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REVIEWS

Primate archaeology

Michael Haslam[1], Adriana Hernandez-Aguilar[1], Victoria Ling[1], Susana Carvalho[1], Ignacio de la Torre[2], April DeStefano[3], Andrew Du[3], Bruce Hardy[4], Jack Harris[3], Linda Marchant[5], Tetsuro Matsuzawa[6], William McGrew[1], Julio Mercader[7], Rafael Mora[8], Michael Petraglia[1], Hélène Roche[9], Elisabetta Visalberghi[10] & Rebecca Warren[4]

All modern humans use tools to overcome limitations of our anatomy and to make difficult tasks easier. However, if tool use is such an advantage, we may ask why it is not evolved to the same degree in other species. To answer this question, we need to bring a long-term perspective to the material record of other members of our own order, the Primates.

Several animal species use tools and selectively manipulate objects[1]. Primate tool use has received particular attention, in part because of the close evolutionary heritage that other primates share with technology-dependent humans. However, the effects of material culture on primate long-term adaptiveness have yet to be systematically explored. Here we review the interface of primatology and archaeology, following a recent intensification of research into the relevance of other primates for understanding hominin technology and behaviour.

Extensive and flexible tool use was once considered a defining human characteristic[2]. Detailed observation since the mid-twentieth century has, however, revealed a wide variety of habitual tool use among wild chimpanzees (*Pan troglodytes*)[3] in Africa, adding to records of less complex tool use by other species. At the same time, stone artefacts made by hominins—the human lineage since the split with chimpanzees some 5–7 Myr ago[4]—have been found dating back 2.6 Myr (ref. 5). Because this earliest Oldowan technology already shows much planning depth, spatial coordination and manual dexterity[6] in its creators, it is probable that earlier, currently unrecognized, tool manufacture occurred. Appeals to phylogenetic proximity therefore posit the last common ancestor of chimpanzees and humans to have been a tool user[7,8], and for many archaeologists chimpanzees have become the dominant referent for modelling early hominin behaviour. However, recent recognition that wild South American bearded capuchin monkeys (*Cebus libidinosus*) also habitually use tools[9], whereas wild bonobos (*Pan paniscus*, the chimpanzee's closest relative) rarely do[10], forces us to rethink the accepted roles of continuity and convergence in primate tool use. We may ask, for example, how many extinct primate groups independently 'invented' tool use during the past several million years, and what circumstances permitted or prevented such discoveries. Questions also arise as to the influence of long-term tool use on non-human-primate anatomy, and the reasons why hominins alone have taken tool use to such an extreme.

A long-standing separation of anthropocentric archaeology from primate ethology has obscured the holistic perspective required to address these questions. Here, our solution is to introduce a new interdisciplinary field—primate archaeology—that examines the past and present material record of all members of the order Primates. This field provides a comprehensive comparative and long-term evolutionary framework for understanding the biological, environmental and social contexts of primate behaviour, through analyses of tool making, tool use and the spatially patterned accumulation of refuse. Examination of the contexts for non-human-primate artefact and landscape use, alongside early hominin equivalents, provides a new understanding of the origins and evolution of human behaviour. Comparisons with the patterned use of material objects by living and extinct taxa outside the Primates will provide the first step towards a universal framework for unravelling the behavioural implications of both human and non-human components of the archaeological record.

The intersection of primatology and archaeology

Since the first systematic recording of wild-chimpanzee tool use, primatologists have stressed its direct relevance to early hominin studies[11]. Beyond phylogeny, the main reasons for this applicability are the convenient physicality and durability of material culture, which permit measurement of behaviour and inference of intentions and abilities even if the user is absent or dead. From an archaeological perspective, definitions of 'tool use'[12] are therefore less important than recognition of the adaptive benefits and interpretive potential of manipulated durable objects.

