**PROCEEDINGS OF
THE ROYAL SOCIETY B**

BIOLOGICAL SCIENCES

Wild chimpanzees select tool material based on efficiency and knowledge

**SCHOLARONE™
Manuscripts**

1　　　**Wild chimpanzees select tool material based on efficiency and knowledge**

2

3　　　Noemie Lamon[1,2]*, Christof Neumann[1], Jennifer Gier[1], Klaus Zuberbühler[1,2,3]†, Thibaud

4　　　　　　　　　　　　　　　　　Gruber[2,4,5]†*

5

6　　　[1]Department of Comparative Cognition, University of Neuchâtel, 2000 Neuchâtel,

7　　　Switzerland

8　　　[2] Budongo Conservation Field Station, Masindi, Uganda;

9　　　[3] School of Psychology and Neuroscience, University of St Andrews, Fife KY16 9JP, UK;

10　　　[4] Swiss Center for Affective Sciences, University of Geneva, 1211 Geneva, Switzerland;

11　　　[5] Department of Zoology, University of Oxford, OX1 3PS, UK

12

13　　　*: Correspondence to: Thibaud Gruber, thibaud.gruber@gmail.com and Noémie Lamon,

14　　　noemie.lamon@gmail.com

15　　　†: joint senior authors

16

17　　　**Keywords: tool use, efficiency, sponges, field experiment, subculture, *Pan troglodytes***

18　　　***schweinfurthii***

19

20 **Abstract**

21 Some animals have basic culture but to date there is not much evidence that cultural traits

22 evolve as part of a cumulative process as seen in humans. This may be due to limits in animal

23 physical cognition, such as an inability to compare the efficiency of a novel behavioural

24 innovation with an already existing tradition. We investigated this possibility with a study on

25 a natural tool innovation in wild chimpanzees, moss-sponging, which recently emerged in

26 some individuals to extract mineral-rich liquids at natural clay-pits. The behaviour probably

27 arose as a variant of leaf-sponging, a tool technique seen in all studied chimpanzee

28 communities. We found that moss-sponges not only absorbed more liquid but were

29 manufactured and used more rapidly than leaf-sponges, suggesting a functional improvement.

30 To investigate whether chimpanzees understood the advantage of moss- over leaf-sponges we

31 experimentally offered small amounts of rainwater in an artificial cavity of a portable log,

32 together with both sponge materials, moss and leaves. We found that established moss-

33 spongers (having used moss at clay-pits) preferred moss to prepare a sponge to access the

34 rainwater, whereas leaf-spongers (never observed using moss) preferred leaves. Survey data

35 finally demonstrated that moss was common in forest areas near clay-pits but nearly absent in

36 other forest areas, suggesting that natural moss-sponging was, at least partly, constrained by

37 ecology, not knowledge. Together, these results suggest that chimpanzees perceive functional

38 improvements in tool quality, a crucial prerequisite for cumulative culture.

39

40   **Introduction**

41   Over the last decades, social network analyses and experiments in the wild and captivity have

42   produced evidence that some animal behaviour can spread socially [1-4] giving ground for the

43   notion of animal cultures [5]. Yet, there is still little compelling evidence for evolution of

44   cultural traits within groups or populations of animals. Consequently, animal cultures remain

45   seen as stagnant, population-level portfolios of behaviour, much in contrast to what is seen in

46   humans [6-8].

47

48   While cultural evolution has become a hot topic in science [9], the term is not uniformly

49   defined, especially when applied to animals. According to some definitions, cultural evolution

50   occurs through stochastic, drift-like processes, as seen in changes in the songs of humpback

51   whale and some birds [10, 11]. Other definitions require that cultural evolution entails some

52   sort of functional improvement, similar to natural selection, a process termed 'Cumulative

53   Cultural Evolution' (CCE). For instance, Schofield et al. [12, p.114] define CCE as "…a

54   modification […] of a cultural trait (i.e., acquired via social learning) that enhances its

55   complexity, efficiency, security, or convenience", a definition we use in this article.

56   Importantly, this view of CCE does not mandate incremental changes in the complexity of

57   behavioural traditions, as proposed by other authors [6-8], as this effectively limits the notion

58   of cultural evolution to humans, a perspective we and others ([13, 14]) find unhelpful for

59   evolutionary studies. Cultural evolution, in our view, is equivalent to cultural change, which

60   also broadens the range of relevant research to include, for example, experimental studies of

61   zebra finch song or route learning in pigeons [15, 16].

62

63   Whatever definition is adopted, the current literature remains weak on examples of cultural

64   change, particularly in wild animals and for tool use, which is astonishing considering the

65   growing interest in animal innovations and traditions [17]. While all current cultural traits

66   must have started off as innovations, most innovations in animals are not copied by others and

67   remain one-off occurrences [e.g. 18]. This is particularly true for chimpanzees (*Pan*

68   *troglodytes*), a species well known for its culturally acquired behaviour [19], where only few

69   of numerous behavioural innovations have spread through communities [20, 21].

70

71   This has led to the hypothesis that, compared to humans, animals experience fundamental

72   limitations in the types of social learning required for high-fidelity spread of novel

73   behaviours, which some authors consider a precondition for CCE [6-8]. For example, while

74   there is consensus that chimpanzees are avid social learners, they may achieve this by

75   stimulus enhancement, local enhancement or emulation [22], but not through imitation or

76   teaching [6, 23]. As a result, chimpanzees may not truly understand the behaviours they learn

77   from others but need to re-invent the wheel anew from one generation to the next [6-8]. A

78   similar point has been made for New Caledonian crows (*Corvus moneduloides*), a species for

79   which there is evidence for local and stimulus enhancement, but not for imitation for

80   behaviour transmission between conspecifics and with humans [24, 25]. Nevertheless, more

81   work is needed in both species to identify the specific social learning mechanisms that

82   contribute to the transmission of tool designs. In addition, others have argued that imitation

83   and teaching are not necessary for CCE to occur, neither in animals nor in humans [26, 27],

84   suggesting that an exclusive focus on social learning mechanisms may prevent a deeper

85   understanding of CCE.

86

87   Another hypothesis for low levels of cultural evolution in animals is based on limitations in

88   physical cognition [e.g. 28]. Individuals may be unable to recognise that a novel behaviour is

89   more suited for a given task compared to a pre-existing one, and thus fail to experience a

90   motivation to adopt the new behaviour, even if it is more advantageous. Animals, in other

91   words, may simply lack the cognitive ability to understand the functional consequences of

92   physical actions upon the environment, which consequently prevents them from improving

93   previously acquired cultural behaviours [29, 30].

94

95   This view is controversial, however, as chimpanzees and other species in the wild have

96   demonstrated some understanding of the physical properties of their tools (e.g. Western

97   chimpanzees (*P.t. verus*) [31], capuchin monkeys (*Sapajus libidinosus*) [32]). For example,

98   most chimpanzees use sticks to fish for termites, but Central chimpanzees (*P.t. troglodytes*)

99   also manufacture more efficient brush-tipped sticks [33], suggesting that the Central African

100   technique emerged from the unmodified technique. Interestingly, migrating female Western

101   chimpanzees adopt a less efficient nut-cracking technique to conform to the prevalent

102   behaviour of their new social group at the cost of personal efficiency [34]. Among non-

103   primates, New Caledonian crows manufacture probing tools to capture invertebrates in trees

104   from the long-barbed edges of palm-like *Pandanus* leaves, but designs differ across groups of

105   animals [35]. In particular, hooked stick tools may have evolved from unmodified stick tools,

106   possibly due to CCE [36, 37].

