

Towards a prehistory of primates

Michael Haslam*

Using the behaviour of related primates to provide analogies for early humans has a long tradition in archaeology. But these primates too have a past, and experienced particular contexts for the adoption of tool-using. In this pioneering review, the author explores distinctions among chimpanzees in ecology, diet and innovation, sets a wider agenda for a prehistory of primates and explains how archaeology could serve it.

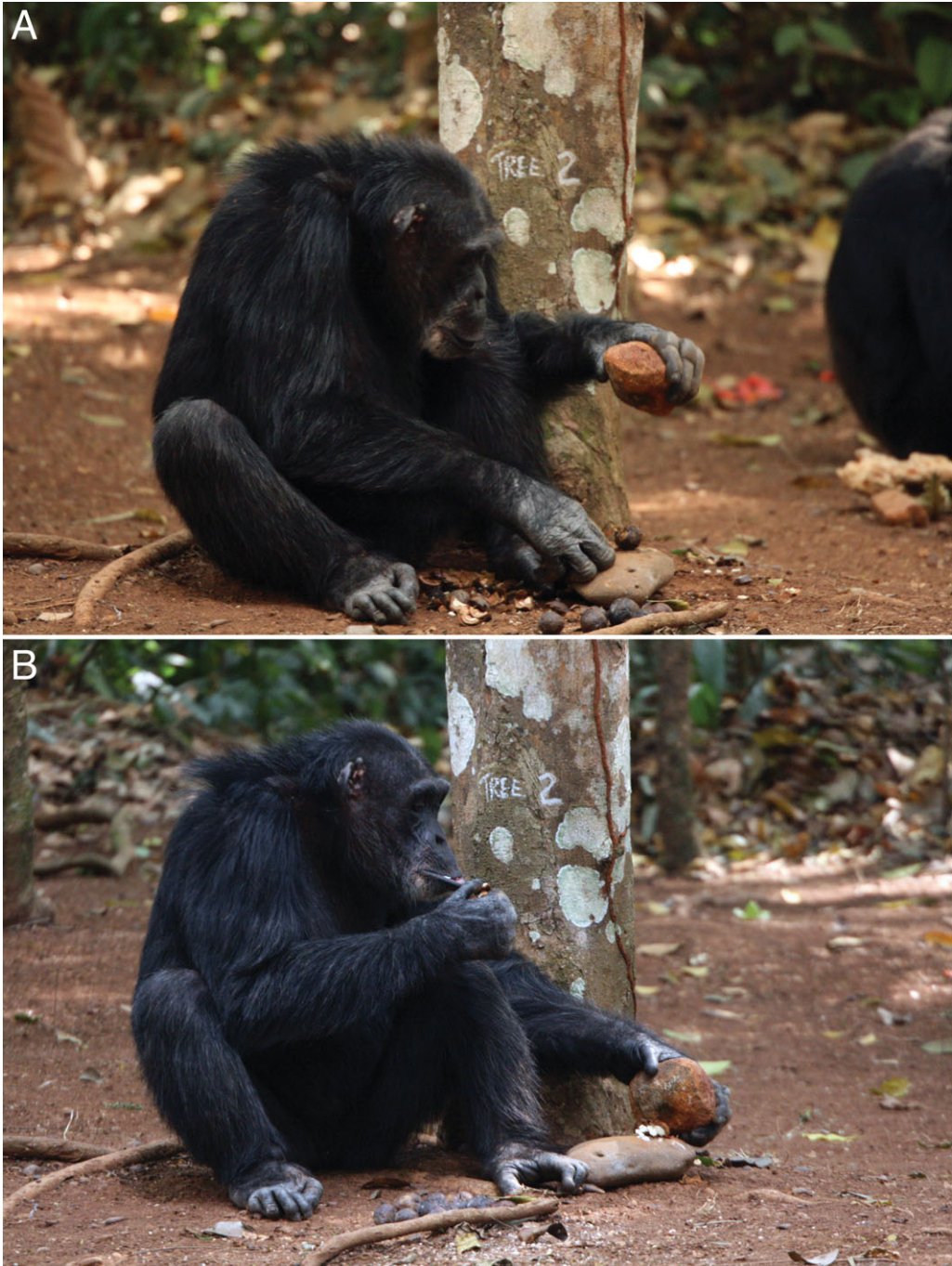
Keywords: primates, modern behaviour, tool-using, chimpanzees

Introduction

The social and technological traits of living non-human primates (henceforth ‘primates’) have contributed significantly to reconstructions of the activities of their past common ancestors with humans (van Schaik *et al.* 2003; Haslam *et al.* 2009; McGrew 2010; Silk 2011; Whiten 2011; Wynn *et al.* 2011). Customary tool-use by wild primates, a key trait of interest to archaeologists, has been recorded in tropical Africa, South America and Southeast Asia, including by chimpanzees (Figure 1), orangutans and bearded capuchin monkeys (McGrew 1992; van Schaik *et al.* 1996; Spagnoletti *et al.* 2011). Less well studied or less prevalent wild tool-use has also been noted among gorillas, bonobos, long-tailed macaques and both yellow-breasted and blonde capuchins (Hohmann & Fruth 2003; Breuer *et al.* 2005; Malaivijitnond *et al.* 2007; Canale *et al.* 2009; Souto *et al.* 2011). Yet there is a great disparity in the observational time span for human and primate behaviour, because the archaeological record of hominins (human ancestors back to our split with the *Pan* lineage) has unusual chronological depth.

At present, hominin technical activities have been detected back ~3.4 million years (McPherron *et al.* 2010), with a well-studied and possibly continuous stone tool record since 2.6 million years ago (mya) (Semaw *et al.* 2003). This record is augmented by non-stone prehistoric technologies for tens, and in some cases hundreds, of thousands of years (e.g. Thieme 1997). In contrast, we have around half a century of systematic chimpanzee behavioural data, and even less for other primates, although anecdotal reports from West Africa extend back around 400 years (Sept & Brooks 1994). When extinct hominin behaviours are compared with those of living primates (e.g. Joulain 1996; Gowlett 2009; Pruett & Bertolani 2009; Toth & Schick 2009; de la Torre 2010; Ungar & Sponheimer 2011), we need to ask whether extant primate behaviour is representative of the several million years of behavioural evolution that preceded it. In other words, when did apes, monkeys and other primates become ‘behaviourally modern’, and how

* Research Laboratory for Archaeology and the History of Art, University of Oxford, Dyson Perrins Building, South Parks Road, Oxford OX1 3QY, UK (Email: michael.haslam@rlaha.ox.ac.uk)



*Figure 1. An adult female western chimpanzee (*Pan troglodytes verus*) using a portable stone hammer and anvil to open a *Coula edulis* nut at the outdoor experimental area, Bossou, Guinea. Note the nut residue visible on the anvil in B. Photographs: Susana Carvalho/PRI-Kyoto.*

would a more complete primate archaeological record change our perspective on human evolution?