Free-living primate populations use a wide variety of plant materials for extractive foraging, social interaction and self-maintenance[9,13–16] (Fig. 1). Wild chimpanzees, orangutans (*Pongo* spp.) and capuchin monkeys use leaf, wood, twig, grass and bark tools, often modifying the items to better suit the targeted task[17–19]. Wild western gorillas (*Gorilla gorilla*) have also recently been reported to use branch tools for postural support[20]. These observations of primate plant-tool use expand the conceptual framework for our interpretations of early hominin behaviour, as hominin wooden artefacts are only known from within the past 800,000 years[21], and poor preservation of organic tools in the archaeological record means a significant amount of information about the origins of human technology is now lost. Use-wear traces and microscopic residues on stone artefacts may provide indirect evidence of plant-tool manufacture in the more remote past[22].

The enforced focus on inorganic archaeological materials has led to the development of highly informative methods of measuring and interpreting stone artefacts[23], often centring on raw-material selection and transport, and on the manufacturing process and resultant forms. The key characteristic distinguishing stone from most organic materials is the potential for controlled formation of acute margins during fracture (that is, detachment of a flake from a larger core), with the degree of

[1]Leverhulme Centre for Human Evolutionary Studies, University of Cambridge, Cambridge CB2 1QH, UK. [2]Institute of Archaeology, University College London, London WC1H 0PY, UK. [3]Department of Anthropology, Rutgers University, New Brunswick, New Jersey 08901, USA. [4]Department of Anthropology, Kenyon College, Gambier, Ohio 43022, USA. [5]Department of Anthropology, Miami University, Oxford, Ohio 45056, USA. [6]Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan. [7]Department of Archaeology, University of Calgary, Calgary, Alberta T2N 1N4, Canada. [8]Division de Prehistoria, Universidad Autonoma de Barcelona, Barcelona 08193, Spain. [9]Maison de l'Archéologie et de l'Ethnologie, CNRS, Paris 92023, France. [10]Istituto di Scienze e Tecnologie della Cognizione, Rome 00197, Italy.

Figure 1 | Chimpanzee plant use. **a**, Plants as tools: fishing for termites (Gombe Stream National Park, Tanzania). Chimpanzee extractive foraging such as this varies culturally between groups, independently of biological or environmental influences. **b**, Plants as construction: sleeping in a nest (Gombe Stream National Park). Chimpanzees make a 'bed' every night, and recent work has shown that reoccupation of the same localities may result in recognizable, patterned debris accumulation. **c**, Plants as activity sites: cracking oil-palm nuts using a tree-branch anvil and stone hammer (Liberia). Photo, A. C. Hannah.

control reflecting motor skill and cognitive capacities[6]. The resulting sharp edges can be used for tasks such as butchering animals, processing plants or trimming wood. Oldowan assemblages dated to ~2.6–1.6 Myr ago typically consist of minimally worked cores and flakes with associated debris, although careful reconstructions have shown that on occasion more than 70 flakes were struck from a single cobble[6]. Oldowan sites also contain battered (not systematically flaked) stone tools (Fig. 2a), and although recognized early on as hammers and anvils[24], only recently have these been analysed in detail and compared with chimpanzee pounding tools[25]. Recovery of cut-marked and damaged fossil bones at some early archaeological sites[26] suggests that cutting edges were exploited primarily for greater access to meat or marrow. However, as a wide variety of plants were available to Oldowan hominins[27], the relative emphasis on vertebrate faunal exploitation over that of vegetation remains hypothetical. Early hominin invertebrate exploitation is little discussed, but is ripe for further enquiry owing to its prevalence in the primate world[28,29].

