

1 **Necessity creates opportunities for chimpanzee tool use**

2

3 Charlotte Grund^{1,2*}, Christof Neumann¹, Klaus Zuberbühler^{1,2,3}, Thibaud Gruber^{2,4,5*}

4

5 ¹Department of Comparative Cognition, University of Neuchâtel, 2000 Neuchâtel, Switzerland

6 ²Budongo Conservation Field Station, Masindi, Uganda;

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

8 ⁴Swiss Center for Affective Sciences, University of Geneva, 1211 Geneva, Switzerland;

9 ⁵Department of Zoology, University of Oxford, OX1 3PS, UK

10

11 Correspondence to: T. Gruber (thibaud.gruber@gmail.com) &

12 C. Grund (grund.charlotte@gmx.de)

13

14

15 SHORT TITLE: Ecology of chimpanzee tool use

16

17

18

19

20

21

22 ABSTRACT

23 While social transmission mechanisms of animal cultures are well studied, little is known about the
24 origins of behavioural innovations, even in established tool-users such as chimpanzees. Previous
25 work has suggested that wild chimpanzees are especially prone to engaging with tools during
26 extended periods of low food availability and after long travel, supporting the hypothesis that
27 cultural innovation is facilitated by necessity revealing opportunities. Here, we tested this
28 hypothesis with a field experiment that directly compared subjects' immediate variation in measures
29 of current energy balance with their interest in a novel foraging problem, liquid honey enclosed in
30 an apparatus accessible by tool use. We found that the previous distance travelled directly predicted
31 subjects' manipulations of both the apparatus and the tool, while previous feeding time was
32 negatively correlated to manipulation time. We conclude that 'necessity' augments chimpanzees'
33 likelihood of engaging with ecological 'opportunities', suggesting that both factors are scaffolding
34 foraging innovation in this and potentially other species.

35

36 Energy constraints are a major driver in behaviour evolution (Aiello and Wheeler, 1995). This is
37 especially true for habitats in which ecological conditions fluctuate, which tends to increase the
38 capacity for behavioural plasticity (Clavel et al., 2011; Sol et al., 2005). One manifestation of
39 behavioural plasticity is the ability to ‘innovate’ (Reader and Laland, 2001), that is, to flexibly
40 respond to environmental changes with novel behavioural patterns. Particularly relevant are
41 innovations that enhance foraging efficiency and the ability to cope with food shortages (Morand-
42 Ferron et al., 2011; Sol et al., 2005). Although rainforests are considered relatively stable habitats
43 with high levels of fruit production (Marshall and Wrangham, 2007), fruiting patterns can fluctuate
44 considerably, which can result in temporary food shortages with corresponding selection pressures
45 on species that strongly depend on fruit (Gruber, 2013; Gruber et al., 2012; Janmaat et al., 2006;
46 Janmaat et al., 2012; Lee and Moura, 2015; Wrangham et al., 1991; Yamakoshi, 1998).

47 Although chimpanzees (*Pan troglodytes*) are typical rainforest dwellers (Boesch and Boesch-
48 Achermann, 2000) they are also found in the savannah (Pruetz and Bertolani, 2009), suggesting that
49 they have been under selection pressure to deal with ecological oscillations. One possible adaptation
50 is their fission-fusion social system (Moscovice et al., 2007), which allows group size and activity
51 patterns to be adjusted to changes in food availability (Chapman et al., 1995), which minimises
52 travel costs (N’guessan et al., 2009). Chimpanzees are also known for their behavioural diversity
53 and flexibility (Whiten et al., 1999) and the fact that they are habitual innovators (Hobaiter et al.,
54 2014; Reader and Laland, 2001) with a large repertoire of foraging-related tool use behaviours to
55 access otherwise inaccessible food resources (Sanz and Morgan, 2013). This has been compellingly
56 illustrated by large differences in behavioural profiles across chimpanzee communities, including
57 tool use (Whiten et al., 1999).