107

108   Causal understanding of tool properties has also been demonstrated in captivity, notably for

109   all great apes [38, 39] and New Caledonian crows [40]. For example, chimpanzees can change

110   from one technique to another if there is a noticeable improvement in efficiency [41, 42]. As

111   always with captive studies, the concern remains that capacities demonstrated by subjects may

112   be a by-product of conditions absent in natural environments. One solution is to carry out

113   controlled experiments with wild-born animals under laboratory conditions [43], as

114   demonstrated for wild-caught New Caledonian crows that discriminate differences in design

115   features of hooked stick tools in captivity [44].

116

117   In sum, the current literature is unable to provide a clear picture regarding the question of

118   whether culturally acquired behaviour in animals can change in directed ways. While captive

119   studies have demonstrated the ability of animals to improve both individually and socially

120   learned techniques, these findings may be artefacts of captive conditions and, as such, of

121   limited value to understand the cultural repertoires described in the wild. Similarly, while

122   field studies have documented naturally occurring changes in behavioural traditions,

123   sometimes with differences in complexity, we are not aware of any documented transition in a

124   cultural trait changing from a less to a more efficient variant, which would provide strong

125   evidence for CCE in wild cultures.

126

127   An interesting consequence of within-group changes in socially acquired behaviour is the

128   establishment of cultural subgroups, defined here as parts of a group engaging in socially

129   acquired behavioural patterns different from the rest of the group [45]. As has been argued for

130   animal culture in general, a key point is that any eventual cultural subgroup is not the result of

131   shared genetics or shared ecology alone [46]. Socially learned subcultures, in other words, are

132   evidence for diversification *within* cultures and are important to investigate cultural evolution

133   [47]. Over longer time periods, the behavioural variant that defines the subculture may

134   continue its cultural sweep, to the effect that it becomes part of the entire group's culture.

135   Alternatively, it may remain restricted to parts of the group [48].

136

137   In this study, we address the question of CCE in animals by capitalizing on recent

138   observations in the Sonso chimpanzee community (*P.t. schweinfurthii*) of Budongo Forest,

139   Uganda [21]. In 2011, a behavioural innovation, moss-sponging, naturally spread within a

140   subset of the community [21]. Moss-sponging is an alternative to commonly found leaf-

141   sponging, a behaviour present in all wild chimpanzee communities studied so far. While leaf-

142   sponging is often referred to as a 'cultural universal' in chimpanzees [19], its widespread

143   presence may also suggest a genetic basis; studies examining the likelihood of its spontaneous

144   emergence are thus needed [49]. Well before the advent of moss-sponging [50], most

145   members of the Sonso community habitually manufactured leaf-sponges to extract various

146   types of liquids from cavities and rivers. Moss-sponging is most likely a variant of leaf-

147   sponging as both consist of harvesting a handful of leafy vegetation or clumps of moss,

148   respectively, subsequently shaped in the mouth into a sponge approximately the size of a golf

149   ball. The sponges are then dipped into the liquid and reinserted and squeezed in the mouth.

150   Moss-sponging was first seen at one specific location in the community's home range, a clay-

151   pit, which consisted of two waterholes in clay ground, filled with mineral-rich suspensions

152   [51]. Immediately after its appearance, the new behaviour spread within a week across seven

153   individuals via proximity-based observational learning [21]. In the subsequent three years,

154   moss-sponging propagated further throughout the community, albeit now mainly within the

155   matrilines of cohort members that initially learned the technique [52]. These two studies show

156   that, compared to leaf-sponging, social learning must have contributed strongly to the spread

157   of moss-sponging. In the meantime, moss-sponging was also observed in the Waibira

158   community of Budongo Forest, which has an overlapping home range with the Sonso

159   community (C. Hobaiter, personal communication).

160

161   The fact that moss-sponging continued to spread through the community, despite the presence

162   of an already existing technique for absorbing liquids (leaf-sponging), led us to hypothesize

163   that the spread may have been caused by a difference in efficiency between the two types of

164   sponge materials. However, one puzzling fact was that, since its emergence, moss-sponging

165   was almost only observed at the site of its original invention, the clay-pit, with only six

166   observations elsewhere in the forest, despite uninterrupted daily focal follows over several

167   years by field assistants and researchers. Leaf-sponging, instead, continued to be observed in

168   a range of contexts and throughout the forest including at the clay-pit.

169

170   A more parsimonious hypothesis may thus have been that moss-sponging was nothing but a

171   context-specific behaviour, triggered by special ecological conditions present at clay-pits, but

172   that chimpanzees did not perceive the more general functional properties of moss as sponge

173   material. Instead, moss-sponging chimpanzees may have simply used moss at the clay-pit in

174   response to ecological (e.g. clay water) or social (e.g. competition) factors encountered at the

175   location, but not because moss-sponging was part of an enriched cultural repertoire.

176

177   To distinguish between these two hypotheses we collected three sets of data. First, we tested

178   whether moss-sponging was indeed more efficient than leaf-sponging, a crucial prerequisite

179   for any argument based on physical cognition. We were interested in two dimensions of

180   efficiency: absorbency (amount of liquid a sponge could contain) and effectiveness (duration

181   of manufacturing and deployment time).

8

182

183   Second, to test whether moss-savvy (but not moss-ignorant) individuals preferred moss-

184   sponging over leaf-sponging, we tested subjects with a standardised field experiment. The

185   experiment consisted of giving subjects a choice between both sponge materials, leaves and

186   moss, presented on a portable log with an artificial cavity filled with natural rainwater [53].

187   Not all members of the community had been observed using moss-sponges at the time of the

188   experiment, suggesting some were 'moss-ignorant'. We thus classified subjects as either

189   'moss-spongers' (i.e. individuals who had been observed manufacturing a moss-sponge at the

190   clay-pit but continued to use leaf-sponges in other contexts, including also at the clay-pit) or

191   'leaf-spongers' (individuals who had never been observed manufacturing moss-sponges but

192   had manufactured leaf-sponges). If moss-sponges are more efficient than leaf-sponges and if

193   chimpanzees can compare tools in terms of efficiency, we predicted that the proportion of

194   moss choices would be higher amongst known moss-spongers than amongst leaf-spongers.

195

196   Third, we investigated whether the lack of moss-sponging by moss-savvy individuals

197   throughout most of the forest was a by-product of uneven moss distribution as chimpanzees

198   generally manufacture their tools near the location of use. To evaluate the ecological

199   correlates of moss-sponging, we conducted a survey of leaf and moss distribution at known

200   chimpanzee sponging locations throughout the forest, including areas of mixed forest where

201   rainwater filled tree-holes were located and swamps where clay-pits were located.

202

203

204   **Material and methods**

205

9

206

Study site and subjects

208   The study was conducted in Budongo Forest Reserve in Western Uganda (1°37'-2°00'N,

209   31°22'-31°46'E) with the Sonso chimpanzee community (*P.t. schweinfurthii*). The reserve

210   consists mainly of moist semi-deciduous tropical forest, at a mean altitude of 1100m. The

211   Sonso community's home range approximately 7 km^2 and members have been habituated to

212   human presence since the mid-1990s [54]. At the time of the study, the community consisted

213   of 68 individuals.