Behavioural modernity

Significant behavioural changes have occurred in the hominin lineage during the past few million years, and archaeologists studying *Homo sapiens* have concentrated on the issue of 'behavioural modernity' (Minugh-Purvis 1995; McBrearty & Brooks 2000; Wadley 2001; d'Errico 2003; Henshilwood & Marean 2003; Renfrew 2007; Conard 2008). At the core of this concept is a search for features that are unique to our species, an attempt to identify the process by which the habits and capacities of past humans came to be recognisably similar to those of humans living today (Klein 2000). While this may be a useful driver of debate (d'Errico & Stringer 2011; Shea 2011), the proposal of a radical behavioural shift, or 'human revolution' (Mellars & Stringer 1989; Bar-Yosef 2002) part way through hominin evolution is unusual when placed in a broader zoological context. There is, for example, no literature on the timing and character of the emergence of 'modern *Macaca* behaviour', or international conferences discussing a possible '*Papio* behavioural revolution'.

From the mid twentieth century onwards, the combination of increasing numbers of hominin fossil discoveries and the establishment of long-term field primatology sites opened up new debates over the similarities between hominins and other African primates (e.g. Leakey 1961; Washburn & DeVore 1961; Holloway 1969; Jolly 1970; Foley 1987). Archaeologists explored the ways that the emerging primate literature could inform topics such as early Pleistocene site creation and social structure (Clark 1960; Isaac 1969), but it was modern, twentieth-century primates that were the point of comparison. Little or no attention was given to possible pre-Anthropocene (Steffen *et al.* 2011) primate behavioural characteristics, except those hypothesised for common human-chimpanzee ancestors (e.g. Parker & Gibson 1979).

The lack of comparative *Pan* fossils can promote the notion of a static phenotype for all chimpanzees, past and present. For example, whereas hominins are represented by a variety of species on charts of brain volume evolution, chimpanzees can only be represented by a modern value (e.g. Aiello & Dean 1990; Gamble *et al.* 2011). Yet a number of ancestral panins (the distinct bonobo-chimpanzee lineage) must have existed during their separate evolution over the past 5–7 million years (Kumar *et al.* 2005). The average time from speciation to extinction for large African mammal species is 2.33 million years (Vrba 2000), while Foley (1993) calculated that African terrestrial primates have a species longevity close to one million years. The one known panin speciation, splitting chimpanzees from bonobos, occurred in the Early Pleistocene (Stone *et al.* 2010; Wegmann & Excoffier 2010). We can therefore posit a minimum of two (and very likely more) extinct direct panin ancestor species since the split from hominins, with an unknown number of dead-end side branches and additional genera (Wood & Harrison 2011).

Cultural variation observed in living chimpanzees and orangutans (Whiten *et al.* 2001; van Schaik *et al.* 2003) suggests that we should not expect the primate archaeological record to be homogeneous in time or space, even when produced by a single species. Extant wild tool-using primates live in a wide range of habitats and have varied social systems (e.g. van

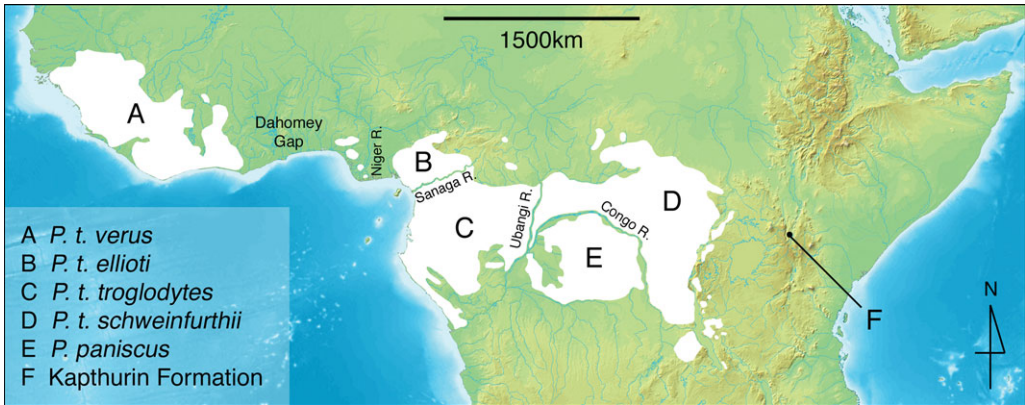


Figure 2. Map of Africa showing the current distribution of *Pan troglodytes* and *Pan paniscus*. Also marked is the Kapthurin Formation, Kenya, the find location of fossil chimpanzee teeth reported by McBrearty & Jablonski (2005). Adapted from data available at www.iucnredlist.org, accessed 14 November 2011.

Schaik *et al.* 1999; McGrew 2004; Mannu & Ottoni 2009; Gumert *et al.* 2011; Shumaker *et al.* 2011), factors that influence the transmission of technological activities (Biro *et al.* 2010). The capacity for cultural variation means that, depending on available materials, non-hominin primates likely experimented with a greater range of tool types than those seen today, including a range of non-stone tools (Panger *et al.* 2002; Byrne 2005; Haslam *et al.* 2009).

A full treatment of these topics lies outside the scope of this review, and I therefore concentrate here on three broad and interlinked categories for which a long-term perspective is important for inter- and intra-species behavioural comparisons: *geographic patterning*, *diet* and *innovation*. These three categories also reflect key adaptive shifts in Pliocene hominin evolution (Potts 2007), and their investigation will assist in understanding the causes of hominin divergence from other primates. My focus is on the most intensively studied living close relative to humans, chimpanzees (Nishida *et al.* 2010), but the concepts are not naturally limited to any one primate (or even non-primate) species.

Towards a prehistory of primates

Geographic patterning

Modern chimpanzees are behaviourally flexible and occupy a wider variety of environments than most primate taxa, including lowland and montane forests, woodlands and drier grasslands or savannah. This adaptability suggests that the current geographic distribution of chimpanzees (Figure 2) is unlikely to directly reflect past distribution. We know that the chimpanzee range is currently shrinking (Butynski 2003), and a significant earlier shift is indicated by the finding of putative chimpanzee fossils in Kenya, ~600km east of the species' current range (McBrearty & Jablonski 2005). The question here is, how did past primate populations spread, split and contract, and how did this affect cultural variation?

Genetic analyses have begun to reveal the population structure and history of the four commonly recognised chimpanzee subspecies: the western (*Pan troglodytes verus*), Nigeria-Cameroon (*P. t. ellioti*), central (*P. t. troglodytes*) and eastern (*P. t. schweinfurthii*) populations (Goldberg 1998; Gagneux *et al.* 2001; Yu *et al.* 2003; Won & Hey 2005; Caswell *et al.* 2008; Hey 2010; Stone *et al.* 2010; Wegmann & Excoffier 2010; Bjork *et al.* 2011). These studies suggest that major rivers in Central Africa (in particular the Niger, Sanaga and Ubangi rivers) act as rarely permeated boundaries to the various subspecies ranges, in addition to isolating the bonobo (*Pan paniscus*) south of the Congo River (Gagneux *et al.* 2001; Bjork *et al.* 2011). Within these regions, the potential importance of Pleistocene refugia in promoting allopatric differentiation has been considered (Lehman & Fleagle 2006), but at least for eastern chimpanzees there is little correlation between posited forest refugia and present-day diversity (Goldberg 1998).

