

1 Primate archaeology evolves

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32 Introduction

33 Archaeology gives humanity access to its past, helping to define who we are. Its method -
34 the scientific study of the material remains of past behaviour – has been extraordinarily
35 successful, resulting in the systematic recovery and interpretation of evidence for human
36 evolution covering more than three million years¹. It is puzzling, therefore, that only
37 recently has the idea emerged that the same approach could be applied to the behaviour of
38 non-human animals. Here, we discuss the development, current state and possible future of
39 the first attempt to move archaeology beyond its anthropocentric borders: primate
40 archaeology².

41

42 Archaeologists looking to expand their discipline at the close of the twentieth century
43 followed the path of early evolution-minded biologists³, by turning to humanity's close
44 relatives: the chimpanzees (*Pan troglodytes*). Initially focused on the spatial patterning of
45 chimpanzee artefacts and behaviour^{4,5}, this work saw a breakthrough in 2002 with the
46 excavation of a chimpanzee nut-cracking site in the Taï Forest, Ivory Coast⁶. The same site
47 and nearby locations were then further excavated in 2003, producing the first radiocarbon
48 dates for non-human tool use of over 4000 years before the present (BP)⁷. Building on
49 decades of research on the Taï chimpanzee communities⁸ as well as a single community at
50 Bossou in Guinea⁹, stone tools became a central research focus, under both natural¹⁰ and
51 human-controlled¹¹ conditions. Along with work on non-stone artefacts, such as nests^{12,13}
52 and plant tools^{14,15}, this research demonstrated that chimpanzees created long-lasting
53 patterns of material culture that could be directly linked to their behaviour.

54

55 In 2009, a review of this incipient work outlined the potential for 'ethoarchaeology'^{6,16-18} –
56 the study of how animal behaviour produces durable, patterned material signatures – to
57 encompass other non-human primates (hereafter, primates)². The discovery only a few
58 years earlier of wild stone-tool-using monkeys – bearded capuchins¹⁹ (*Sapajus libidinosus*) in
59 Brazil and Burmese long-tailed macaques²⁰ (*Macaca fascicularis aurea*) in Thailand – meant
60 that for the first time the social and environmental contexts of lithic technology in multiple
61 primate species could be compared with that of humans and our direct ancestors (the
62 hominins) (Fig. 1). That review, and subsequent elaborations²¹⁻²⁴, identified two main areas
63 that could benefit from an archaeological approach to the primate past: (i) a deeper

64 understanding of the specific technological and cultural trajectories taken by other primate
65 species, and (ii) the collection of comparative primate data useful to palaeoanthropologists
66 and archaeologists working on the emergence of hominin tool use¹. There were also specific
67 goals proposed in the review, namely greater collaboration (including joint fieldwork)
68 between primatologists, archaeologists and palaeoanthropologists, standardization of site
69 and artefact recording procedures, and a greater focus on use-damage patterns as a means
70 of analysing recovered tools². As outlined below, each of these goals has seen rapid
71 advancement in recent years, although fundamental challenges still remain.

72

73

74 **Figure 1: Locations and examples of stone-tool-use by wild non-human primates and early**
75 **hominins.** (A) Bearded capuchin monkey (*Sapajus libidinosus*), Brazil. Photo by MH. (B) West
76 African chimpanzee (*Pan troglodytes verus*), Guinea. Photo by TM. (C) Burmese long-tailed
77 macaque (*Macaca fascicularis aurea*), Thailand. Photo by MH. (D) Stone tools from Lomekwi
78 3, Kenya, dated to 3.3 million years ago. From ref. ¹. (E) Stone tool from Gona, Ethiopia,
79 dated to 2.6 million years ago. From ref. ²⁵.

80

81 **The role of primate archaeology**

82 Primatology was established in the first half of the twentieth century initially as an
83 interdisciplinary field by researchers trained in zoology, psychology and physical
84 anthropology^{26–28}. In its formative years, it lacked significant inter-disciplinary collaboration
85 with archaeology, despite the latter being also sometimes considered a branch of
86 anthropology²⁹, a situation that saw little improvement up to the 1990s¹⁶. As primatology
87 developed into the premier field for the study of primates, it therefore did so as a discipline
88 rooted firmly in the present. Where past primates were considered, it was their bones that
89 typically drew attention, rather than their tools³⁰. This focus on close observation of
90 behaviour, physiology, social relationships and diets in living animals meant that reports
91 from both wild and captive animals could be considered, despite the drastically altered
92 living conditions of the latter³¹. However, it left a situation rife with temporal uncertainty,
93 concisely summarised by McGrew: ‘Termite fishing [in Gombe] may just as well have been
94 invented in 1959, the year before Jane Goodall arrived, or a million years ago’¹⁶.