214

Tool features

216   Tool efficiency was assessed in terms of *absorbency,* defined as the weight of liquid that a

217   leaf-sponge or a moss-sponge could carry, the assumption being that the more water it could

218   absorb, the more efficient it was. '*Leaf-sponging*' was defined as using a wad of crumpled or

219   folded leaves to absorb and consume liquid; '*moss-sponging*' as using a clump of moss or

220   mixture of moss and leaves for the same purpose (fig.1). Sponges manufactured by

221   chimpanzees during daily follows and experiments were collected whenever possible and

222   their absorbency measured. Over 153 days of focal follows and experiments between January

223   2013 and February 2015, we collected 96 sponges on 48 separate days from 28 identified and

224   three unidentified individuals. We measured the absorbency for N=62 of them for whom the

225   manufacturer was identified (N=48 leaf-sponges; N=14 moss-sponges), collected during

226   natural sponging at clay-pits, tree holes and rivers (N=44) and during experiments (N=18).

227   Absorbency was determined by dipping the sponge in water and then squeezing it, comparing

228   the weight before and after squeezing with a scale (Factory weigh™PRO-VA1234, precision:

229   0.01g). Each sponge was tested within a few hours after being collected in the forest, ruling

230   out systematic environmental effects (e.g. [55]). Each sponge was then submerged in a

231   container with rainwater, removed, weighed, squeezed until water stopped dripping, and

232   weighed again. This procedure was repeated 10 times for each sponge, following Biro and

233   colleagues [56]. To account for possible degradation between repeated squeezes, we included

234   measurement number as a covariate in the statistical analyses. While we measured weight of

235   absorbed liquid, for simplicity we refer to absorbency as volume.

236

237   *Availability*

238   We carried out a survey to assess the availability of sponging material (leaves and moss)

239   around locations where chimpanzees had been observed sponging. The prediction was that

240   swamp areas where clay-pits are located contained more moss than mixed forest areas where

241   natural tree holes are rather located. To this end, in December 2016, we surveyed all locations

242   where chimpanzees had previously been observed sponging from tree holes or clay-pits (28

243   locations, N=8 in swamp areas and N=20 in mixed forest areas). The survey zone was a 5m

244   radius around the water source, up to three meters off the ground. To assess leaf availability,

245   we counted all stems of *Acalypha spp.* and *Lasiodiscus mildraedii,* the species most

246   frequently picked by the chimpanzees to manufacture leaf-sponges. We considered a stem as

247   a plant axis that carried at least four leaves. To assess moss availability, we calculated the

248   surface covered by moss in the survey zone. As moss species, we were able to identify

249   *Orthostichella welwitschii* (mostly hanging from tree branches), *Porotrichum elongatum*, and

250   *Plagiochila spp* (a liverwort). We assessed moss coverage by using surfaces of 20cm x 20cm,

251   using a cardboard reference unit. If the whole surface was covered by moss, we attributed a

252   value of 1; if half, 0.5; a quarter, 0.25; otherwise 0.

253

11

254   *Experiment*

255   To investigate what tool 'leaf-spongers' and 'moss-spongers' would select if given the choice

256   of the two materials in a controlled context, we manufactured a portable log (length:33.5cm;

257   diameter:14cm, fig.SF10) with an artificial cavity drilled in the centre (opening:8.0x8.5cm;

258   depth:8.0cm), filled with 20ml of rainwater. The apparatus was a modified version of a

259   honey-trap apparatus used in previous experiments [53]. To minimize the risk of disease

260   transmission from humans to chimpanzees, we boiled rainwater collected from tin roofs prior

261   to each experiment. We chose rainwater rather than mineral suspensions to remove any

262   potential inherent advantage that moss might have over leaves in absorbing minerals [57]. We

263   positioned the apparatus in the absence of any individuals and supplied tool material at equal

264   distance from the hole (fig.SF10) in the form of two clumps of moss (*Orthostichella*

265   *welwitschii*) and two leafy branches of *Acalypha spp*.

266

267   We aimed to test subjects in isolation to rule out social influence or competitive pressure. We

268   thus targeted specific individuals by anticipating subjects' travel direction, presenting the

269   apparatus when they were alone (except for mothers with dependent offspring). The choice of

270   subjects was therefore opportunistic and not blind. Since individuals were unconstrained in

271   their daily movement patterns, it was unavoidable that, in some trials (8 of 20), the subject

272   arrived at the apparatus while another individual was already engaging with it. In another

273   case, the subject joined two group members already engaging with the log (Supplementary

274   material). If both materials were still available when the subject arrived, we included its

275   choices in the analysis. If an individual participated several times, we only took the first trial

276   into account. Trials had to be repeated occasionally, with at least 24-hour intermissions, if the

277   subject interacted with the log but did not manufacture a sponge. All trials were filmed by two

12

278   experimenters (NL and her field assistant) with Panasonic HC-X909 video cameras to get two

279   different angles of the scene. Data included: the identity of the subject and eventual

280   bystanders; whether the subject had been seen moss-sponging before; and the technique used

281   to retrieve the water from the hole.

282

283   There were two experimental periods (January 2014 and January 2015) corresponding to the

284   annual dry season, when chimpanzees are most likely to search for water in tree holes. 20

285   individuals participated in the experiment, all of which had been observed manufacturing leaf-

286   sponges prior to the experiment: six adult females, five adult males, two subadult females, one

287   subadult male, four juvenile females and two juvenile males. 9 of 20 individuals were

288   classified as 'moss-spongers' as they had moss-sponged at least once before the experiment

289   (Table ST1), while the remaining 11 were classified as 'leaf-spongers' by default [52].

290

291   The absorbency of the sponges (9 moss-sponges and 9 leaf-sponges) manufactured during the

292   experiment was measured as described above. We additionally evaluated efficiency by

293   extracting manufacturing time (latency between first touching the material and removing the

294   fabricated sponge from the mouth) and deployment time (latency between touching the

295   sponge material, fabricating the sponge, and transferring the liquid-filled sponge into the

296   mouth) from videos recorded during the experiments for N=17 leaf-sponges and N=8 moss-

297   sponges. For both measures, the assumption was that the faster a tool could be manufactured

298   and used, the more efficient it was.

299

300   ***Statistical analyses***

301   To assess differences in sponge absorbency we fitted a linear mixed model (LMM) with

302   Gaussian error distribution with the lme4 package in R3.4.0 [58, 59]. The response variable

303   was the volume of water a given moss absorbed. Type of material (moss/leaf), context

304   (natural observation/experiment) and sponge weight were entered as fixed effects. In addition,

305   we fitted measurement number as control variable to account for the possibility that

306   absorbency degraded within a sponge over repeated squeezes. Our main interest was the

307   effect of the sponge material. As the degradation effect of repeated squeezes could differ

308   between the two materials or the effects of material differ between the two contexts, we

309   included two 2-way interactions in our model: (1) material and measurement number and (2)

310   material and context. We fitted sponge ID (due to multiple measurements per sponge) nested

311   in manufacturer ID as random intercept. Finally, we fitted material and context as

312   uncorrelated random slopes in manufacturer ID. Model fit was assessed visually (distribution

313   and homogeneity of residuals) and numerically (variance inflation factors), and neither check

314   indicated severe violations of assumptions (Supplementary material). We also fitted a null

315   model with material (our factor of primary interest) removed but random effects structure

316   unchanged. The difference between full and null model was assessed using a likelihood ratio

317   test (LRT) [60].

318

319   To assess differences in manufacturing and deployment time during the experiment, we fitted

320   two LMMs with material (moss/leaf) as fixed effect, sponge manufacturer as random

321   intercept, and material as uncorrelated random slope in manufacturer ID. In the first model,

322   we used manufacturing time as the response variable. In the second model, we used

323   deployment time as the response variable. As with the absorbency models, we removed the

324   major factor of interest (material) of these full models to fit corresponding null models, which

14

325   were also tested with LRTs. We also fitted both models as generalized linear mixed models

326   with Poisson error and log-link function.

