Chimpanzee Ethnography Reveals Unexpected Cultural Diversity

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48 **Abstract**

49 Human ethnographic knowledge covers hundreds of societies, whereas chimpanzee ethnography

50 encompasses at most 15 communities. Using termite fishing as a window into the richness of

51 chimpanzee cultural diversity, we address a potential sampling bias with 39 additional communities

52 across Africa. Previously, termite fishing was known from eight locations with two distinguishable

53 techniques observed in only two communities. Here, we add nine previously unstudied termite-

54 fishing communities revealing 38 different technical elements as well as community-specific

55 combinations of three to seven elements. Thirty of those were not ecologically constrained,

56 permitting the investigation of chimpanzee termite fishing culture. The number and combination of

57 elements shared among individuals were more similar within than between communities, thus

58 supporting community-majority conformity via social imitation. The variation in community-specific

59 combinations of elements parallels cultural diversity in human greeting norms or chopstick etiquette.

60 We suggest that termite fishing in wild chimpanzees shows some elements of cumulative cultural

61 diversity.

62

63 **Introduction**

64 Comparative cultural studies are hampered by the fact that humans are by far the most intensively

65 studied species with many hundreds of well-known different societies[1-2], while non-human species

66 are mostly known from a few populations reaching one dozen in the second most studied species,

67 the chimpanzee[3,4]. Notwithstanding, chimpanzee cultural abilities have been proposed to be limited

68 to simple elements that could be invented independently by each individual performing a given

69 technique[5-7]. Multiple captive studies with chimpanzees and other animal species tend to support

70 this conclusion, and suggest that culture, if present, is not based on a faithful learning mechanism

71 nor any form of teaching, limiting it to simple elements[5-7].

4

72 Studies on chimpanzee communities have frequently revealed undocumented behavioral variants for

73 the species, such as algae fishing, accumulative stone throwing, water dipping, cave use, or

74 sequential tool use [8-12]. Additionally, recent research on neighboring chimpanzee communities has

75 revealed the persistence of cultural differences within the same environment[13,14]. Both suggest that

76 incomplete sampling could lead to underestimated chimpanzee cultural complexity[4]. In an attempt

77 to overcome this limitation, we launched a large-scale cross-sectional study with the aim of sampling

78 additional chimpanzee communities for addressing questions about cultural complexity and their

79 potential ecological and social drivers[15]. Here, we present a detailed ethnographic analysis of

80 chimpanzee termite fishing observed at 10 communities, with the three following goals: 1) document

81 the technical elements used by chimpanzees when extracting termites living in a) aerial (epigeal), and

82 b) underground mounds, 2) test whether community-specific techniques are present, and if so 3)

83 assess inasmuch these community-specific techniques could represent a case of cumulative cultural

84 evolution. Given that we investigated variation in the termite-fishing techniques of chimpanzees, any

85 evidence for conformity (i.e., a pattern of within-group homogeneity), in the absence of ecological

86 constraints, would support process-oriented imitation rather than end-state emulation or trial and

87 error learning[5,16] since termite extraction was successful in all instances.

88 We collected a total of 1,463 one-minute camera-trap videos of chimpanzee termite fishing from 10

89 communities (range: 14 to 184 for aerial termite fishing; 60 to 336 for underground termite fishing).

90 These videos were analyzed by CB, who has over 40 years' experience observing wild chimpanzees.

91 The termite-fishing ethogram describing individual technical elements was created by CB was tested

92 for reliability with SP, an expert on great ape gestures, on a randomly chosen 10% of videos (N=169)

93 from all 10 termite-fishing communities without SP knowing the community nor the element

94 distribution between communities. Inter-observer agreement in the classification of termite-fishing

95 behaviours was 85% for technical elements, 90% for body part(s) used to fish, 100% for body part(s)

96 used for support and 64% for position of the wrist (Cohen's Kappa test: all p<0.001). In addition, two

97   additional independent observers blind to the aim and hypothesis of the study, naïve to the

98   ethogram, and to the origin of the videos, coded the same videos with an average inter-observer

99   agreement of 93% (average Kappa=0.657; N=31 technical elements, with a Kappa higher than 0.8 for

100   11 of them and 30 out of 31 Kappa values reaching significance at p<= 0.05; N=73 videos). An open-

101   access video library demonstrates the variation in the technical elements coded for termite-fishing

102   behaviour for the different chimpanzee communities (see

103   www.eva.mpg.de/primat/staff/boesch/termite-fishing-video-library.html). For all elements

104   identified, we further inferred whether the element could potentially be explained as the

105   chimpanzees' response to ecological challenges presented by the termite mound structure, and if it

106   was not, we assumed differences reflect social preferences (see Supplementary Table 3 for details).