Chimpanzees and capuchins use stone hammer-and-anvil combinations to crack hard-shelled nuts[18,30] (Fig. 2b, c), as well as anvils for opening hard-shelled fruits[31,32]. Island-dwelling long-tailed macaques (*Macaca fascicularis*) use stones to crack molluscs and crabs[33], and bearded capuchins use stones to dig for tubers and to process

Figure 2 | Primate stone-tool use. **a**, Three ~1.7–1.6-Myr-old Oldowan pounding tools from Olduvai Gorge, Tanzania. Provenance (left to right): FLK North level 1–2; FLK North level 5; FLK North sandy conglomerate. Scale bars, 1 cm. **b**, Chimpanzee cracking nuts with a stone hammer and anvil (Bossou, Guinea). The full social complexity of this activity cannot be reconstructed from the archaeological record alone. **c**, Adult male capuchin cracking nuts using a stone hammer and wood anvil (Boa Vista, Brazil). Note erect body position and relatively large (1.44-kg) hammer.

plants such as cactus[19,34]. These tools can become fractured, abraded or pitted as a result of repeated impact damage, leaving potentially diagnostic use-wear patterns (Fig. 3). Although non-human primates have not been seen systematically creating sharp stone flakes, fortuitous breakage of an anvil margin while processing plant foods has been hypothesized as a first step towards deliberate stone knapping[32]. The origins of intentionally flaked stone technology are therefore an important meeting point between primatology and archaeology, and archaeologists regularly invoke chimpanzee plant-processing behaviour in discussions of either pounding tools or the accidental creation of flakes from anvils[35,36]. Continued input from both fields is required to resolve incongruities between the hypotheses that vegetal processing led to the critical discovery of stone flaking, but that meat and marrow processing were the first uses of the discovery.

The oldest archaeological sites have no hominin fossils in direct association with stone artefacts[5,6]. *Homo habilis*, currently the earliest recognized member of genus *Homo*, lived ~2.4–1.4 Myr ago[37] and was hypothesized to be the creator of the initial Oldowan tools[38]. However, the time gap between the start of systematic stone flaking and the earliest *Homo* fossils suggests that earlier hominin taxa could be the innovators[39]. The relative brain sizes and manipulative abilities of the hominin species potentially ancestral to early *Homo* (that is, *Australopithecus africanus*, *Australopithecus afarensis* and *Australopithecus garhi*) appear to be roughly equivalent to those of the extant great apes[8,40–42]. This has prompted studies of non-human-primate capabilities. When they are motivated, captive orangutans[43], bonobos[44] and capuchin monkeys[45] are capable of rudimentary stone reduction leading in some cases to sharp-edged, flaked cutting tools. The bonobo results are distinguishable from Oldowan artefacts, although the main bonobo subject displayed an unprompted inclination throughout the study to break rocks by throwing them onto a hard substrate, rather than using the typical Oldowan method of striking one hand-held stone against another[46]. This suggests an alternative avenue through which australopithecines and earlier hominins may have obtained sharp stone edges, and raises the possibility that extinct panins (the chimpanzee lineage since the split with humans) may have used the same technique.

Aspects of modern primate anatomy, such as a capacity for bipedal posture and the structure of the forelimb, wrist and hands[47], provide

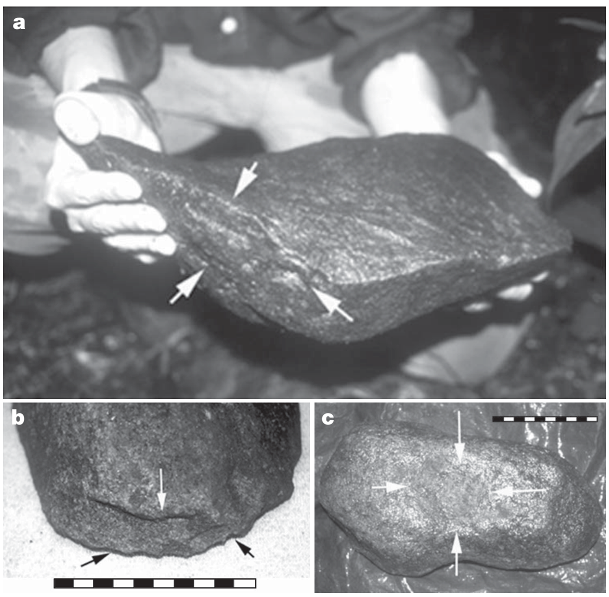

Figure 3 | Wear patterns on chimpanzee pounding stone tools. Repeated use of favoured hammers and anvils builds up distinctive damage patterns, permitting archaeological identification of these tools. **a**, **b**, Flaking, crushing, pitting and corner removals. **c**, Cavity formation. Scale bar divisions, 1 cm. Photos, C. Boesch and J.M. (Taï National Park, Côte d'Ivoire).