95

96 Adding time-depth to primate behaviour is one of the novel contributions made by
 97 researchers using primate archaeological methods. Taking a long-term perspective allows us
 98 to identify when and where tool use innovation or tool use loss may have occurred within a
 99 primate population, and to track the spread of such behaviour between groups. To
 100 chimpanzee nut-cracking, we can now add macaque shellfish-pounding in Thailand³²,
 101 capuchin stone-on-stone percussive³³, and capuchin cashew processing³⁴ to the list of
 102 archaeologically excavated and reconstructed primate behaviours (Fig. 2). The latter has
 103 been traced back at least 700 years in northeast Brazil, recording around 100 generations of
 104 capuchin social transmission. There is every reason to expect that earlier sites and forms of
 105 tool use will be found; recall that it took centuries of investigation into the human
 106 archaeological record to push its origins back into the Pliocene¹. As with all excavations,
 107 context is key, and identification of older sediments likely to preserve primate tools³⁵ will be
 108 important in refining this process. However, archaeology is not only concerned with the
 109 distant past. For example, analysis of activity areas recently abandoned by non-habituated
 110 chimpanzees in the Tai Forest allowed reconstruction of their cultural preference for stone
 111 versus wooden nut-cracking hammers³⁶. By recording the ratio of wood to stone tools at
 112 abandoned sites, this report was first to enumerate chimpanzee cultural differences solely
 113 from archaeological deposits, a practice that is commonplace in hominin archaeology.

114

115

116 **Figure 2: Archaeologically excavated stone tools used in percussive activities.** (A) Lomekwi
 117 3 site (Kenya), 3.3 million years old, tool user unknown but possibly *Kenyanthropus*
 118 *platyops*. From ref. ¹. (B) Panda 100 site (Ivory Coast), used by West African chimpanzees
 119 (*Pan troglodytes verus*). Photos by TP. (C) LS5 site (Thailand), used by Burmese long-tailed
 120 macaques (*Macaca fascicularis aurea*). From ref. ³². (D) Lasca OIT2 site (Brazil), used by
 121 bearded capuchin monkeys (*Sapajus libidinosus*). From ref. ³³. All scales are in cm.

122

123 The fact that we can now demonstrate how multiple, phylogenetically-diverse species
 124 produce distinct lithic records across parts of Africa, Asia and South America opens up new
 125 opportunities for identifying unsuspected primate tool use in the past. It also offers a
 126 chance to explore why few populations have adopted tool use, even where it seems primed
 127 to develop from closely related forms such as stone handling in three species of macaque³⁷.

128 In each instance, stone-tool-using primates have lived alongside hominins, leaving
129 archaeological records that may be either separate but contemporaneous³⁴, or even
130 intermingled⁷. For now, we should assume that the same circumstance occurred at other
131 times and places, over the millions of years that hominins and other primates have shared
132 landscapes³⁸. The primates that happened to be alive during the geologically recent birth of
133 primatology as a science are very likely not the only ones that used or potentially even
134 made stone tools. Further, we should not assume that the hominin stone tool record is
135 somehow comprised of a single unbroken lineage of tool use from first appearance to the
136 modern day. The primate evidence indicates that we should expect multiple, independent
137 inventions of hominin stone tool use.

138

139 Time-depth can be assessed either directly, for example using radiocarbon dating of organic
140 material found with stone tools^{7,34}, or indirectly, for example through genetic data. Genetic
141 studies can estimate the longevity of individual primate communities, and based on Y-
142 chromosome data a number of East African chimpanzee (*P. t. schweinfurthii*) communities
143 were found to likely have existed as stable entities for hundreds to thousands of years³⁹.
144 Decoding of chimpanzee subspecies genomes makes it clear that Central African
145 chimpanzees (*P. t. troglodytes*) retain ancestral genes, with West African *P. t. verus* as a later
146 offshoot⁴⁰. Since West African chimpanzees are the only known *Pan* stone tool users
147 (possibly along with the even more recently-diverged Nigerian-Cameroon *P. t. ellioti*⁴¹),
148 current evidence puts the emergence of chimpanzee stone technology in the late Middle
149 Pleistocene, perhaps as recently as 200,000-150,000 years ago⁴². In the same line of
150 reasoning, when comparing chimpanzees with their close relatives the bonobos (*Pan*
151 *paniscus*), there is no clear stone-tool-use link back to their common ancestor with
152 humans⁴². The bonobo-chimpanzee-human common ancestor may have used stone tools –
153 although we have no evidence for it as yet – but as things stand we cannot assess whether
154 its behaviour resembled the tool use actions of modern chimpanzees⁴³. Recognising just
155 which parts of the chimpanzee (or any primate species) behavioural repertoire are actually
156 valid for use in referential models is an ongoing process^{44,45}, and progress will require
157 primatologists and archaeologists to more regularly engage with each other, in the field and
158 in the scientific literature.

