly folivorous and rarely engage in extractive foraging in natural conditions—in the few occasions that they do engage in extractive foraging (for instance when they eat nuts or termites) they can access the food sources by hand or by using their teeth (Breuer et al., 2005). Nevertheless, sporadic anecdotal observations of wild gorilla tool use have been described in the context of foraging (Kinani and Zimmerman, 2015) and for balancing and testing the depth of a pool (Breuer et al., 2005). In captivity, Parker et al. (1999) found that 93% of the surveyed captive gorillas used tools as missiles, sponges and probes (see also Fontaine et al., 1995). Studies exploring the physical cognition underlying tool use in captive great apes have indicated that gorillas perform at an equivalent level to the other great ape species (Herrmann et al., 2008). Therefore, it is likely that, similar to bonobos, there may be environmental and/or motivational factors that dissuade the emergence of tool use in wild gorillas. In line with this view, Lonsdorf et al. (2009) reported less frequent object manipulation and less social tolerance at an artificial foraging task in captive gorillas compared to captive chimpanzees, both of which could contribute to inhibiting the emergence of tool use behaviours.

**Gorilla conclusion.** Given their limited tool use repertoires and their lack of stone tool use, gorillas have rarely been used as models for investigating early hominin technologies. Instead, gorillas have occasionally been used to investigate social structure (Morrison et al., 2019) and anatomy (Stokstad, 2000) in early hominins, although these topics are beyond the scope of the current manuscript. Still, as is also the case for bonobos, evidence from captive gorilla studies has demonstrated that species without frequent tool use (including stone tool use) in their wild behavioural repertoire may still have the capacity for it in captive settings. Further research of this type with gorillas may yet find that this species has the capacity for percussive tool use (perhaps even stone tool use) under particular conditions, despite not displaying it in the wild. Gorillas could be valuable models for other aspects of early hominin behaviour (e.g., Morrison et al., 2019; Stokstad, 2000) and/or in comparative studies with other non-human primates. However, as long as gorillas are not found to use stone tools, the validity of this species as model for early hominin stone tool behaviours is limited compared to other primates when considered independently.

**Modern humans.** Modern humans (*Homo sapiens*) have been used extensively in experimental studies on various aspects of pre-modern hominin behaviour, including stone tool use (Johnson et al., 1978). These experimental studies using modern human knappers have focused on different aspects of lithic technology (often simultaneously), such as which techniques hominins may have used to produce the stone tools found in the archaeological record (e.g., Faisal et al., 2010; Putt, 2015; Byrne et al., 2016; Pargeter and de la Peña, 2017); the relationship between stone tool production and other cognitive abilities such

as language (e.g., Stout and Chaminade, 2012; Cataldo et al., 2018), working memory (e.g., Haidle, 2010) or future planning (e.g., Pargeter et al., 2019); the learning mechanisms underlying the acquisition of knapping abilities by naïve individuals (e.g., Putt et al., 2014; Stout et al., 2015; Morgan et al., 2015; Lombao et al., 2017; Pargeter et al., 2019); the decision making process (or absence of it) during knapping (e.g., Nonaka et al., 2010; Moore and Perston, 2016; Muller et al., 2017); brain activity during stone tool production and use (e.g., Stout et al., 2000, 2008, 2015) and stone tool use-wear in order to infer potential tool function (e.g., Lemorini et al., 2014; Pederagnana and Ollé, 2017).

Most of these studies used participants from Western, Educated, Industrialised, Rich and Democratic (WEIRD) countries (Henrich et al., 2010). The almost exclusive use of WEIRD participants in cognitive and psychological (including knapping) experiments has been criticised by many on the grounds that participants with this profile represent a very small proportion of the current human population and an even smaller proportion of the human species as a whole. Cross-cultural studies have demonstrated variation in how information is transmitted to infants (Little et al., 2016), in the value attached to behavioural conformity (Clegg et al., 2017), and in teaching styles (Clegg et al., 2020) across cultures. The possibility that particular social learning strategies or pedagogical techniques may differ cross-culturally raises the concern that conclusions drawn from studies focused on the social learning of stone tool production (e.g., Morgan et al., 2015) may be limited by their reliance on WEIRD participants, who may share culturally influenced social learning preferences. In contrast to contemporary WEIRD societies, for most of our evolutionary history as a species, *Homo sapiens* practiced a hunting-gathering, nomadic lifestyle. Consequently, using modern hunter-gatherer populations as participants in experiments aimed at reconstructing early hominin stone tool repertoires may be more informative from an evolutionary perspective than solely testing WEIRD society members (see also Marlowe, 2005; Hewlett et al., 2011).

Human children have also been used as models of physical cognition, tool-making, and tool-using capacities of pre-modern hominins. One benefit of studying the tool-making abilities of children rather than adults is that, through the combination of novel tasks and children's more limited experience of the world compared to adults, researchers hope to reduce the likelihood of participants drawing analogies between experimental tasks and real-world experiences. These types of experiments thus provide insight into what kinds of problems children are capable of solving without (or with only limited) social information and prior experience. For example, Reindl et al. (2016) presented 2- to 3.5-year-old children with novel tasks designed to approximate wild great ape tool use. All but one task (nut-cracking) was solved by at least two children, suggesting that human children possess the physical cognition required to produce this set of great ape tool use behaviours. Reindl et al. (2016) argued that these behaviours are likely to comprise part of a phylogenetic "basic state" (or "zone of latent solutions") which the LCA of humans and great apes also could have expressed. This research approach was recently expanded and replicated by Neldner et al. (2020), who confirmed the above finding using a cross-cultural sample (children from the!Xun, Khwe, and ≠Khomani Bushmen communities in South Africa, and children from metropolitan Australia). Neldner et al. (2020) additionally found that one child in each of their tested cultures solved the nut-cracking task. This type of experiment allows arguments to be made about species-level, cross-cultural behaviour in humans. Brill and Foucart (2005) tested children in a nut-cracking task focusing on tool choice and performance. The authors found that exploration of tool properties decreased with age whereas the use of anvils increased with

age. In addition, older children chose functional hammers more frequently than younger children and only the youngest participants (3 year olds) did not succeed in the task.

Although testing children in tool using tasks presents some advantages over testing adults (e.g., less experience with a narrower tool repertoire), it should be noted that even young children with limited experience of the world have been raised in contemporary human social and technological settings, and may therefore not be ‘blank slates’ from a technological perspective. Whilst the children in the above studies may not have previously encountered tool use problems like the ones presented, it is unclear how their previous social and technological experiences may have shaped their responses.

*Traditional stone knappers.* Modern human communities that still use stone tools in traditional social contexts have also been the focus of ethnographic studies of stone tool production and use (Stout, 2002; McCall, 2012). For example, Tindale (1977) reported that members of the Kaiadilt community in Australia use stone bifaces as hammering tools to remove oysters from their conglomerates (though note that Cane, 1992 states that stone tools are no longer made by societies in Australia, suggesting that stone tool production ceased after Tindale’s publication).

Later, Stout (2002) conducted an ethnographic study among adze makers in Langda, in the Indonesian Irian Jaya. An adze is a hafted stone tool, with a cutting edge perpendicular to its handle, traditionally used in Langda to clear land and for shaping wood. Perhaps of greatest interest for the current review is Stout’s (2002) discussion of the cognitive requirements of adze-making, which highlights the potential role of shared ideas, strategic planning, and perceptual-motor skills in adze production. Stout also highlights the social context of skill-learning in adze production, noting that “apprentices participate in a structured and meaningful community of practice that provides scaffolding and motivation for the learning process” (2005, p. 337). However, McCall (2012) cautions against drawing broad conclusions from ethnoarchaeological research, pointing out that in Stout’s (2002) study, the learning process is likely influenced by the fact that only one type of stone tool is being produced (making the combination between raw material and tool production predictable for learners). Furthermore, it is important to consider that adze are nowadays largely non-functional and instead valued for their aesthetic appearance as a symbol of wealth (McCall, 2012). While Stout (2005) notes that a modern actualistic research, including both ethnographic and experimental approaches, cannot reveal the details of prehistoric social organisation, he suggests that such research can pinpoint the conditions necessary for certain kinds of behaviour to emerge.

More recently, Arthur (2010) conducted an ethnographic study with Konso women in Ethiopia, who make and use flaked stone tools for processing hides. Like Stout (2002), Arthur (2010) highlights the social context of stone tool making in this community, in which flaked stone tool making may be learnt through selective apprenticeships between female relatives.

*Human conclusion.* Experimental approaches involving modern humans as models for early hominin knapping abilities have both strengths and limitations. A clear advantage of using modern humans as test subjects is that participants can be instructed and tutored on a variety of testing methodologies. Furthermore, the vast majority of studies of this kind employ university students, meaning that studies can be conducted quickly and minimising experimental costs. Studies involving modern human models have the additional advantage that being closely related to early hominins (closer than any living non-human great ape), phylogenetic inferences regarding the behaviour and cognition of early

hominins can be perhaps drawn more easily. However, it is also possible that modern humans might not be as representative of early hominins as it is often assumed. Certain cognitive mechanisms present in modern humans have been argued to be the result of cultural rather than genetic evolution, meaning that they were absent or much less developed in our hominin ancestors (Heyes, 2019 but see also Shipton, 2010; Morgan et al., 2015; Putt et al., 2014 for studies which used modern humans as models for early hominin tool use). The reliance of modern humans on these cognitive mechanisms (such as language, imitation, or literacy) to learn novel behaviours might limit the generalizability of modern human studies to our hominin ancestors. In an attempt to test modern human subjects that are less reliant on these mechanisms crucial for living in a modern cultural environment, multiple researchers have turned to children as behavioural models of early hominin material culture. However, assuming that modern human children are not as embedded as adults in the modern human cultural environment is unlikely to be a valid a priori assumption. Before the age of two, infants are already physically engaging in the tool use behaviours of their culture (Connolly and Dalgleish, 1989; McCarty et al., 2001) and object manipulation begins even earlier (Rochat, 1989; Bakeman et al., 1990). Moreover, infants encounter objects within the social context of their culture and are capable within their first year of socially learning the ways in which objects can be manipulated (Fagard and Lockman, 2009). Therefore, even when tested at a relatively young age, modern children are likely to have spent large amounts of time engaging in tool use and object manipulation, much of which may be socially influenced.

Another limitation of modern human stone tool studies is the fact that most modern human cultures do not make or use stone tools any more because we have access to more efficient materials and tools to fulfill our technological needs. Furthermore, how previous knowledge of other technological artefacts influences the behaviour of the participants in experimental stone tool studies is often unaccounted for (although see exceptions in Roux and David, 2005; Geribàs et al., 2010; Nonaka et al., 2010; Pargeter et al., 2019). Ethnographic studies of contemporary stone tool makers and users partially solve some of these limitations by studying lithic technology within its cultural context. However, even studies focusing on traditional stone knappers present certain caveats. For instance, studies of contemporary stone tool use have generally been conducted with sedentary populations, whereas our ancestors during most of our evolutionary history were mobile foragers (McCall, 2012). Therefore, whilst ethnographic studies of current lithic technology production have the potential to highlight universal processes, such as the role of social learning and apprenticeship on stone tool production, it is important to consider that they involve complex contemporary societies. As Stout points out, each study can only provide a single example of the “myriad ways in which lithic technologies might be incorporated into modern human societies” (Stout, 2002, p. 696).