valuable comparisons in assessing the capacities of hominins living before 2.6 Myr ago. Primate dentition is sufficient for many scraping, slicing, crushing and trimming tasks[40,48], and this has been offered as an explanation for the apparent absence of stone flaking among wild non-human primates. Documenting the selective feedback from both technology and environment in shaping anatomical traits therefore forms an important research focus of primate archaeology. That both 45-kg chimpanzees and 3-kg capuchins use stone hammers averaging around 1 kg or more in mass[30,49] demonstrates that we cannot posit an a-priori relationship between the size of a primate and its potential tools. Similarly, *Cebus* has a significantly higher encephalization quotient (the ratio of brain size to expected brain size as calculated from body mass or metabolism) than do most other primates, including *Pan* and the extinct hominins before *Homo*[50]. Ideally, comparative anatomy allows us to track the divergent paths taken by the various primate lineages since their split. For panins, however, we are hindered by an almost total lack of fossils[51]. The hominin fossil record is better represented, but the likelihood of past adaptive radiations makes it unclear which of the known extinct species are direct ancestors of the human line.

It is also unclear which of the extinct hominins were tool users. *Australopithecus garhi* has been suggested as being responsible for cut-marked bones dated to 2.5 Myr ago in Ethiopia[26], and *Australopithecus robustus* has been posited as being a potential bone-tool user in South Africa[28]. Chimpanzees show cultural variation in their tool use; for example, not all populations use stone tools to crack nuts[14], and wild bonobos and gorillas have not been observed to use extractive tools of any kind[10]. Thus, we should not assume that groups of extinct hominins were homogenous in their forms of material culture. Moreover, the parsimonious explanation that widespread *Homo* and chimpanzee material culture indicates a tool-using common ancestor cannot reasonably be extended to the common ancestor of apes and *Cebus* or *Macaca*. The New and Old World monkeys split from the line leading to the apes around 35 and 25 Myr ago, respectively[52], and wild tool use in these lineages is rare. Convergence in tool use among primates is therefore plausible, probably owing to similar adaptive pressures, foraging requirements and physiological constraints. Significantly, acceptance of convergence in monkeys opens the door to the possibility of repeated gain and loss of tool use among extinct primates in multiple lineages over millions of years. From this perspective, it is unreasonable to expect that the only tool-using, non-hominin primates are extant species.

For a comprehensive comparative study of the development of technology, we must establish the antiquity and form of tools used by non-human-primate ancestors (and potentially also tool-using species outside the primates), along with their ecological contexts. This aim has been advanced through excavation of chimpanzee nut-cracking sites in Taï National Park, Côte d'Ivoire[53,54], where finds of accumulated cultural refuse dating back at least 4,300 years helped establish the legitimacy of primate-archaeological research. Recovered tools were interpreted as fragments of pounding stones used for processing nuts, supported by discriminatory analysis of adhering starch residues. Ongoing studies at Bossou and Diecke in Guinea focus on chimpanzee tool selection, spatial patterning and functional characteristics for a number of surface-context, present-day nut-cracking localities[55] (Fig. 4a). Similarly, research on wild bearded capuchins has examined such factors as the wear traces left by repeated use of anvils for pounding hard-shelled nuts[30], tool transport and selectivity[56] and the kinematics and energetics of nut cracking[57]. Capuchins consistently select hammer stones that are appropriate for the task by size and weight, displaying planning abilities and the rapid employment of visual, acoustic and haptic clues to correctly identify suitable tools[58]. Preferential accumulation of such materials at sites with appropriate anvils—the latter identifiable from wear traces—produces a capuchin 'activity area' (Fig. 4b), the remains of which may last for millennia.