Pounding stone use has been included in the list of cultural traits charted in multi-site chimpanzee studies (Whiten *et al.* 1999, 2001). These studies recognise clear geographic variation, with wild chimpanzees from different study sites using different combinations of stone and wood hammers and anvils, or alternatively not using stones to crack nuts even when both are available. Explanations offered for this variation include the variety and hardness of available nut species (Boesch & Boesch 1990; McGrew *et al.* 1997) and limited spatial diffusion of nut-cracking knowledge between sites (McGrew 1992). However, causal mechanisms are difficult to infer over short time spans, and differentiating between cases in which primate cultural variants are absent because knowledge has been lost from a particular site or region, or absent because they were never invented by the resident groups (Wrangham 2006; Whiten *et al.* 2009), is very difficult without a referent chronological sequence. Experimental evidence from captive primates (e.g. Hayashi *et al.* 2005; Marshall-Pescini & Whiten 2008b) has limited ability to address this issue, and studies that seek to generalise findings from captive primate subjects may have to acknowledge the limited scope of those findings for understanding primate behaviour before the twentieth century (Boesch 2007; Leavens *et al.* 2010; Whiten 2011).

It would be particularly interesting to see if chimpanzee use of pounding stones has persisted throughout periods where shifting climates altered the available nut and fruit resources (Dupont *et al.* 2010), or whether such tool-use disappears and re-appears in tune with environmental changes. In this regard, it is important to note that chimpanzee pounding stone use is currently localised to west Africa (and *P. t. verus*), which may limit the archaeological study of such traditions and their correlates to this part of the modern chimpanzee range, although recent anecdotal evidence for stone tool-using Nigeria-Cameroon chimpanzees (Morgan & Abwe 2006) suggests that this behaviour might be more widespread. Nonetheless, as a starting point we can hypothesise that stone tool-use as a behaviourally modern trait in *Pan* is limited by the time of genetic divergence (as a proxy for physical separation) of the western chimpanzees from the central-eastern clade. Present consensus places this process $\sim 1\text{--}0.5\text{mya}$ (Becquet *et al.* 2007; Caswell *et al.* 2008; Stone *et al.* 2010; Wegmann & Excoffier 2010), and more likely towards the younger end of that spectrum. Viewed as a specific West African innovation, and not as a remnant behaviour of the hominin-panin last common ancestor, the most plausible hypothesis is that chimpanzee stone tool-use began some time closely prior to 500 000 years ago. While tool-use traits do

not always align with genetic divisions in chimpanzees (Lycett *et al.* 2010), stone tool-use currently does, and excavation of the African primate archaeological record is the only way to test this hypothesis.

Emerging genetic data for the capuchin monkeys of Central and South America (Lynch Alfaro *et al.* 2011) similarly provide targets for future archaeological investigation. The capuchin *Cebus* genus has recently been reclassified into two genera (the gracile *Cebus* and the more robust *Sapajus*), the result of a late Miocene split potentially related to the establishment of the Amazon River (Hoorn *et al.* 2010). Use of pounding stones to open palm nuts in the wild is currently only known among *Sapajus* (Figure 3), in the drier *cerrado* (grassland to scrub woodland) and *caatinga* (dry forest and thorn scrub) environments that separate the Brazilian Atlantic and Amazon forests (Moura & Lee 2004; Visalberghi *et al.* 2007; Canale *et al.* 2009). *Sapajus* began to diversify from an origin zone somewhere in the Atlantic Forest around 3–2.5mya, before expanding west into the drier habitats, a movement postulated to have occurred around 0.7mya (Casado *et al.* 2010; Lynch Alfaro *et al.* 2011). As forest dwelling capuchins have not been observed to use stone tools, the genetic data therefore provide an initial prospective date for the origins of lithic technology among the capuchins, with the intriguing possibility that it was this specific technological innovation that permitted their dispersal into the previously uninhabited areas. The data further suggest that the north-western members of these dispersing groups subsequently moved into the Amazon rainforest (already occupied by *Cebus*) after 0.4mya (Lynch Alfaro *et al.* 2011). We can only speculate at present, but the absence of stone pounding tools among modern Amazonian *Sapajus* populations may well result from loss of a technological adaptation that was strongly tied to the palm nuts found in the *cerrado* and *caatinga*. In this scenario, testable through archaeological exploration, the lithic technologies of both 'behaviourally modern' capuchins and chimpanzees therefore have a Middle Pleistocene origin.

Beyond genetic reconstructions, the recovery of stone (or other) tools used by primates is strong proxy evidence of the presence of those primates at a given time and place. Fortunately, chimpanzees and capuchins transport and accumulate stone materials (Boesch & Boesch 1984; Visalberghi *et al.* 2007; Canale *et al.* 2009; Carvalho *et al.* 2009; Spagnoletti *et al.* 2011), creating recognisable sites and constructing technological niches that may structure subsequent activity (Figure 3). Redundant patterning has also been documented for chimpanzee nesting sites (Sept 1998; Hernandez-Aguilar 2009), further concentrating group behaviour.

The archaeological study of chimpanzee activity areas is currently in its infancy (Mercader *et al.* 2002; Carvalho *et al.* 2008), and a primary difficulty is in distinguishing primate tools from naturally occurring stones, or from hominin behavioural debris. Primate preference for stones of particular density, size and material assist in their discernment (although this approach is less useful once outside the range of preferences seen among living primates), as can the careful documentation of characteristic wear patterns and adhering residues (Mercader *et al.* 2007). In the Americas, the task is aided by the absence of hominins prior to the terminal Pleistocene (Goebel *et al.* 2008), meaning that stone pounding tools dated prior to this time may in theory be attributed to non-human primates.



Figure 3. Formation of a primate archaeological site, Fazenda Boa Vista, Piauí, Brazil: A) an adult male wild bearded capuchin monkey (*Sapajus libidinosus*) using a quartzite pounding stone and fixed sandstone anvil to open palm nuts; B) the resulting site. Note the concurrence of durable material elements, including the use-worn anvil, hammerstones and nut debris both on the anvil and concentrated in the immediate area (scale is 10cm). Photographs: Michael Haslam/EthoCebus Project.

Diet

Chimpanzees have a mixed and variable diet, including fruits, herbaceous vegetation, insects, vertebrates and secondary products such as honey (e.g. McGrew *et al.* 1988; Milton 1999; McGrew 2001; Tweheyo *et al.* 2004; Laden & Wrangham 2005; Sanz & Morgan 2009). Ideally, the recovery of archaeological evidence for past chimpanzee behaviour would allow us to assess the representativeness of modern primate diets, compared to their ancestors throughout the past few million years. As discussed earlier, the adaptability of chimpanzees to a variety of conditions and ability to range across wide areas may act as a buffer to local climate-driven changes in resources; however, it is reasonable to hypothesise that some of the now extinct panin species were more specialised and/or localised than living populations, based on the variation known from the hominin lineage (e.g. the hyper-robust *Paranthropus*, or the island dwelling *Homo floresiensis*) and the orangutan lineage (Ungar & Sponheimer 2011; Wood & Harrison 2011). At its simplest, the question that arises is to what extent the range of potential chimpanzee dietary niches were actually exploited by past panin species.

