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Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task

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Population and group-specific behavioural differences have been taken as evidence for animal cultures [1-10], a notion that remains controversial with sceptics arguing that ecological or genetic factors, rather than social learning, provide a more parsimonious explanation [11-14]. Work with captive chimpanzees has addressed this criticism by showing that experimentally created traditions can be transmitted through socially aided learning [15-17]. Recent fieldwork further suggests that ecological and genetic factors are insufficient to explain all the behavioural differences seen in chimpanzees, but the data are only observational [18, 19]. Here we present the results of a field experiment [20, 21] that compared the performance of chimpanzees

26 **(*P. t. schweinfurthii*) from two Ugandan communities, Kanyawara and Sonso, on an**

27 **identical task in the physical domain -- extracting honey from holes drilled into**

28 **horizontal logs. Kanyawara chimpanzees, who occasionally use sticks to acquire honey**

29 **[4], spontaneously manufactured sticks to extract the experimentally provided honey. In**

30 **contrast, Sonso chimpanzees, who possess a considerable leaf technology but no food-**

31 **related stick use [4, 22], relied on their fingers, but some individuals also produced leaf-**

32 **sponges to access the honey. Our results indicate that, when genetic and environmental**

33 **factors are controlled, wild chimpanzees rely on their cultural knowledge when**

34 **confronted with a novel cognitive task.**

35

36

37 **Results and Discussion**

38

39 Some of the strongest evidence for animal culture comes from studies on wild chimpanzees

40 comparing the behavioural patterns of different populations in Africa [4, 5]. Population-

41 specific behavioural differences are particularly evident in tool use. However, the

42 observational nature of most field studies makes it difficult to draw definitive conclusions, as

43 it is impossible to rule out all potential ecological or genetic explanations for behavioural

44 variation attributed to culture [12]. Although social transmission has been observed in

45 captivity, with good evidence that chimpanzees can socially learn arbitrary behaviours [16], it

46 is currently unclear to what degree this finding can be applied to the wild. For example, it is

47 possible that chimpanzees re-solve a particular problem with trial-and-error learning because

48 they operate under the same conditions every time they confront it, not because they have

49 acquired cultural knowledge. Testing cultural knowledge, therefore, requires field

50 experiments by which individuals of the same genetic background are tested with a novel

51   problem under the same environmental conditions, thus controlling for all other potential

52   sources of explanations.

53

54   We conducted a field experiment with two communities of East African chimpanzees, *P. t.*

55   *schweinfurthii*, to investigate how their cultural knowledge determined the way they solved a

56   simple cognitive task under identical ecological conditions. The genetic differences between

57   the two communities are negligible and insufficient to assign an individual to a particular

58   community, making it unlikely that any difference in behaviours is the result of underlying

59   genetic differences [23]. Individuals of the Sonso community of Budongo Forest and the

60   Kanyawara community of Kibale National Park, Uganda, were allowed to encounter an

61   artificial hole of 4x5 cm, drilled into a horizontally situated log, which was filled with natural

62   honey. Honey, produced by bees of the *Apis*, *Meliponula* and *Xylocopa* genera*,* is found in

63   both forests and consumed by members of both communities [22, Muller & Wrangham,

64   personal observations]. A rectangular shape was chosen to provide a visually novel stimulus

65   that differed from the entrance of the beehives chimpanzees naturally encounter in the wild. In

66   another difference the hole was presented in the horizontal plane. Natural beehive entrances

67   are usually found on the vertical sides of trunks (see online supplemental material) but

68   chimpanzees may also access the hives after the supporting trees have fallen down. In such

69   cases, honey is easily accessible and chimpanzees do not use sticks on such trees (Gruber,

70   personal observations). Finally, experimental honey was provided as a liquid substrate as

71   opposed to the waxy honey naturally encountered by the chimpanzees. This accumulation of

72   differences generated a task sufficiently different from what chimpanzees usually encounter in

73   the forest, while conserving the basic natural features. This way we were able to ensure that

74   individuals were not relying blindly on simple stimulus-response algorithms acquired

75   previously for example by operant conditioning. Moreover, we made sure that chimpanzees

76 would not associate the presence of honey with humans by filling the holes when no

77 individual was present.

78

79 The experimental logs were selected so that they were located in a relatively open area of at

80 least 5x5 m often visited by the chimpanzees. Individuals had unrestricted access to the hole

81 during the experimental phase, and no efforts were made to attract individuals or to encourage

82 engagement with the hole.