Overall, modern humans represent the most comparable models to investigate early hominin stone tool behaviours, and particularly knapping. Modern humans are the living species phylogenetically closest to early hominins, with the most similar anatomy from all living primates. Despite potential cognitive and behavioural differences between modern human populations and between our species and our hominin ancestors, modern humans are still the most representative models to reconstruct early hominin stone tool repertoires. Indeed, so far, modern humans are the only known species that intentionally produces and uses stone tools.

**Macaques.** Macaques (*Macaca* spp.) have rarely been used as models for early hominin tool use compared to other primate



species. This is perhaps due to the fact that the LCA between *Homo* and *Macaca* lived 23 Ma (Glazco and Nei, 2003; but see Perelman et al., 2011). In addition, despite early reports of tool use in wild populations (oyster-hammering; Carpenter, 1887), macaques have only recently started to be included in comparative studies of tool use after these early reports were confirmed in some populations of Burmese long-tailed macaques *Macaca fascicularis aurea* (henceforth: *Mfa*) from Southeast Thailand (Malaivijitnond et al., 2007). *Mfa* have been described to use stone tools to process encased foods such as shellfish, sea almonds, and oil palm nuts via ‘pound-hammering’ and rock oysters using ‘axe-hammering’ (Falótico et al., 2017). Moreover, these macaques have been shown to choose certain types of stone tools based on the food they are processing: pounding hammers are used to open nuts and shellfish on stone anvils, whilst naturally occurring axe hammers are used to pick at rock oysters attached to stone substrates (Gumert et al., 2009). One peculiarity of these stone tool behaviours is that they seem to be restricted to only the *Mfa* subspecies of macaques, as *Macaca fascicularis fascicularis* (henceforth: *Mff*), who share the same habitat as *Mfa*, have never been observed to use stones in the wild or captivity (Malaivijitnond et al., 2007; Bandini and Tennie, 2018). However, hybrid *Mfa* × *Mff* populations exist, and within these populations, the individuals that were identified as having a more “*Mfa* phenotype” were also more likely to use stone tools, therefore suggesting a strong genetic component to this behaviour (Gumert et al., 2019).

Macaques have been proposed to represent useful model organisms to reconstruct hominin stone tool use in coastal environments (Gumert and Malaivijitnond, 2012). Due to the relative climatic stability of coastal environments, some have argued that early hominins may have used them as refuge landscapes during times of high climatic unpredictability (Joordens et al., 2019). Thus, understanding how different species, such as long-tailed macaques, exploit coastal resources can provide insight into how early hominins may have survived and exploited these environments. Gumert and Malaivijitnond (2012, p. 454) argued that “it is highly likely that historically humans, and potentially other hominins, may have captured and consumed coastal resources in an individualistic fashion like macaques”. Indeed, the axe-hammering behaviour observed in *Mfa* is similar to behaviours practiced until recently by some populations of modern humans (e.g., Tindale, 1977). In the first archaeological excavation of a Burmese macaque stone hammering site, Haslam et al. (2016) identified ten macaque stone tools based on superficial use-wear patterns such as pitting or crushing beneath an overhanging basalt boulder with abundant oysters. The authors even reported step-terminated fractures similar to those found in human archaeological sites in some of the stone tools recovered (Haslam et al., 2016).

More recently, wild long-tailed macaques in Thailand have been described to engage in yet another stone percussive behaviour, namely nut-cracking of oil palm nuts from an abandoned plantation using stone hammers and anvils (Luncz et al., 2017). Proffitt et al. (2018b) conducted the first technological and use-wear characterisation of 13 hammerstones identified as having been used for nut-cracking of oil palm nuts. The tools showed evidence of extensive battering and crushing and six of the analysed hammerstones possessed overlapping flake scars indicative of unintentionally detached stone pieces. Furthermore, some of the recovered fractured stones were detached from naturally occurring acute angles and presented conchoidal fracture (typical of flakes of anthropogenic origin, Proffitt et al., 2018b). These stone detachments were considered to be unintentional and resulting from miss-hits.

Other than for opening encased food sources, some reports exist of captive macaques using stones to push out food from inside tubes (Tokida et al., 1994), and stone handling behaviours (albeit not strictly tool use) have been observed in various macaque species both in the wild and captivity (Nahallage and Huffman, 2007). Indeed, stone handling and play behaviours in juveniles have been suggested to be pre-requisites for the development of later stone tool use in long-tailed macaques (Tan, 2017).

**Macaque conclusion.** Given that long-tailed macaques are phylogenetically distantly related to humans and that they do not fracture stones intentionally, it might seem unlikely that they represent appropriate models to better understand early hominin knapping. However, this species’ stone tool repertoire can be useful for inferring other aspects of hominin stone technologies. The fact that two subspecies of long-tailed macaques (*Mfa* and *Mff*) have developed different strategies to exploit coastal environments (with and without tools) calls for further study of their stone tool repertoires (see also Gumert and Malaivijitnond, 2012; Gumert et al., 2019; Haslam et al., 2013) and of the role that genetic predispositions play in the development of stone tool behaviours in primates (Gumert et al., 2019). Long-tailed macaques’ stone tool behaviours can also be useful to reconstruct the potential stone tool repertoires employed by early humans in coastal environments, which likely played an important role in human evolution (Joordens et al., 2019). Indeed, coastal environments may have been used by early hominins as refuges during periods of climatic instability, allowing them to gradually distribute themselves inland via humid corridors across different environments (Cuthbert et al., 2017; Joordens et al., 2019). In addition, *Mfa* stone tools for pound- and axe-hammering represent the first comparative use-wear catalogue generated by a non-human primate species of the marks produced on stone tools by the exploitation of coastal prey. The fact that some traditional stone knapping societies also used stone tools to remove oysters from conglomerates makes axe-hammering in macaques a particularly salient behaviour for cross-species comparisons. Finally, macaque nut-cracking provides an additional comparative sample to that of chimpanzees and modern humans to reconstruct the form of this behaviour as well as the signature that it might leave in archaeological artefacts.

**Capuchins.** Capuchin monkeys (encompassing the *Sapajus* and *Cebus* genera), possess the broadest stone tool use repertoires among non-human primate species, using stone tools for a variety of foraging purposes both in the wild and captivity (Mannu and Ottoni, 2009; Monteza-Moreno et al., 2020; Arroyo et al., 2021). Bearded capuchins (*Sapajus libidinosus*) use stones as digging tools to access underground storage organs of plants as well as trapdoor spiders in Serra da Capivara National Park, Brazil (Falótico et al., 2017). This same capuchin population uses stones to smash deciduous wood in order to access larvae and worms (Ottoni and Izar, 2008), and female capuchins in this population have been observed to throw stones as a courtship behaviour (Falótico and Ottoni, 2013). Mannu and Ottoni (2009) observed three instances of wild bearded capuchins using small stones to dislodge larger ones from conglomerate rock, with the large stones then being used as hammerstones either to pound tree trunks or pulverise other stones. These observations were interpreted as indicative of a capacity for sequential stone tool use in this species (Mannu and Ottoni, 2009). White-faced capuchins (*Cebus capucinus imitator*) in Coiba National Park, Panama, use stones and anvils to access encased foods in coastal areas such as seeds, hermit crabs, terrestrial crabs and marine snails (Barrett

et al., 2018). Yet, one of the most studied stone tool use behaviour in capuchins is nut-cracking using stone hammers and anvils, which is present in all tool-using capuchin repertoires. Nut-cracking seems to be a behaviour that can be acquired relatively easily by capuchins, demonstrated by the fact that naïve, captive capuchins (*Sapajus [Cebus] apella*) spontaneously started cracking nuts with stone hammers when presented with all necessary materials, and without requiring any a priori demonstrations (Visalberghi, 1987). These findings suggest that certain species of capuchins may have some genetic predispositions for stone tool use, or at least stone manipulation (Hayashi, 2015).

Following excavations of a wild bearded capuchin nut-cracking site, this behaviour in Serra da Capivara National Park has been estimated to be at least 2400 years old (Falótico et al., 2019). The authors identified several hammerstones with flake detachments but concluded that “the capuchin hammerstones at Caju BPF2 do not show the same percussive damage as typical human knapping hammerstones. Instead, it consists of repeated, superimposed incipient cones of percussion often located on flat surfaces, typical of capuchin percussive activities” (Falótico et al., 2019). Modern wild bearded capuchins from the same population where these excavations were conducted have also been observed to unintentionally detach sharp-edged stones, some of which present certain superficial morphological resemblance to Oldowan flakes (Proffitt et al., 2016). Most capuchin sharp-edged stones are a by-product of a behaviour known as ‘stone on stone’ (SoS) percussion, in which the capuchins use a hammerstone to strike (and often fracture) other stones embedded in a conglomerate (Proffitt et al., 2016). Despite the capuchins often producing sharp edges as a by-product of SoS percussion, they have never been observed using them (Proffitt et al., 2016), suggesting that sequential tool use in this species does not extend to the production and use of sharp stones. Although the purpose behind this behaviour is still unclear, it has been suggested that the capuchins may lick the dust produced during SoS percussion in order to ingest minerals (Proffitt et al., 2016).

Recently, Arroyo and colleagues (2021) analysed wild bearded capuchin pounding tools used for three different purposes in Serra da Capivara National Park: digging tools, pounding tools for soft encased foods, and pounding tools for SoS behaviour. This analysis demonstrated that the tool function could be determined based on the use-wear patterns observed on the tools (Arroyo et al., 2021). However, some tools (primarily the ones used for digging) did not display clear macroscopic modifications, leading the authors to suggest that the rate of digging behaviours in capuchins and early hominins is likely under-represented in the primate and Plio-pleistocene archaeological record. Studies such as the one conducted by Arroyo et al. (2021) contribute to a growing reference collection of stone tools used across extant primates that allow for inferences on potential percussive behaviours of early hominins.

In captivity, an earlier study investigated whether capuchins (*Sapajus apella*) would intentionally make flake-like objects and use them when provided with the right materials and the motivation to do so in the form of a food-baited puzzle box (Westergaard and Suomi, 1994). The study followed a similar testing paradigm to that pioneered by Wright (1972) and later used with Kanzi the bonobo (Toth et al., 1993). Westergaard and Suomi (1994) reported that the naïve capuchins, who were unenculturated and had not been provided with any training or demonstrations of stone tool making or using behaviour, spontaneously detached flake-like stones. In a later experimental condition, the authors found that capuchins used stones provided by humans (presumably with sharp-edges) as cutting tools to open a puzzle box. Furthermore, in this second condition, one capuchin made and subsequently used a flake-like stone as a

cutting tool to open a baited puzzle box. This study currently constitutes the only evidence that a non-human primate can intentionally make a sharp-edged stone *and* use it as a cutting tool. Westergaard and Suomi (1994, p. 403) interpreted their findings as suggesting that: “the ability to make and use stone tools is a primitive behavioural capacity that may have been ‘discovered’ numerous times and utilised by more than one hominoid genus and species” (see also Whiten et al., 2009; Tennie et al., 2017).