Fortunately, tool-use is pervasive in chimpanzee dietary foraging (McGrew 1992), particularly in the extraction of embedded nutrient rich resources such as nuts, termites, underground storage organs (USOs) and honey (e.g. Boesch & Boesch-Achermann 2000; Deblauwe *et al.* 2006; Hernandez-Aguilar *et al.* 2007; Sanz & Morgan 2009). The spearing tools used by Fongoli chimpanzees to disable small prey hidden in tree holes (Pruetz & Bertolani 2007) could similarly be seen as targeting 'embedded' food. Tool-use allows us to record diet-related activities beyond direct observation for primates that are either unhabituated (Sanz *et al.* 2004; Fowler & Sommer 2007; Canale *et al.* 2009; Koops *et al.* 2010) or even deceased (Mercader *et al.* 2002). Most of the tools manufactured and used by chimpanzees are made of plant materials, which will survive in the short-term (perhaps decades in the case of nests made by modifying living trees; Stewart *et al.* 2011), but are unlikely to enter the long-term archaeological record other than through fortuitous discard in a waterlogged or hyper-arid setting. Nonetheless, standardisation of the size and physical characteristics of many of these tools (McGrew 2004; Boesch *et al.* 2009; Sanz *et al.* 2009) means that they are both recognisable when encountered, and encode information about the traditions and dietary habits of the group that created them.

Even more promising for studying long-term changes in diet is the use of stone and hard wood pounding tools for opening nuts and other food items, as practised by chimpanzees, capuchin monkeys and long-tailed macaques (Boesch & Boesch 1990; Ottoni & Izar 2008; Canale *et al.* 2009; Carvalho *et al.* 2009; Gumert *et al.* 2009). The use of anvil stones has been presented as a plausible mechanism for the initial stage leading to deliberate stone tool fracture among hominins (Marchant & McGrew 2005), and if this is the case then it is worth exploring the reasons why present-day chimpanzees have not followed a similar path to stone tool manufacture. Stone tools used by chimpanzees have a demonstrated antiquity of over 4000 years in the Taï Forest of Côte d'Ivoire (Mercader *et al.* 2007), and there is no reason to suspect that the stone tool record left by past primates in Africa, Asia and South America is not still present and awaiting study by archaeologists and primatologists.

As pounding tools are currently recognised as primarily a dietary adaptation, then at a minimum the antiquity of embedded food exploitation can be investigated through

systematic excavation and analysis of these artefacts. However, there are also more complex diet-related questions that may be addressed through the analysis of stone artefacts used by chimpanzees and other primates. For example, the relationship between the physical character (shape, size and density) of selected stone tools and the food types exploited with them deserves greater attention. Chimpanzees and capuchins choose stone tools based on their performance characteristics and fitness for the task at hand (Boesch & Boesch 1982; Visalberghi *et al.* 2009), an ability we may reasonably expect panin ancestors to also have possessed. Along with microscopic residues adhering to used tools (Mercader *et al.* 2007; Haslam *et al.* 2010), the search for correlations of form and function would allow assessment of the composition, size and hardness of the foods targeted by past primates. With added chronological resolution, such assessments will permit the reconstruction of a behavioural component to primate diet evolution, which can then be further refined through concurrent environmental reconstruction of artefact find spots and consideration of dental morphologies and wear (Ungar 1998).

The exploitation of embedded foods provides a nutritional advantage to tool-using primates (Wrangham 2006). While it is rarely considered that either a chimpanzee direct ancestor or a side branch of the panin lineage may have developed radically different or perhaps even more complex technology than extant individuals, the selective impetus is there, in the form of nutrient and calorie-rich nuts, as well as in underground starchy foods (Hernandez-Aguilar *et al.* 2007). Each primate lineage has had millions of years in which to discover, spread, lose and re-discover the benefits of technology, and it is unlikely that the forms of stone tool-use observed among living primates are the only ones ever to have evolved. The increased energetic returns gained by accessing embedded resources is a plausible reason to hypothesise that tool-use traditions at least equivalent in complexity to modern behaviour may have been repeatedly discovered by past primate, and hominin, populations.

Innovation

Cumulative cultural change plays a key role in behavioural studies attempting to differentiate primate and human learning processes (Marshall-Pescini & Whiten 2008a), with investigation into mechanisms such as imitation and emulation (Tennie *et al.* 2009). Studies of human behavioural modernity have turned in recent years to the impact of demography on permitting and sustaining behavioural innovations and patterns (Shennan 2001; Powell *et al.* 2009; Richerson *et al.* 2009). Chimpanzee research has also begun to explore these connections (Mitani 2006; Lycett *et al.* 2009), with a correlation shown between larger female group sizes and the number of habitual and customary cultural traits in several wild chimpanzee communities (Lind & Lindenfors 2010). This again raises the possibility that chimpanzee groups affected by recent human activities may not be behaviourally representative of past panins.

The same genetic studies that seek to identify past chimpanzee population expansions and contractions (e.g. Won & Hey 2005; Caswell *et al.* 2008) also provide spatio-temporal targets for investigating the occurrence of periods of more and less rapid cultural innovation. Mitochondrial studies that reconstruct female population size trends may be of special

interest in this regard, if females were a primary vector for cultural transmission in the past (Lycett *et al.* 2010). Unfortunately, genetic studies do not provide precise information on the timing of past bottlenecks and expansions, with date estimates varying widely depending on the model and calibration points used (Stone *et al.* 2010). However, archaeological evidence for origins and changes in primate cultural traditions could assist in narrowing the error margins of genetic studies, as it has done for calibrations of the human mitochondrial 'clock' (Soares *et al.* 2009).

Each of the chimpanzee subspecies may have been genetically distinct for longer than *H. sapiens* has existed as a species (Wegmann & Excoffier 2010; but see Gonder *et al.* 2011), which leaves a significant amount of time over which any cumulative effects of cultural innovation may have operated among the panins. Analysis of material culture left by primate populations that were larger and better connected than those of today would provide a much needed comparison to short-term laboratory-based studies that suggest chimpanzees do not accumulate modifications (Tennie *et al.* 2009). In particular, the long-term perspective provided by archaeology allows for assessment of whether panin accumulative processes operate on a slower scale than has been observable in the few decades of chimpanzee research.

Genetic data show that Central African chimpanzee populations have the largest current effective population size, and that unlike the western and eastern subspecies they did not go through a substantial population bottleneck in the Pleistocene (Wegmann & Excoffier 2010). The strong bottleneck effects seen for the western and eastern populations, as well as for the bonobos, might suggest that central populations are the ones to look to for cultural continuities and accumulation over the past few million years (Sanz & Morgan 2010). However, *P. t. troglodytes* have received less intensive field study than the western and eastern populations; for the 19 (out of 39) cultural variants identified by Whiten *et al.* (2001) that involve tool-use, 11 have insufficient data for assessing their presence among one or both of the Central African Goualougo and Lopé communities (Lycett *et al.* 2010). It is therefore not possible on present evidence to identify whether the presence of larger populations over longer time periods has had an impact on the innovation and cultural retention rates of modern chimpanzees. Nevertheless, a reasonable prediction based on demography would be that cultural innovation rates were consistently highest among past Central African panins, with cultural founder effects active among the diverging western and then eastern chimpanzee subspecies from around 500 000 years ago.