159

160 Using the same genetic dating approach as that applied to *Pan*, the origins of robust
161 capuchin stone tool use very likely post-dates the emergence of *S. libidinosus* and its
162 occupation of the semi-arid Brazilian interior during the Middle Pleistocene^{21,46}. If this turns
163 out to be the case, then it may be that the subsequent Late Pleistocene expansion of these
164 capuchins north into the Amazon forests, where no tool use has been observed, reflects a
165 loss of cultural knowledge in the Amazonian groups owing to a change of environment⁴⁶. A
166 similar process of forest variation through time has been proposed to help explain the
167 absence of probe tool use, common among almost all chimpanzee communities⁴⁷, in the
168 modern Sonso chimpanzee community in Uganda⁴⁸.

169

170 When primates make use of durable raw materials , they generate landscape-scale patterns
171 of artefact discard that are amenable to archaeological surveys. Again, with a few notable
172 exceptions^{13,49–52}, these patterns have been typically not investigated by primatologists.
173 Archaeologists are familiar with the kind of mixed assemblages that this repeated behaviour
174 creates, but the additional feature of being able to observe living animals creating these
175 palimpsests puts primate archaeology in a unique position. Foraging activities that occur
176 across multiple tool-use areas require knowledge of material transport in particular, and
177 recently both capuchin⁵³ and chimpanzee studies⁵⁴ have demonstrated the cumulative
178 effects of long-term stone tool transport. In the chimpanzee example, the weight
179 distribution of hammerstones used for cracking *Panda* nuts in the Taï Forest was found to
180 follow a similar distance-decay curve to that seen at hominin sites in East Africa⁵⁵. This
181 finding suggests that, just as chimpanzee short-term planning of tool movements⁵⁶ is
182 obscured in their archaeological record, there are likely to be similar hidden components to
183 hominin transport events. For capuchins, the repeated use of favoured natural sites not only
184 guides foraging patterns and results in an archaeological signature, but it also acts to build
185 up repositories of tools and anvils that scaffold the efforts of young monkeys learning to
186 crack nuts⁵⁷.

187

188 Much of primate archaeology can be differentiated from traditional primatology in its focus
189 on ethoarchaeology¹⁸. This perspective combines detailed observations of modern animals
190 with the ‘lifeways’ of the inanimate objects with which they interact, although in the case of
191 unhabituated primates the emphasis is heavily on the latter type of evidence. For example,

192 a study of wild Thai macaques⁵⁸ found stone-tool-assisted consumption of up to 63 oysters
193 by a macaque in a single feeding bout, while also recording how the distance moved by each
194 individual tool contributed to the formation of archaeologically-recognisable sites. In
195 another recent study, West African chimpanzees were observed accumulating stones in and
196 around trees, leaving (unintentionally or otherwise) durable and salient landscape
197 markers⁵⁹. Of course, wild primates continue to use sites in the absence of human
198 observers, meaning that surveys of materials accumulated as a result of natural primate
199 activity are more directly comparable to the build-up of tools seen at hominin
200 archaeological sites than the short-term recording of specific tool-use events or
201 experiments¹¹. Primate archaeologists can return repeatedly to the same site⁵³ to observe
202 site formation as an active process.

203

204 **Primate archaeology and hominin evolution**

205 One of the early aims of primate archaeology was the recovery and reporting of primate
206 data in forms that would allow comparison with the evidence from early hominin
207 behaviour^{4,5}. In recent years, this aim has been advanced in three primary areas: identifying
208 and interpreting tools versus natural stones, framing the emergence of hominin stone
209 flaking, and ascertaining which primate species can act as models for hominin tool-use
210 behaviour.