Although Westergaard and Suomi (1994) acknowledge that the stone production methods used by the capuchins were ‘primitive’ compared to those hypothesised for hominins 2 Ma, the authors argue that lithic technologies may have evolved in the hominin lineage earlier than suggested in the literature. The extensive stone tool culture observed in capuchins compared to other primates, and the fact that they provide (at least for now) the only evidence of intentional stone production outside the human lineage, suggests that capuchins may be an overlooked species when modelling the early stages of hominin lithic culture (see also McGrew et al., 2019). Even anatomically, some have argued that capuchins may be better models for pre-modern hominins than other primates. For example, Sayers et al. (2012) write that despite their small body size and more primitive forelimbs, “Old World monkeys are still functionally preferable as subjects [...] because their longer and much more mobile spines provide at least partial amelioration of the otherwise compulsory bent-hip-bent-knee gait dictated by the highly specialised African ape pelvis and lumbar spine”.

*Capuchin conclusion.* The findings from studies on stone tool-using capuchins (including both *Cebus* spp. and *Sapajus* spp.) suggest that these species may provide relevant insight into the emergence of lithic technologies in primates (see also McGrew et al., 2019). Whilst it is acknowledged that capuchins have extensive stone tool use repertoires, many still favour chimpanzees (or great apes more generally) as models over capuchins, most likely due to the closer phylogenetic relationship to our species (e.g., see Whiten, 2015 but see McGrew et al., 2019). Yet, the capuchin stone tool use repertoire may actually be the most relevant among non-human primates to understand the stone behaviours that might have preceded the emergence of lithic technologies in our lineage. The fact that capuchins are (so far) the only non-human primate species that has been found to spontaneously make *and* use flake-like objects (without prior human training and demonstrations; Westergaard and Suomi, 1994) suggests that this ability might be an example of convergent evolution in the primate lineage (at least once in the human lineage and once in capuchins, Bandini et al., 2021). As making and using flakes is not a common behaviour in capuchins, and currently only occurs in specific human-manipulated environments (in which the need to make such tools is artificially created), this provides an invaluable opportunity to explore the mechanisms behind the emergence of knapping in a non-human species. Therefore, contrary to the current approach in the literature of using great apes (and especially chimpanzees) as models of early hominin cognition associated with lithic technologies, some species of monkeys such as capuchins may be an even more appropriate model species than previously acknowledged.

Overall, further capuchin experiments might provide valuable insight into the initial developmental stages of hominin knapping. In addition, capuchin species can help us build more informed hypothesis regarding the diversity of early hominin stone tool repertoire. Lastly, capuchin percussive tools represent important references to investigate the signature marks that different percussive behaviours leave on stone implements.

**Other animals.** Although less often discussed, some non-primate species have also been observed to unintentionally fracture stones. For example, domestic donkeys have been reported to produce seemingly complex cores with conchoidal breakages during “self-trimming” of their hooves that present morphological characteristics traditionally used to identify hominin artefacts (Domínguez-Solera et al., 2021). Other non-primate species have been observed using stones as tools, both in the wild and in captivity. For example, sea otters (*Enhydra lutris*) use stone tools to pound open encased invertebrate prey (Fujii et al., 2015), a behaviour that has been compared to macaque pound-hammering. Similar to the macaques, sea otters use rocks as hammers to break the exoskeleton of encased food or as anvils to pry them open from underwater rocks (Fujii et al., 2015). Recent studies have shown that, as is the case with macaque pounding, the stone foraging behaviour of sea otters leaves traces on the substrate that can be recognised and analysed using archaeological methods (Haslam et al., 2019). Although sea otters are currently the only otter species known to use tools, the majority of otter species have been observed to manipulate stones and practice stone handling behaviour, thus suggesting that otters may have a genetic predisposition to handle stones (Bandini et al., 2021).

Stone tool use has also been described in several species of birds (Lefebvre et al., 2002). Wild bristle-thighed curlews (*Numenius tahitiensis*) across various Pacific Islands drop coral stones on top of albatross eggs in order to ingest the egg’s contents (Marks and Hall, 1992); captive black breasted buzzards (*Hamirostra melanosternon*) have also been observed to drop stones to crack open eggs (Debus, 1991) and both wild and captive Egyptian vultures (*Neophron percnopterus*) have been reported to use stones to hammer eggs from different species (Barcell et al., 2015) as well as to smash lizards (van Lawick-Goodall, 1971). Multiple bird species (rooks: *Corvus frugilegus*, Eurasian jays: *Garrulus glandarius*, New Caledonian crows: *Corvus moneduloides*, great-tailed grackles: *Quiscalus mexicanus*, and western scrub-jays: *Aphelocoma californica*) have been tested in captive settings using the Aesop’s fable paradigm, in which stones are dropped into water to raise the level of a floating reward (reviewed by Jelbert et al., 2015; Ghirlanda and Lind, 2017). Recently, this paradigm was adapted for use with raccoons (*Procyon lotor*; Stanton et al., 2017).

While using stones in contexts such as the Aesop’s fable task may not provide direct insights into hominin stone tool behaviours, this research may reveal the capacity of non-primate species to reason about the causal properties of stones (for example, selecting large over small stones to complete the task; Bird and Emery, 2009). However, a recent meta-analysis demonstrated that apparent causal understanding inferred from Aesop’s fable experiments may be better explained by trial-and-error learning (Ghirlanda and Lind, 2017).

Among arthropods, digger wasps (*Ammophila urinaria* and *Ammophila aberti*) seal their burrows where they lay eggs with soil, which then they proceed to compact using a pebble held between their mandibles (Brockmann, 1985).

**Other animals conclusion.** Unintentional stone fracturing by primate (Proffitt et al., 2016) and non-primate animals (such as donkeys, Domínguez-Solera et al., 2021), serve as a reminder that non-anthropogenic processes can generate material traces that could be confounded with hominin artefacts. Although non-primate tool use is less relevant than primate tool use to reconstruct the evolution of technology in our lineage (see Table 1), some insight for hominin stone tool repertoires can be drawn from studying other animals. Indeed, tool-using animals outside of the primate taxon represent an important source of

comparative data to investigate the ecological, cognitive, and neurological drivers of the evolution of tool use (including stone tool use) in the animal kingdom in general, and in our lineage specifically (Bentley-Condit and Smith, 2010; Hunt et al., 2013). Food scarcity (Moura and Lee, 2004), brain size (Lefebvre et al., 2002), energetic costs derived from travel (Gruber et al., 2016), genetic factors (Gumert et al., 2019) and innovation rate (Reader and Laland, 2003), to cite a few, have been deemed important correlates of tool use. However, the ways in which these and other factors interact and lead to the emergence of tool use in some species (like certain hominin species) but not in others, remains an open question attracting growing research efforts (Beck, 1980; Hunt et al., 2013).

## Conclusions

Given the impossibility of directly investigating the stone tool repertoire of early hominins, there are obvious advantages to using extant primates as behavioural models for understanding the extent of early hominin stone tool abilities. Our goal in this review has been to highlight the different contributions that each species can make to further our knowledge on the emergence and expression of stone tool behaviours. However, as discussed above, there are also limitations to the conclusions that can be drawn from primate studies, and care should be taken when directly extrapolating extant primate behaviour to early hominins (see also Table 1). For example, in some cases, capuchin monkeys might represent more appropriate models to investigate early hominin knapping than chimpanzees, given that capuchins fracture stones intentionally and have been reported to use sharp-edged stones as cutting tools in captivity. Furthermore, studies including multiple stone tool-using species have more potential than single-species studies to reveal environmental and/or social factors that might have fueled the emergence and expression of lithic technologies in our lineage. For instance, comparative studies of macaque, capuchin, chimpanzee, and modern human nut-cracking might provide valuable data to better understand when and why this percussive foraging behaviour was practiced by our hominin ancestors.

Although their value as models to reconstruct early hominin stone tool repertoires is limited, non-stone tool-using species in the wild such as orangutans, bonobos, and gorillas can provide useful information to reconstruct the social structure, anatomical features and plant tool repertoires of various early hominin species. Wood artefacts are extremely rare in Palaeolithic archaeological assemblages (Oakley et al., 1977; Thieme, 1997) and therefore it is particularly in this context that extant primates are valuable models of early hominin material culture. For instance, studies on great ape termite and ant foraging (McBeath and McGrew, 1982; Nishida and Hiraiwa, 1982; Sanz et al., 2004; Lonsdorf, 2006; Bogart and Pruetz, 2008) alongside modern human studies, have been invaluable in formulating hypotheses about patterns of insectivory in early hominins. Similarly, primatological and ethnographic studies of plant tool selection (Almeida-Warren et al., 2017; Pascual-Garrido, 2018, 2019; Pascual-Garrido and Almeida-Warren, 2021) and plant tool use (Motes-Rodrigo et al., 2019) provide a unique set of data to formulate hypotheses about the use of perishable materials by early hominins, and the behavioural precursors of stone tool use, a behavioural set almost completely invisible in the archaeological record.

In terms of human primates, modern WEIRD humans and traditional stone knapping populations can be useful for inferring early hominin stone tool use, both in terms of knapping and percussive behaviours. Despite being one of the best models to investigate early hominin stone tool repertoires, it is important to

**Table 1 Summary table of the strengths and limitations of using different primate species as models of early hominin stone behaviours as well as a description of the most appropriate use of each species in comparative studies aimed at reconstructing early hominin stone repertoires.**

