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9 **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<sup>1-2</sup>, while non-human species  
66 are mostly known from a few populations reaching one dozen in the second most studied species,  
67 the chimpanzee<sup>3,4</sup>. 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<sup>5-7</sup>. 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<sup>5-7</sup>.

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<sup>8-12</sup>. Additionally, recent research on neighboring chimpanzee communities has  
75 revealed the persistence of cultural differences within the same environment<sup>13,14</sup>. Both suggest that  
76 incomplete sampling could lead to underestimated chimpanzee cultural complexity<sup>4</sup>. 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<sup>15</sup>. 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<sup>5,16</sup> 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  $p \leq 0.05$ ; 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](http://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<sup>17</sup>. 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<sup>10</sup>. 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<sup>18</sup>  
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<sup>7,19,20</sup>. 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<sup>21,22</sup> 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<sup>23,24</sup> 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<sup>7</sup>, others recognize that this improvement can also manifest itself in  
178 social improvements, comfort or well-being, which remain difficult to measure<sup>19</sup>. 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.<sup>20</sup>), 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<sup>5</sup>, while the response to environmental challenges may be supported by more  
187 individual learning mechanisms<sup>7</sup>.

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<sup>25,26</sup>, 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 (Goulougo). The study examined termite fishing camera-trap videos  
217 collected via the PanAf from all 10 communities. Individual chimpanzees were identified both within

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<sup>9</sup>, 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<sup>27</sup>.  
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<sup>23,24</sup>. 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<sup>28</sup>, 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)<sup>29</sup> with binomial error structure and logit link  
259 function<sup>30</sup>, 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<sup>30</sup>. Since

265 tests of random effects are somewhat problematic<sup>31</sup>, and since the elements were in part mutually  
266 exclusive, we decided to conduct a permutation test<sup>32</sup> 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)<sup>33</sup> using the function  
277 glmer of the package lme4 (version 1.1-17)<sup>34</sup>, 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<sup>35</sup>. This is calculated as follows:

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

305 where  $N_{sharedPres}$  is the number of technical elements present in both individuals  $i$  and  $j$ , and  $N_{only i}$  and  
306  $N_{only j}$  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<sup>36</sup>, 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<sup>18</sup> 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<sup>37</sup> 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

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**



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.  
470 E.A.A., A.B., C.C., V.E.E., J.M.F., D.F., R.A.H.A., V.H., P.K., M.K., M.L., E.N.M., G.M., D.M., M.M., E.N.,  
471 S.N., L.J.O., R.O., L.P., A.P., C.S., L.S., F. S., N.T., E.G.W., and J.W. collected data in the field.

#### 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.**<sup>38</sup> 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 **Figure 2: Cultural diversity when fishing termites from underground nests in six different**  
486 **chimpanzee communities.**<sup>38</sup> 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 Goulougo (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

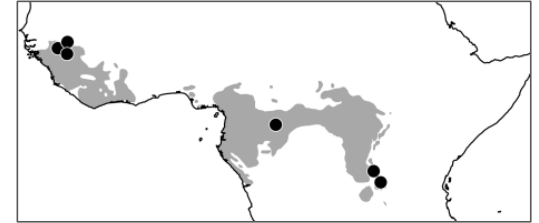
498 **Figure 3: Occurrence of technical elements in 10 different chimpanzee communities for (a) aerial**  
499 **termite nests and (b) underground termite nests.** The black fraction of the circles depicts the  
500 proportion of sequences in which the respective element was present, and the area of 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 **Figure 4: 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.

# Aerial termite fishing



Arriving at nest

Arrive with 1 stick

Tool type

Rigid sticks

Soft sticks

Tool modification

Bite end of stick

Hand technique

Shake up-and-down inserted stick

Scratch tunnel opening with fingers

One hand brings stick to mouth

Lean on forearm to fish

One hand brings stick to mouth

Both hands extract stick from mound

Shake sideways inserted stick

One hand brings stick to mouth

Support with wrist from below

Forearm follows stick to mouth

Dindéfelo

Goualougo

Gombe

Kayan

Bafing

Issa



# Underground termite fishing



**Arriving at nest**

Use long thick stick

Use short thick stick

**Perforation**

Perforate with 2 hands + foot

Perforate with 1 hand + foot

**Body Position**

Sit to fish

Lean on elbow to fish

Lie sideways to fish

**Tool modification**

Pull through teeth to make short brush

Open fibers to make long brush

Insert stick near elbow

**Hand technique**

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

Goulougo

Campo Maan

Mont Cristal

La Belgique

Korup

Wonga Wongue

G

WW

G

K

WW

MC