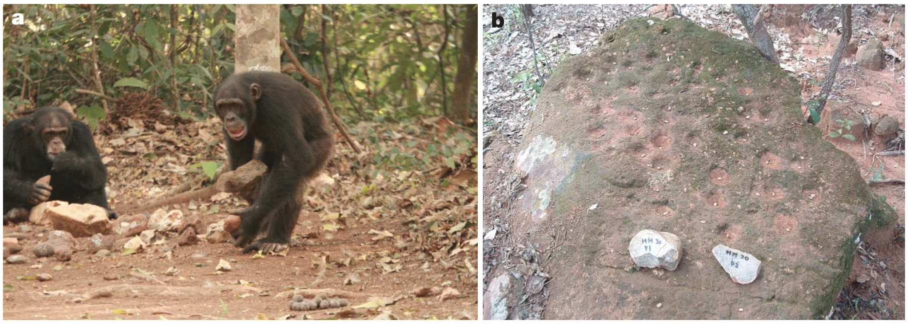

Figure 4 | Primate site creation. **a**, Selective transport of a stone hammer and anvil by an adolescent male chimpanzee (Bossou, Guinea). Over time, this behaviour accumulates artefacts in preferred tool-use sites. **b**, Stone anvil pitted by capuchin nut-cracking activity (Boa Vista, Brazil). Two stone hammers were found on the anvil, and nut debris was removed from the anvil before recording. Image from ref. 30.

Chimpanzee and capuchin spatial concentration of pounding tools such as anvils and hammer stones, and repeated, frequently seasonal, re-use of locations such as nut-tree sites, can form recognizable non-human archaeological assemblages[53]. The viability of identifying pounding tools from pre-Oldowan times onwards is strengthened by modern actualistic studies—of nut cracking, meat processing, marrow extraction, digging-stick manufacture and stone-tool manufacture—that leave distinct use-damage patterns on the tools and act as proxies for identifying past pounding activities. Recording use-wear traces on experimental anvils and hammer stones, and on those used by free-ranging primates, also gives a clearer understanding of the dynamic behavioural and decision-making processes involved. Such cross-taxa comparative work is still in its infancy; however, ongoing research applying this methodology to Plio-Pleistocene anvils from Koobi Fora, Kenya, and Olduvai Gorge[25] suggests that the various pounding activities may be differentiated by their use traces. Field experiments exposing wild chimpanzees to a variety of raw materials for extractive foraging complement this work[59], as does the study of percussion-marked fossil bones[60].

Pioneering studies applying archaeological recording methods to the spatial distribution of chimpanzee nests[61,62] suggested that chimpanzees accumulate organic artefacts through repeated occupation of a site. Current work confirms this hypothesis[63], providing insight into early hominin site formation processes. A recent report of wooden digging tools used by savanna-woodland chimpanzees also demonstrates the importance of an archaeological approach to primate plant-tool use[15]. The presence of digging tools, holes, masticated underground storage organs, faeces and knuckle prints indicated that chimpanzees had been digging for underground storage organs, despite the absence of direct observations of this activity. Wild capuchins also use sticks to probe[19]; moreover, they exhibit repeated use of caves to sleep in at night, to thermoregulate during the hottest part of the day, and to seek refuge in during heavy rain (Etho*Cebus* project, unpublished observations). All primates leave remnants that can enter the archaeological record (for example faeces as coprolites), and behavioural patterns that emphasize repeated use of particular tree, cliff or cave sites[64,65] may result in spatially patterned and therefore detectable accumulations in both open and forested environments. These findings have clear parallels with the archaeological interpretation of hominin activity areas; however, recognition of the highly uneven preservation of this ephemeral evidence in the archaeological record is challenging.