Species	Strengths	Limitations	Valuable models for
Chimpanzees ( <i>Pan troglodytes</i> )	<ul style="list-style-type: none"> <li>• Close phylogenetic ties to humans (Langergraber et al., 2012)</li> <li>• Large body of research on both wild and captive chimpanzee behaviours</li> <li>• Most extensive tool use repertoires among primates (Whiten et al., 1999)</li> <li>• Some (but not all) populations use stone tools for percussive behaviours, including some present in modern humans</li> </ul>	<ul style="list-style-type: none"> <li>• 6 Ma of independent evolution from hominins (e.g., Sayers et al., 2012)</li> <li>• Difference in behaviour across chimpanzee subspecies; therefore no ‘one’ chimpanzee model</li> <li>• No evidence of intentional or systematic sharp stone production</li> <li>• Extant chimpanzees live in different environments to early hominins or the LCA (Sayers et al., 2012)</li> </ul>	<ul style="list-style-type: none"> <li>• Percussive stone foraging behaviours, particularly nut-cracking and its signature in archaeological artefacts</li> </ul>
Bonobos ( <i>Pan paniscus</i> )	<ul style="list-style-type: none"> <li>• Close phylogenetic ties to humans (Langergraber et al., 2012)</li> <li>• Have the ability to use tools (Gruber and Clay, 2016), including stone tools (Neufuss et al., 2017)</li> </ul>	<ul style="list-style-type: none"> <li>• Much less intensive research effort on bonobos than chimpanzees</li> <li>• Rarely use tools and have a much smaller tool use repertoire</li> <li>• Currently the only study on bonobo stone tool manufacture and use tested enculturated bonobos, limiting the conclusions that can be drawn at the species level</li> </ul>	<ul style="list-style-type: none"> <li>• Drawing more robust conclusions about the stone tool using abilities of the Pan-Homo LCA (Dual-Pan model; Gruber and Clay, 2016)</li> <li>• Hominin species that had the ability to use tools but did not express it</li> </ul>
Orangutans ( <i>Pongo abelii</i> )	<ul style="list-style-type: none"> <li>• Second most extensive tool use repertoires among primates, after chimpanzees (van Schaik et al., 2003)</li> <li>• Engage in lithic and non-lithic percussive behaviour in captivity (Motes-Rodrigo et al., 2022; Bandini et al., 2021)</li> </ul>	<ul style="list-style-type: none"> <li>• Oldest common ancestor between hominins and non-human great apes (-13 Ma, Glazco and Nei, 2003)</li> <li>• No currently known stone tool behaviours in the wild</li> </ul>	<ul style="list-style-type: none"> <li>• Reconstructing the tool use repertoires of hominoid species that lived in the forest canopy and rarely foraged on the ground, as well as of more solitary species</li> </ul>
Gorillas ( <i>Gorilla gorilla</i> )	<ul style="list-style-type: none"> <li>• Have the ability to use tools in captivity (e.g. Lonsdorf et al., 2009)</li> </ul>	<ul style="list-style-type: none"> <li>• Distantly related to humans (-7 Ma, Glazco and Nei, 2003)</li> <li>• Rarely use tools in the wild</li> <li>• No evidence yet for stone tool use (Bandini and Tennie, 2020)</li> </ul>	<ul style="list-style-type: none"> <li>• Comparative studies with stone tool using great apes</li> </ul>
Modern Humans ( <i>Homo sapiens</i> )	<ul style="list-style-type: none"> <li>• Very closely related to various early hominin species</li> <li>• Easily accessible as test subjects</li> <li>• Can instruct subjects as to the aims and requirements of the study</li> <li>• Can test children and traditional stone knapper communities for cross-cultural and ontogenetic studies</li> <li>• Engage in intentional sharp-edged stone detachment and lithic percussive behaviours</li> </ul>	<ul style="list-style-type: none"> <li>• Most easily accessible test subjects are from predominantly WEIRD backgrounds, limiting the ability to generalise findings to all populations (Henrich et al., 2010)</li> <li>• Certain cognitive mechanisms present in modern humans are likely the result of cultural rather than genetic evolution (Heyes, 2018), meaning that they may have been absent or much less developed in our hominin ancestors</li> <li>• The vast majority of modern human cultures do not make or use early stone tools any more</li> <li>• Studies of contemporary stone tool use have generally been conducted with sedentary populations, whereas our ancestors during most of our evolutionary history were mobile foragers</li> </ul>	<ul style="list-style-type: none"> <li>• Hominin knapping (particularly studies with non-WEIRD populations)</li> <li>• Hominin lithic percussion (particularly studies with non-WEIRD populations)</li> </ul>
Macaques ( <i>Macaca fascicularis</i> )	<ul style="list-style-type: none"> <li>• Some subspecies use stone tools to forage for food in coastal environments (e.g., Gumert et al., 2009), including behaviours that are, or used to be, present in traditional stone knapping communities (Tindale, 1977)</li> <li>• Present a repertoire of stone tool use behaviours</li> </ul>	<ul style="list-style-type: none"> <li>• Distantly related to humans (-23 Ma, Glazco and Nei, 2003)</li> <li>• Most macaque species do not use stone tools</li> </ul>	<ul style="list-style-type: none"> <li>• Reconstructing stone percussive repertoires in coastal environments (Gumert and Malaivijitnond, 2012)</li> <li>• Further understanding of early hominin nut cracking and its signature in archaeological artefacts</li> </ul>
Capuchins ( <i>Sapajus libidinosus/apella</i> )	<ul style="list-style-type: none"> <li>• Extensive tool use repertoires including the widest range of stone tool use repertoires of all tool-using primates (Arroyo et al., 2021)</li> <li>• Evidence for dissociated sharp stone production and use abilities in captive</li> </ul>	<ul style="list-style-type: none"> <li>• Distantly related to humans and other great apes (-33 Ma, Glazco and Nei, 2003)</li> <li>• No evidence of intentional or systematic sharp stone production in the wild</li> </ul>	<ul style="list-style-type: none"> <li>• Initial stages of hominin lithic technologies (knapping) and precursors of intentional stone tool manufacture</li> <li>• Potential diversity of behaviours included in the early hominin stone tool use repertoire</li> </ul>

**Table 1 (continued)**

Species	Strengths	Limitations	Valuable models for
Other animals	<p>capuchins and some evidence for intentional sharp stone tool production in captivity (Westergaard and Suomi, 1994)</p> <ul style="list-style-type: none"> <li>• Various species use stone tools, including for percussion</li> <li>• Provide a different perspective on stone tool use (e.g., outgroup)</li> </ul>	<ul style="list-style-type: none"> <li>• Very distantly related to humans, therefore inferences based on phylogenetic similarities cannot be made</li> <li>• Often these animals live in very different environments to early hominins</li> </ul>	<ul style="list-style-type: none"> <li>• Further understanding of early hominin percussive behaviours (e.g. nut cracking) and their signature in archaeological artefacts</li> <li>• Further insight into the conditions behind the emergence of stone tool use in animals with different environmental pressures and cognitive demands/abilities</li> </ul>

recognise the limitations of extrapolating from modern humans to extinct hominins, considering how much our cognition and dependency on language and culture has changed in the last 3 million years. The same argument can be made for some extant primates like the *Pan* species, who have undergone 6–7 Ma of evolution since the last common ancestor of *Pan* and *Homo*.

Some of the studies that we have highlighted in this review involved individuals living in captivity, which might raise questions regarding the validity of these subjects as representative of their wild counterparts. This concern is often driven by the fact that individuals in captivity are not subject to the same pressures and stressors as in the wild, which some have argued could alter captive animals' priorities, needs, and behaviour (Boesch and Boesch-Achermann, 2000). However, this conclusion may be premature. Dedicated research into concrete differences between captive and wild subjects is still scarce, and more detailed evaluations on a case by case basis are required before dismissing test subjects as non-representative of their wild conspecifics. Recently, Webster and Rutz (2020) proposed the STRANGE framework to evaluate the suitability of an individual for a particular experiment (but see Farrar and Ostojic, 2020). The authors argue that a list of factors should be systematically evaluated when conducting animal cognition studies: Social background, Trappability, Rearing history, Acclimation, Natural changes in responsiveness, Genetic makeup, and Experience (forming the acronym, STRANGE). We agree that evaluations such as those proposed by Webster and Rutz (2020), rather than captivity per se, should be conducted to evaluate the suitability of animal subjects for comparative studies.

Over the last decade, a growing number of initiatives and collaborations between archaeologists, primatologists and anthropologists have been established focusing on primates as extant behavioural models of early hominins. Indeed, the new field of primate archaeology (Haslam et al., 2017) fosters the application of standardized methods to collect and analyse primate tools so they can be compared with archaeological artefacts. However, there are still gaps in the literature. For instance, with regards to studying the conditions behind the emergence of flaked stone technology in the archaeological record, early primate knapping studies (Wright, 1972; Toth et al., 1993; Westergaard and Suomi, 1994) should be replicated and extended to unenculturated and untrained subjects (e.g., Bandini et al., 2021; Motes-Rodrigo et al., 2022). Further studies investigating the stone-related abilities of apes and monkeys under controlled conditions (e.g., Bandini and Tennie, 2018) would also allow us to examine the value of these testing paradigms and to explore the extents and limitations of primate abilities to make and use stone tools.

Finally, primate studies are intrinsically interesting in their own right, and it is not always essential that findings from primatology be tied back to early hominins and the evolution of our own species. Often, primate behaviour studies attempt to relate their

findings to early hominins, even in cases where the justification for doing so may be weak. This may be partly due to an incentive for high-impact publications to include claims regarding the broader evolutionary implications of study results and to relate them to our own species. Perhaps it is time to lift this pressure from primate researchers to link their findings back to human evolution, and to recognise the contributions and limitations of using extant primates as behavioural models for extinct hominins.

### Data availability

Data sharing not applicable to this article as no datasets were generated or analysed.

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### References

- Almeida-Warren K, Sommer V, Piel AK, Pascual-Garrido A (2017) Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, Western Tanzania. *Am J Phys Anthropol* 164:292–304. <https://doi.org/10.1002/ajpa.23269>
- Andrefsky W (2009) The analysis of stone tool procurement, production, and maintenance. *J Archaeol Res* 17:65–103. <https://doi.org/10.1007/s10814-008-9026-2>
- Arroyo A, Falótico T, Burguet-Coca A, Expósito I, Quinn P, Proffitt T (2021) Use-wear and residue analysis of pounding tools used by wild capuchin monkeys (*Sapajus libidinosus*) from Serra da Capivara (Piauí, Brazil). *J Archaeol Sci* 35:102690. <https://doi.org/10.1016/j.jasrep.2020.102690>
- Arroyo A, Hirata S, Matsuzawa T, de la Torre I (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:e0166788. <https://doi.org/10.1371/journal.pone.0166788>
- Arthur KW (2010) Feminine knowledge and skill reconsidered: women and flaked stone tools. *Am Anthropol* 112:228–243. <https://doi.org/10.1111/j.1548-1433.2010.01222.x>
- Bakeman R, Adamson LB, Konner M, Barr RG (1990) !Kung infancy: the social context of object exploration. *Child Dev* 61:794. <https://doi.org/10.2307/1130964>
- Bandini E, Bandini M, Tennie C (2021) A short report on the extent of stone handling behaviour across other species. *Anim Behav Cogn* 8:15–22. <https://doi.org/10.26451/abc.08.01.02.2021>
- Bandini E, Motes-Rodrigo A, Archer W, Minchin T, Axelsen H, Hernandez-Aguilar RA, McPherron SP, Tennie C (2021) Naïve, unenculturated chimpanzees fail to make and use flaked stone tools. *Open Res Eur* 1:20. <https://doi.org/10.12688/openreseurope.13186.1>
- Bandini E, Tennie C (2018) Naïve, captive long-tailed macaques (*Macaca fascicularis fascicularis*) fail to individually and socially learn pound-hammering, a tool-use behaviour. *R Soc Open Sci* 5:171826. <https://doi.org/10.1098/rsos.171826>
- Bandini E, Tennie C (2020) Exploring the role of individual learning in animal tool-use. *PeerJ* 8:e9877. <https://doi.org/10.7717/peerj.9877>
- Bandini E, Grossmann J, Funk M, Albiach-Serrano A, Tennie C (2021) Naïve orangutans (*Pongo abelii* and *Pongo pygmaeus*) individually acquire nut-cracking using hammer tools. *Am J Primatol* 83:e23304. <https://doi.org/10.1002/ajp.23304>
- Barcell M, Benitez JR, Solera F, Román B, Donazar JA (2015) Egyptian vulture (*Neophron percnopterus*) uses stone-throwing to break into a Griffon vulture