Discussion: a primate archaeological perspective

The three aspects of primate behaviour considered briefly here, diet, geographic variation and innovation, were chosen to point up the benefits of bringing an archaeological approach to primatology (Haslam *et al.* 2009). This approach improves our understanding of primate behavioural evolution in its own right, complementing studies of psychological and manual skills (e.g. Byrne 2005), in addition to generating comparative data for the study of human evolution. The reviewed topics are not mutually exclusive, since geographical expansions may stimulate or derive from innovations, and new innovations that relate to diet may be preferentially taken up by other individuals and groups (Nishida *et al.* 2009). It is also

important to remember that, even among humans, seemingly adaptive behaviours can be lost (Henrich 2004). Without knowing just how chequered the temporal pattern of cultural variation may be (Wrangham 2006), we should not automatically regard living tool-using primates (or indeed any cultural species) as representative of their entire ancestral lineages. For example, based on emerging genetic data, I have hypothesised that stone tool-use observed in Brazilian capuchin monkeys may be no more than 700 000 years old, and the same behaviour among West African chimpanzees perhaps little more than 500 000 years old. But across these taxa (and others) there may have been numerous instances of technological discovery, loss and re-discovery over that time period, dependent on demography and the availability of suitable tools and dietary targets. Now that the conceptual constraint of a lone *Homo-Pan* stone tool-using clade is abandoned, a key task is to examine the independent technological trajectory of each tool-using group.

The idea of cross-referencing hominin and primate activities is not new in archaeology, but directly investigating the activities of past primates does involve a shift away from humans and our ancestors as the sole focus of prehistoric study. In practice, the methods required differ little from those used in Palaeolithic archaeology. Surveys are necessary to determine the prevalence and distribution of tool materials, and their geographical intersection with habitats suitable for resources such as palm nuts and social insects, regardless of whether these are currently used by extant primates. The Brazilian *cerrado* and *caatinga* zones certainly hold promise in this regard, as does the Dahomey Gap savannah that separates the Upper and Lower Guinea rainforests (Mayr & O'Hara 1986) (Figure 2). Forest expansion in the latter area is linked to an increase in the pioneer oil palm *Elaeis guineensis* (Salzmann & Hoelzmann 2005), favoured for nut-cracking and pestle-pounding by the extant Bossou chimpanzees of Guinea (Sugiyama 1994).

Excavations are needed both within and outside the current range of tool-using primate species, especially in areas where environmental reconstructions indicate the previous existence of suitable habitats (e.g. Dupont *et al.* 2010). Information on changes to major river systems, as barriers to both gene and information flow, may assist in setting temporal limits to cultural processes. Initial dating programs also need to target durable, culturally relevant materials such as broken nut shells. Use-wear and residue analyses will continue to be valuable in distinguishing primate tools from natural objects, including use-wear on concentrations of broken stone debris that may reveal tool re-use behaviours akin to the early stages of hominin stone knapping. Key plant residues include starches found in nuts and USOs, the lipids and resins found in these same sources, and fragments of nut shells and structural tissue pounded into tool surfaces. Animal residues may include hair (such as the bushbaby hair found adhering to a chimpanzee spear in Senegal: Pruetz & Bertolani 2007), termite and ant parts, fats and marrow (Boesch & Boesch 1989), blood and by-products such as honey (Boesch *et al.* 2009; Sanz & Morgan 2009).

Realistically, the initial age estimates provided in this review for the origins of extant primate stone tool-use will require revision. These estimates are partly based on genetic dates, which have wide error margins, and in any case population genetic divergence cannot by default be assumed to correlate with material culture changes in any animal (including hominins). Finally, we should remember that hominins have filled the niche of cognitively advanced, large bodied, tool-using primate for the past few million years, which probably

had a negative impact on the evolution of similar roles among our close relatives. Debatably, this impact may have included intermittent hominin occupation of African forests from the Middle Pleistocene onwards (Mercader 2002). It is possible that we and our ancestors are the reason modern chimpanzees display limited rates of cultural evolution, and it is likely that the survival of extant primate species in Africa is to some extent a function of their ability to co-exist with hominins (Jablonski 2002). Outside Africa, the Asian macaques also have a long shared history with *Homo*, while in the Americas a lack of Pleistocene hominins may have permitted greater primate technological experimentation. Our ability to address issues such as these will strongly benefit from an archaeological approach, and an ability to see beyond behaviourally modern primates will offer new perspectives on both the relevance of primatological referents to human evolution, and on the variability and time depth of non-human primate behaviour.

Acknowledgements

I am grateful to Dora Biro, Bill McGrew, Susana Carvalho, Elisabetta Visalberghi, Dorothy Fragaszy and three anonymous reviewers for discussions and helpful comments on earlier drafts. I would also like to thank all the researchers working on the evolution of primate technology, on whose insightful work this review draws. The author received funding from a UK Arts and Humanities Research Council Early Career Fellowship, and European Research Council Starting Grant No. 283959 (PRIMARCH).

References

- AIELLO, L. & C. DEAN. 1990. *An introduction to human evolutionary anatomy*. London: Academic Press.
- BAR-YOSEF, O. 2002. The Upper Palaeolithic revolution. *Annual Review of Anthropology* 31: 363–93.
- BECQUET, C., N. PATTERSON, A. STONE, M. PRZEWSORSKI & D. REICH. 2007. Genetic structure of chimpanzee populations. *PLoS Genetics* 3: e66.
- BIRO, D., S. CARVALHO & T. MATSUZAWA. 2010. Tools, traditions, and technologies: interdisciplinary approaches to chimpanzee nut cracking, in E. Lonsdorf, S. Ross & T. Matsuzawa (ed.) *The mind of the chimpanzee: ecological and experimental perspectives*: 141–55. Chicago (IL): University of Chicago Press.
- BJORK, A., W. LIU, J. WERTHEIM, B. HAHN & M. WOROBAY. 2011. Evolutionary history of chimpanzees inferred from complete mitochondrial genomes. *Molecular Biology and Evolution* 28: 615–23.
- BOESCH, C. 2007. What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology* 121: 227–40.
- BOESCH, C. & H. BOESCH. 1982. Optimization of nut-cracking with natural hammers by wild chimpanzees. *Behaviour* 83: 265–86.
- 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates* 25: 160–70.
- 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology* 78: 547–73.
- 1990. Tool use and tool making in wild chimpanzees. *Folia Primatologica* 54: 86–99.
- BOESCH, C. & H. BOESCH-ACHERMANN. 2000. *The chimpanzees of the Tai Forest. Behavioural ecology and evolution*. Oxford: Oxford University Press.
- BOESCH, C., J. HEAD & M. ROBBINS. 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution* 56: 560–69.
- BREUER, T., M. NDOUNDOU-HOCKEMBA & V. FISHLOCK. 2005. First observation of tool use in wild gorillas. *PLoS Biology* 3(11): e380.
- BUTYNSKI, T. 2003. The robust chimpanzee *Pan troglodytes*: taxonomy, distribution, abundance, and conservation status, in R. Kormos, C. Boesch, M. Bakarr & T. Butynski (ed.) *West African chimpanzees. Status survey and conservation action plan*: 5–12. Cambridge: IUCN.
- BYRNE, R. 2005. The maker not the tool: the cognitive significance of great ape manual skills, in V. Roux & B. Brill (ed.) *Stone knapping: the necessary conditions for a uniquely hominid behaviour*: 159–69. Cambridge: McDonald Institute for Archaeological Research.