83

84 Two types of hole were drilled at each site. The first was 11 cm deep with honey filled up to 6

85 cm below the surface. This allowed the chimpanzees to get most of the honey by using their

86 fingers only. Tool-use was not required. Honeycombs were scattered around the hole to

87 provide a visual cue (Fig. 1a). In the second experiment, the same hole was re-drilled to a 16

88 cm depth, with honey filled up to 10 cm beneath the surface. In this condition, it was no

89 longer possible to access the honey with the fingers. Again, honeycombs were positioned to

90 provide visual cues, this time covering the hole to prevent insects from exploiting the honey

91 before the chimpanzees arrived (see methods) (Fig. 1b).

92

93 At both sites, individuals initially showed similar responses to the artificial holes by

94 consuming all available honeycombs. However, their subsequent behaviours differed in

95 striking ways. At Sonso, most individuals relied on their hands only to access the honey in

96 both experimental conditions (table 1) but some of them also used leaves (fig. 2a; see online

97 supplemental material). For the 11 cm hole, tool use was not required, but two of 13

98 individuals nevertheless inserted leaves to extract honey (RE and PS). In the second

99 condition, tool use was necessary and two further individuals of 11 in total were observed to

100 compress leaves in their mouth to produce a leaf-sponge. One of them, a sub-adult male

101   (HW), proceeded to sponge the honey. In comparison, most chimpanzees at Kanyawara

102   prepared sticks to access the honey (fig. 2b; 11 cm hole: 6 of 10 individuals; 16 cm hole: 11 of

103   12 individuals; see online supplemental material). No individual at Kanyawara used leaf-

104   sponging, although the behaviour is customary in the community in other contexts [4].

105

106   Overall, there was significantly more tool use at Kanyawara than Sonso in both the 11 cm

107   (non-obligatory) shallow (Fisher exact test, $p < 0.05$) and the 16 cm (obligatory) deep

108   condition ($p = 0.001$). Using the Freeman-Halton extension of the Fisher test [24], we found

109   that the overall distribution of the three categories of responses (no tool use, sticks, leaves)

110   was significantly different from the null hypothesis, i.e. , the two populations being identical

111   in their techniques to access the honey ($p < 0.01$ and $p < 0.001$, respectively), providing

112   statistical evidence that Kanyawara and Sonso chimpanzees responded in a group-specific

113   manner. To assess the size of this difference, we calculated the Lambda value for predicting

114   tool use (yes or no) and for predicting the response category (no tool, stick, leaf). The Lambda

115   test is a non-parametric variable that gives the proportional reduction in error when group

116   membership is used as a variable to predict behaviour [25]. For predicting tool use, we

117   obtained lambda values of 0.400 (shallow condition) and 0.857 (deep condition). For

118   predicting the response category, we obtained lambda values of 0.6 and 1 (see methods).

119   Although in the shallow condition the range of response choices was larger than in the deep

120   condition, both lambda values demonstrated that group identity was a strong predictor of

121   behaviour in both conditions.

122

123   The Kanyawara chimpanzees engaged significantly longer ($n = 18$, mean time of 1177 s, SD =

124   2044 s) with the two holes than the Sonso chimpanzees ($n = 22$, mean time of 126 s, SD = 132

125   s) (Mann-Whitney test, $Z = -3.453$, $p = 0.001$), but this difference could not explain why

126   Sonso chimpanzees never used sticks. As time before manufacturing a tool did not differ

127   significantly between the two conditions in Kanyawara (shallow hole, n = 4, mean = 30.5, SD

128   = 41.5; deep hole, n = 7, mean = 20, SD = 15.6; Mann-Whitney test, Z = -0.38, p = 0.704), we

129   pooled the data and excluded cases where an individual had engaged previously with the hole

130   before manufacturing a tool. The mean Kanyawara duration from first encounter to choosing a

131   tool was 23 s (n = 11, range 0 – 88 s). Most chimpanzees at Sonso spent more than 23 s

132   engaging with the hole, so that they would have had sufficient time to select a stick.

133   Moreover, the three Sonso individuals who produced tools during their first engagement with

134   the hole did so in the time range of the Kanyawara chimpanzees (n = 3; range 4 – 61 s).

135   Crucially, Sonso chimpanzees have never been observed using sticks to acquire food in over

136   15 years of continuous observations.