- (*Gyps fulvus*) egg. *J Rapt Res* 49:521–522. <https://doi.org/10.3356/rapt-49-04-521-522.1>
- Barrett BJ, Monteza-moreno CM, Dogandžić T, Zwyns N, Ibáñez A, Crofoot MC (2018) Habitual stone-tool aided extractive foraging in white-faced capuchins, *Cebus Capucinus*. *Anim Behav Cogn* <https://doi.org/10.1101/351619>
- Beck BB (1980) Animal tool behavior: the use and manufacture of tools. Garland Press, New York
- Bentley-Condit V, Smith (2010) Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour* 147:185–32A. <https://doi.org/10.1163/000579509X12512865686555>
- Bird CD, Emery NJ (2009) Rooks use stones to raise the water level to reach a floating worm. *Curr Biol* 19:1410–1414. <https://doi.org/10.1016/j.cub.2009.07.033>
- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T (2003) Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 6(4):213–223. <https://doi.org/10.1007/s10071-003-0183-x>
- Biro D, Sousa C, Matsuzawa T (2006) Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut cracking and leaf folding. In: Matsusaka T, Tomonaga M, Tanaka M (eds.) *Cognitive development in chimpanzees*. Springer, Tokyo
- Boesch C, Boesch H (1983) Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behavior* 83:265–286. <https://doi.org/10.1163/156853983X00192>
- Boesch C, Boesch H (1984) Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *J Hum Evol* 13:415–440. [https://doi.org/10.1016/s0047-2484\(84\)80055-x](https://doi.org/10.1016/s0047-2484(84)80055-x)
- Boesch C, Boesch-Achermann H (2000) *The chimpanzees of the Tai Forest: behavioural ecology and evolution*. Oxford University Press, Oxford
- Bogart SL, Pruett JD (2008) Ecological context of savanna chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *Am J Primatol* 70:605–612. <https://doi.org/10.1002/ajp.20530>
- Breuer T, Ndongou-Hockemba M, Fishlock V (2005) First observation of tool use in wild gorillas. *PLoS Biol* 3:e380. <https://doi.org/10.1371/journal.pbio.0030380>
- Bril B, Foucart J (2005) Enacting the perception of the affordances of potential tools. I: the case of children hammering. In: Heft H, Marsh KL (eds.) *Studies in perception and action VIII*. Lawrence Erlbaum Associates, Mahwah, pp. 3–6
- Bril B, Parry R, Dietrich G (2015) How similar are nut-cracking and stone-flaking? A functional approach to percussive technology. *Philos Trans R Soc Lond B: Biol Sci* 370:20140355. <https://doi.org/10.1098/rstb.2014.0355>
- Brockmann HJ (1985) Tool use in digger wasps (*Hymenoptera: Sphecinae*). *Psyche* 92:309–329. <https://doi.org/10.1155/1985/73184>
- Bunn HT (1981) Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291:574–577. <https://doi.org/10.1038/291574a0>
- Byrne F, Proffitt T, Arroyo A, de la Torre I (2016) A comparative analysis of bipolar and freehand experimental knapping products from Olduvai Gorge, Tanzania. New approaches to the study of Quartz lithic industries. *Quat Int* 424:58–68. <https://doi.org/10.1016/j.quaint.2015.08.018>
- Cane S (1992) Aboriginal perceptions of their stone tool technology: a case study from the Western Desert, Australia. *Aust Archaeol* 35:11–31. <https://doi.org/10.1080/03122417.1992.11681466>
- Carpenter A (1887) Monkeys opening oysters. *Nature* 36:53–53. <https://doi.org/10.1038/036053d0>
- Carvalho S, Biro D, McGrew WC, Matsuzawa T (2009) Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Anim Cogn* 12:103–114. <https://doi.org/10.1007/s10071-009-0271-7>
- Carvalho S, Cunha E, Sousa C, Matsuzawa T (2008) Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *J Hum Evol* 55:148–163. <https://doi.org/10.1016/j.jhevol.2008.02.005>
- Carvalho S, McGrew WC (2012) The origins of the Oldowan: why chimpanzees (*Pan troglodytes*) still are good models for technological evolution in Africa. In: Domínguez-Rodrigo M (ed.) *Stone tools and fossil bones: debates in the archaeology of human origins*. Cambridge University Press, Cambridge, pp. 222–244
- Carvalho S, Matsuzawa T, McGrew WC (2013) From pounding to knapping: how chimpanzees can help us to model hominin lithics. In: Sanz CM, Call J, Boesch C (eds.) *Tool use in animals: cognition and ecology*. Cambridge University Press, Cambridge, pp. 225–241
- Cataldo DM, Miglano AB, Vinicius L (2018) Speech, stone tool-making and the evolution of language. *PLoS ONE* 13:e0191071. <https://doi.org/10.1371/journal.pone.0191071>
- Chavaillon J (1976) Evidence for the technical practices of early Pleistocene Hominids, Shungura Formation, Lower Omo Valley, Ethiopia. In: Coppens Y, Howell FC, Isaac G, Leakey L (eds.) *Earliest man and environments in the lake Rudolf Basin*. University of Chicago Press, Chicago, p 565–573
- Clegg JM, Wen NJ, DeBaylo PH, Alcott A, Keltner EC, Legare CH (2020) Teaching through collaboration: flexibility and diversity in caregiver–child interaction across cultures. *Child Dev* <https://doi.org/10.1111/cdev.13443>
- Clegg JM, Wen NJ, Legare CH (2017) Is non-conformity WEIRD? Cultural variation in adults' beliefs about children's competency and conformity. *J Exp Psychol Gen* 146:428–441. <https://doi.org/10.1037/xge0000275>
- Connolly K, Dagleish M (1989) The emergence of a tool-using skill in infancy. *Dev Psychol* 25:894–912. <https://doi.org/10.1037/0012-1649.25.6.894>
- Cuthbert MO, Gleeson T, Reynolds SC, Bennett MR, Newton AC, McCormack CJ, Ashley GM (2017) Modelling the role of groundwater hydro-refugia in East African hominin evolution and dispersal. *Nat Comm* 8:15696. <https://doi.org/10.1038/ncomms15696>
- Davidson I, McGrew WC (2005) Stone tools and the uniqueness of human culture. *J R Anthropol Inst* 11:793–817. <https://doi.org/10.1111/j.1467-9655.2005.00262.x>
- de Beaune SA (2004) The invention of technology: prehistory and cognition. *Curr Anthropol* 45:139–162. <https://doi.org/10.1086/381045>
- Debus SJS (1991) Further observations on the black-breasted buzzard *Hamirostra melanosternon* using stones to break eggs. *Aust Field Ornithol* 14:138–143. <https://doi.org/10.3316/informit.583733742203342>
- Domínguez-Solera SD, Maíllo-Fernández J-M, Baquedano E, Domínguez-Rodrigo M (2021) Equids can also make stone artefacts. *J Archaeol Sci* 40:103260. <https://doi.org/10.1016/j.jasrep.2021.103260>
- Domínguez-Rodrigo M, Alcalá L (2016) 3.3-million-year-old stone tools and butchery traces? More evidence needed. *Paleoanthropology* 2016:46–53. <https://doi.org/10.4207/PA.2016.ART99>
- Dunmore CJ, Skinner MM, Bardo A, Berger LR, Hublin JJ, Pahr DH, Rosas A, Stephens NB, Kivell TL (2020) The position of *Australopithecus sediba* within fossil hominin hand use diversity. *Nat Ecol Evol* 4:911–918. <https://doi.org/10.1038/s41559-020-1207-5>
- Fagard J, Lockman JJ (2009) Change in imitation for object manipulation between 10 and 12 months of age. *Dev Psychobiol* 52:90–9. <https://doi.org/10.1002/dev.20416>
- Faisal A, Stout D, Apel J, Bradley B (2010) The manipulative complexity of Lower Paleolithic stone toolmaking. *PLoS ONE* 5:e13718. <https://doi.org/10.1371/journal.pone.0013718>
- Falótico T, Ottoni EB (2013) Stone throwing as a sexual display in wild female bearded capuchin monkeys, *Sapajus libidinosus*. *PLoS ONE* 8:e79535. <https://doi.org/10.1371/journal.pone.0079535>
- Falótico T, Proffitt T, Ottoni EB, Staff RA, Haslam M (2019) Three thousand years of wild capuchin stone tool use. *Nat Ecol Evol* 3:1034–1038. <https://doi.org/10.1038/s41559-019-0904-4>
- Falótico T, Siqueira JO, Ottoni EB (2017) Digging up food: excavation stone tool use by wild capuchin monkeys. *Sci Rep* 7:62–78. <https://doi.org/10.1038/s41598-017-06541-0>
- Falótico T, Spagnoletti N, Haslam M, Luncz LV, Malaivijitnond S, Gumert M (2017) Analysis of sea almond (*Terminalia catappa*) cracking sites used by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). *Am J Primatol* 79:e22629. <https://doi.org/10.1002/ajp.22629>
- Farrar BG, Ostojic L (2020) It's not just the animals that are STRANGE. *Learn Behav* <https://doi.org/10.3758/s13420-020-00442-5>
- Fontaine B, Moisson PY, Wickings EJ (1995) Observations of spontaneous tool making and tool use in a captive group of western lowland gorillas (*Gorilla gorilla gorilla*). *Folia Primatol* 65:219–223. <https://doi.org/10.1159/000156892>
- Forss SIF, Motes-Rodrigo A, Hrubesch C, Tennie C (2019) Differences in novel food response between Pongo and Pan. *Am J Primatol* 81:e22945. <https://doi.org/10.1002/ajp.22945>
- Fox EA, Sitompul AF, van Schaik CP (1999) Intelligent tool use in Sumatran orangutans. In: Parker ST, Mitchell RW, Miles HL (eds.) *The mentalities of Gorillas and Orangutans*. Cambridge University Press, Cambridge
- Fujii JA, Ralls K, Tinker MT (2015) Ecological drivers of variation in tool-use frequency across sea otter populations. *Behav Ecol* 26:519–526. <https://doi.org/10.1093/beheco/aru220>
- Furlong EE, Boose KJ, Boysen ST (2008) Raking it in: the impact of enculturation on chimpanzee tool use. *Anim Cogn* 11:83–97. <https://doi.org/10.1007/s10071-007-0091-6>
- Furuichi T, Koops K, Ryu H, Sanz C, Sakamaki T, Morgan D, Tokuyama N (2015) Why do wild bonobos not use tools like chimpanzees do? *Behaviour* 152:425–460. <https://doi.org/10.1163/1568539x-00003226>
- Geribas N, Mosquera M, Vergés JM (2010) What novice knappers have to learn to become expert stone toolmakers. *J Archaeol Sci* 37:2857–2870. <https://doi.org/10.1016/j.jas.2010.06.026>
- Ghirlanda S, Lind J (2017) 'Aesop's fable' experiments demonstrate trial-and-error learning in birds, but no causal understanding. *Anim Behav* 123:239–247. <https://doi.org/10.1016/j.anbehav.2016.10.029>
- Glazco GV, Nei M (2003) Estimation of divergence times for major lineages of primate species. *Mol Bio Evol* 20:424–434. <https://doi.org/10.1093/molbev/msg050>
- Goodall J (1964) Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* 201:1264–1266. <https://doi.org/10.1038/2011264a0>