327

328   We used two tests to assess subjects' choices during the experiment. First, we ran a proportion

329   test to address the hypothesis that, given their presumed differences in knowledge, moss-

330   spongers were more likely to choose moss than leaf-spongers and that leaf-spongers were

331   more likely to choose leaves than moss-spongers. Because this was a directed hypothesis, we

332   opted to provide a one-tailed p-value here. In addition, if effects were significant, but opposite

333   to what we predicted, we would consider the result as non-significant, i.e., the same

334   interpretation as if accepting the null hypothesis [61].

335

336   Second, we addressed the same question but framed the problem as correlational, i.e., how

337   strongly material choice was correlated with presumed knowledge. For this, we investigated

338   the correlation between the likelihood of individuals to use moss in the experiment (yes=1;

339   no=0) and their presumed knowledge of the moss-sponging technique (yes=1; no=0). This

340   coding allows the calculation of repeatability R (intra-class correlation coefficient) between

341   choice of material during the experiment and presumed knowledge [62, 63]. This metric can

342   be interpreted as the proportion of total variance accounted for by differences between

343   individuals [62]. At its highest (R=1), there is no within-subject variance, i.e., in our case the

344   matching between choices during the experiment and subjects' knowledge would be perfect.

345   We computed a null distribution of expected R values based on 2000 permuted data sets and

346   assessed statistical significance as the proportion of R values from these permuted data sets

347   that were larger or equal to our observed R value [63].

348

15

349   Finally, we compared the frequencies of materials to manufacture sponges between different

350   locations/forest types using a Mann-Whitney *U* test.

351

352

353   **Results**

354

355   *Absorbency*

356   The model assessing the absorbency of moss-sponges manufactured by chimpanzees in both

357   natural and experimental contexts differed significantly from the null model (LMM, LRT:

358   χ^2_3=36.25, p<0.0001). We found that sponges made of moss absorbed significantly more

359   liquid than sponges made of leaves, and this difference was more pronounced for the sponges

360   manufactured in the experimental context (LRT, χ^2_1=28.69, p<0.0001, Table 1, fig.2). Not

361   surprisingly, heavier sponges, independently of the material used to manufacture them,

362   absorbed more liquid than lighter sponges (1g increase in weight corresponded to 0.85ml

363   more liquid absorbed, table 1). In the natural context, moss-sponges absorbed an average of

364   13.1ml; leaf-sponges an average of 8.4ml of liquid (fig.2). In the experimental context, moss-

365   sponges absorbed an average of 26.3ml; leaf-sponges an average of 9.5ml of liquid (fig.2).

366

367

368   **Table 1│ Results of the LMM testing differences in absorbency.** Each sponge was

369   measured 10 times.

	Beta	Standard error	t
Intercept	2.58	0.86	2.99
Material (moss or leaves)	16.87	3.17	5.32
Context (experimental or natural)	-1.03	0.92	-1.12
Measurement number (10 dips)	-0.38	0.06	-5.92
Weight (g)	0.85	0.07	12.09
Material * Measurement number	-0.06	0.13	-0.45
Material * Context	-12.23	2.02	-6.06

370

371   *Manufacturing and deployment time*

372   The model comparing manufacturing time only between experimentally manufactured moss-

373   and leaf-sponges was marginally significantly different from the null model (LMM: N=25

374   sponges by 15 individuals, LRT: χ^2_1=3.44, p=0.0635, Table 2, fig.3). Moss-sponges took on

375   average 7.2s to manufacture while leaf-sponges took on average 11.2s.

376

377   The model comparing deployment time (manufacturing plus first use) between experimentally

378   manufactured moss-and leaf-sponges differed significantly from the null model (LRT:

379   χ^2_1=4.46, p=0.0347, Table 2, fig.3). Here, the combined time was on average 9.0s for moss-

380   sponges and on average 12.8s for leaf-sponges.

381

382   In both cases, GLMMs with Poisson error structure revealed very similar results (see

383   supplemental materials).

384

385   **Table 2│ Results of the LMMs testing differences in manufacturing and deployment**

386   **time between moss and leaf-sponges.**

	Beta	Standard error	*t*
Manufacturing time			
Intercept	11.18	1.56	7.16
Material (moss vs. leaf)	-3.99	2.00	-2.00
Deployment time			
Intercept	12.79	1.56	8.20
Material (moss vs. leaf)	-3.80	1.68	-2.26

387   ***Experiment***

388   We tested 20 individuals. In line with our predictions, the proportion of individuals that used

389   moss for sponge production was higher amongst known moss- than leaf-spongers (proportion

390   test: χ^2_1=3.23, one-tailed p=0.0361, moss-spongers: 7/9, leaf-spongers: 3/11, Table ST1).

391

392   To assess the correlation between presumed knowledge and choice during the experiment, we

393   calculated the repeatability of the material chosen. The repeatability estimate was *R*=0.52

394   (p=0.009, range of permuted *R*: 0.00-0.81, see fig.SF8). These results indicate that individuals

395   were more likely to choose the material in the experiment that corresponded to their presumed

396   knowledge.

397

398

399   *Availability*

400   We found that both *Acalypha spp.* and *Lasiodiscus mildraedii* were more readily available

401   around tree-hole sponging locations in mixed forest areas (N=20 locations) than in swamp

402   areas (N=8 locations) although this difference was not statistically significant (Wilcoxon test,

403   W=105.5, p=0.2034, fig.4). However, there was significantly less moss material available at

404   known sponging locations in mixed forest than in the swamp areas, where the clay-pits were

405   located (Wilcoxon test, W=5, p<0.001, fig.4).

406

407

408   **Discussion**

409

410   We tested experimentally whether the spread of moss-sponging, first observed in the Sonso

411   chimpanzees of Budongo Forest in 2011, could be connected to differences in efficiency

412   between this behavioural innovation and the ancestral leaf-sponging variant, and whether this

413   led to the establishment of a new subculture in the community. We report three sets of

414   findings that are directly relevant to this question and to the topic of cultural evolution more

415   generally. In the first set, we found that moss-sponges represented a functional improvement

416   compared to ancestral leaf-sponges. Moss-sponges were both more effective in absorbing

417   rainwater and were fabricated and used more quickly than leaf-sponges. Our results are thus

418   in line with an ongoing discussion on tool efficiency as an indicator of cumulative culture,

419   exemplified by data on New Caledonian crows whose hooked tools are more efficient than

420   non-hooked tools [36, 37] and central African chimpanzees whose brush-tipped termite

421   fishing tools are more efficient than non-brushed tools [33].

422

19

423   Our second finding was to show experimentally that chimpanzees who already had experience

424   with moss-sponges preferred moss over leaves as material to fabricate sponges when

425   presented with a novel problem unrelated to the original socio-ecological context of moss-

426   sponging, i.e., independent of location, liquid type and social competition. In contrast,

427   individuals that had never been observed moss-sponging mainly chose leaves, suggesting they

428   did not perceive moss as a suitable sponge material in this novel situation. These results

429   demonstrate that moss-sponging is not tied to a particular ecological condition but generally

430   available to individuals who have learned the novel technique beforehand. Our experimental

431   results are also supported by the natural observations of Sonso individuals using moss-

432   sponges outside the context of the clay-pit, which suggest that moss-sponging is in the process

433   of being applied more widely.