58 In some chimpanzee communities, tool use is observed during periods of food shortage, suggesting
59 that it serves as a backup strategy, similar to consuming ‘fall-back’ foods (Bulindi: McLennan,
60 2015; Kahuzi: Yamagiwa and Basabose, 2009; Bossou: Yamakoshi, 1998). In a meta-analysis on
61 primate innovation, Reader and Laland (2001) found that in 47% (N=36) of all relevant studies

62 “innovation was prompted by ecological challenges, such as periods of food shortage, dry seasons,
63 or habitat degradation”. Innovation in chimpanzees and other animals, in this view, is borne out of
64 the need to acquire nutrients, as stated by the ‘necessity’ hypothesis (Fox et al., 1999). Further
65 support for the necessity hypothesis comes from energy-deprived guppies that were more likely to
66 locate novel food sources than control animals (Laland and Reader, 1999). Additionally, Sol et al.
67 (2005) found that foraging innovations in wild bird species were more common in the winter, again
68 suggesting that energy needs are an important driving factor. Similarly, in common mynas
69 (*Acridotheres tristis*), individuals with high feeding motivation (and low neophobia) were more
70 likely to engage and solve an experimental task that required operations than controls (Sol et al.,
71 2012). Necessity also appears to have an effect within groups of animals, since subordinates often
72 experience higher necessity than dominant individuals due to reduced access to resources, and this
73 tends to make them better innovators (Griffin and Guez, 2014; Reader and Laland, 2001).

74 However, there are alternative hypotheses to explain the presence of tool use. Specifically, some
75 studies failed to find significant correlations between tool behaviour and reduced food availability
76 (Koops et al., 2013; Sanz and Morgan, 2013), suggesting that other mechanisms may be at work,
77 alternatively or simultaneously. One such idea, the ‘opportunity’ hypothesis, proposes that
78 behavioural innovations, such as tool use in chimpanzees, are better explained by individuals being
79 exposed to specific environmental conditions, specifically encountering a resource in the presence
80 of potential tool material (Koops et al., 2014). In Sumatran orang-utans (*Pongo abelii*), for instance,
81 differences in tool-based insectivory correlate with site differences in insect abundance, but not with
82 changes in the availability of preferred foods (Fox et al., 2004). Another example is the
83 chimpanzees in the Goulougo Triangle (Republic of Congo) where no increase in stick-based
84 foraging was observed during periods of fruit shortage (Sanz and Morgan, 2013).

85 Beyond opportunity and necessity, additional hypotheses have been discussed. For example, Rutz
86 and St Clair (2012) have proposed the 'relative profitability hypothesis' to explain disparities in tool
87 use within and between crow species. Here, the idea is that tool use occurs if it is relatively more

88 profitable than alternative non-tool based foraging strategies. In sum, despite large interest, the
89 current literature is inconclusive about what drives behavioural innovations and the emergence of
90 tool use in animals.

91 The Sonso chimpanzee community is interesting to test hypotheses of tool innovation and use, as
92 members of this group do not use tools to extract food other than liquids, in contrast to other well-
93 studied chimpanzee communities (Whiten et al., 1999). In previous experiments, we let individuals
94 encounter natural liquid honey, presented in an artificial cavity dug in a large, fallen tree, designed
95 to foster tool use (Gruber et al., 2009). Strikingly, some individuals manufactured a tool, a leaf-
96 sponge to access the honey, but there was much variance in how long individuals engaged with the
97 task and whether they used a tool (Gruber et al., 2011). Leaf-sponges are used community-wide to
98 access water from tree holes, puddles and clay pits, suggesting that the honey-sponging individuals
99 applied an “old solution to a new problem” (Kummer and Goodall, 1985).

100 Subsequent research on the same community showed that periods with much travelling and low
101 fruit consumption resulted in extended problem-solving efforts with different honey-provisioning
102 devices (Gruber et al., 2016), suggesting that an unfavourable energy balance increases
103 chimpanzees’ interest in difficult, out-of-reach food resources. Interest was highest following
104 extended unfavourable conditions, while actual tool use was best predicted by extensive travel
105 effort before an experiment. Although relevant, this study was hampered by the fact that estimates
106 of both travel and feeding efforts were only indirect and patchy, as they were assessed via long-term
107 data from behavioural scans. The relative paucity of scans also prevented us from investigating
108 immediate effects on explorative and tool interaction behaviour although such data are crucial for
109 theories of tool innovation.