- CANALE, G.R., C.E. GUIDORIZZI, M.C.M. KIERULFF & C.A.F.R. GATTO. 2009. First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). *American Journal of Primatology* 71: 366–72.
- CARVALHO, S., E. CUNHO, C. SOUSA & T. MATSUZAWA. 2008. *Chânes opératoires* and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution* 55: 148–63.
- CARVALHO, S., D. BIRO, W. C. MCGREW & T. MATSUZAWA. 2009. Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeological invisible steps in the technological evolution of early hominins? *Animal Cognition* 12: S103–S114.
- CASADO, F., C. BONVICINO, C. NAGLE, B. COMAS, T. MANZUR, M. LAHOS & H. SEUANEZ. 2010. Mitochondrial divergence between 2 populations of the hooded capuchin, *Cebus (Sapajus) cay* (Platyrrhini, Primates). *Journal of Heredity* 101: 261–69.
- CASWELL, J., S. MALLICK, D. RICHTER, J. NEUBAUER, C. SCHIRMER, S. GNERRE & D. REICH. 2008. Analysis of chimpanzee history based on genome sequence alignments. *PLoS Genetics* 4(4): e1000057.
- CLARK, J.D. 1960. Human ecology during Pleistocene and later times in Africa south of the Sahara. *Current Anthropology* 1: 307–324.
- CONARD, N. 2008. A critical view of the evidence for a southern African origin of behavioural modernity. *South African Archaeological Society Goodwin Series* 10: 175–79.
- D'ERRICO, F. 2003. The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evolutionary Anthropology* 12: 188–202.
- D'ERRICO, F. & C. STRINGER. 2011. Evolution, revolution or saltation scenario for the emergence of modern cultures? *Philosophical Transactions of the Royal Society B* 366: 1060–69.
- DE LA TORRE, I. 2010. Insights on the technical competence of the early Oldowan, in A. Nowell & I. Davidson (ed.) *Stone tools and the evolution of human cognition*: 45–65. Boulder (CO): University Press of Colorado.
- DEBLAUWE, I., P. GUISLAIN, J. DUPAIN & L. VAN ELSACKER. 2006. Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, southeast Cameroon. *American Journal of Primatology* 68: 1191–96.
- DUPONT, L., S. JAHNS, F. MARRET & S. NING. 2010. Vegetation change in equatorial West Africa: time-slices for the last 150 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology* 155: 95–122.
- FOLEY, R. 1987. *Another unique species*. New York: Longman Scientific & Technical.
- 1993. African terrestrial primates: the comparative evolutionary biology of *Theropithecus* and hominids, in N. Jablonski (ed.) *Theropithecus – the rise and fall of a primate genus*: 245–70. Cambridge: Cambridge University Press.
- FOWLER, A. & V. SOMMER. 2007. Subsistence technology of Nigerian chimpanzees. *International Journal of Primatology* 28: 997–1023.
- GAGNEUX, P., M. GONDER, T. GOLDBERG & P. MORIN. 2001. Gene flow in wild chimpanzee populations: what genetic data tell us about chimpanzee movement over space and time. *Philosophical Transactions of the Royal Society B* 356: 889–97.
- GAMBLE, C., J.A.J. GOWLETT & R. DUNBAR. 2011. The social brain and the shape of the Palaeolithic. *Cambridge Archaeological Journal* 21: 115–35.
- GOEBEL, T., M.R. WATERS & D. O'ROURKE. 2008. The Late Pleistocene dispersal of modern humans in the Americas. *Science* 319: 1497–502.
- GOLDBERG, T. 1998. Biogeographic predictors of genetic diversity in populations of eastern African chimpanzees (*Pan troglodytes schweinfurthi*). *International Journal of Primatology* 19: 237–54.
- GONDER, M., S. LOCATELLI, L. GHOBRIAL, M. MITCHELL, J. KUJAWSKI, F. LANKESTER, C.-B. STEWART & S. TISHKOFF. 2011. Evidence from Cameroon reveals differences in the genetic structure and histories of chimpanzee populations. *Proceedings of the National Academy of Sciences of the USA* 108: 4766–71.
- GOWLETT, J.A.J. 2009. Artefacts of apes, humans, and others: towards comparative assessment and analysis. *Journal of Human Evolution* 57: 401–410.
- GUMERT, M., M. KLUCK & S. MALAIVIJITNOND. 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. *American Journal of Primatology* 71: 594–608.
- GUMERT, M., L.K. HOONG & S. MALAIVIJITNOND. 2011. Sex differences in the stone tool-use behavior of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). *American Journal of Primatology* 73: 1–11.
- HASLAM, M., A. HERNANDEZ-AGUILAR, V. LING, S. CARVALHO, I. DE LA TORRE, A. DE STEFANO, A. DU, B.L. HARDY, J. HARRIS, L. MARCHANT, T. MATSUZAWA, W. MCGREW, J. MERCARDER, R. MORA, M. PETRAGLIA, H. ROCHE, E. VISALBERGHI & R. WARREN. 2009. Primate archaeology. *Nature* 460: 339–44.

- HASLAM, M., S. CARVALHO, A. CROWTHER & T. MATSUZAWA. 2010. Residue analysis of modern and ancient chimpanzee pounding tools from Bossou and Diecké, Guinea: defining a primate archaeological signature. Paper presented at the 23rd International Primatological Society Congress, Kyoto.
- HAYASHI, M., Y. MIZUNO & T. MATSUZAWA. 2005. How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. *Primates* 46: 91–102.
- HENRICH, J. 2004. Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *American Antiquity* 69: 197–214.
- HENSHILWOOD, C.S. & C.W. MAREAN. 2003. The origin of modern human behavior. *Current Anthropology* 44: 627–51.
- HERNANDEZ-AGUILAR, A. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *Journal of Human Evolution* 57: 350–64.
- HERNANDEZ-AGUILAR, A., J. MOORE & T. PICKERING. 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceedings of the National Academy of Sciences of the USA* 104: 19210–13.
- HEY, J. 2010. The divergence of chimpanzee species and subspecies as revealed in multipopulation isolation-with-migration analyses. *Molecular Biology and Evolution* 27: 921–33.
- HOHMANN, G. & B. FRUTH. 2003. Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology* 44: 563–71.
- HOLLOWAY, R. 1969. Culture: a human domain. *Current Anthropology* 10: 395–412.
- HOORN, C., F. WESSELINGH, H. TER STEEGE, M. BERMUDEZ, A. MORA, J. SEVINK, I. SANMARTIN, A. SANCHEZ-MESEGUER, C. ANDERSON, J. FIGUEIREDO, C. JARAMILLO, D. RIFE, F. NEGRI, H. HOOGHIEMSTRA, J. LUNDBERG, T. STADLER, T. SÄRKINEN & A. ANTONELLI. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330: 927–31.
- ISAAC, G.L. 1969. Studies of early culture in East Africa. *World Archaeology* 1: 1–28.
- JABLONSKI, N. 2002. The fossil record of Old World monkeys: the Late Neogene radiation, in W. Hartwig (ed.) *The primate fossil record*: 255–99. Cambridge: Cambridge University Press.
- JOLLY, C. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5: 5–26.
- JOULIAN, F. 1996. Comparing chimpanzee and early hominid techniques: some contributions to cultural and cognitive questions, in P. Mellars & K. Gibson (ed.) *Modelling the early human mind*: 173–89. Cambridge: McDonald Institute for Archaeological Research.
- KLEIN, R.G. 2000. Archeology and the evolution of human behavior. *Evolutionary Anthropology* 9: 17–36.
- KOOPS, K., W.C. MCGREW & T. MATSUZAWA. 2010. Do chimpanzees (*Pan troglodytes*) use cleavers and anvils to fracture *Treculia africana* fruits? Preliminary data on a new form of percussive technology. *Primates* 51: 175–78.
- KUMAR, S., A. FILIPSKI, V. SWARNA, A. WALKER & S.B. HEDGES. 2005. Placing confidence limits on the molecular age of the human–chimpanzee divergence. *Proceedings of the National Academy of Sciences of the USA* 102: 18842–47.
- LADEN, G. & R. WRANGHAM. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. *Journal of Human Evolution* 49: 482–98.
- LEAKEY, L. 1961. *The progress and evolution of Man in Africa*. Oxford: Oxford University Press.
- LEAVENS, D., K. BARD & W. HOPKINS. 2010. BIZARRE chimpanzees do not represent ‘the chimpanzee’. *Behavioral and Brain Sciences* 33: 100–101.
- LEHMAN, S. & J. FLEAGLE. 2006. Biogeography and primates: a review, in S. Lehman & J. Fleagle (ed.) *Primate biogeography*: 1–58. New York: Springer.
- LIND, J. & P. LINDENFORS. 2010. The number of cultural traits is correlated with female group size but not with male group size in chimpanzee communities. *PLoS One* 5: e9241.
- LYCETT, S., M. COLLARD & W. C. MCGREW. 2009. Cladistic analyses of behavioural variation in wild *Pan troglodytes*: exploring the chimpanzee culture hypothesis. *Journal of Human Evolution* 57: 339–47.
- LYCETT, S., M. COLLARD & W.C. MCGREW. 2010. Are behavioral differences among wild chimpanzee communities genetic or cultural? An assessment using tool-use data and phylogenetic methods. *American Journal of Physical Anthropology* 142: 461–67.
- LYNCH ALFARO, J., J. BOUBLI, L. OLSON, A. DI FIORE, B. WILSON, G. GUTIERREZ-ESPELETA, K. CHIOU, M. SCHULTE, S. NEITZEL, V. ROSS, D. SCHWOCHOW, M. NGUYEN, I. FARIAS, C. JANSON & M. ALFARO. 2011. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *Journal of Biogeography*. doi: 10.1111/j.1365-2699.2011.02609.x.