107   **Results**

108   *Aerial termite fishing*

109   Aerial termite-fishing requires an individual to insert one thin twig into a tunnel, deep enough into

110   the termite mound for the soldiers to bite[17]. We discovered chimpanzees of three previously

111   unstudied communities performing this technique (Figures 1). In total, we distinguished 17 different

112   elements for aerial termite fishing, of which 14 were inferred to be primarily socially transmitted, as

113   no ecological constraints could be identified to explain the differences (N=476 videos providing 85

114   independent sequences of termite fishing including 116 individuals). There were strong community

115   differences in the combinations of elements observed in the majority of individuals within a

116   community (Figure 1; Supplementary Table 1).

117   *Underground termite fishing*

118   Underground termite-fishing involves the use of a tool-set comprising two different-sized sticks: a

119   thick one to perforate (or puncture) the ground to gain access into the mound and a thinner one

120   inserted into the tunnel made by the perforator to fish for termite soldiers[10]. We discovered three

121   previously unstudied chimpanzee communities performing this technique, all located in Central

122   Africa (Figure 2). We observed 21 different technical elements in some, or only one, community

123   (N=987 videos from 107 independent sequences including 132 individuals; Supplementary Table 2).

124   We found strong community differences in the combinations of elements observed in the majority of

125   individuals within a community (Figure 2), and 16 of these elements were inferred to be social

126   preferences.

127   ***Testing for group-specific combinations in termite fishing***

128   To investigate whether the combinations of elements observed for termite fishing (Figures 1 and 2)

129   were community specific, we first tested whether the frequency of occurrence of technical elements

130   was community specific, and second, whether individuals from the same community shared more

131   elements than with individuals from different communities. Using a Generalized Linear Mixed Model,

132   we found that individuals shared significantly more elements within a community than with

133   individuals from other communities (permutation test of the contribution of the combination of

134   community and technical elements for aerial nests: standard deviation, sd=3.28, 95% confidence

135   interval (CI): 2.358 to 4.040, P=0.001; underground nests: sd=11.87, CI: 13.157 to 23.468, P=0.001;

136   Figure 3). As seen in Figure 3, some elements were community specific differentiating them from

137   others, such as 'lean elbow', which was, only detected in Korup chimpanzees, while 'lay side' was

138   specific to the Wonga Wongue chimpanzees. At the other extreme, 'bite' or 'scratch' occurred in all

139   communities but with different frequencies. Repeating the analysis by permuting mounds rather

140   than individuals did not substantially affect the result (aerial nests: sd=3.21, CI: 2.253 to 4.163,

141   P=0.003; underground nests: sd=10.97, CI: 12.336 to 22.599, P=0.001). The combination of elements

142   exhibited by an individual was also significantly more similar to those of other individuals of the same

143   community, compared with those of other communities (Sørensen similarity index considering only

144   the putatively socially driven elements, leaving 14 elements for the aerial and 16 for the

145   underground data: average similarity of combinations: aerial, different communities: 0.453, different

146 individuals from the same community: 0.741, difference (CI): 0.289 (0.215 to 0.364); underground,

147 different communities: 0.244, different individuals from the same community: 0.873, difference:

148 0.629 (0.495 to 0.739); both P=0.001; Figure 4a). The fishing technique of the Korup chimpanzees

149 was uniquely characterized by always including 'perfore 1h', 'lean elbow', 'lip shake', 'near elbow'

150 and 'head eat', while in Goualougo chimpanzees the 'long stick' is always combined with 'sit' and

151 'support 2h', and in the majority, with 'perfore 2h'. Meanwhile the La Belgique chimpanzees combine

152 'perfore 1h' always with 'long brush' and 'wrist eat' (Figure 3). Finally, a cultural fixation analysis[18]

153 confirmed that elements where alternative elements are present clearly deviated from a random

154 distribution (Figure 4c) with some technical elements showing a strong signal of cultural fixation

155 (group 8 and 11 for underground termite fishing in Supplementary Table 3), and others with more

156 moderate separations between communities (group 2, 4 and 6 in Supplementary Table 3).