110 In this study, we readdressed the role of necessity and opportunity in chimpanzee tool use and
111 cultural behaviour more generally by experimentally exposing subjects in a standardised way to a
112 foraging problem, while simultaneously measuring participants’ immediate prior travel effort and
113 food intake. To this end, we followed subjects during their daily foraging, sampling their feeding

114 activities and movements in their home range over a roughly 24h period before presenting them
115 with a portable apparatus that contained encased liquid honey. Although we could not directly
116 measure metabolic data (or ‘energy balance’) we were able to assess them indirectly via food intake
117 and physical activity (e.g. Hoyt et al., 2006). This protocol thus allowed us to relate the energy
118 balance of subjects to their interest in problem-solving behaviour when encountering artificially
119 provided honey. As in previous experiments, subjects had to engage with a specific mechanism to
120 access the honey, this time by manipulating a stick in a predetermined way (fig. 1). Based on
121 previous results (Gruber et al. 2016), we expected that individuals who had travelled more and/or
122 fed less over the previous 24h period than other individuals would engage more with both the
123 apparatus and the tool when encountering the experimentally-provided feeding opportunity.

124

125 METHODS

126 Study site and community

127 The study was conducted with the Sonso community whose home range includes the ‘Budongo
128 Conservation Field Station’ (Reynolds, 2005) in Western Uganda from January 2016 to May 2016.
129 The Sonso chimpanzees have previously taken part in other field experiments involving encased
130 honey (Gruber, 2016; Gruber et al., 2012; Gruber et al., 2016).

131

132 Experimental apparatus

133 The experimental device consisted of a 40 cm long natural wooden log with a 25 cm radius and a 17
134 cm deep cavity that could carry a plastic receptacle filled 10cm deep with liquid honey (fig. 1). The
135 only possible way to access the honey was by operating a stick that protruded through a 1 cm wide
136 hole in the cavity’s lid. The stick could be freely moved within the cavity, which allowed subjects
137 to extract honey by pulling the stick out from the honey pool. However, as the stick was blocked at
138 one end it was not possible to remove it completely from the apparatus. This made it impossible for

139 subjects to discard the stick and to search for alternative tool solutions, as they have done in
140 previous experiments (for a review, see Gruber, 2016). Hence, the current device differed from
141 previously used ones in the diameters of the hole and stick, as well as the fact that the stick was
142 permanently connected to the device, which prevented subjects from exploring other solutions. This
143 allowed us to directly compare motivation of subjects. Conversely, the lack of pay-off could also
144 drive them away quickly if they were not successful in obtaining honey (see results).

145

146 Subjects

147 At the time of the study, the Sonso community consisted of 68 individuals (12 adult males and 23
148 adult females with their offspring). We carried out focal animal follows on N=6 individuals selected
149 due to previously demonstrated interest in similar experiments (2009 – 2015, supplemental table
150 S1; see also Gruber et al. 2016). Prior to these experiments, none of the subjects was ever observed
151 using a stick in a natural or experimental foraging context. Since we did not aim to influence party
152 composition, subjects never encountered the device alone, such that N=16 further individuals
153 participated in the experiment, in addition to the N=6 subjects. All encounters were filmed and
154 analysed by CG with BORIS v 2.981 software (Friard and Gamba, 2016). Behavioural activity and
155 interactions of individuals were coded following a predefined ethogram (supplementary table S2).

156

157 Experimental design

158 To investigate the relationship between travel distance, foraging success and propensity to innovate,
159 we conducted our field experiment with the following design. Each trial lasted two days (fig. 2). On
160 day 1 we located one of the six focal animals in the morning and tried to follow it until it nested in
161 the evening ('day 1 focal follows'). On day 2, we localised the same individual early in the morning
162 and continued to follow it until a good opportunity for an experimental trial arose ('day 2 focal
163 follows'). During all focal follows, GPS data were collected using a GARMIN 64s, while
164 behavioural data were collected using continuous focal animal sampling (Altmann, 1974). For every

165 feeding event, we noted the type of food consumed (fruit, leaves, flowers, bark, wood, meat, termite
166 soil, others) and (whenever possible) the food species.

167

168 To calculate travel effort and feeding behaviour prior to an experiment, we first determined the
169 subject's travel speed (number of metres travelled per 1 hour of observation time) and the
170 proportion of time it spent feeding (feeding time per 1 hour of observation time) on day 1. We
171 subsequently extrapolated the obtained travel speeds and feeding proportions to 10 hours (fig. 2;
172 8am – 6pm), resulting in a given subject's 'day 1 feeding time and travel distance'. The experiment
173 was carried out on day 2 at different times, depending on opportunities (range 07:16 – 13:38 local
174 time). As a consequence, observation times on day 2 varied accordingly (average 3.5 h). For better
175 comparability, we used the average observation time to calculate the 'day 2 feeding time and travel
176 distance' of each subject, extrapolating its day 2 travel distances and feeding proportions to 3.5 h.
177 Overall, travel distance and feeding behaviour were assessed over both days by adding the
178 calculated travel distances and feeding times of day 1 and day 2, referred to as 'estimated travel
179 effort' and 'estimated feeding time', respectively. Once a subject was given the opportunity to
180 interact with the apparatus other individuals were usually also present, such that several individuals
181 could sometimes be tested during the same trial. We analysed their behaviours separately, provided
182 individuals had unconstrained access to the apparatus.