The role of primate archaeology

Acknowledging that only some primate taxa exhibit technology, despite their inherited biological similarities, primate archaeology has the following interconnected aims. The first goal is to use concurrent archaeological and primatological methods for recording living non-human-primate tool use to learn about the evolutionary trajectories of primate behaviour from both anthropocentric and 'primatocentric' perspectives. The second is to employ comparative studies of similar technologies across human and primate taxa (for example pounding, probing and digging tools) to investigate the origins of tool use among primates and its social, physiological, biomechanical and environmental contexts. The third is to examine the spatially patterned behavioural characteristics of primates that do not use tools, to determine whether these patterns are recognizable in the material record and how they might inform us about the likely activities of extinct primates (including hominins that did not use tools). The fourth aim is to identify how convergence has shaped primate tool use, and the implications that this has for the technologies of extinct primate taxa.

In implementing this agenda, the most complex results will probably derive from stone-tool-using species such as humans, chimpanzees, capuchins and macaques, as these generate a durable material record. However, until research methods in this field are much more rigorous and well established, it would be premature to make decisions on the potential contribution of any one taxon. Much of our knowledge is very recent: a mere decade ago the list of known wild-primate stone-tool users included only humans and chimpanzees, and half a century ago solely humans.

Despite a number of research projects that examine pre-*sapiens* contexts, most archaeological investigations worldwide remain focused on the activities of *Homo sapiens*, largely within the past few tens of millennia. This agrees well with definitions of archaeology as an anthropocentric science. However, we contend that archaeology should be viewed as a set of methods for the recovery and interpretation of behavioural evidence, irrespective of the species creating the record. This view is already common in the study of species that may be our direct ancestors (for example *H. habilis*), as well as those that are not (for example *Homo neanderthalensis* and *Homo floresiensis*). The difference is that the comparative study of dynamic living-primate behaviour offers greater potential for hypothesis testing and data generation than any study of static objects left by extinct hominins. Furthermore, although terms such as 'chimpanzee archaeology'[55] and 'cultural panthropology'[66] have been used previously, they exclude non-ape primates; an inclusive term for these endeavours promotes common methods and encourages cross-taxa comparisons.

Non-human primates display stone and plant-material selection, processing and accumulation behaviours that challenge the conventional view of hominins as the sole creators of archaeological sites. If geographical and palaeoecological data suggest that a site was habitable by both hominins and other (potentially extinct) tool-using primates, then ambiguity arises over the extent to which either taxon contributed to any recovered assemblage. The only dated chimpanzee archaeological site faces this problem, human and chimpanzee stone tools being present in the same deposit[54]. The known innovative abilities of tool-using primates should therefore act as a cautionary brake in automatically assigning assemblages from such sites to any one taxon[40].

Whereas there is only one extant species of hominin and two of panin, there are eight living capuchin species[67], only one of which

(*C. libidinosus*) is known to use tools frequently in the wild[9]. Primate archaeological research into the contexts of *Cebus* long-term tool selection, tool manipulation and spatial and social organizational strategies therefore offers one of the clearest opportunities to uncover important variables in the emergence of material culture. For example, we need to quantify the energetic costs of being a habitual tool user, and assess how these costs affect differential survival. As mentioned above, acceptance of the convergent evolution of tool use among Old and New World monkeys means that we should reasonably expect other species to have discovered, employed and then lost tool use throughout the past. On the basis of extant primate behaviour, we can expect some of these instances to have involved stone tools, and for those artefacts still to be recoverable today. Primate archaeology enables us to discover whether or not the long record of stone-tool use in the hominin line (at present covering around half the period since the common ancestor with *Pan*) is exceptional.