157 **Discussion**

158 By carrying out an unprecedented ethnographic analysis of one of the best-studied chimpanzee

159 cultural traits — termite fishing — we show that chimpanzee cultural diversity is currently

160 underestimated due to an under-sampling of different populations. By studying additional

161 communities, we have increased our knowledge about termite-fishing variation from two to 38

162 elements found in 10 communities. Our results emphasize that community specificity in termite

163 fishing is not only about the absence or presence of elements, but also about the combinations of

164 different elements in each community (Figures 1 and 2). This adds a completely new dimension to

165 the characterization of chimpanzee cultures.

166 We found that the combinations of elements form community-specific techniques in termite fishing

167 resembled a process of cumulative cultural evolution[7,19,20]. As our study was cross-sectional rather

168 than longitudinal, we do not have historical records to reconstruct the order of invention and

169 inclusion of those elements over time, nor whether they were invented by one or many individuals

170   (but see[21,22] for such evidence in other nonhuman animals). However, given the community

171   specificity of the combinations of elements, when alternatives are present within communities, our

172   results are best explained by a high-fidelity social learning mechanism. The mound structure of the

173   most commonly consumed *Macrotermes* sp. varies extensively depending on the local microclimatic

174   conditions[23,24] and would thus not explain the community-specific distribution of elements. This

175   suggests that in chimpanzees, social influences were stronger than ecological ones.

176   Although some scholars argue that the accumulation of elements should lead to successive

177   improvements in the cultural trait[7], others recognize that this improvement can also manifest itself in

178   social improvements, comfort or well-being, which remain difficult to measure[19]. For example, in our

179   study, comfort may have driven the variation across communities of chimpanzees lying, sitting or

180   leaning whilst termite fishing (Supplementary Table 1 and 2). Thus, at present, our observations are

181   compatible with accumulated culture (sensu Dean et al.[20]), while a conclusion about true cumulative

182   culture would require data on fishing efficiency being improved by the combinations of elements.

183   The observation that potentially ecologically-dependent technical elements were distributed more

184   widely across communities than socially inferred ones (Supplementary Table 1 and 2) reinforces the

185   suggestion that social transmission is accompanied by a faithful copying mechanism, such as process-

186   oriented imitation[5], while the response to environmental challenges may be supported by more

187   individual learning mechanisms[7].

188   The present study is not without limitations. Due to the methodology used, we could only record

189   spatially fixed behaviours. This led us to underestimate technical elements that occurred outside the

190   field of view of the camera, or when individuals were positioned behind the mound or with their

191   back towards the camera. While this may not affect the assessment of cultural diversity whenever

192   we had a large number of videos for a community, this was not the case for Bafing, Kayan and Campo

193   Ma'an. Therefore, we may still underestimate cultural diversity in chimpanzee termite fishing.

194   Limited population sampling has biased our knowledge of chimpanzee culture, preventing us from

195   fully understanding human cultural uniqueness. We showed that chimpanzees have a larger termite-

196   fishing diversity than previously assumed. More importantly, our findings suggest that 'chimpanzee

197   etiquette', similar to human forms of etiquette[25,26], is likely based on a high-fidelity social

198   transmission mechanism among individuals of a population, resulting in an accumulation of

199   community-specific elements. Therefore, this study notably decreases the gap between chimpanzee

200   and human cultural abilities.

201

202   **Methods**

203   This study uses non-invasive behavioural observations collected on wild chimpanzees as part of the

204   Pan African Programme: The Cultured Chimpanzee ('PanAf'). All field research complied with the

205   ethical regulations and standards set by the relevant government authorities present within each

206   host country (see Acknowledgements for full list of governmental bodies that provided

207   authorizations for this study). Moreover, no experiments on animals were conducted therefore

208   randomization of experimental protocols was not necessary. The sampling strategy for the PanAf was

209   to conduct a minimum of 1 year of fieldwork on wild chimpanzee communities that were unknown

210   or poorly known behaviourally to scientists to better capture the variation present in this species.