183

184 Once a subject encountered the apparatus on day 2, we recorded its behaviour on video. The
185 subject's behaviour was subsequently coded by CG. First, we calculated the 'device engagement
186 time' as an expression of an individual's motivation to access the encased honey (supplementary
187 table S2). 'Device engagement time' included all the subject's physical contacts with the apparatus,
188 including licking leaked honey, touching the apparatus and licking the fingers, or manipulating the
189 apparatus or stick. From this, we then extracted the 'stick touching time' as an expression of an
190 individual's propensity to engage with the only suitable tool, a precondition to successfully solving

191 the task. Engagement with the log or stick was considered as terminated when the individual let go
192 of the apparatus or tool and left the experimental setup. We managed to conduct a total of N=16
193 successful trials over a period of 3.5 months between January and May 2016, involving N=22
194 individuals, some of which encountered the log more than once (see table S3). From these trials, we
195 managed to extract N=8 trials for which we also had focal follow data (see below).

196

197 Statistical analyses

198 We conducted focal follows for N=6 individuals, who subsequently contributed to N=8
199 experimental trials, i.e. providing both data on previous travel effort and feeding history and
200 subsequent performance at the apparatus. This resulted in a final dataset of N=9 datapoints because
201 in one of eight experimental trials we had focal data on the previous behaviour of two present
202 individuals, KC and KX. We entered them as separate data points since both subjects took turns in
203 accessing the device without any visible signs of tension.

204 Given the low sample size, we analysed the data with univariate, non-parametric procedures instead
205 of generalized linear mixed models. We carried out two sets of analyses. In the results section, we
206 used the full N=9 dataset whereas in the supplement we present additional analyses with each
207 individual represented only once.

208

209 RESULTS

210 Behavioural responses

211 In eight of 16 experimental trials we could estimate the previous travelling and feeding activities of
212 at least one of the participating individuals (for one trial we had previous focal data on two
213 individuals; range of individuals with or without focal data engaging with the device in these eight
214 experimental trials: 0–4, see table S3). The mean engagement time with the apparatus in the eight
215 experiments was 10s (range: 1–61s, including individuals with and without focal data). In seven of

216 the eight trials, engagement included some form of stick contact by one or two individuals (see
217 table S3), mainly touching and pulling the stick. Mean stick interaction time during instances of log
218 engagement in the eight experiments was 11s (range: 0–45s, including individuals with and without
219 focal data). In two cases stick use was successful insofar as subjects managed to extract honey (KB,
220 KU; table S3). Here, both individuals pulled out the stick to lick honey pasted to its lower end (fig.
221 3), which led to the highest stick touching times (KU: 31s; KB: 45s) of all trials. Remarkably,
222 however, no individual solved the problem in the sense that it showed repeated, controlled up-and-
223 down movements of the stick by hand (or foot) to access the honey.

224

225 Travel and feeding history and interest in honey

226 For N=9 cases we were able to estimate the subjects' previous travel effort and feeding time as part
227 of N=8 experimental trials (table 1). 'Estimated travel effort' ranged from 1.0 – 4.4km whereas
228 'estimated feeding time' ranged from 1.8 – 11.0h. Mean device engagement time was 19s (range:
229 0–50s) and mean stick touching time was 13s (range 0–45s; see table 1).

230

231 Relationship between previous energy expenditure and interest in device

232 Individuals showed increased interest in the apparatus with increased distance travelled before a
233 trial (Spearman's rank correlation $\rho = 0.85$, N = 9 trials, fig. 4, table S5). In contrast, 'estimated
234 feeding time' was weakly negatively correlated with 'engagement time' with the device
235 (Spearman's rank correlation $\rho = -0.49$, N = 9 trials, fig. 4, table S5).