211

212 The question of how to identify a tool from an unused stone has vexed archaeology since its
213 inception. In general, repeated conchoidal fracturing of a stone using controlled strikes^{60,61},
214 whether or not this results in a pre-determined shape⁶², has been accepted as a sign of
215 hominin agency (although see below regarding capuchin flake manufacture). For stones that
216 have not been deliberately flaked, however, including those used by modern primates and
217 past humans for simple food pounding tasks, the form of the stone gives little clue to its
218 artefactual nature. Fortunately, the sophistication and specificity of use-wear investigations
219 have seen significant advances in the past few years. These studies use either
220 experimental⁶³ or surface morphology^{64–66} analyses to locate the damaged portions of tools,
221 and to reconstruct the behaviour that produced the damage. This method can identify likely
222 pounding tools from any time period; for example, two stones from the Tulu Bor Member at
223 Koobi Fora in Kenya⁶⁴ – a formation dated at over three million years⁶⁷ – possess use-wear

224 that matches patterns on Pleistocene and experimental pounding tools, and that differs
225 significantly from natural damage. If verified by further study, these tools would be the
226 oldest yet identified by use-wear damage alone, joining early flaked assemblages¹.

227

228 Expanding out from tools to sites, primate archaeology gives us a new perspective on the
229 densities of stone tools left behind by primate (including hominin) activities. Tool densities
230 are fundamental to locating archaeological sites, and even for recognizing sites as discrete
231 activity areas in the first place⁶⁸. Research on modern nut-cracking sites at Bossou²³
232 revealed that chimpanzees left behind tools at a density of 0.002-0.05 tools/m², while
233 capuchin cashew processing sites at Serra da Capivara National Park (SCNP)³⁴ had orders of
234 magnitude higher average stone tool densities of 0.45 m⁻², with a maximum of 13 m⁻².

235 Compared with artefact scatters from early hominin sites in East Africa⁶⁹, which typically
236 have densities of 1-10 m⁻² but in exceptional cases >100 m⁻², the capuchins are towards the
237 lower range of the hominins. This overlap means that traditional archaeological methods
238 are apt for locating buried capuchin sites at SCNP, and this has proved to be the case³⁴.

239 However, the Bossou chimpanzees discard such low numbers of tools – one stone in 20 m²
240 at the densest²³ – that detecting and correctly interpreting such sites in an archaeological
241 excavation will be more challenging. The contribution of use-wear data will be of greatest
242 aid in such cases⁶⁵.

243

244 Environmental variability likely played a leading role in the evolution of early hominin
245 technologies⁷⁰, and primate archaeology offers the opportunity to track the effects of
246 environmental shifts on other technological primates. For example, the parts of coastal
247 Thailand occupied by stone-tool-using macaques have seen dramatic changes in sea levels
248 over the past twenty thousand years^{71,72}. Given that these macaques are well adapted to
249 foraging on inter-tidal resources, identifying when and where such resources existed will
250 assist in identifying periods suitable for the spread of lithic technology in this taxon. Useful
251 parallels for the macaque research in this regard may be found in archaeological debates
252 over the importance of sea levels in the Bering Strait for human dispersal into North
253 America⁷³, and the importance of marine resources to the emergence of behaviourally
254 modern humans in southern Africa⁷⁴. In each of these cases, the exposure of coastal lands at
255 times of lowered sea level, and the inundation of those lands during high stands, is critical

256 for assessing how archaeological sites were situated within the ancient landscape. Assessing
257 the interconnectedness of past African forests is similarly important, to determine whether
258 tool-use behaviours have multiple origin points or spread through contact between
259 neighbouring chimpanzee communities^{21,48}.

260

261 The initial emergence of hominin stone flaking is not considered the start of tool use in our
262 lineage^{75,76}, but it does remain the most visible manifestation of this phenomenon. There is
263 no evidence that the last common ancestor of bonobos, chimpanzees and humans used
264 stone tools⁴², and one of the stalwarts of hominin uniqueness has been the fact that we
265 alone invasively flake stones⁷⁷ to obtain sharp edges. Chimpanzees damage the edges and
266 corners of their stone hammers and anvils during use⁷⁸, and may even split them into still-
267 usable chunks¹¹. These breakage events are essentially random and inadvertent, however,
268 and no wild chimpanzee has been observed directly and repeatedly striking two stones
269 together – an essential component of hominin flaking – in order to damage them. It is
270 significant, therefore, that wild capuchins at SCNP have been documented performing
271 precisely this behaviour^{79,80}. The capuchins strike hammer stones onto other cobbles
272 embedded within a natural conglomerate, unintentionally producing recurrent sharp-edged,
273 conchoidally fractured flakes that are technologically indistinguishable from simple,
274 intentionally made flakes³³. In some cases, the capuchins use this technique to extract a
275 cobble that is then used as a hammer in its own right⁷⁹, although they have not been
276 observed using the sharp-edged flakes that they produce.