434

435   In a third set of findings, we reported that the most likely reason natural moss-sponging was

436   not seen outside its original clay-pit context was the uneven availability of moss throughout

437   the forest. Survey data showed that the two most common plant species to manufacture leaf-

438   sponges were abundant throughout the forest and present at the 28 locations where

439   chimpanzees had been observed leaf-sponging. In contrast, moss was rare in the forest, except

440   in swamp areas where clay-pits are located, which effectively prevented moss-spongers from

441   executing their behaviour because of a lack of opportunities [64, 65]. Nevertheless,

442   chimpanzees do not transport moss-sponges from moss-rich areas to moss-depleted ones,

443   suggesting that the functional improvements may not be enough to modify chimpanzees'

444   preference entirely.

445

446　The core evidence for cultural evolution was the result of our field experiment, which

447　essentially suggested the presence of a cultural subgroup in tool use within the Sonso

448　community. Our experiment did not specifically address the role of social learning in sponge

449　manufacturing, as this was done in previous studies [21, 52]. More importantly, the current

450　study suggests that most leaf-spongers did not perceive moss as a potential sponge material

451　[29], suggesting a lack of underlying cultural knowledge.

452

453　Nevertheless, 3 of 11 classified leaf-spongers (Table ST1) chose moss to manufacture a

454　sponge during the experiment, which requires some explanation. For one individual, KH, we

455　cannot exclude that she was socially influenced by observing an individual before her using

456　moss. However, this argument does not apply for other trials, such as when ST, roughly the

457　same age, chose moss, even after having observed an individual before her using a leaf-

458　sponge (Supplementary material). It is also possible that the three new moss-spongers (a)

459　were simply oblivious to the choices offered, (b) recognised the advantages of moss as sponge

460　material in situ, or (c) were curious to try out its properties in the absence of any prior social

461　learning. Generally, however, we find explanations based on ad-hoc trial and error

462　experimenting less plausible because multiple studies with this community have already

463　shown a remarkable resistance to using novel tools in experimental situations [64, 66]. The

464　most likely explanation, in our view, is that these three individuals had acquired moss-

465　sponging behaviour prior to the experiment, but never showed it during observer presence. It

466　would be important to monitor these previously unidentified moss-spongers to check whether

467　moss-sponging remains present. We have observations for one individual, KH, who was

468　subsequently observed moss-sponging at the clay-pit.

469

470   Also relevant is that two of nine known moss-spongers opted for the traditional leaf-sponging

471   technique in the experiment. This might have been the result of individual differences in

472   conservatism, manufacturing skills, or taste. For example, some individuals may prefer the

473   technique they are more used to, even if they understand differences in efficiency [53].

474   Leaves are the more habitual material to manufacture a sponge, which may have hindered

475   some individuals from seeing the more efficient moss solution [29]. Social conformity may

476   also cause some chimpanzees to opt for a less efficient technique [34]. In sum, while we

477   showed consistency between attributed prior knowledge and choice in the experiment, our

478   results suggest that context and individual differences interact with each other and determine

479   an individual's choice of tool material, even in controlled situations [66].

480

481   Overall, these results provide, to our knowledge, the first evidence that wild chimpanzees can

482   switch from an older, less efficient variant towards a newer, more efficient, socially learned

483   technique. Whether or not moss-spongers preferentially chose moss because they understood

484   and compared the physical properties of the two materials seems very plausible but can

485   ultimately not be decided by our data. While it is possible that experience with moss led to an

486   understanding that moss is more efficient than leaves, moss-spongers may have simply

487   become more familiar with moss compared to other chimpanzees, such that differences in

488   habits were ultimately responsible for our findings. We do not find this a very strong

489   argument because all individuals, including the moss-spongers, continued to use leaf-sponges

490   regularly outside the context of the clay-pit over the years following the appearance of moss-

491   sponging, predicting that all subjects should have chosen leaves in the experiment.

492

493   In sum, our findings are consistent with the interpretation that the innovation and social

494   spread of moss-sponging effectively led to the formation of a tool-related cultural subgroup in

495   the Sonso community. This outcome may be based on a cognitive ability to perceive and

496   compare the functional properties and efficacy of tools. Cognitively 'less demanding'

497   explanations, for example that chimpanzees simply chose the more locally abundant material,

498   were ruled out by our experiment, which controlled for the availability of tool materials. Our

499   data further highlight a potential role of efficiency as a driver of cultural evolution, insofar as

500   more efficient traits are favoured and eventually come to dominate, while less efficient traits

501   are neglected and eventually abandoned. In our case, one reason why moss-sponging did not

502   spread as much as its efficiency suggested might be the mere lack of available resources.

503   There is no doubt ecological factors generally have a strong influence on the emergence and

504   maintenance of cultural behaviour [64]. The Sonso chimpanzees had been observed for over

505   20 years before moss-sponging appeared, with dozens of chimpanzees visiting the swamp

506   forest but no one innovating the behaviour before 2011. One explanation for this is that other

507   nutrient resources, such as *Raphia* pith, became less abundant due to human activities, forcing

508   chimpanzees to look for alternative sources, such as mineral-rich water found in clay-pits

509   [57]. Moss-sponges then spread socially in a subgroup of the current generation of

510   chimpanzees, who adopted the more efficient form compared to the ancestral trait. It will be

511   interesting to see how new generations of Sonso chimpanzees, regularly exposed to moss-

512   sponging demonstrators, magistrate between the old tradition, leaf-sponging, and the more

513   recent tradition, moss-sponging, in tool-assisted drinking contexts.

514

515   **Data availability**

516   All data and code used in this study are available in the supplementary materials.

517

518   **Acknowledgements**

525

References

1.   Aplin L.M., Farine D.R., Morand-Ferron J., Cockburn A., Thornton A., Sheldon B.C. 2015 Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538-541.

2.   Boogert N.J., Giraldeau L.-A., Lefebvre L. 2008 Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour* **76**, 1735-1741.

3.   Alem S., Perry C.J., Zhu X., Loukola O.J., Ingraham T., Søvik E., Chittka L. 2016 Associative Mechanisms Allow for Social Learning and Cultural Transmission of String Pulling in an Insect. *PLOS Biology* **14**(10), e1002564.

4.   Ladds Z., Hoppitt W., Boogert N.J. 2017 Social learning in otters. *Royal Society Open Science* **4**(8). (doi:10.1098/rsos.170489).

5.   Whiten A., Goodall J., McGrew W.C., Nishida T., Reynolds V., Sugiyama Y., Tutin C.E.G., Wrangham R.W., Boesch C. 1999 Cultures in chimpanzees. *Nature* **399**(6737), 682-685.

6.   Tennie C., Call J., Tomasello M. 2009 Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B* **364**, 2045-2415.

7.   Boyd R., Richerson P.J. 1996 Why culture is common but cultural evolution is rare. *Proceedings of the British Academy* **88**, 77-93.

8.   Dean L.G., Vale G.L., Laland K.N., Flynn E., Kendal R.L. 2014 Human cumulative culture: A comparative perspective. *Biol Rev Cambridge Philosophic Soc* **89**, 284-301.

9.   Brewer J., Gelfand M., Jackson J.C., MacDonald I.F., Peregrine P.N., Richerson P.J., Turchin P., Whitehouse H., Wilson D.S. 2017 Grand challenges for the study of cultural evolution. *Nature Ecology Evolution* **1**, 0070. (doi:10.1038/s41559-017-0070).

549   10.   Lynch A., Baker A.J. 1993 A Population Memetics Approach to Cultural-Evolution in

550   Chaffinch Song - Meme Diversity within Populations. *Am Nat* **141**, 597–620.

551   11.   Filatova O.A., Burdin A.M., Hoyt E. 2013 Is killer whale dialect evolution random?