236

237 Additionally, we found that subjects interacted more with the stick following a longer compared to
238 a shorter estimated distance travelled (median travel distance with stick interaction: 3.4km; N = 6;
239 without stick interaction: 2.3km; N = 3; Mann Whitney *U* test, $W = 0$, $N_1 = 3$, $N_2 = 6$; fig. 5). There
240 was no major difference in estimated feeding time between experiments with and without stick

241 interaction (Mann Whitney U test, $W = 12.5$, $N_1 = 3$, $N_2 = 6$), although subjects that spent more
242 time feeding were less likely to interact with the stick (fig. 5).

243

244 DISCUSSION

245 In the current study we investigated whether tool use in wild chimpanzees is a direct consequence
246 of necessity (in terms of food intake and energy spent during travel) or opportunity (in terms of
247 encountering difficult-to-access high quality food). In particular, we were interested in the short-
248 term effects of individuals' travel and foraging histories on their subsequent interest in a task that
249 required a tool-based behavioural innovation. We investigated this using a portable apparatus that
250 supplied high quality food, liquid honey, to subjects in a standardised way. Based on a previous
251 analysis of experimental and long-term observational data (Gruber et al., 2016), we predicted that
252 unfavourable energy balances (i.e., high travel costs, low feeding time) would foster high interest in
253 the device and the proposed tool, and, as a consequence, increase the probability of a behavioural
254 innovation.

255 To this end, we collected focal data from $N=6$ subjects over a continuous period covering much of
256 two consecutive days. The relationship between our experimental data and the behavioural data
257 acquired for each subject suggested that extended travel and low feeding time prior to encountering
258 a difficult feeding opportunity indeed favoured both exploratory and tool use behaviour. Based on
259 our results and previous studies, we first discuss possible drivers of behavioural innovation in wild
260 chimpanzees and then propose a new model of chimpanzee foraging innovation, which scaffolds
261 opportunity and necessity with one another (see also Rutz & St Clair, 2012 for a similar framework
262 in New Caledonian crows).

263

264 **Drivers of behavioural innovations in wild chimpanzees**

265 Chimpanzees are widely considered the most 'cultural' of all non-human animals, evidenced by

266 behavioural profiles that differ drastically between communities (Whiten et al., 1999). Although
267 much is known about the social learning mechanisms that favour the spread of novel behaviours in
268 chimpanzees (Whiten et al., 2009), very little is known about the mechanisms underlying behaviour
269 innovations (Gruber et al., 2010; Reader et al., 2016). For chimpanzees, the current literature has
270 focussed on two main scenarios to explain the origins of innovations: opportunity and necessity
271 (Koops et al., 2014). The ‘opportunity hypothesis’ predicts that animals acquire novel behaviours,
272 such as tool use, because they encounter the key ingredients in spatio-temporally favourable
273 conditions. The ‘necessity hypothesis’, in contrast, predicts that animals become more motivated to
274 solve problems if their favourite staple food is lacking, which forces them to meet their nutritional
275 needs from alternative, but typically more difficult to access (e.g. embedded) food sources. There is
276 evidence in support of both hypotheses as causal factors of tool innovations, which has triggered an
277 ongoing debate in the literature.

278 Our study was designed to address this impasse and our results suggest that both necessity and
279 opportunity can play a role in interlinked ways, a proposal that, surprisingly, has not received much
280 attention so far (but see Rutz & St Clair, 2012). We found that wild chimpanzees that travelled
281 more before an experiment spent more time trying to access high value food and were more likely
282 to engage with a provided tool the following day than individuals that travelled less, possibly due to
283 the fact that they had spent less energy. Persistence in problem solving is widely thought to be
284 essential for foraging innovations in animals (Benson-Amram and Holekamp, 2012; Cauchard et
285 al., 2013). In the present study, we also found that engagement time was above average on trials
286 when subjects successfully retrieved honey using the stick. Necessity, in other words, may drive
287 individuals to explore novel food sources and increase their willingness to devote time to solving
288 unfamiliar problems. This will increase chances of behaviour innovations through basic trial-and-
289 error or more complex processes, but only if a relevant ecological opportunity is in place.

