1   **Primate archaeology evolves**

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Introduction

Archaeology gives humanity access to its past, helping to define who we are. Its method - the scientific study of the material remains of past behaviour – has been extraordinarily successful, resulting in the systematic recovery and interpretation of evidence for human evolution covering more than three million years[1]. It is puzzling, therefore, that only recently has the idea emerged that the same approach could be applied to the behaviour of non-human animals. Here, we discuss the development, current state and possible future of the first attempt to move archaeology beyond its anthropocentric borders: primate archaeology[2].

Archaeologists looking to expand their discipline at the close of the twentieth century followed the path of early evolution-minded biologists[3], by turning to humanity's close relatives: the chimpanzees (*Pan troglodytes*). Initially focused on the spatial patterning of chimpanzee artefacts and behaviour[4,5], this work saw a breakthrough in 2002 with the excavation of a chimpanzee nut-cracking site in the Taï Forest, Ivory Coast[6]. The same site and nearby locations were then further excavated in 2003, producing the first radiocarbon dates for non-human tool use of over 4000 years before the present (BP)[7]. Building on decades of research on the Taï chimpanzee communities[8] as well as a single community at Bossou in Guinea[9], stone tools became a central research focus, under both natural[10] and human-controlled[11] conditions. Along with work on non-stone artefacts, such as nests[12,13] and plant tools[14,15], this research demonstrated that chimpanzees created long-lasting patterns of material culture that could be directly linked to their behaviour.

In 2009, a review of this incipient work outlined the potential for 'ethoarchaeology'[6,16–18] – the study of how animal behaviour produces durable, patterned material signatures – to encompass other non-human primates (hereafter, primates)[2]. The discovery only a few years earlier of wild stone-tool-using monkeys – bearded capuchins[19] (*Sapajus libidinosus*) in Brazil and Burmese long-tailed macaques[20] (*Macaca fascicularis aurea*) in Thailand – meant that for the first time the social and environmental contexts of lithic technology in multiple primate species could be compared with that of humans and our direct ancestors (the hominins) (Fig. 1). That review, and subsequent elaborations[21–24], identified two main areas 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 use[1]. 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 tools[2]. 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   anthropology[29], a situation that saw little improvement up to the 1990s[16]. 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 tools[30]. 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 latter[31]. 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 Thailand[32],

101   capuchin stone-on-stone percussion[33], and capuchin cashew processing[34] 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 Pliocene[1]. As with all excavations,

107   context is key, and identification of older sediments likely to preserve primate tools[35] 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 hammers[36]. 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 macaque[37].

128 In each instance, stone-tool-using primates have lived alongside hominins, leaving

129 archaeological records that may be either separate but contemporaneous[34], or even

130 intermingled[7]. 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 landscapes[38]. 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 years[39].

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 offshoot[40]. 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 ago[42]. 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 humans[42]. 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 chimpanzees[43]. 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 environment[46]. 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 communities[47], in the

168 modern Sonso chimpanzee community in Uganda[48].

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 capuchin[53] and chimpanzee studies[54] 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 Africa[55]. This

181 finding suggests that, just as chimpanzee short-term planning of tool movements[56] 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 nuts[57].

187

188 Much of primate archaeology can be differentiated from traditional primatology in its focus

189 on ethoarchaeology[18]. 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 macaques[58] 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 markers[59]. 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 experiments[11]. Primate archaeologists can return repeatedly to the same site[53] 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 shape[62], 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 experimental[63] 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 Kenya[64] – a formation dated at over three million years[67] – 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 assemblages[1].

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 place[68]. Research on modern nut-cracking sites at Bossou[23]

232   revealed that chimpanzees left behind tools at a density of 0.002-0.05 tools/m^2, 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 Africa[69], 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 case[34].

239   However, the Bossou chimpanzees discard such low numbers of tools – one stone in 20 m^2

240   at the densest[23] – 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 cases[65].

243

244   Environmental variability likely played a leading role in the evolution of early hominin

245   technologies[70], 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   America[73], and the importance of marine resources to the emergence of behaviourally

254   modern humans in southern Africa[74]. 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 tools[42], and one of the stalwarts of hominin uniqueness has been the fact that we

265 alone invasively flake stones[77] to obtain sharp edges. Chimpanzees damage the edges and

266 corners of their stone hammers and anvils during use[78], and may even split them into still-

267 usable chunks[11]. 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 flakes[33]. In some cases, the capuchins use this technique to extract a

275 cobble that is then used as a hammer in its own right[79], 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 prey[81], a closer

282 approximation to reconstructions of early hominin carcass processing[77] 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 handedness[83], (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, (vi) a threshold for brain size, (vii)

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 nuts[86]. 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 nuts[89].

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 biosphere[90]. 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 users[93–95].

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 animals[31] – 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. Hundreds[34] to thousands[7] 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 processing[99], 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 primates[101]. 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   survival[102]. 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

403

404   **Author contributions**

405   MH, AHA, LL and TP conceived the paper. MH wrote the paper, with contributions from all

406   other authors. TP prepared the figures, with assistance from MH.

407

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