211   The communities were selected following different criteria: 1) a balanced number of communities for

212   each African region, 2) a balanced representation of the main ecosystems inhabited by chimpanzees,

213   3) previous information on the presence of chimpanzees available for the site, and 4) sufficient

214   security for our field teams. After 8 years of collecting data at 46 chimpanzee communities across the

215   species range, for a range of 1-30 months, we observed 10 communities termite fishing, 1 of which

216   was already known to do so (Goualougo). The study examined termite fishing camera-trap videos

217   collected via the PanAf from all 10 communities. Individual chimpanzees were identified both within

10

218   and across each termite fishing sequence (i.e., across multiple videos). As in previous studies on

219   chimpanzee tool-use using camera-trap data[9], individuals were identified using a combination of

220   sexual characteristics, facial features, and conspicuous markings or injuries.

221   ***Ecological versus socially inferred behavioural elements***

222   To distinguish whether a technical element is primarily socially or ecologically driven, we used the

223   following two definitions: a technical element for which the chimpanzee had different alternatives

224   which are not constrained by ecological parameters was defined to be driven by social factors. In

225   Supplementary Table 3, the alternative elements are identified by similarly numbered groups. On the

226   other hand, a technical element that was obviously ecologically constrained was defined to be driven

227   by ecological factors (Supplementary Table 3). Examples of ecological constraints include the

228   structure and depth of the termite mound that could affect stick length, the hardness of the soil that

229   could affect perforation technique, or the availability of raw material that could affect stick rigidity[27].

230   Detailed studies on the architecture of the *Macrotermes bellicosus* mounds, the most-often fished

231   species by chimpanzees, revealed extensive variability within the same local area due to specific

232   microclimatic conditions[23,24]. Still, some ecological aspects could partly affect the use of other

233   technical elements, however we classified them as social as long as we observed that chimpanzees

234   possess alternative elements with which they can respond. For example, the defensive behaviour of

235   the termites could affect the stick shaking movements, but since chimpanzees shake the stick in

236   different ways, we classified these elements as being socially driven (group 3 in Supplementary Table

237   3). Similarly, the termites may bite with differing efficiency at a stick with different ends, but since

238   chimpanzees were seen to make small and long brushes, and bite or peel the extremity we classified

239   these elements as being socially driven (group 5 and 9 in Supplementary Table 3).

240   ***Inter-observer Reliability***

241 In order to determine reliability, two raters independently coded 23 technical elements (Christophe

242 Boesch and Simone Pika, and later Julia Riedel and Isabel Ordaz Németh). We only included in the

243 final analyses elements that occurred at a minimum of eight times across different communities and

244 videos. We then measured reliability using Cohen's Kappa[28], separately for behaviour, body part,

245 supporting position, body part supporting, and, wrist position. For each of these, we determined

246 Kappa twice, once considering cases in which the second rater did not see an element noted by the

247 first rater as a mismatch, and once excluding such cases. We further evaluated reliability on the level

248 of the individual behavioural elements using a one-tailed binomial test. To this end, we counted the

249 number of times the second rater coded the same behaviour as the first one. We then set the

250 expected proportion of chance agreement to the product of the numbers of times both raters coded

251 the behaviour in question, divided by the squared total of coded behaviours. As before, we applied

252 this approach twice, once considering the cases, in which the second rater did not see an element as

253 a mismatch, and once excluding such cases. Details for the agreement between CB and SP are

254 provided in Supplementary Tables 4 and 5.

255 ***Statistical analysis***

256 *Distribution of different technical elements across communities*

257 As overall tests of whether the occurrence of technical elements was community specific, we fitted

258 two Generalized Linear Mixed Models (GLMM)[29] with binomial error structure and logit link

259 function[30], one for the aerial termite data and one for the underground termite data. Into these, we

260 included, besides the intercept as the sole fixed effect, random intercepts for the community, the

261 mound, the individual, the technical element, and the combination of community and technical

262 element. This latter random intercept accounts for community-specific preferences for the utilization

263 of technical elements. Furthermore, to account for varying observation times per combination of

264 individual and mound, we included it (log-transformed) as an offset term into the model[30]. Since

12

265   tests of random effects are somewhat problematic[31], and since the elements were in part mutually

266   exclusive, we decided to conduct a permutation test[32] of whether the random intercept of the