290 We assumed that travel effort and foraging success have metabolic consequences on what we called
291 ‘energy balance’. Previous studies in humans (e.g. Hoyt et al., 2006; Plasqui and Westerterp, 2004)

292 and nonhuman animals (see review in Asensio et al., 2009) have linked physical activity with
293 energy balance, despite the fact that the relationship is complex and depends on additional socio-
294 ecological factors (Clutton-Brock and Janson, 2012; Pontzer, 2017). For instance, individuals differ
295 in energy requirements depending on their age/sex class or reproductive state. Moreover, quality
296 and size of food patches differ throughout a home range, whereas the size of the travel party will
297 determine the amount of travel effort necessary to obtain sufficient energy (Asensio et al., 2009).
298 For example, N'guessan et al. (2009) found a negative relation between food availability and
299 feeding time because chimpanzees travelled longer distances while increasing feeding time during
300 periods of poor food availability. Other studies also suggest that chimpanzees increase foraging
301 efforts during periods of food scarcity (Doran, 1997; Murray et al., 2006). In contrast, in Bornean
302 orangutans (*Pongo pygmaeus*), travel significantly increased with feeding opportunities (defined as
303 the percentage of feeding trees in a given plot), despite the fact that the size of the ranging area
304 became smaller when fruit abundance increased (Wartmann et al., 2010). Reduced food availability
305 also has a direct connection to group size, down-regulating the foraging subgroups of a community
306 to a size that still allows the individual to forage efficiently (Asensio et al., 2009; Matsumoto-Oda,
307 2002). As a consequence, subgroup size can be positively correlated with travel time (e.g. long-tail
308 macaques, van Schaik et al., 1983) or food availability (e.g. chimpanzees, Anderson et al., 2002).
309 Although these are all important factors for more informed models of tool innovation and use, the
310 design of our study did not allow us to address any such social correlates of foraging behaviour.

311

312 **A model of behavioural innovation and spread**

313 Based on our findings and the current literature, we propose a three-step model for foraging-related
314 tool innovations and spread in chimpanzees, and possibly other animals more generally (fig. 6).
315 Step 1 describes the innovation process, fostered by both necessity and opportunity; step 2 describes
316 the social spread of an innovation; step 3 describes the maintenance or eventual disappearance of
317 the innovation within a group.

319 1) *Behavioural innovation*: Our hypothesis is that foraging-related innovations are directly
320 influenced by resource shortages that render current behavioural coping mechanisms and foraging
321 patterns less effective (Gruber, 2013). Based on previous work (e.g. Gruber et al., 2012; Gruber et
322 al., 2016), we assume that shortages are either sustained or acutely severe. As a result, individuals
323 are driven to explore alternative resources and, by doing so, they exploit new ecological
324 opportunities that are already present (but so far overlooked) or that have appeared recently because
325 of a change in their environment. Hard-to-access, well-protected, energy-rich foods are likely to be
326 of specific interest (e.g., nuts, larvae, honey, Ungar, 2007), a situation modelled by our experiment.
327 Our data suggest that unfavourable energy balances caused by reduced intake and/or high
328 expenditure increase individuals' motivation to access such a difficult-to-access, high-value food.
329 Necessity, in other words, increases the time and attention an individual directs towards ecological
330 opportunities (substrate and tool material) already present in their environments, and both factors
331 combined increase the likelihood of behavioural innovations. Necessity, in short, creates new
332 opportunities.

333 2) *Community-wide spread*: In our study, two individuals successfully operated the apparatus by
334 manipulating the stick in the correct way, although there was no indication that they learned the
335 novel tool use behaviour as they did not display the behaviour repeatedly. Yet, with more
336 opportunities to engage in trial-and-error exploration, these subjects may have acquired a
337 behavioural innovation that enabled them to access the novel food resource, which would give them
338 an advantage over others in their energy balance. Chimpanzees are remarkable social learners,
339 suggesting that behavioural innovations could spread quickly to other community members (Gruber
340 et al., 2015a; Lamon et al., 2017; Ramsey et al., 2007). If the new behaviour persists in the
341 community, it becomes part of the community's cultural profile, beyond the ecological context in
342 which it originated. If only parts of the community display the behaviour, the behavioural
343 innovation can also become part of a subculture, as previously demonstrated for moss-sponging in

344 the Sonso chimpanzee community (Lamon et al., 2018).