552   *Behav Processes* **99**, 34–41.

553   12.   Schofield D.P., McGrew W.C., Takahashi A., Hirata S. 2018 Cumulative culture in

554   nonhumans: overlooked findings from Japanese monkeys? *Primates* **59**(2), 113-122.

555   (doi:10.1007/s10329-017-0642-7).

556   13.   Whiten A. in press A second inheritance system: The extension of biology through

557   culture. *Royal Society Interface Focus*.

558   14.   McGrew W.C. 2017 Ourselves explained. *Human Ethology Bulletin* **3**, 141-144.

559   15.   Fehér O., Wang H., Saar S., Mitra P.P., Tchernichovski O. 2009 De novo

560   establishment of wild-type song culture in the zebra finch. *Nature* **459**, 564–568.

561   16.   Sasaki T., Biro D. 2017 Cumulative culture can emerge from collective intelligence in

562   animal groups. *Nature Communications* **8**, 15049. (doi:10.1038/ncomms15049).

563   17.   Reader S.M., Morand-Ferron J., Flynn E. 2016 Animal and human innovation: novel

564   problems and novel solutions. *Philosophical Transactions of the Royal Society of London B:*

565   *Biological Sciences* **371**(1690). (doi:10.1098/rstb.2015.0182).

566   18.   Yamamoto S., Yamakoshi G., Humle T., Matsuzawa T. 2008 Invention and

567   modification of a new tool use behavior: Ant-fishing in trees by a wild chimpanzee (*Pan*

568   *troglodytes verus*) at Bossou, Guinea. *American Journal of Primatology* **70**, 699-702.

569   19.   Whiten A., Goodall J., McGrew W.C., Nishida T., Reynolds V., Sugiyama Y., Tutin

570   C.E.G., Wrangham R.W., Boesch C. 2001 Charting cultural variation in chimpanzees.

571   *Behaviour* **138**, 1481-1516.

572   20.   Nishida T., Matsusaka T., McGrew W.C. 2009 Emergence, propagation or

573   disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: A

574   review. *Primates* **50**, 23-36.

575   21.   Hobaiter C., Poisot T., Zuberbühler K., Hoppitt W., Gruber T. 2014 Social network

576   analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLOS*

577   *Biology* **12**(9), e1001960.

578   22.   Nagell K., Olguin R.S., Tomasello M. 1993 Processes of Social-Learning in the Tool

579   Use of Chimpanzees (*Pan troglodytes*) and Human Children (*Homo sapiens*). *Journal of*

580   *Comparative Psychology* **107**(2), 174-186.

581   23.   Whiten A., McGuigan N., Marshall-Pescini S., Hopper L.M. 2009 Emulation,

582   imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical*

583   *Transactions of the Royal Society B: Biological Sciences* **364**, 2417-2428.

584   24.   Logan C.J., Breen A.J., Taylor A.H., Gray R.D., Hoppitt W.J.E. 2016 How New

585   Caledonian crows solve novel foraging problems and what it means for cumulative culture.

586   *Learn Behav* **44**, 18-28.

587   25.   Kenward B., Rutz C., Weir A.A.S., Kacelnik A. 2006 Development of tool use in New

588   Caledonian crows: inherited action patterns and social influences. *Animal Behaviour* **72**,

589   1329-1343.

590   26.   Caldwell C.A., Millen A.E. 2009 Social learning mechanisms and cumulative cultural

591   evolution: is imitation necessary? *Psychological Science* **20**, 1478-1483.

592   27.   Zwirner E., Thornton A. 2015 Cognitive requirements of cumulative culture: teaching

593   is useful but not essential. *Scientific Reports* **5**, 16781.

594   28.   Povinelli D.J. 2000 *Folk physics for apes: The chimpanzee's theory of how the world*

595   *works*. Oxford, OUP.

27

596   29.   Gruber T., Zuberbühler K., Clément F., van Schaik C.P. 2015 Apes have culture but

597   may not know that they do. *Frontiers in Psychology* **6**, 91. (doi:10.3389/fpsyg.2015.00091).

598   30.   Csibra G., Gergely G. 2011 Natural pedagogy as evolutionary adaptation.

599   *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 1149-1157.

600   31.   Sakura O., Matsuzawa T. 1991 Flexibility of wild chimpanzee nut-cracking behavior

601   using stone hammers and anvils: an experimental analysis. *Ethology* **87**, 237-248.

602   32.   Visalberghi E., Adessi E., Truppa V., Spagnoletti N., Ottoni E., Izar P., Fragaszy D.

603   2009 Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*

604   **19**, 213-217.

605   33.   Sanz C.M., Call J., Morgan D. 2009 Design complexity in termite-fishing tools of

606   chimpanzees (Pan troglodytes). *Biol Lett* **5**, 293–296.

607   34.   Luncz L.V., Sirianni G., Mundry R., Boesch C. 2018 Costly culture: differences in

608   nut-cracking efficiency between wild chimpanzee groups. *Animal Behaviour* **137**, 63-73.

609   (doi:https://doi.org/10.1016/j.anbehav.2017.12.017).

610   35.   Hunt G.R., Gray R.D. 2003 Diversification and cumulative evolution in New

611   Caledonian crow tool manufacture. *Proceedings of the Royal Society B: Biological Sciences*

612   **270**, 867-874.

613   36.   Sugasawa S., Klump B.C., St Clair J.J.H., Rutz C. 2017 Causes and Consequences of

614   Tool Shape Variation in New Caledonian Crows. *Current biology* **27**(24), 3885-3890.e3884.

615   (doi:10.1016/j.cub.2017.11.028).

616   37.   St Clair J.J.H., Klump B.C., Sugasawa S., Higgott C.G., Colegrave N., Rutz C. 2018

617   Hook innovation boosts foraging efficiency in tool-using crows. *Nature Ecology & Evolution*

618   **2**(3), 441-444. (doi:10.1038/s41559-017-0429-7).

619	38.	Manrique H.M., Gross A.N.-M., Call J. 2010 Great apes select tools on the basis of

620	their rigidity. *J Exp Psychol Anim Behav Process* **36**, 409–422.

621	39.	Lehner S.R., Burkart J.M., van Schaik C.P. 2011 Can captive orangutans (*Pongo*

622	*pygmaeus abelii*) be coaxed into cumulative build-up of techniques? *Journal of Comparative*

623	*Psychology* **125**, 446-455.

624	40.	Chappell J., Kacelnik A. 2002 Tool selectivity in a non-primate, the New Caledonian

625	crow (Corvus moneduloides). *Animal Cognition* **5**(2), 71-78.

626	41.	Yamamoto S., Humle T., Tanaka M. 2013 Basis for cumulative cultural evolution in

627	chimpanzees: Social learning of a more efficient tool-use technique. *Plos ONE* **8**(1), e55768.

628	42.	Davis S.G., Vale G.L., Schapiro S.J., Lambeth S.P., Whiten A. 2016 Foundations of

629	cumulative culture in apes: improved foraging efficiency through relinquishing and

630	combining witnessed behaviors in chimpanzees (Pan troglodytes). *Sci Rep* **6**, 35953.

631	43.	Gruber T., Singleton I., van Schaik C.P. 2012 Sumatran orangutans differ in their

632	cultural knowledge but not in their cognitive abilities. *Current Biology* **22**(23), 2231-2235.

633	(doi:10.1016/j.cub.2012.09.041).