267   combination of community and technical element significantly contributed to explaining the

268   response. To this end, we randomized the assignment of individuals to communities. We conducted

269   1,000 permutations into which we included the original data as one permutation. As the test statistic,

270   we chose the estimated variance (precisely the standard deviation) in the response attributed to

271   variation among the levels of the random effect of the combination of community and technical

272   element. We determined the P-value as the proportion of permutations revealing a test statistic at

273   least as large as that of the original data. We indicate model estimates (standard deviations

274   associated with the random intercepts effect of the combination of community and technical

275   element) as a measure of effect size and determined their 95% confidence intervals by means of a

276   parametric bootstrap (N=1,000). The models were fitted in R (version 3.4.4)[33] using the function

277   glmer of the package lme4 (version 1.1-17)[34], and we bootstrapped model estimates using the

278   function bootMer of the same package. The sample sizes for aerial nests in these models were 1546

279   total presences/absences (comprising 517 presences) of 17 technical elements for 71 individuals

280   from five communities, observed at 23 mounds, and 85 combinations of community and technical

281   elements. For underground nests, the data included 1788 total presences/absences (comprising 490

282   presences) of 21 technical techniques for 90 individuals from six communities and comprising 120

283   combinations of community and technical elements. From both data sets, we dropped combinations

284   of individual and technical elements for which we could not reliably code the presence or absence of

285   the behaviour.

286   However, potential differences between communities could also be largely driven by specificities of

287   the particular mounds rather than individual preferences differing systematically between

288   communities. We hence decided to run an additional permutation test in which we randomly

289   shuffled the assignment of communities (and their individual members) among termite mounds.

290   Since a few individuals had been observed at several different termite mounds, creating

291   complications regarding the random assignment of communities to mounds, we excluded them from

292   this analysis. Hence, this analysis is more conservative due to a smaller sample size in terms of the

293   number individuals included in combination with fewer units (i.e., mounds rather than individuals)

294   being permuted. The sample sizes for these models were 1,064 total presences/absences (comprising

295   350 presences) of 17 technical elements for 62 individuals from five communities observed at 13

296   mounds, and comprising 85 combinations of community and technical elements (aerial mounds) and

297   1,200 total presences/absences (comprising 324 presences) of technical elements for 77 individuals

298   from six communities observed at 29 mounds, and comprising 119 combinations of community and

299   technical elements (underground mounds).

300   *Sharing of technical elements within compared to across communities*

301   To estimate whether individuals belonging to the same community shared more technical elements

302   than individuals belonging to different communities, we measured the dyad-wise overlap between

303   combinations of individuals by means of Sørensen's similarity index[35]. This is calculated as follows:

304    $$\text{Sørensen}_{i,j} = 2 \times N_{\text{sharedPres}} / (2 \times N_{\text{sharedPres}} + N_{\text{only } i} + N_{\text{only } j})$$

305   where $N_{\text{sharedPres}}$ is the number of technical elements present in both individuals i and j, and $N_{\text{only } i}$ and

306    $N_{\text{only } j}$ are the number of technical elements observed only in individual i and j, respectively. It is

307   worth noting that Sørensen's index considers only technical elements present in at least one of the

308   two individuals of a given dyad.

309   We tested whether individuals of the same community shared on average more technical elements

310   than individuals of different communities by means of a Mantel like permutation test[36], which

311   permuted the individuals across communities. As a test statistic, we used the absolute difference

312   between the average similarity indices between individuals of the same and different communities,

313   respectively. We conducted 1,000 permutations into which we included the original data as one

314   permutation and determined the P-value as the proportion of permutations revealing a test statistic

315   at least as large as that of the original data. We conducted this test twice, separately for the aerial

316   and underground nest data (Figure 4a and b, respectively). As a measure of effect size we indicate

317   the difference between the mean similarity indices between individuals of the same and different

318   populations. We determined the 95% confidence interval of this measure by means of a non-

319   parametric bootstrap (N=1,000), sampling the individuals. Since the individuals contributed differing

320   numbers of sequences to the data, the bootstrapped data sets usually differed from the original one

321   in terms of the number of sequences. For these analyses, we considered only those individuals for

322   which all the behaviour elements considered in a data set (aerial or underground, respectively) could

323   be reliably coded. Hence, the sample sizes for these analyses are smaller than for the models

324   described above, namely a total 877 absences and 371 presences observed for 86 sequences of 60

325   individuals (aerial data) and 991 absences and 311 presences observed for 100 sequences of 68

326   individuals (underground data).