137

138   It is theoretically possible that the stick use by the Kanyawara chimpanzees is the result of

139   prior individual rather than social learning. Although our study does not address the previous

140   learning history of our animals, a number of points make individual learning a less likely

141   ontogenetic mechanism. First, the speed, determination, and accuracy of the tool-using

142   individuals in both communities strongly suggest that ad hoc individual learning on a trial-

143   and-error basis is an unlikely explanation for the observed differences. Affordance learning

144   can also be ruled out by the fact that the physical properties of the task were kept identical,

145   due to the design of the experiment, yet the chimpanzees responded in community-specific

146   ways. Finally, due to the ecological and genetic similarities between the two communities, the

147   individual learning hypothesis predicts that individuals in both groups should be equally likely

148   to learn stick use to obtain natural honey, which was not the case. Because of all these reasons

149   and the fact that chimpanzees in both communities selected tools quickly and in community-

150   specific ways it is more likely that their decisions were based on cultural knowledge in line

151   with the evidence from captivity [17]. To our knowledge, this experiment is the first to

152   compare two genetically undistinguishable populations of the same subspecies [23] with the

153   same task, thereby controlling for both genetic and environmental factors [13]. By using a

154   standardized hole, filled with the same type and amount of honey, under the same

155   environmental conditions, any differences in observed behaviour are most parsimoniously

156   attributed to the individuals' prior learning histories or, more specifically, the differences in

157   their cultural backgrounds [4, 5].

158

159   The behavioural results obtained with this experiment also reflect subtle differences in dietary

160   habits between the two communities [26, 27]. The Kanyawara chimpanzees eat *Apis* honey

161   about once per month and unsuccessfully try to obtain honey at a similar rate (Kibale

162   Chimpanzee Project, unpublished data, 1991-2001). By comparison, honey consumption is

163   rare in Sonso, but this has nothing to do with the anti-predator behaviour of the bees, which

164   fiercely attack chimpanzees at both sites (Gruber, personal observation). In our experiment,

165   Kanyawara individuals engaged longer with the hole, and revisited the experimental spot

166   regularly when feeding in the vicinity. At Sonso honey consumption appeared to be much

167   more opportunistic, coinciding with feeding at a nearby *Rafia farinifera* tree [28].

168

169   From a cognitive point of view, our results suggest that chimpanzees rely on their cultural

170   knowledge to solve a novel foraging problem. Kanyawara chimpanzees occasionally attempt

171   to acquire small amounts of honey (ca. 1-5 mg) available in the nests of solitary carpenter

172   bees (*Xylocopa* spp.). Such attempts always involve a probing stick used to obtain the waxy

173   honey. They continued to use this technique when the food was encountered in the spatially

174   and visually novel setting of our field experiment. In contrast, the Sonso chimpanzees do not

175   use tools to access food and, consequently, their first approach to the problem was to use their

176   fingers. The Sonso chimpanzees produce leaf-sponges to retrieve water from hollows in trees,

177   and some individuals applied this technique to the novel problem of the experimental

178   situation. The fact that they consumed the combs beforehand, possibly perceived the smell of

179   honey and perceived the presence of bees, makes it improbable that they anticipated finding

180   water in the artificial hole.

181

182   As argued before, the fact that all the chimpanzees reacted in a community-specific way

183   supports a culturally-based rather than individual acquisition of the behaviour. We define

184   culture as a community-specific set of behaviours that an individual is exposed to and can

185   socially learn from. According to this view, the Sonso chimpanzees do not use sticks during

186   feeding because they have never seen another chimpanzee using sticks in this context, but

187   once someone invents the technique, it may spread through the community through socially-

188   aided processes [21, 29]. Our experiment does not show how individuals originally acquired

189   their set of foraging behaviours, only how individuals apply their knowledge when confronted

190   with novel problems. As a final point, our study highlights the fact that the 'exclusion

191   method', commonly used to identify cultural differences among populations [10], may be

192   suitable to identify all cultural variants. As mentioned, both chimpanzee populations have

193   been observed to use leaf-sponges but only the Sonso individuals applied this technique to the

194   experimental condition, suggesting that the complexity of a behaviour and its contextual use

195   should be taken into account when comparing cultural differences between populations [30].

196

197   From a methodological point of view, we have demonstrated that, by using simple cognitive

198   tests to which there are several solutions, the disparate influences that affect behaviour can be

199   studied systematically in the wild. We were able to control for the genetic, environmental and

200   task-related influences, leaving cultural differences as the most plausible explanation. Field

201 experiments of this kind, when combined with the necessary observational studies and

202 supported by more controlled studies in the laboratory, can provide a robust test to

203 systematically compare cultural differences in wild animals.

204

205

206 **Experimental Procedures**

207

208 <u>Subjects and study sites</u>

209 The Sonso community (01°43'N, 31°32'E) has been studied in the Budongo Forest since

210 1990 and has been fully habituated to human observers since 1994. At the time of the study,

211 the community consisted of 69 individuals. The Kanyawara community (00°33'N, 30°21'E)

212 has been continuously studied in Kibale National Park since 1987 and has been fully

213 habituated since 1994. At the time of the study, the community consisted of 46 individuals.