277

278 The fact that capuchins perform activities that appear to resemble human flaking more than
279 does chimpanzee stone tool use highlights one way that single-species comparative primate
280 models may be limited in their usefulness for understanding hominin ancestors. By the
281 same token, macaques use stone tools primarily to process animal prey⁸¹, a closer
282 approximation to reconstructions of early hominin carcass processing⁷⁷ than the focus on
283 nut-cracking seen among capuchins or chimpanzees. Overall, those characteristics
284 universally (and convergently) shared by known stone-tool-using primates form a stronger
285 analogical basis for reconstructing hominin stone tool use than any single species does
286 referentially. At present, known stone-tool-use universals for primates include: (i) selective
287 transport and accumulation of both modified and unmodified stones at activity areas; (ii)

288 use of stone tools by all members of a primate group at a given site, including females,
289 males and juveniles; (iii) a multi-year learning process for juveniles to become fully
290 proficient tool-users, with evidence of juvenile learning left at sites (e.g., inefficient
291 materials and tool sizes, mis-struck stones); and (iv) use of stone anvils as pounding
292 surfaces, even if wooden anvils are preferred at some sites. All species on occasion move
293 food to hammers and anvils, hammers and anvils to food, and all three elements to a
294 separate site^{11,34,58,82}. There is no reason why these same behaviours should not have been
295 present among hominins throughout their range and temporal distribution, and this
296 fundamental knowledge can help guide both the search for, and interpretation of, hominin
297 stone-tool-use sites.

298

299 In contrast, characteristics not shared among the extant lithic primates – including modern
300 humans – require further explanation and justification if applied to extinct hominins. These
301 species-specific characters include (i) the presence of human-level handedness⁸³, (ii) a
302 preference for wooded, grassy or coastal environments, (iii) the use of language to transmit
303 tool traditions, (iv) a focus on plant vs animal prey, (v) a threshold for brain size, (vi)
304 reliance on a particular form of locomotion (bipedal or quadrupedal), and (viii) the
305 relationship between body size or strength and tool sizes. The size and hardness of primate
306 stone tools are typically selected (when possible) to match the target food item^{10,84,85}, to the
307 extent that tool size is, on first principles, a proxy for the hardness of processed encased
308 foods. The primary exception to this rule is found among capuchins that use heavier stone
309 tools to process softer cashew nuts⁸⁶. In that instance, it may be that the larger stones act
310 more as a shield against the caustic liquid in these cashews than as a necessity for opening
311 the nuts. Naturally, these character lists are not solely retrodictive, and they need to be
312 tested against future discoveries of additional stone-tool-using species, to assess their
313 robustness in the face of new data.

314

315 **Challenges for the future**

316 Despite the steps taken in the past decade or so, there is much left to do in bringing
317 primatology, palaeoanthropology and archaeology closer together, and fundamental
318 questions remain unanswered. For example, it is not yet clear how we should measure
319 change in primate tool use through time, when their technologies are (in comparison to

320 modern humans) far simpler to begin with. This question is tied to the fact that our search
321 image for past primate tools is heavily guided by our knowledge of present-day tools, to the
322 extent that changes may be difficult to recognize in the first place. However, the same
323 issues confront researchers dealing with simple hominin technologies, where debates over
324 the extent and meaning of possible changes during the first million years of the Oldowan
325 are longstanding and unresolved^{60,87,88}. One solution is to continue extending the primate
326 archaeological record further back in time, assessing it for change at major climatic
327 boundaries (e.g., the Pleistocene-Holocene transition), and using present-day ties between
328 primate tool sizes and processed foods to assess past variation. Another solution is to
329 investigate species dispersals into new environments; for example, bearded capuchin tool
330 use may have evolved in concert with their expansion into more arid environments,
331 increasing their encounters with and potential reliance on hard, encased palm nuts⁸⁹.