345 3) *Maintenance and disappearance*: Once subjects have learned socially to exploit a novel food
346 resource, there is no reason why its consumption should be restricted to particular periods of the
347 year, suggesting that ‘necessity’ is less relevant in its maintenance as long as ecological conditions
348 do not change. ‘Opportunity’, in contrast, is likely to continue playing a key role in maintenance.
349 For example, if there is a reduction in the availability of tool material or food resource, the
350 prediction is that the socially acquired behavioural innovation is likely to disappear again.
351 Disappearance is also predicted by necessity, especially if alternative foraging opportunities appear
352 and provide a stable food supply. Budongo Forest, for example, has been subjected to selective
353 removal of tropical hardwoods, which has benefitted various fig tree species whose fruits are
354 consumed by chimpanzees throughout most of the year (Reynolds, 2005). This finding has been
355 interpreted as a potential factor in the loss of stick use in the Budongo chimpanzees (reduced
356 ecological necessity, Gruber et al., 2012). In sum, both necessity and opportunity are likely factors
357 in the disappearance of socially learned behavioural innovations, mainly because of demonstrations
358 and social learning opportunities become less common, which interrupts the social transmission
359 process and leads to cultural loss (Gruber, 2013).

360

361 In line with previous findings, our field experiment indicates that chimpanzees’ propensities to
362 engage with foraging opportunities may be linked to unfavourable energy balances. While the
363 current study has focused on the relationship between ecological challenges and behavioural
364 innovations, additional factors need to be taken into account in the future. In addition to the social
365 factors already discussed above, individual variation in curiosity and persistence is likely to
366 influence how individuals respond to necessity, in addition to factors such as age, sex and social
367 rank, which are also known to influence performance in problem-solving (Gruber, 2016; Reader
368 and Laland, 2001). It may also be argued that the Sonso chimpanzees are unable to represent sticks
369 as a material basis for tools (see discussion in Gruber, 2016; Gruber et al., 2015b). Furthermore, the

370 natural availability of honey-providing beehives within the chimpanzees' home range is likely to
371 influence individual behaviour (Sanz and Morgan, 2013; Sommer et al., 2012). Future studies may
372 also want to provide more direct measures of energy balance, such as by tracking urinary C-peptide
373 levels (Emery Thompson et al., 2009). A drawback of our study is indeed that we did not have
374 physiological measures of energy balance, and had to rely on indirect ways to assess variation. A
375 combination of field experiments with physiological markers would be an important next step in
376 linking internal variables and tool use behaviour. We also acknowledge that we base our
377 conclusions in the current experiment on a small sample size, despite the fact that they confirm an
378 hypothesis drawn from a previously larger indirect study (Gruber et al., 2016). More work is thus
379 needed to disentangle how opportunity and necessity interact together to lead to tool use. In
380 particular, it may be that future work finds different patterns connecting these two factors (e.g. more
381 travel and/or less feeding lead to less engagement with a given opportunity). If this happens, an
382 exciting avenue of research will be to compare the various contexts that lead to these effects, to
383 understand how variations in the respective weight of each factor can influence tool use innovation.

384

385 In conclusion, experimental problem-solving tasks are a valuable way of assessing the propensity
386 for behavioural innovations in wild animals and can be used to investigate the role of necessity and
387 opportunity. Our experiment focused exclusively on a tool-operated mechanism, but it is also
388 important to explore non-tool based foraging tasks. First, comparing tool and non-tool-based
389 foraging tasks may allow isolating pressures that solely act on tool use. Second, non-tool based
390 tasks will also allow testing our model in other environments or with species that have developed
391 alternative strategies to cope with ecological pressures (Snaith and Chapman, 2008). Both tool and
392 non-tool-based experimental tasks will thus lead us to better understand the dynamic interactions
393 between opportunity and necessity in fostering behavioural innovation. It is also important to keep
394 in mind that the current ecological conditions observed by researchers may be different from the
395 conditions in which an innovation originated, suggesting that current conditions are more valuable

396 in understanding the maintenance of cultural behaviour than its origins. Foraging experiments, as
397 the one presented in this study, may provide insights into how rare situations can lead to novel
398 behaviour, which, if adaptive, may then spread to become established into a cultural repertoire.

399

400 DATA AVAILABILITY

401 All data are available either in the main manuscript or in the Supplemental Material online.

402

403 FUNDING

404 This work was funded by the European Research Council (FP7/2007-2013 / ERC grant number n°
405 283871) and the Swiss National Science Foundation (grant numbers 310030_143359 to KZ;
406 CR13II_162720, P300PA_164678 to TG).

407

408 ACKNOWLEDGMENTS

409 We thank UNCST and UWA for permission to conduct our research in Budongo Forest Reserve
410 and the Royal Zoological Society of Scotland for supporting BCFS. We thank all staff at BCFS for
411 assistance in the field. We thank two anonymous reviewers and the editor for their insightful
412 comments that contributed to enhance the quality of our article.