214 The distance between the two sites is about 250 km.

215

216 <u>Experimental procedure</u>

217 Natural honey was acquired from local bee farmers of the Masindi District, Uganda, whose

218 bees of the genus *Apis* forage freely in Budongo Forest. At both sites, the experimental holes

219 were drilled in dead logs using a manual drill. At Budongo, the holes were drilled into a

220 *Cleistopholis patens* tree that had fallen recently. At Kibale, the holes were drilled into a

221 *Strychnos mitis* tree that had also fallen recently. At both sites, the tree fall had generated a

222 relatively open area of about 25 m², surrounded by thick vegetation. Twigs, climbers and

223 leaves were available as potential raw material for tools in large quantities at both sites. At

224 Budongo, the log was located next to a *Raphia farinifera* tree where chimpanzees often came

225 to feed [28]. The site was usually visited by small groups that also used the place as a resting

226   area. At Kibale, the log was located 30 m from a fruiting *Aningeria altissima* tree, in a cleared

227   area where chimpanzees usually came for grooming and resting after feeding. Both situations

228   were similar in that there were no particularly interesting objects in the vicinity that might

229   have prevented them from exploring the environment.

230

231   Every morning, honey was poured in the hole by the experimenter (TG). The 11-cm (non-

232   obligatory) shallow hole was filled with 90 ml of honey up to 6 cm beneath the surface. The

233   16-cm (obligatory) deep hole was filled up to 10 cm beneath the surface. Additionally,

234   honeycombs were providing around the 11-cm hole or covering the 16-cm hole (fig. 1a & b)

235   to provide a conspicuous visual cue and to attract the chimpanzees. The change in the

236   arrangement of the combs was made to better protect the liquid honey from wild bees, which

237   had started to forage into the hole at the time the second experiment started.

238

239   A motion-sensitive video camera PixController DVREye™ was positioned to survey the hole

240   and the immediate area (20 m²). All experiments were set up in the absence of any

241   chimpanzees. Access to the honey spot was unrestricted, and no additional means were used

242   to attract individuals to the hole or to encourage them to engage with it. The experimenter

243   then left the area, only to come back while following a group of chimpanzees on their daily

244   ranging. Additional video recordings were made by the experimenter with a Canon FS100

245   handy video camera. No interaction happened between the experimenter and any of the

246   animals. Experiments at Budongo took place between 20 Feb and 25 March 2009 and at

247   Kibale between 2 and 22 April 2009.

248

249   All statistical tests were calculated with SPSS v 16.0 (Copyright © SPSS Inc.) except for the

250   Freeman-Halton extension of the Fisher Test, which was calculated using the Vassar College

251 method (http://faculty.vassar.edu/lowry/VassarStats.html). Fisher exact tests give a

252 measurement of the difference between populations but no indication of effect strength. To

253 estimate the size of the effect (i.e. how different the two populations were), we calculated

254 Goodman and Kruskal's λ, a measure of proportional reduction in error. It indicates the extent

255 to which the modal categories and frequencies for each value of the independent variable

256 differ from the overall modal category and frequency, i.e. for all values of the independent

257 variable together. Values for λ range from zero (no association between independent and

258 dependent variables) to one (perfect association between the two). λ is calculated with the

259 equation

260 $$\lambda = (\varepsilon_1 - \varepsilon_2) / \varepsilon_1$$

261 where ε_1 is the overall non-modal frequency, and ε_2 the sum of the non-modal frequencies for

262 each value of the independent variable.

263

264

265 **Acknowledgements**

266

276

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357

358

359

360 Table 1: Summary of the chimpanzees of the Sonso and Kanyawara communities engaging in

361 the honey acquisition task

362

363 Data points are sorted per individuals and community. Individuals are presented in

364 alphabetical order, sorted by community. Several individual engaged with the holes in the two

365 experiments. Time is given in seconds. For each individual, the community of origin (Sonso

366 or Kanyawara) and age class is given (adult, sub-adult, juvenile). Infants were not taken into

367 account, as they merely played and did not try to acquire the honey. Measurements were taken

368 as mode of contact with the hole by hand (H), mouth (M) or tool (S: stick, L: leaves),

369 excluding visual information acquired by gaze. For each individual and setting (deep 16 cm

370 hole; shallow 11 cm hole) tool use was scored (yes/no). Total time engaging with the hole is

371 given for both settings separately and combined. Latency to tool manufacture is calculated

372 from an individual's first engagement with the hole. All cases where individuals had a

373 previous knowledge of the hole were excluded. * individual manufactured tool but did not use

374 it. **: delay in the onset of the automatic video camera did not allow exact time measures

375 before taking a tool. ***: individuals with prior knowledge of the hole (either with a previous

376 setting or a previous non-tool engagement) excluded from the analysis. ¤: individuals missing

377 a hand because of a snare. §: engagement with the combs only, not with the hole.