- MALAIVITTOND, S., C. LEKPRAYOON, N. TANDAVANITTI, S. PANHA, C. CHEEWATHAM & Y. HAMADA. 2007. Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology* 69: 227–33.
- MANNU, M. & E. OTTONI. 2009. The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools. *American Journal of Primatology* 71: 242–51.
- MARCHANT, L.F. & W.C. MCGREW. 2005. Percussive technology: chimpanzee baobab smashing and the evolutionary modeling of hominid knapping, in V. Roux & B. Bril (ed.) *Stone knapping: the necessary conditions for a uniquely hominin behaviour* 341–50. Cambridge: McDonald Institute for Archaeological Research.
- MARSHALL-PESCINI, S. & A. WHITEN. 2008a. Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Animal Cognition* 11: 449–56.
- 2008b. Social learning of nut-cracking behavior in East African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *Journal of Comparative Psychology* 122: 186–94.
- MAYR, E. & R.J. O'HARA. 1986. The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution* 40: 55–67.
- MCBREARTY, S. & A. BROOKS. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39: 453–563.
- MCBREARTY, S. & N. JABLONSKI. 2005. First fossil chimpanzee. *Nature* 437: 105–108.
- MCGREW, W.C. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.
- 2001. The other faunivory: primate insectivory and early human diet, in C. Stanford & H. Bunn (ed.) *Meat-eating and human evolution*: 160–78. Oxford: Oxford University Press.
- 2004. *The cultured chimpanzee: reflections on cultural primatology*. Cambridge: Cambridge University Press.
- 2010. In search of the last common ancestor: new findings on wild chimpanzees. *Philosophical Transactions of the Royal Society B* 365: 3267–76.
- MCGREW, W.C., P. BALDWIN & C. TUTIN. 1988. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *American Journal of Primatology* 16: 213–26.
- MCGREW, W.C., R.M. HAM, L.J.T. WHITE, C. TUTIN & M. FERNANDEZ. 1997. Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology* 18: 353–74.
- MCPHERRON, S.P., Z. ALEMSEGED, C.W. MAREAN, J. WYNN, D. REED, D. GERAADS, R. BOBE & H. BEARAT. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466: 857–60.
- MELLARS, P. & C. STRINGER (ed.). 1989. *The human revolution: behavioral and biological perspectives on the origins of modern humans*. Edinburgh: Edinburgh University Press.
- MERCADER, J. 2002. Forest people: the role of African rainforests in human evolution and dispersal. *Evolutionary Anthropology* 11: 117–24.
- MERCADER, J., M. PANGER & C. BOESCH. 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296: 1452–55.
- MERCADER, J., H. BARTON, J. GILLESPIE, J. HARRIS, S. KUHN, R.T. TYLER & C. BOESCH. 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences of the USA* 104(9): 3043–48.
- MILTON, K. 1999. Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition* 15: 488–98.
- MINUGH-PURVIS, N. 1995. The modern human origins controversy: 1984–1994. *Evolutionary Anthropology* 4: 140–47.
- MITANI, J. 2006. Demographic influences on the behavior of chimpanzees. *Primates* 47: 6–13.
- MORGAN, B. & E. ABWE. 2006. Chimpanzees use stone hammers in Cameroon. *Current Biology* 16: R632–R33.
- MOURA, A. & P. LEE. 2004. Capuchin stone tool use in caatinga dry forest. *Science* 306: 1909.
- NISHIDA, T., T. MATSUSAKA & W.C. MCGREW. 2009. Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates* 50: 23–36.
- NISHIDA, T., K. ZAMMA, T. MATSUSAKA, A. INABA & W.C. MCGREW. 2010. *Chimpanzee behavior in the wild: an audio-visual encyclopedia*. Tokyo: Springer.
- OTTONI, E. & P. IZAR. 2008. Capuchin monkey tool use: overview and implications. *Evolutionary Anthropology* 17: 171–78.
- PANGER, M., A. BROOKS, B.G. RICHMOND & B. WOOD. 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology* 11: 235–45.
- PARKER, S. & K. GIBSON. 1979. A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences* 2: 367–408.