- Goren-Inbar N, Sharon G, Melamed Y, Kislev M (2002) Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. *PNAS* 99:2455–2460. <https://doi.org/10.1073/pnas.032570499>
- Green DJ, Alemseged Z (2012) *Australopithecus afarensis* scapular ontogeny, function, and the role of climbing in human evolution. *Science* 338:514–517. <https://doi.org/10.1126/science.1227123>
- Gruber T, Clay Z (2016) A comparison between bonobos and chimpanzees: a review and update. *Evol Anthropol* 25:239–252. <https://doi.org/10.1002/evan.21501>
- Gruber T, Clay Z, Zuberbühler K (2010) A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the Pan lineage. *Anim Behav* 80:1023–1033. <https://doi.org/10.1016/j.anbehav.2010.09.005>
- Gruber T, Zuberbühler K, Neumann CC (2016) Travel fosters tool use in wild chimpanzees. *eLife* 5:e16371. <https://doi.org/10.7554/eLife.16371>
- Grund C, Neumann C, Zuberbühler K, Gruber T (2019) Necessity creates opportunities for chimpanzee tool use. *Behav Ecol* 30:1136–1144. <https://doi.org/10.1093/beheco/anz062>
- Gumert MD, Kluck M, Malaivijitnond S (2009) The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. *Am J Primatol* 71:594–608. <https://doi.org/10.1002/ajp.20694>
- Gumert MD, Malaivijitnond S (2012) Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *Am J Phys Anthropol* 149:447–457. <https://doi.org/10.1002/ajpa.22143>
- Gumert D, Tan AWY, Luncz LV, Chua CT, Kulik L, Switzer AD, Haslam M, Iriki A, Malaivijitnond S (2019) Prevalence of tool behaviour is associated with pelage phenotype in intraspecific hybrid long-tailed macaques (*Macaca fascicularis aurea* × *M. f. fascicularis*). *Behavior* 156:1083–1125. <https://doi.org/10.1163/1568539X-00003557>
- Gumert M, Tan AWY, Malaivijitnond S (2019) Long-tailed macaque stone tool use in intertidal habitats. In: Barnett A, Matsuda I, Nowak K (eds.) *Primates in flooded habitats: ecology and conservation*. Cambridge University Press, Cambridge, pp. 144–147
- Harmand S, Lewis JE, Feibel CS, Lepre CJ, Prat S, Lenoble A et al. (2015) 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521:310–315. <https://doi.org/10.1038/nature14464>
- Haslam M (2014) On the tool use behavior of the bonobo-chimpanzee last common ancestor, and the origins of hominine stone tool use: Tool use in the bonobo-chimpanzee LCA. *Am J Primatol* 76:910–918. <https://doi.org/10.1002/ajp.22284>
- Haslam M, Fujii J, Espinosa S, Mayer K, Ralls K, Tinker MT, Uomini N (2019) Wild sea otter mussel pounding leaves archaeological traces. *Sci Rep* 9:4417. <https://doi.org/10.1038/s41598-019-39902-y>
- Haslam M, Gumert MD, Biro D, Carvalho S, Malaivijitnond S (2013) Use-wear patterns on wild macaque stone tools reveal their behavioural history. *PLoS ONE* 8:e72872. <https://doi.org/10.1371/journal.pone.0072872>
- Haslam M, Hernandez-Aguilar RA, Proffitt T, Arroyo A, Falótico T, Fragaszy D, Gumert M, Harris JWK, Huffman MA, Kalan AK, Malaivijitnond S, Matsuzawa T, McGrew W, Ottoni EB, Pascual-Garrido A, Piel A, Pruetz J, Schuppli C, Stewart F, Tan A, Visalberghi E, Luncz LV (2017) Primate archaeology evolves. *Nat Ecol Evol* 1:1431–1437. <https://doi.org/10.1038/s41599-017-0286-4>
- Haslam M, Luncz L, Pascual-Garrido A, Falótico T, Malaivijitnond S, Gumert M (2016) Archaeological excavation of wild macaque stone tools. *J Hum Evol* 96:134–138. <https://doi.org/10.1016/j.jhevol.2016.05.002>
- Hayashi M, Mizuno Y, Matsuzawa T (2005) How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. *Primates* 46:91–102. <https://doi.org/10.1007/s10329-004-0110-z>
- Hayashi M (2015) Perspectives on object manipulation and action grammar for percussive actions in primates. *Philos Trans R Soc Lond B: Biol Sci* 370:20140350. <https://doi.org/10.1098/rstb.2014.0350>
- Haidle MN (2010) Working-memory capacity and the evolution of modern cognitive potential: Implications from animal and early human tool use. *Curr Anthropol* 51:S149–S166. <https://doi.org/10.1086/650295>
- Henrich J, Heine SJ, Norenzayan A (2010) The weirdest people in the world? *Behav Brain Sci* 33:61–83. <https://doi.org/10.1017/S0140525X0999152X>
- Hernandez-Aguilar RA, Moore J, Pickering TR (2007) Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proc Natl Acad Sci USA* 104:19210–19213. <https://doi.org/10.1073/pnas.0707929104>
- Herrmann E, Wobber V, Call J (2008) Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *J Comp Psychol* 122:220–230. <https://doi.org/10.1037/0735-7036.122.2.220>
- Hewlett BS, Fouts HN, Boyette AH, Hewlett BL (2011) Social learning among Congo basin hunter-gatherers. *Philos Trans R Soc Lond B: Biol Sci* 366:1168–1178. <https://doi.org/10.1098/rstb.2010.0373>
- Heyes C (2018) *Cognitive gadgets: the cultural evolution of thinking*. Harvard University Press, USA
- Heyes C (2019) Précis of cognitive gadgets: the cultural evolution of thinking. *Behav Brain Sci* 42:e169. <https://doi.org/10.1017/S0140525X18002145>
- Hirata S, Morimura N, Houki C (2009) How to crack nuts: acquisition process in captive chimpanzees (*Pan troglodytes*) observing a model. *Anim Cogn* 12:87–101. <https://doi.org/10.1007/s10071-009-0275-3>
- Hunt GR, Gray RD, Taylor AH (2013) Why is tool use rare in animals? In: Sanz C, Call J, Boesch C (eds.) *Tool use in animals*. Cambridge University Press, Cambridge, pp. 89–118. <https://doi.org/10.1017/CBO9780511894800.007>
- Inskeep RR (1969) Some problems relating to the early stone age in South Africa. *S Afr Archaeol Bull* 24:174–181. <https://doi.org/10.2307/3888299>
- Isaac GL, Harris JWK, Krolle M (1997) The stone artefact assemblages: a comparative study. In: Isaac GL (ed.) *Koobi Fora Research Project*. Oxford University Press, Oxford, pp. 262–362
- Jelbert SA, Taylor AH, Gray RD (2015) Investigating animal cognition with the Aesop's Fable paradigm: current understanding and future directions. *Commun Integr Biol* 8:e1035846. <https://doi.org/10.1080/19420889.2015.1035846>
- Johnson LL, Behm JA, Bordes F, Cahen D, Crabtree DE, Dincuze DF, Hay CA, Hayden B, Hester TR, Katz PR, Knudson R, McManamon FP, Malik SC, Müller-Beck H, Newcomer MH, Paddaya K, Price-Beggerly P, Ranere AJ, Sankalia HD, Sheets PD (1978) A history of flint-knapping experimentation, 1838–1976 [and Comments and Reply]. *Curr Anthropol* 19:337–372. <https://doi.org/10.1086/202078>
- Joordens JC, Feibel CS, Vonnhof HB, Schulp AS, Kroon D (2019) Relevance of the eastern African coastal forest for early hominin biogeography. *J Hum Evol* 131:176–202. <https://doi.org/10.1016/j.jhevol.2019.03.012>
- Keeley LH, Toth N (1981) Microwear polishes on early stone tools from Koobi Fora, Kenya. *Nature* 293:464–465. <https://doi.org/10.1038/293464a0>
- Kinani J-F, Zimmerman D (2015) Tool use for food acquisition in a wild mountain gorilla (*Gorilla beringei beringei*): tool use in a mountain gorilla. *Am J Primatol* 77:353–357. <https://doi.org/10.1002/ajp.22351>
- Koops K, Furuichi T, Hashimoto C (2015) Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Sci Rep* 5:11356. <https://doi.org/10.1038/srep11356>
- Koops K, McGrew WC, Matsuzawa T (2010) Do chimpanzees (*Pan troglodytes*) use cleavers and anvils to fracture *Treulia africana* fruits? Preliminary data on a new form of percussive technology. *Primates* 51:175–178. <https://doi.org/10.1007/s10329-009-0178-6>
- Koops K, Visalberghi E, van Schaik CP (2014) The ecology of primate material culture. *Biol Lett* 10:20140508. <https://doi.org/10.1098/rstb.2014.0508>
- Langergraber KE, Prüfer K, Rowney C, Boesch C, Crockford C, Fawcett K et al. (2012) Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proc Natl Acad Sci USA* 109:15716–15721. <https://doi.org/10.1073/pnas.1211740109>
- Lefebvre L, Nicolakakis N, Boire D (2002) Tools and brains in birds. *Behaviour* 139:939–973. <https://doi.org/10.1163/156853902320387918>
- Lemorini C, Plummer TW, Braun DR, Crittenden AN, Ditchfield PW, Bishop LC, Hertel F, Oliver JS, Marlowe FW, Schoeninger MJ, Potts R (2014) Old stones' song: use-wear experiments and analysis of the Oldowan quartz and quartzite assemblage from Kanjera South (Kenya). *J Hum Evol* 72:10–25. <https://doi.org/10.1016/j.jhevol.2014.03.002>
- Little EE, Carver LJ, Legare CH (2016) Cultural variation in triadic infant-caregiver object exploration. *Child Dev* 87:1130–1145. <https://doi.org/10.1111/cdev.12513>
- Lombao D, Guardiola M, Mosquera M (2017) Teaching to make stone tools: new experimental evidence supporting a technological hypothesis for the origins of language. *Sci Rep* 7:14394. <https://doi.org/10.1038/s41598-017-14322-y>
- Lonsdorf EV (2006) What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Anim Cogn* 9:36–46. <https://doi.org/10.1007/s10071-005-0002-7>
- Lonsdorf EV, Ross SR, Linick SA, Milstein MS, Melber TN (2009) An experimental, comparative investigation of tool use in chimpanzees and gorillas. *Anim Behav* 77:1119–1126. <https://doi.org/10.1016/j.anbehav.2009.01.020>
- Luncz LV, Proffitt T, Lars K, Haslam M, Wittig RM (2016) Distance-decay effect in stone tool transport by wild chimpanzees. *Proc R Soc B: Biol Sci* 283:20161607. <https://doi.org/10.1098/rspb.2016.1607>
- Luncz LV, Svensson MS, Haslam M, Malaivijitnond S, Proffitt T, Gumert M (2017) Technological response of wild macaques (*Macaca fascicularis*) to anthropogenic change. *Int J Primatol* 38:872–880. <https://doi.org/10.1007/s10764-017-9985-6>
- Malaivijitnond S, Lekprayoon C, Tandavanitt N, Panha S, Cheewatham C, Hamada Y (2007) Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *Am J Primatol* 69:227–233. <https://doi.org/10.1002/ajp.20342>
- Mannu M, Ottoni EB (2009) The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools. *Am J Primatol* 71:242–251. <https://doi.org/10.1002/ajp.20642>
- Marchant LF, McGrew WC (2005) Percussive technology: Chimpanzee baobab smashing and the evolutionary modelling of hominin knapping. In: Roux V, Bril B (eds.) *Stone knapping: the necessary conditions for a uniquely hominin behaviour*. McDonald Institute for Archaeological Research, Cambridge