327   *Calculating the cultural fixation index*

328   To compare the proportion of variation in technical elements exhibited within and between

329   populations, we calculated a cultural F_{ST}. Cultural F_{ST} is negatively correlated with within-group

330   similarity, meaning higher F_{ST} values reflect more between group differences than within. We used

331   an approach similar to Bell and colleagues[18] but with a modification since the original method leads

332   to F_{ST} values larger than 1 in highly differentiated populations. This modified cultural F_{ST} method was

333   originally developed by Handley and Mathew[37] to account for variation in sample size and

334   populations having unique traits specific to them. We calculated the F_{ST} separately for each group of

335   putatively socially driven technical elements and also separately for aerial and underground nests. In

336   order to determine cultural F_{ST} values we processed the data as follows. In a first step, we

337   determined for each sequence of each individual which element of a given group of mutually

338   exclusive elements it had used (see Supplementary Table 3 and Supplementary Data 7 for details of

15

339   the F_{ST} calculation). This led to two matrices (one for aerial and one for underground nests), each

340   with one row per sequence and one column for each group of mutually exclusive elements. Since

341   some groups of mutually exclusive elements rarely occurred (when more than 50% of the sequences

342   did not have an entry for the respective group), we excluded them from the data and subsequently

343   excluded all sequences in which for at least one of the remaining groups none of the mutually

344   exclusive elements appeared. This subsetting of the data aimed at using the same sample size per

345   each element of a given group of mutually exclusive patterns when calculating the cultural F_{ST}. The

346   final sample for the aerial data consisted of 80 sequences from 53 individuals out of five communities

347   with behaviours from three groups (2, 4, and 6) of mutually exclusive technical elements, and the

348   final sample for the underground data consisted of 78 sequences from 58 individuals out of six

349   communities with behaviours from two groups (8 and 11) of mutually exclusive technical elements.

350   Since some of the individuals varied with regard to which particular element of a group of mutually

351   exclusive elements they used in a given sequence, we then randomly selected one sequence per

352   individual (generating a population of 'haploid' individuals) and then determined the cultural F_{ST} for

353   each group of mutually exclusive elements. In order to remove the effects of any particular random

354   selection, we repeated this 1,000 times and report average results and their variation (Figure 4c). F_{ST}

355   values were small in group 2, 4, and 6 and comparatively large in group 8 and 11 (Figure 4c).

356   Furthermore, particularly within group 4 and 11, F_{ST} values varied considerably between different

357   random selections of technical elements per individual.

358

359   **Data Availability**

360   The data for this study have been uploaded as part of the supplementary files (Supplementary Data

361   1-6).

362   **Code Availability**

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363 The custom code used for all statistical analyses has been uploaded as part of the supplementary

364 files (Supplementary Data 7 and 8).

365

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447

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466   **Author Contributions**

467   C.B., M.A., and H.S.K., designed the study and oversaw data collection; C.B., M.A., and P.D. compiled

468   data for this study; C.B., R.M., S.P., I.O-N., J.R. and A.K.K. analyzed the data; C.B., R.M. and A.K.K.

469   prepared figures; C.B., A.K.K., M.A. and H.S.K. wrote the manuscript with input from all coauthors.

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472   **Competing Interests**

473   The authors declare no competing interests.

474

475   **Figure Legends**

476   Figure 1: **Cultural diversity when fishing termites from aerial nests in six different chimpanzee**

477   **communities.**[38] Only elements observed in at least 50% of the individuals of a community and

478   differing between communities are included (Table S1). For Gombe chimpanzee, no quantification is

479   provided (in brown). Each element in a box interconnects with the other elements present within

480   each community and connections do not reflect a hierarchy, but highlight the combinations of

481   elements in each community. The variation in the combinations observed partly reflects different

482   ecological challenges and social preferences (see Table S1), while the number of elements within

483   each community reflects an assumed accumulation process. I=Issa chimpanzees only.