634	44.	St Clair J.J.H., Rutz C. 2013 New Caledonian crows attend to multiple functional

635	properties of complex tools. *Philosophical Transactions of the Royal Society B: Biological*

636	*Sciences* **368**(1630). (doi:10.1098/rstb.2012.0415).

637	45.	Mann J., Stanton M.A., Patterson E.M., Bienenstock E.J., Singh L.O. 2012 Social

638	networks reveal cultural behaviour in tool-using dolphins. *Nature Communications* **3**, 980.

639	(doi:10.1038/ncomms1983).

640	46.	Laland K.N., Janik V.M. 2006 The animal cultures debate. *Trends in Ecology and*

641	*Evolution* **21**(10), 542-547.

642   47.   Newson L., Richerson P.J., Boyd R. 2007 Cultural evolution and the shaping of

643   cultural diversity. In *Handbook of cultural psychology* (eds. S. Kitayama, Cohen D.), pp. 454-

644   476. New York, NY, The Guilford Press.

645   48.   Matsuzawa T. 2003 Koshima monkeys and bossou chimpanzees: Long-term research

646   on culture in nonhuman primates. In *Animal Social Complexity* (eds. F. B. M. de Waal, Tyack

647   P.), pp. 374-387. Cambridge, MA, Harvard University Press.

648   49.   Bandini E., Tennie C. 2017 Spontaneous reoccurrence of "scooping", a wild tool-use

649   behaviour, in naïve chimpanzees. *PeerJ* **5**, e3814. (doi:10.7717/peerj.3814).

650   50.   Gruber T., Muller M.N., Strimling P., Wrangham R.W., Zuberbühler K. 2009 Wild

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

652   *Current Biology* **19**, 1806-1810.

653   51.   Reynolds V., Lloyd A.W., Babweteera F., English C.J. 2009 Decaying *Raphia*

654   *farinifera* palm trees provide a source of sodium for wild chimpanzees in the Budongo Forest,

655   Uganda. *PLoS ONE* **4**(7), e6194.

656   52.   Lamon N., Neumann C., Gruber T., Zuberbühler K. 2017 Kin-based cultural

657   transmission of tool use in wild chimpanzees. *Science Advances* **3**(4), e1602750.

658   53.   Gruber T., Muller M.N., Reynolds V., Wrangham R.W., Zuberbühler K. 2011

659   Community-specific evaluation of tool affordances in wild chimpanzees. *Scientific Reports* **1**,

660   128. (doi:10.1038/srep00128).

661   54.   Reynolds V. 2005 *The Chimpanzees of the Budongo Forest: Ecology, Behaviour, and*

662   *Conservation*. Oxford, Oxford University Press.

663   55.   Songok J., Salminen P., Toivakka M. 2014 Temperature effects on dynamic water

664   absorption into paper. *Journal of Colloid and Interface Science* **418**, 373-377.

665   (doi:https://doi.org/10.1016/j.jcis.2013.12.017).

666   56.   Biro D., Sousa C., Matsuzawa T. 2007 Ontogeny and cultural propagation of tool use

667   by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In

668   *Cognitive development in chimpanzees* (eds. T. Matsuzwa, M. Tomonaga, Tanaka M.), pp.

669   476-508, Springer.

670   57.   Reynolds V., Lloyd A.W., English C.J., Lyons P., Dodd H., Hobaiter C., Newton-

671   Fisher N., Mullins C., Lamon N., Schel A.-M., et al. 2015 Mineral acquisition from clay by

672   Budongo Forest chimpanzees. *Plos ONE* **10**(7), e0134075.

673   58.   R_Development_Core_Team. 2015 R: A language and environment for statistical

674   computing. In *R Foundation for Statistical Computing at <http://wwwr-projectorg/>* (

675   59.   Bates D., Maechler M., Bolker B., Walker S. 2014 lme4: Linear mixed-effects models

676   using Eigen and S4. R package version 1.1-7. (

677   60.   Dobson A.J. 2002 *An Introduction to Generalized Linear Models*, Chapman and Hall.

678   61.   Ruxton G.D., Neuhäuser M. 2010 When should we use one-tailed hypothesis testing?

679   *Methods Ecol Evol* **1**(2), 114-117. (doi:doi:10.1111/j.2041-210X.2010.00014.x).

680   62.   Nakagawa S., Schielzeth H. 2010 Repeatability for Gaussian and non-Gaussian data: a

681   practical guide for biologists. *Biol Rev Cambridge Philosophic Soc* **85** 935–956.

682   63.   Stoffel M.A., Nakagawa S., Schielzeth H. 2017 rptR: repeatability estimation and

683   variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol* **8**,

684   1639–1644.

685   64.   Gruber T., Zuberbühler K., Neumann C. 2016 Travel fosters tool use in wild

686   chimpanzees. *eLife*, 10.7554/eLife.16371.

687   65.   Sanz C.M., Morgan D.B. 2013 Ecological and social correlates of chimpanzee tool

688   use. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*

689   **368**(1630). (doi:10.1098/rstb.2012.0416).

690   66.   Gruber T. 2016 Great apes do not learn novel tool use easily: Conservatism, functional

691   fixedness, or cultural influence? *International Journal of Primatology* **37**(2), 296-316.

692   (doi:10.1007/s10764-016-9902-4).

693

694

695   **Legends**

696

697   **Figure 1. Two examples of sponge tools manufactured during a log experiment.** a) Leaf-

698   sponge made of *Alchornea floribunda*, b) moss-sponge made of *Orthostichella welwitschii*.

699

700   **Figure 2. Comparison of absorbency for natural and experimental sponges**. Each square

701   represents the mean volume absorbed by one sponge across 10 repeated measurements.

702   Circles represent model predictions. Lines are 95% confidence intervals.

703

704   **Figure 3. Comparison of moss and leaf manufacturing (left) and deployment (right)**

705   **time.** Raw data are shown as squares and model estimates as circles with 95% confidence

706   intervals.

707

708   **Figure 4. Availability of sponge material across forest types.**

709

710   *Ethics Statement*

711   Field protocols were reviewed and permission to conduct this research was given by the

712   Uganda Wildlife Authority (UWA), the Ugandan National Council for Science and

713   Technology (UNCST), the National Forestry Authority (NFA), and the resident veterinary

714   section at Budongo Conservation Field Station (BCFS).

715

716   *Funding statement*

717   This work was funded by the European Research Council (FP7/2007-2013/ERC n°283871)

718   and the Swiss National Science Foundation (grants 310030_143359 to KZ; CR13I1_162720

719   and P300PA_164678 to TG).

720

721   *Competing interests statement*

722   We declare we have no competing interests

723

724   *Author contributions*

725   Data collection: N.L. and J.G.; statistical analysis: C.N. and N.L.; experimental design: N.L.,

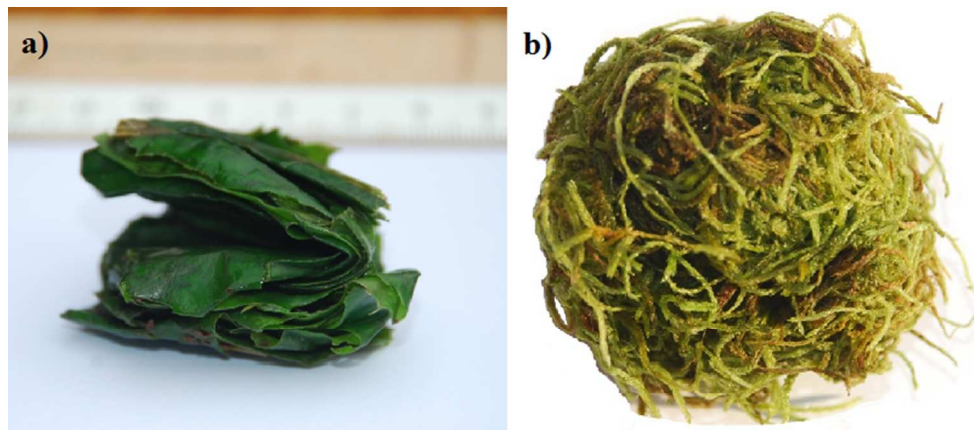726   T.G., and K.Z.; manuscript writing: N.L., T.G., C.N., and K.Z.; funding: K.Z.