- Marks JS, Hall CS (1992) Tool use by bristle-thighed curlews feeding on albatross eggs. *Condor* 94:1032–1034. <https://doi.org/10.2307/1369308>
- Marlowe FW (2005) Hunter-gatherers and human evolution. *Evol Anthropol* 14:54–67. <https://doi.org/10.1002/evan.20046>
- McBeath NM, McGrew WC (1982) Tools used by wild chimpanzees to obtain termites at Mt Assirik, Senegal: the influence of habitat. *J Hum Evol* 11:65–72. [https://doi.org/10.1016/S0047-2484\(82\)80032-8](https://doi.org/10.1016/S0047-2484(82)80032-8)
- McBrearty S, Brooks AS (2000) The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J Hum Evol* 39:453–563. <https://doi.org/10.1006/jhev.2000.0435>
- McCall GS (2012) Ethnoarchaeology and the organization of lithic technology. *J Archaeol Res* 20:157–203. <https://doi.org/10.1007/s10814-011-9056-z>
- McCarty ME, Clifton RK, Collard RR (2001) The beginnings of tool use by infants and toddlers. *Infancy* 2:233–256. [https://doi.org/10.1207/S15327078IN0202\\_8](https://doi.org/10.1207/S15327078IN0202_8)
- McGrew WC, Falótico T, Gumert MD, Ottoni EB (2019) A simian view of the Oldowan: reconstructing the evolutionary origins of human technology. In: *Squeezing minds from stones*. Oxford University Press, pp. 13–41
- McGrew W, Marchant L, Wrangham RW, Klein H (1999) Manual laterality in anvil use: wild chimpanzees cracking *Strychnos* fruits. *Laterality* 4:79–87. <https://doi.org/10.1080/03069887600760101>
- McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, Geraads D et al. (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466:857–860. <https://doi.org/10.1038/nature09248>
- Mercader J, Barton H, Gillespie J, Harris J, Kuhn S, Tyler R, Boesch C (2007) 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. *PNAS* 104:3043–3048. <https://doi.org/10.1073/pnas.0607909104>
- Mercader J, Panger M, Boesch C (2002) Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296:1452–1455. <https://doi.org/10.1126/science.1070268>
- Merrick HV, Merrick JPS (1976) Archaeological occurrences of earlier Pleistocene age, from Shungura Formation. In: Coppens FC, Howell GL, Isaac GL, Leakey L (eds.) *Earliest man and environments in the Lake Rudolf Basin: stratigraphy, paleoecology, and evolution*. University of Chicago Press, Chicago, pp. 574–584
- Meulman EJM, Van Schaik CP (2013) Orangutan tool use and the evolution of technology. In: Sanz CM, Call J, Boesch C (eds.) *Tool use in animals: cognition and ecology*. Cambridge University Press, Cambridge, pp. 176–202
- Monteza-Moreno CM, Dogandžić T, McLean KA, Castillo-Caballero PL, Mijangoramos Z, Del Rosario-Vargas E, Crofoot MC, Barrett BJ (2020) White-faced capuchin, *Cebus capucinus imitator*, hammerstone and anvil tool use in riparian habitats on Coiba Island, Panama. *Int J Primatol* 41:429–433. <https://doi.org/10.1007/s10764-020-00156-5>
- Moore MW, Perston Y (2016) Experimental insights into the cognitive significance of early stone tools. *PLoS ONE* 11:e0158803. <https://doi.org/10.1371/journal.pone.0158803>
- Mora R, De la Torre I (2005) Percussion tools in Olduvai Beds I and II (Tanzania): implications for early human activities. *J Anthropol Archaeol* 24:179–192. <https://doi.org/10.1016/j.jaa.2004.12.001>
- Morgan BJ, Abwe EE (2006) Chimpanzees use stone hammers in Cameroon. *Curr Biol* 16:R632–R633. <https://doi.org/10.1016/j.cub.2006.07.045>
- Morgan TJ, Uomini NT, Rendell LE, Chouinard-Thuly L, Street SE, Lewis HM, Cross CP, Evans C, Kearney R, de la Torre I, Whiten A, Laland KN (2015) Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nat Commun* 6:6029. <https://doi.org/10.1038/ncomms7029>
- Morrison RE, Groenenberg M, Breuer T, Manguette ML, Walsh PD (2019) Hierarchical social modularity in gorillas. *Proc R Soc B: Biol Sci* 286:20190681. <https://doi.org/10.1098/rspb.2019.0681>
- Motes-Rodrigo A, McPherron S, Archer W, Hernandez-Aguilar RA, Tennie C (2022) Experimental investigation of orangutans' lithic percussive and sharp stone tool behaviours. *PLoS ONE* 17:e0263343. <https://doi.org/10.1371/journal.pone.0263343>
- Motes-Rodrigo A, Majlesi P, Pickering TR, Laska M, Axelsen H, Minchin T, Tennie C, Hernandez-Aguilar RA (2019) Chimpanzee extractive foraging with excavating tools: experimental modeling of the origins of human technology. *PLoS ONE* 14:e0215644. <https://doi.org/10.1371/journal.pone.0215644>
- Moura ADA, Lee PC (2004) Capuchin stone tool use in Caatinga dry forest. *Science* 306:1909. <https://doi.org/10.1126/science.1102558>
- Muller A, Clarkson C, Shipton C (2017) Measuring behavioral and cognitive complexity in lithic technology throughout human evolution. *J Anthropol Archaeol* 48:166–180. <https://doi.org/10.1016/j.jaa.2017.07.006>
- Nahallage C, Huffman M (2007) Acquisition and development of stone handling behavior in infant Japanese macaques. *Behaviour* 144:1193–1215. <https://doi.org/10.1163/156853907781890959>
- Neldner K, Reindl E, Tennie C, Grant J, Tomaselli K, Nielsen M (2020) A cross-cultural investigation of young children's spontaneous invention of tool use behaviours. *R Soc Open Sci* 7:192240. <https://doi.org/10.1098/rsos.192240>
- Neufuss J, Humle T, Cremaschi A, Kivell TL (2017) Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference, hand grips and efficiency. *Am J Primatol* 79:e22589. <https://doi.org/10.1002/ajp.22589>
- Nishida T, Hiraiwa M (1982) Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *J Hum Evol* 11:73–99. [https://doi.org/10.1016/S0047-2484\(82\)80033-X](https://doi.org/10.1016/S0047-2484(82)80033-X)
- Nonaka T, Brill B, Rein R (2010) How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. *J Hum Evol* 59:155–167. <https://doi.org/10.1016/j.jhevol.2010.04.006>
- Oakley KP, Andrews P, Keeley LH, Clark JD (1977) A reappraisal of the Clacton Spear Point. *Proc Prehist Soc* 43:13–30. <https://doi.org/10.1017/S0079497X00010343>
- Ottoni EB, Izar P (2008) Capuchin monkey tool use: overview and implications. *Evol Anthropol* 17:171–178. <https://doi.org/10.1002/evan.20185>
- Pargeter J, Khreisheh N, Stout D (2019) Understanding stone tool-making skill acquisition: experimental methods and evolutionary implications. *J Hum Evol* 133:146–166. <https://doi.org/10.1016/j.jhevol.2019.05.010>
- Pargeter J, de la Peña P (2017) Milky quartz bipolar reduction and lithic miniaturization: experimental results and archaeological implications. *J Field Archaeol* 42:551–565. <https://doi.org/10.1080/00934690.2017.1391649>
- Parker ST, Kerr M, Markowitz H, Gould J (1999) A survey of tool use in zoo gorillas. In: Parker ST, Mitchell RW, Miles HL (eds.) *The mentalities of Gorillas and Orangutans*. Cambridge University Press, Cambridge, pp. 188–194
- Pascual-Garrido A (2018) Scars on plants sourced for termite fishing tools by chimpanzees: towards an archaeology of the perishable. *Am J Primatol* 80:e22921. <https://doi.org/10.1002/ajp.22921>
- Pascual-Garrido A (2019) Cultural variation between neighbouring communities of chimpanzees at Gombe, Tanzania. *Sci Rep* 9:1–12. <https://doi.org/10.1038/s41598-019-44703-4>
- Pascual-Garrido A, Almeida-Warren K (2021) Archaeology of the perishable. *Curr Anthropol* 62:333–362. <https://doi.org/10.1086/713766>
- Pedergnana A, Ollé A (2017) Monitoring and interpreting the use-wear formation processes on quartzite flakes through sequential experiments. *Quat Int* 427:35–65. <https://doi.org/10.1016/j.quaint.2016.01.053>
- Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, Moreira MA, Pecon-Slattery J (2011) A molecular phylogeny of living primates. *PLoS Genet* 7:e1001342. <https://doi.org/10.1371/journal.pgen.1001342>
- Potts R, Shipman P (1981) Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature* 291:577–580. <https://doi.org/10.1038/291577a0>
- Pradhan GR, Tennie C, van Schaik CP (2012) Social organization and the evolution of cumulative technology in apes and hominins. *J Hum Evol* 63:180–90. <https://doi.org/10.1016/j.jhevol.2012.04.008>
- Proffitt T, Haslam M, Mercader JF, Boesch C, Luncz LV (2018a) Revisiting Panda 104, the first archaeological chimpanzee nut-cracking site. *J Hum Evol* 124:117–139. <https://doi.org/10.1016/j.jhevol.2018.04.016>
- Proffitt T, Luncz LV, Falótico T, Ottoni EB, de la Torre I, Haslam M (2016) Wild monkeys flake stone tools. *Nature* 539:85–88. <https://doi.org/10.1038/nature20112>
- Proffitt T, Luncz LV, Malaivijitnond S, Gumert M, Svensson MS, Haslam M (2018b) Analysis of wild macaque stone tools used to crack oil palm nuts. *R Soc Open Sci* 5:171904. <https://doi.org/10.1098/rsos.171904>
- Pruetz JD, Bertolini P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Curr Biol* 17:412–417. <https://doi.org/10.1016/j.cub.2006.12.042>
- Prüfer K, Munch K, Hellmann I, Akagi K, Miller JR, Walenz B et al. (2012) The bonobo genome compared with the chimpanzee and human genomes. *Nature* 486:527–531. <https://doi.org/10.1038/nature11128>
- Putt SS (2015) The origins of stone tool reduction and the transition to knapping: an experimental approach. *J Archaeol Sci* 2:51–60. <https://doi.org/10.1016/j.jasrep.2015.01.004>
- Putt SS, Woods AD, Franciscus RG (2014) The role of verbal interaction during experimental bifacial stone tool manufacture. *Lithic Technol* 39:96–112. <https://doi.org/10.1179/0197726114Z.00000000036>
- Reader SM, Laland KN (2003) Animal innovation: an introduction. In: Reader SM, Laland KN (eds.) *Animal innovation*. Oxford University Press, Oxford, pp. 3–36
- Reeves JS, Proffitt T, Luncz LV (2021) Modeling a primate technological niche. *Sci Rep* 11:1–9. <https://doi.org/10.1038/s41598-021-01849-4>
- Reindl E, Beck SR, Apperly IA, Tennie C (2016) Young children spontaneously invent wild great apes' tool-use behaviours. *Proc R SocB: Biol Sci* 283:20152402. <https://doi.org/10.1098/rspb.2015.2402>
- Rochat P (1989) Object manipulation and exploration in 2- to 5-month-old infants. *Dev Psychol* 25:871–884. <https://doi.org/10.1037/0012-1649.25.6.871>
- Roffman I, Savage-Rumbaugh S, Rubert-Pugh E, Ronen A, Nevo E (2012) Stone tool production and utilization by bonobo-chimpanzees (*Pan paniscus*). *PNAS* 109:14500–14503. <https://doi.org/10.1073/pnas.1212855109>
- Rolian C, Carvalho S (2017) Tool use and manufacture in the last common ancestor of *Pan* and *Homo*. In: Muller MN, Wrangham RW, Pilbeam DR (eds.) *Chimpanzees and human evolution*. The Belknap Press of Harvard University Press, USA, Cambridge, pp. 602–644