484

485 <u>Figure 2</u>: **Cultural diversity when fishing termites from underground nests in six different**

486 **chimpanzee communities.**[38] Only elements observed in at least 50% of the individuals of a

487 community and differing between communities are included (Table S2). Each element in a box

488 interconnects with the other elements found within each community. Some elements are unique to a

489 community (e.g., "peel the bark" of the stick in La Belgique chimpanzees, or "shake with the lips" the

490 inserted stick in Korup (K) chimpanzees), while others are shared among communities. The

491 connections do not reflect a hierarchical order in performing the technique, but highlight the

492 distinguishing features of the combination of elements in each community. The Goualougo (G)

493 technique is typified by 6 elements, including a unique perforation element as well as elements

494 shared with other communities, "sit to fish" shared with Campo Ma'an, Mont Cristal (MC), and La

495 Belgique, while "pull through teeth to make short brush", "support with two hands" and "insert stick

496 with both hands" are shared with Campo Ma'an and Mont Cristal. WW=Wonga Wongue.

497

498 <u>Figure 3</u>: **Occurrence of technical elements in 10 different chimpanzee communities for (a) aerial**

499 **termite nests and (b) underground termite nests.** The black fraction of the circles depicts the

500 proportion of sequences in which the respective element was present, and the area of the circles

501 depicts the number of sequences observed (range: 1 to 54; variation of sample size within

502 communities is due to occasional missing values that occurred when it could not be reliably seen

503 whether a given element was present in a given sequence). See also Supplementary Table 1 and 2.

504

505 <u>Figure 4</u>: **Similarity (Sørensen's similarity index) between combinations of putative social elements**

506 **only, compared for individuals belonging to different or the same community, for elements**

507 **observed at (a) aerial and (b) underground nests.** Indicated are medians (thick horizontal lines)

508 quartiles (boxes), and 2.5 and 97.5% quantiles (vertical lines). (**c) Cultural F$_{ST}$ values for five groups of**

509 **mutually exclusive technical elements** (2, 4 and 6 for aerial and 8 and 11 for underground nests, see

510 Supplementary Table 3). Indicated are medians, quartiles, and 2.5 as well as 97.5 quantiles of the F_{ST}-

511 values obtained from different random selection of sequences. F_{ST} values close to 1 indicates

512 complete separation between communities, like for groups 8 and 11, values between 0.1 and 0.4

513 indicates weaker separations between communities, like for groups 2, 4 and 6.
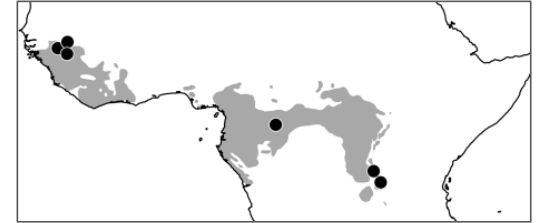
Underground termite fishing

Arriving at nest
- Use long thick stick
- Use short thick stick

G — WW

Perforation
- Perforate with 2 hands + foot
- Perforate with 1 hand + foot

G

Body Position
- Sit to fish
- Lean on elbow to fish
- Lie sideways to fish

G   K   WW

Tool modification
- Pull through teeth to make short brush
- Open fibers to make long brush

Hand technique

MC

- Insert stick with both hands
- Tap ground with stick
- Insert stick near elbow
- Support with second hand to eat
- Side wrist supports stick to eat
- Move head to eat from stick
- Move head to eat from supported
- Share stick with offspring
- Eat termites from support wrist
- Shake stick with lips
- Share stick with offspring

Goualougo | Campo Maan | Mont Cristal | La Belgique | Korup | Wonga Wongue

(a) Bafing, Dindef., Goual., Issa, Kayan

Rigid, Soft, Scratch, Insert 1h, Insert 2h, Shake, Shake u–d, Sit, Lean elbow, Bite, Brush, Wrist help, Mop, Stick 2h, Forearm, Hand takes, Stick 1h

(b) Campo M., Goual., Korup, La Belg., Mt Cr., Wonga W.

Tap, Perfore 2h, Perfore 1h, Long stick, Lean Elbow, Lay Side, Sit, Short brush, Long brush, Peel, Lip shake, Near elbow, Insert 2h, Support 2h, Sidewrist, Wrist eat, Head stick, Head eat, Mop, Share, Leave