- POTTS, R. 2007. Environmental hypotheses of Pliocene human evolution, in R. Bobe, Z. Alemseged & A. K. Behrensmeyer (ed.) *Hominin environments in the East African Pliocene: an assessment of the faunal evidence*: 25–49. Dordrecht: Springer.
- POWELL, A., S. SHENNAN & M. THOMAS. 2009. Late Pleistocene demography and the appearance of modern human behavior. *Science* 324: 1298–301.
- PRUETZ, J. & P. BERTOLANI. 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology* 17: 412–17.
- 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: implications for hominin adaptations to open habitats. *PaleoAnthropology* 2009: 252–62.
- RENFREW, C. 2007. *Prehistory: making of the human mind*. London: Weidenfeld & Nicolson.
- RICHERSON, P.J., R. BOYD & R.L. BETTINGER. 2009. Cultural innovations and demographic change. *Human Biology* 81: 211–35.
- SALZMANN, U. & P. HOELZMANN. 2005. The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. *The Holocene* 15: 190–99.
- SANZ, C. & D. MORGAN. 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology* 30: 411–27.
- 2010. The complexity of chimpanzee tool-use behaviors, in E. Lonsdorf, S. Ross, T. Matsuzawa & J. Goodall (ed.) *The mind of the chimpanzee: ecological and experimental perspectives*: 127–40. Chicago: University of Chicago Press.
- SANZ, C., D. MORGAN & S. GULICK. 2004. New insights into chimpanzees, tools and termites from the Congo Basin. *American Naturalist* 164: 567–81.
- SANZ, C., J. CALL & D. MORGAN. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters* 5: 293–96.
- SEMAW, S., M.J. ROGERS, J. QUADE, P. RENNE, R.F. BUTLER, M. DOMINGUEZ-RODRIGO, D. STOUT, W.S. HART, T. PICKERING & S.W. SIMPSON. 2003. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution* 45: 169–77.
- SEPT, J. 1998. Shadows on a changing landscape: comparing nesting patterns of hominids and chimpanzees since their last common ancestor. *American Journal of Primatology* 46: 85–101.
- SEPT, J. & G.E. BROOKS. 1994. Reports of chimpanzee natural history, including tool use, in 16th- and 17th-century Sierra Leone. *International Journal of Primatology* 15: 867–78.
- SHEA, J.J. 2011. *Homo sapiens* is as *Homo sapiens* was. Behavioral variability versus ‘behavioral modernity’ in Paleolithic archaeology. *Current Anthropology* 52: 1–35.
- SHENNAN, S. 2001. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal* 11: 5–16.
- SHUMAKER, R., K. WALKUP & B. BECK. 2011. *Animal tool behavior: the use and manufacture of tools by animals*. Baltimore (MD): John Hopkins University Press.
- SILK, J. 2011. The path to sociality. *Nature* 479: 182–83.
- SOARES, P., L. ERMINI, N. THOMSON, M. MORMINA, T. RITO, A. ROHL, A. SALAS, S. OPPENHEIMER & M. RICHARDS. 2009. Correcting for purifying selection: an improved human mitochondrial molecular clock. *American Journal of Human Genetics* 84: 740–59.
- SOUTO, A., C. BIONE, M. BASTOS, B. BEZERRA, D. FRAGASZY & N. SCHIEL. 2011. Critically endangered blonde capuchins fish for termites and use new techniques to accomplish the task. *Biology Letters*. doi: 10.1098/rsbl.2011.0034.
- SPAGNOLETTI, N., E. VISALBERGHI, E. OTTONI, P. IZAR & D. FRAGASZY. 2011. Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of Human Evolution* 61: 97–107.
- STEFFEN, W., J. GRINEVALD, P. CRUTZEN & J. MCNEILL. 2011. The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A* 369: 842–67.
- STEWART, F., A. PIEL & W.C. MCGREW. 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. *Journal of Human Evolution* 61: 388–95.
- STONE, A., F. BATTISTUZZI, L. KUBATKO, G.H. PERRY, E. TRUDEAU, H. LIN & S. KUMAR. 2010. More reliable estimates of divergence times in *Pan* using complete mtDNA sequences and accounting for population structure. *Philosophical Transactions of the Royal Society B* 365: 3277–88.
- SUGIYAMA, Y. 1994. Tool use by wild chimpanzees. *Nature* 367: 327.
- TENNIE, C., J. CALL & M. TOMASELLO. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B* 364: 2405–15.
- THIEME, H. 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385: 807–10.
- TOTH, N. & K. SCHICK. 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology* 38: 289–305.

- TWEHEYO, M., K. LYE & R. WELADJI. 2004. Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* 188: 267–78.
- UNGAR, P. 1998. Dental allometry, morphology, and wear as evidence for diet in fossil primates. *Evolutionary Anthropology* 6: 205–17.
- UNGAR, P. & M. SPONHEIMER. 2011. The diets of early hominins. *Science* 334: 190–93.
- VAN SCHAİK, C., E. FOX & A. SITOMPUL. 1996. Manufacture and use of tools in wild Sumatran orangutans. *Naturwissenschaften* 83: 186–88.
- VAN SCHAİK, C., R. DEANER & M. MERRILL. 1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution* 36: 719–41.
- VAN SCHAİK, C., M. ANCRENAZ, G. BORGÉN, B. GALDIKAS, C. KNOTT, I. SINGLETON, A. SUZUKI, S.S. UTAMI & M. MERRILL. 2003. Orangutan cultures and the evolution of material culture. *Science* 299: 102–105.
- VISALBERGHI, E., D. FRAGASZY, E. OTTONI, P. IZAR, M. DE OLIVEIRA & F. ANDRADE. 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology* 132: 426–44.
- VISALBERGHI, E., E. ADDESSI, V. TRUPPA, N. SPAGNOLETTI, E. OTTONI, P. IZAR & D. FRAGASZY. 2009. Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology* 19: 213–17.
- VRBA, E. 2000. Major features of neogene mammalian evolution in Africa, in T. Partridge & R. Maud (ed.) *Cenozoic geology of southern Africa*: 277–304. Oxford: Oxford University Press.
- WADLEY, L. 2001. What is cultural modernity? A general view and a South African perspective from Rose Cottage Cave. *Cambridge Archaeological Journal* 11: 201–21.
- WASHBURN, S. & I. DEVORE. 1961. Social behavior of baboons and early man, in S. Washburn (ed.) *Social life of early Man*: 91–105. New York: Wenner-Gren Foundation for Anthropological Research.
- WEGMANN, D. & L. EXCOFFIER. 2010. Bayesian inference of the demographic history of chimpanzees. *Molecular Biology and Evolution* 27: 1425–35.
- WHITEN, A. 2011. The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society B* 366: 997–1007.
- WHITEN, A., J. GOODALL, W.C. MCGREW, T. NISHIDA, V. REYNOLDS, Y. SUGIYAMA, C. TUTIN, R. WRANGHAM & C. BOESCH. 1999. Cultures in chimpanzees. *Nature* 399: 682–85.
- 2001. Charting cultural variation in chimpanzees. *Behaviour* 138: 1481–516.
- WHITEN, A., K. SCHICK & N. TOTH. 2009. The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. *Journal of Human Evolution* 57: 420–35.
- WON, Y.-J. & J. HEY. 2005. Divergence population genetics of chimpanzees. *Molecular Biology and Evolution* 22: 297–307.
- WOOD, B. & T. HARRISON. 2011. The evolutionary context of the first hominins. *Nature* 470: 347–52.
- WRANGHAM, R. 2006. Chimpanzees: the culture-zone concept becomes untidy. *Current Biology* 16: R634–R635.
- WYNN, T.G., A. HERNANDEZ-AGUILAR, L.F. MARCHANT & W.C. MCGREW. 2011. ‘An ape’s view of the Oldowan’ revisited. *Evolutionary Anthropology* 20: 181–97.
- YU, N., M. JENSEN-SEAMAN, L. CHEMNICK, J. KIDD, A. DEINARD, O. RYDER, K. KIDD & W.-H. LI. 2003. Low nucleotide diversity in chimpanzees and bonobos. *Genetics* 164: 1511–18.

Received: 6 May 2011; Accepted: 6 October 2011; Revised: 8 December 2011