332

333 Primate archaeology is much more reliant on stone tool evidence than is traditional human
334 archaeology, at least for the past few thousand years, because of human innovations in the
335 use of shell, bone, ceramic, metal, glass and synthetic materials. For example, in terms of
336 tool types the majority of chimpanzee technology is based on plant materials^{47,77,90}, and
337 while hominins have also long made use of wood and fragile organic artefacts^{91,92}, the
338 added contextual information derived from non-lithic hominin artefacts has enriched our
339 understanding of how hominin behaviour evolved. This problem is confounded by primate
340 habitation of tropical zones, especially forests, where organic materials are rapidly recycled
341 back into the biosphere⁹⁰. The result is that forested early primate sites may not be
342 recognized (or recognizable), whereas the presence of artificial materials such as ceramics
343 or even elaborately shaped stone tools immediately signal past hominin presence. In these
344 circumstances, the main positive aspect is that extant primate non-lithic tools can suggest
345 possible missing elements of the hominin record, particularly as the great apes in general
346 are more prolific plant than stone tool users⁹³⁻⁹⁵.

347

348 A final challenge lies in distinguishing hominin from non-hominin tools. In some cases, this
349 may be relatively straightforward even within the one site, for example when the fracture
350 characteristics of intentionally flaked stones contrast with the blocky fractures produced by
351 chimpanzees^{7,78}. In other cases there is no easy solution, and for the earliest stone tools

352 there are no directly associated hominin bones that may give confidence in assigning a
353 particular species as their creator^{1,96}. If an ancestor of any primate was breaking stones (for
354 whatever reason) more than two million years ago in Eastern or Southern Africa, we simply
355 would not know. The ability of primates to make use of materials provided by humans –
356 seen repeatedly in studies of captive animals³¹ – increases the likelihood that early primate
357 stone tool behaviour may involve the same raw materials, and even the same sites, as those
358 exploited by hominins. The rationale for such behaviour may also be difficult to discern or
359 unexpected; for example, the stone-flaking wild capuchins of SCNP do not use the sharp
360 edges they create, instead they lick and sniff the damaged stone surfaces. These behaviours
361 have not been posited for Pliocene hominins, yet these and other as-yet-unimagined
362 activities may have been exhibited by them in the past. Primate traditions can be
363 ephemeral, lasting only a few generations^{97,98}, yet in that time a primate group could easily
364 create thousands of damaged stones across their home range. Hundreds³⁴ to thousands⁷ of
365 years of primate activity will leave a correspondingly greater footprint.

366

367 The assignation of particular sites and assemblages to particular species, or even more
368 problematically cultural groups within a species, is an unresolved issue. However, when
369 researchers of different backgrounds work together at the same locations and on the same
370 material, it can help diminish the effect of any discipline-specific biases, increasing the
371 chance of producing a more accurate understanding of the studied behaviour. For example,
372 primatologists and archaeologists with experience of wild capuchin nut cracking have
373 applied their field methods directly to wild macaque nut processing⁹⁹, and archaeologists
374 have conducted site formation experiments with wild monkeys as a guide to excavating
375 former sites produced by that same monkey group^{58,100}. This cross-pollination of people and
376 ideas was, as noted earlier, a tenet of the original establishment of primate archaeology as a
377 discipline, and its continuation and expansion will undoubtedly provide unforeseen
378 solutions to currently intractable issues.

379

380 At the turn of the twenty-first century, we possessed an archaeological record for only one
381 lineage, our own. Fewer than two decades later, we now have four primate lineages with
382 excavated archaeological evidence, adding the New World monkeys, Old World monkeys,
383 and apes to what had been for centuries an exclusively human club. Other animals will

384 inevitably also be added in, including from outside the primates¹⁰¹. The question is
 385 therefore no longer whether the archaeology of non-human animals is possible, but which
 386 questions should be the next ones to address using these methods. Whatever answers we
 387 come up with, the crucial ethoarchaeological component of this work needs to continue,
 388 and even accelerate, as anthropogenic forces constantly reduce the chances for primates'
 389 survival¹⁰². Increasing anthropogenic modification of primate habitats provides an
 390 opportunity to observe whether and how these animals adjust their technologies in
 391 response to environmental and social disturbances^{37,103}, but this is a poor trade for
 392 ultimately losing the animals themselves. It is not enough to ensure the existence of cultural
 393 species in isolated zoos or sanctuaries, where they are divorced from the social and physical
 394 environments that produced their unique characteristics. Instead, culturally-healthy free-
 395 ranging populations need to be preserved, maintaining the ability of animals to transfer
 396 naturally between groups and to access the foods and tool materials on which their
 397 traditions depend. Only then will we ensure that the remarkable behaviour of primates
 398 continues to evolve.

399

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407

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