Figure 1. Two examples of sponge tools manufactured during a log experiment. a) Leaf-sponge made of Alchornea floribunda, b) moss-sponge made of Orthostichella welwitschii.
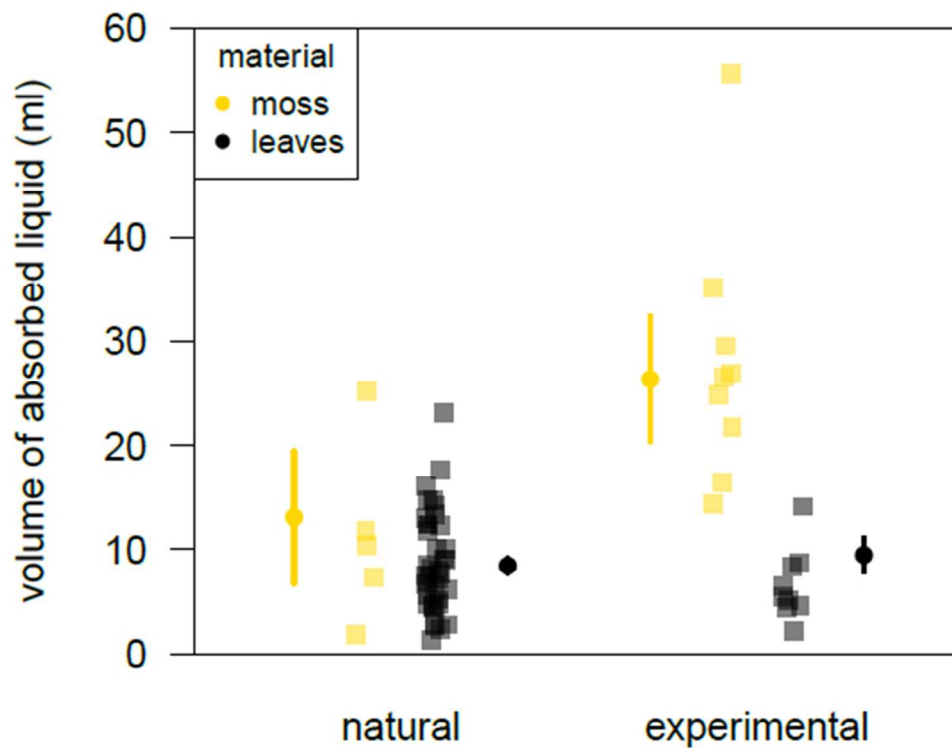
69x29mm (300 x 300 DPI)

Figure 2. Comparison of absorbency for natural and experimental sponges. Each square represents the mean volume absorbed by one sponge across 10 repeated measurements. Circles represent model predictions. Lines are 95% confidence intervals.
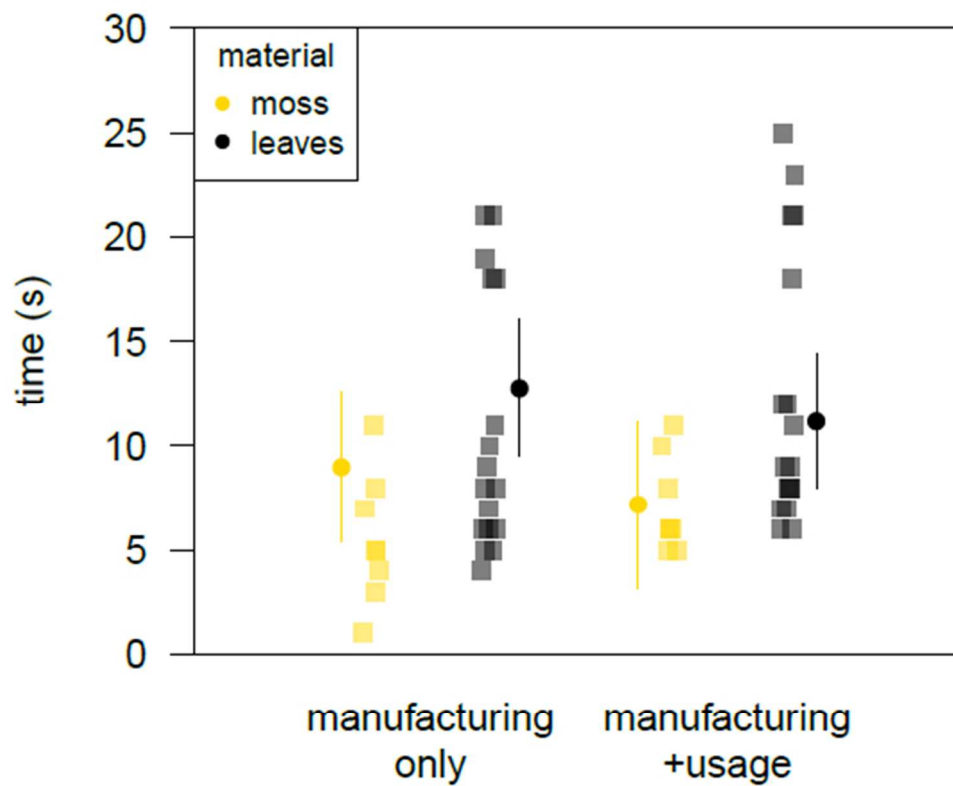
47x35mm (300 x 300 DPI)

Figure 3. Comparison of moss and leaf manufacturing (left) and deployment (right) time. Raw data are shown as squares and model estimates as circles with 95% confidence intervals.
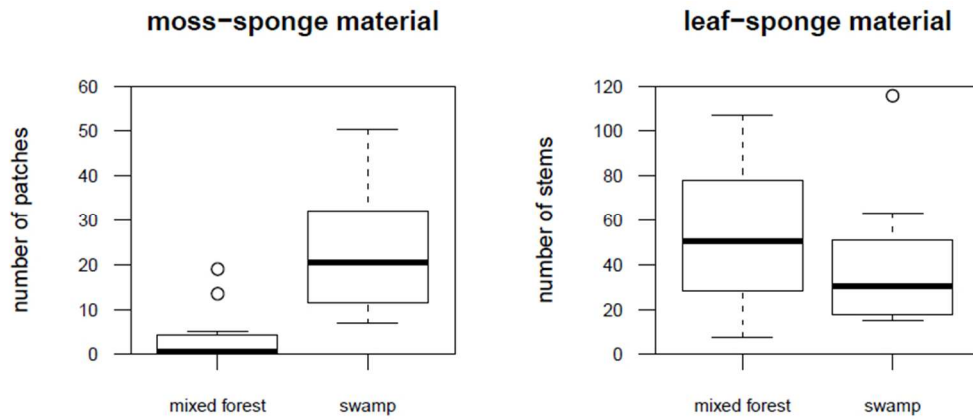
47x38mm (300 x 300 DPI)

Figure 4. Availability of sponge material across forest types.

71x30mm (300 x 300 DPI)