Sharp-edged tools are not the only stone artefacts produced during the Oldowan and later periods, and more material was used for percussion than for flaking at some early sites[25]. A perspective that emphasizes hominin systematic flaking obscures the potential contribution of non-hominin primates to the known archaeological record, and inhibits meaningful discussion of the factors behind cross-taxa parallels evident in other areas of technology. These factors include energy trade-offs between diet and tool manufacture, inter- and intraspecies variability in resource exploitation and tool function, intentionality in tool material and attribute selection, and modes of social transmission. From a longer-term perspective, primate archaeology also contributes essential data to debates over the necessity and sufficiency of tool use in the evolution of bipedalism and terrestriality.

Comparisons between taxa that have close morphological and genetic affinities with humans form a naturally strong research basis. However, the rationale behind primate archaeology applies also to non-primates, because any animal that accumulates or modifies durable materials will leave a signature in the archaeological record. Animals as diverse as crows[68], dolphins[69], beavers[70] and bowerbirds[71] selectively manipulate material objects in regular patterns for extractive foraging, niche construction and sexual display. Animals that use stones to break open resources, for example the portable anvils of Californian sea otters[72] or fixed nut-cracking anvils of New Caledonian crows[73], may leave recoverable impact signatures that inform on the time depth and adaptive value of tool use in these species. Animal behavioural studies typically concentrate on current abilities rather than evidence for the evolutionary development of object manipulation, and even those field sites with multidecadal research data (for example Gombe Stream National Park for chimpanzees) have recorded only a tiny fraction of the lifespan of a species. A clearer understanding of the behavioural remnants of non-human animals provides a 'control experiment' on the uniqueness of human artefacts.

The future of primate archaeology

Primate archaeology places the entirety of human behavioural evolution into its wider comparative biological context, and its establishment clarifies the need for refinement of existing research programs. First, there is a need for systematic collaboration: few archaeologists have seen a wild primate use a tool, and few primatologists have taken part in archaeological excavations. Integrated involvement of disciplines outside these areas, including comparative anatomy, cognitive science and evolutionary ecology, will also be essential. Second, standardization of recording procedures will combine an archaeological focus on material attributes and actions with the comprehensive spatially, temporally and socially patterned behavioural data generated by primatology. Third, creation of a comprehensive database comparing cross-taxa tool making and tool use in their environmental, biological and social contexts will enable exploration of the selective costs and benefits involved, with the ultimate aim of identifying those circumstances driving the uptake and continuance of tool use among primates, including human ancestors. Finally, direct documentation of the use of both human- and non-human-primate tools will allow us to tie specific actions to resultant residues and wear patterns, in turn helping us to understand why archaeologically recovered artefacts were created or chosen, producing valuable data on cognitive evolution.

Greater recognition of the value of primate tool use and site creation to human evolutionary studies can only help in the protection of rapidly declining primate populations. Field observation of the frequency of site visitation and the processes of site accumulation produces clues to the timescales represented at known hominin sites. Linking data to identified individuals within a primate group provides rich contextual information on cultural transmission and demographic variation in tool use within social and kinship networks[74], as well as emphasizing the roles of age, sex and experience in phenomena such as tool standardisation, connecting artefacts to social roles and ontogeny. All such data help clarify those characteristics of technology that differentiate primates from other tool-using species. Crucially, excavation of primate activity areas adds time depth to these observations; other than for the later hominins, the span of time over which any species has used tools is currently unknown.

Recent years have seen the first observations of wild tool use by populations of orangutans, capuchins and macaques, and a dramatic increase in our knowledge of the range, variability and time depth of chimpanzee material culture. We have also seen the announcement of the world's oldest hominin tools and the revelation of unexpected skill in their manufacture. With the likelihood of even earlier hominin tool use, the proposed addition of new taxa to the hominin family tree[42,75,76] has added new complexity to our evolutionary history. Primate archaeology provides the necessary methodology and scope to incorporate these developments into a coherent framework for the systematic location and interpretation of evolutionarily significant material culture, opening up new avenues in our understanding of the place of technology in primate and human societies.

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