- Roux V, David E (2005) Planning abilities as a dynamic perceptual-motor skill: an actualist study of different levels of expertise involved in stone knapping. In: Bril B, Roux V (eds.) Stone knapping: the necessary conditions for a uniquely hominin behaviour. McDonald Institute for Archaeological Research, USA, Cambridge, pp. 91–116
- Rutz C, St Clair JJ (2012) The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behav Process* 89:153–165. <https://doi.org/10.1016/j.beproc.2011.11.005>
- Samuni L, Lemieux D, Lamb A, Galdino D, Surbeck M (2021) Tool use behavior in three wild bonobo communities at Kokolopori. *Am J Primatol* (online):e23342
- Sanz CM, Morgan DB, Gulick S (2004) New insights into chimpanzees, tools, and termites from the Congo Basin. *Am Nat* 164:567–581. <https://doi.org/10.1086/424803>
- Sanz CM, Deblauwe I, Tagg N, Morgan DB (2014) Insect prey characteristics affecting regional variation in chimpanzee tool use. *J Hum Evol* 71:28–37. <https://doi.org/10.1016/j.jhevol.2013.07.017>
- Savage-Rumbaugh S, Fields WM (2006) Rules and tools: beyond anthropomorphism. In: Toth N, Schick K (eds.) The Oldowan: case studies into the earliest stone age. Stone Age Institute Press, Gosport, pp. 223–241
- Sayers K, Lovejoy CO (2008) The Chimpanzee has no clothes: a critical examination of *Pan troglodytes* in models of human evolution. *Curr Anthropol* 49:87–114. <https://doi.org/10.1086/523675>
- Sayers K, Raghanti MA, Lovejoy CO (2012) Human evolution and the chimpanzee referential doctrine. *Annu Rev Anthropol* 41:119–138. <https://doi.org/10.1146/annurev-anthro-092611-145815>
- Van Schaik CP, Deaner RO, Merrill MY (1999) The conditions for tool use in primates: implications for the evolution of material culture. *J Hum Evol* 36:719–741. <https://doi.org/10.1006/jhev.1999.0304>
- van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M (2003) Orangutan cultures and the evolution of material culture. *Science* 299:102–105. <https://doi.org/10.1126/science.1078004>
- van Schaik CP, Ancrenaz M, Djojoasmoro R, Knott CD, Morrogh-Bernard HC, Nuzuar OK, Odom K, Atmoko SSU, Van Noordwijk MA (2009) Orangutan cultures revisited. In: Wich SA, Setia TM, Van Schaik CP (eds.) Orangutans: geographic variation in behavioral ecology and conservation. Oxford University Press, Oxford, pp. 299–309
- van Schaik CP, Fox EA, Fechtman LT (2003) Individual variation in the rate of use of tree-hole tools among wild orang-utans: implications for hominin evolution. *J Hum Evol* 44:11–23. [https://doi.org/10.1016/S0047-2484\(02\)00164-1](https://doi.org/10.1016/S0047-2484(02)00164-1)
- van Schaik CP, Knott CD (2001) Geographic variation in tool use on *Neesia* fruits in orangutans. *Am J Phys Anthropol* 114:331–342. <https://doi.org/10.1002/ajpa.1045>
- Schick KD, Toth NP (1994) Making silent stones speak: human evolution and the dawn of technology. Simon and Schuster, New York
- Schick K, Toth N (2006) An overview of the Oldowan industrial complex: the sites and the nature of the evidence. In: Toth N, Schick K (eds.) The Oldowan: case studies into the earliest Stone Age. Stone Age Institute Press, Gosport
- Schick KD, Toth N, Garufi G, Savage-Rumbaugh ES, Rumbaugh D, Sevcik R (1999) Continuing investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *J Archaeol Sci* 26:821–832. <https://doi.org/10.1006/jasc.1998.0350>
- Shumaker RW, Walkup KR, Beck BB (2011) Animal tool behavior: the use and manufacture of tools by animals. Johns Hopkins University Press, Baltimore
- Stanton L, Davis E, Johnson S, Gilbert A, Benson-Amram S (2017) Adaptation of the Aesop's Fable paradigm for use with raccoons (*Procyon lotor*): considerations for future application in non-avian and non-primate species. *Anim Cogn* 20:1147–1152. <https://doi.org/10.1007/s10071-017-1129-z>
- Stokstad E (2000) Human evolution: Hominid ancestors may have knuckle walked. *Science* 287:2131a–22132. <https://doi.org/10.1126/science.287.5461.2131a>
- Stout D (2002) Skill and cognition in stone tool production: an ethnographic case study from Irian Jaya. *Curr Anthropol* 43:693–722. <https://doi.org/10.1086/342638>
- Stout D (2005) The social and cultural context of stone-knapping skill acquisition. In: Roux V, Bril B (eds.) Stone knapping: the necessary conditions for a uniquely hominin behaviour. McDonald Institute for Archaeological Research, Cambridge, pp. 331–340
- Stout D, Chaminade T (2012) Stone tools, language and the brain in human evolution. *Philos Trans R Soc Lond B: Biol Sci* 367:75–87. <https://doi.org/10.1098/rstb.2011.0099>
- Stout D, Hecht E, Khreisheh N, Bradley B, Chaminade T (2015) Cognitive demands of lower Paleolithic toolmaking. *PLoS ONE* 10:e0121804. <https://doi.org/10.1371/journal.pone.0121804>
- Stout D, Toth KD, Schick K, Chaminade T (2008) Neural correlates of Early Stone Age tool-making: technology, language and cognition in human evolution. *Philos Trans R Soc Lond B: Biol Sci* 363:1939–1949. <https://doi.org/10.1098/rstb.2008.0001>
- Stout D, Toth N, Schick K, Stout J, Hutchins G (2000) Stone tool-making and brain activation: position emission tomography (PET) studies. *J Archaeol Sci* 27:1215–1223. <https://doi.org/10.1006/jasc.2000.0595>
- Tan AWY (2017) From play to proficiency: the ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. *J Comp Psychol* 131:89–114. <https://doi.org/10.1037/com0000068>
- Telegi G (1974) Chimpanzee subsistence technology: materials and skills. *J Hum Evol* 3:575–594. [https://doi.org/10.1016/0047-2484\(74\)90018-9](https://doi.org/10.1016/0047-2484(74)90018-9)
- Tennie C, Premo LS, Braun DR, McPherron SP (2017) Early stone tools and cultural transmission: resetting the null hypothesis. *Curr Anthropol* 58:652–672. <https://doi.org/10.1086/693846>
- Tennie C (2019) Could nonhuman great apes also have cultural evolutionary psychology? *Behav Brain Sci* 42:E184. <https://doi.org/10.1017/S0140525X19001055>
- Thieme H (1997) Lower Palaeolithic hunting spears from Germany. *Nature* 385:807–810. <https://doi.org/10.1038/385807a0>
- Tindale NB (1977) Further report on the Kaiadilt people of Bentinck Island, Gulf of Carpentaria, Queensland. In: Allen J, Golson J, Jones R (eds.) Sunda and Sahul: prehistoric studies in Southeast Asia, Melanesia and Australia. Academic Press, New York, pp. 247–273
- Tokida E, Tanaka I, Takefushi H, Hagiwara T (1994) Tool-using in Japanese macaques: use of stones to obtain fruit from a pipe. *Anim Behav* 47:1023–1030. <https://doi.org/10.1006/anbe.1994.1140>
- de la Torre I (2004) Omo revisited: evaluating the technological skills of Pliocene hominids. *Curr Anthropol* 45:439–465. <https://doi.org/10.1086/422079>
- de la Torre I (2010) Insights on the technical competence of the early Oldowan. In: Nowell A, Davidson I (eds.) Stone tools and the evolution of human cognition. University of Colorado Press, Boulder, pp. 45–65
- Toth N, Schick KD, Savage-Rumbaugh ES, Sevcik RA, Rumbaugh DM (1993) Pan the tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *J Archaeol Sci* 20:81–91. <https://doi.org/10.1006/jasc.1993.1006>
- Toth N, Schick K, Semaw S (2006) A comparative study of the stone tool-making skills of Pan, Australopithecus, and *Homo sapiens*. In: Toth N, Schick K (eds.) The Oldowan: case studies into the earliest Stone Age. Stone Age Institute Press, Gosport
- van Lawick-Goodall J (1971) Tool-using in primates and other vertebrates. In: Lehrman DS, Hinde RA, Shaw E (eds.) Advances in the study of behavior. Academic Press vol. 3, pp. 195–249. [https://doi.org/10.1016/S0065-3454\(08\)60157-6](https://doi.org/10.1016/S0065-3454(08)60157-6)
- Visalberghi E (1987) Acquisition of nut-cracking behaviour by 2 capuchin monkeys (*Cebus apella*). *Folia Primatol* 49:168–181. <https://doi.org/10.1159/000156320>
- Webster MM, Rutz C (2020) How STRANGE are your study animals? *Nature* 582:337–340. <https://doi.org/10.1038/d41586-020-01751-5>
- Westergaard GC, Suomi SJ (1994) A simple stone-tool technology in monkeys. *J Hum Evol* 27:399–404. <https://doi.org/10.1006/jhev.1994.1055>
- Whiten A (2015) Experimental studies illuminate the cultural transmission of percussive technologies in *Homo* and *Pan*. *Philos Trans R Soc Lond B: Biol Sci* 370:20140359. <https://doi.org/10.1098/rstb.2014.0359>
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399:682–685. <https://doi.org/10.1038/21415>
- Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM (2009) Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philos Trans R Soc B* 364:2417–2428. <https://doi.org/10.1098/rstb.2009.0069>
- Whiten A, Schick K, Toth N (2009) The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. *J Hum Evol* 57:420–435. <https://doi.org/10.1016/j.jhevol.2008.12.010>
- Wright RVS (1972) Imitative learning of a flaked stone technology—the case of an orangutan. *Mankind* 8:296–306. <https://doi.org/10.1111/j.1835-9310.1972.tb00451.x>
- Wynn T, Hernandez-Aguilar RA, Marchant LF, McGrew WC (2011) “An ape’s view of the Oldowan” revisited. *Evol Anthropol* 20:181–197. <https://doi.org/10.1002/evan.20323>
- Wynn T, McGrew WC (1989) An ape’s view of the Oldowan. *Man* 24:383–398. 2802697

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The authors declare no competing interests.

### Ethical approval

Ethical approval not applicable to this article as no novel data were collected or analysed.

**Informed consent**

This article does not contain any studies with human participants performed by any of the authors.

**Additional information**

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