413

414

415 REFERENCES

- 416 Aiello LC, Wheeler P, 1995. The expensive-tissue hypothesis: the brain and the digestive system in human
417 and primate evolution. *Current Anthropology* 36:199-221.
- 418 Altmann J, 1974. Observational study of behavior: Sampling methods. *Behaviour* 49:227-267.
- 419 Anderson DP, Nordheim EV, Boesch C, Moermond TC, 2002. Factors affecting fission-fusion grouping in
420 chimpanzees in the Taï National Park, Côte d'Ivoire. *Behavioural diversity in chimpanzees and*
421 *bonobos* Cambridge: Cambridge University Press. p. 90-101.
- 422 Asensio N, Korstjens AH, Aureli F, 2009. Fissioning minimizes ranging costs in spider monkeys: a
423 multiple- level approach. *Behavioral Ecology and Sociobiology* 63:649- 659.
- 424 Benson-Amram S, Holekamp KE, 2012. Innovative problem solving by wild spotted hyenas. *Proc Biol Sci B*
425 *279:4087-4095*.
- 426 Boesch C, Boesch-Achermann H, 2000. *The chimpanzees of the Taï forest: Behavioural ecology and*
427 *evolution*. Oxford: Oxford University Press.
- 428 Cauchard L, Boogert NJ, Lefebvre L, Dubois F, Doligez B, 2013. Problem-solving performance is correlated
429 with reproductive success in a wild bird population. *Animal Behaviour* 85:19-26.
- 430 Chapman CA, Wrangham RW, Chapman LJ, 1995. Ecological Constraints on Group-Size - an Analysis of
431 Spider Monkey and Chimpanzee Subgroups. *Behavioral Ecology and Sociobiology* 36:59-70.
- 432 Clavel J, Julliard R, Devictor V, 2011. Worldwide decline of specialist species: toward a global functional
433 homogenization? *Frontiers in Ecology and the Environment* 9:222-228.
- 434 Clutton-Brock T, Janson C, 2012. Primate socioecology at the crossroads: Past, present, and future.
435 *Evolutionary Anthropology: Issues, News, and Reviews* 21:136-150. doi: doi:10.1002/evan.21316.
- 436 Doran D, 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping
437 patterns in Tai chimpanzees. *International Journal of Primatology* 18:183-206.
- 438 Emery Thompson M, Muller MN, Wrangham RW, Lwanga JS, Potts KB, 2009. Urinary C-Peptide tracks
439 seasonal and individual variation in energy balance in wild chimpanzees. *Hormones and Behavior*
440 *55:299-305*.
- 441 Fox EA, Sitompul AF, van Schaik CP, 1999. Intelligent tool use in wild Sumatran orangutans. In: S. Parker,
442 L. Miles, Mitchell A, editors. *The Mentality of Gorillas and Orangutans* Cambridge: Cambridge

443 University Press. p. 99-117.

444 Fox EA, van Schaik CP, Sitompul A, Wright DN, 2004. Intra- and interpopulational differences in orangutan
445 (*Pongo pygmaeus*) activity and diet: Implications for the invention of tool use. American Journal of
446 Physical Anthropology 125:162-174.

447 Friard O, Gamba M, 2016. BORIS: a free, versatile open-source event-logging software for video/audio
448 coding and live observations. Methods Ecol Evol 7:1325–1330.

449 Griffin AS, Guez D, 2014. Innovation and problem solving: a review of common mechanisms. Behavioural
450 Processes 109:121- 134.

451 Gruber T, 2013. Historical hypotheses of chimpanzee tool use behaviour in relation to natural and human-
452 induced changes in an East African rain forest. Revue de Primatologie 5:document 66. doi:
453 10.4000/primatologie.1690.

454 Gruber T, 2016. Great apes do not learn novel tool use easily: Conservatism, functional fixedness, or cultural
455 influence? International Journal of Primatology 37:296-316. doi: 10.1007/s10764-016-9902-4.

456 Gruber T, Muller MN, Reynolds V, Wrangham RW, Zuberbühler K, 2011. Community-specific evaluation
457 of tool affordances in wild chimpanzees. Scientific Reports 1:128. doi: 10.1038/srep00128.

458 Gruber T, Muller MN, Strimling P, Wrangham RW, Zuberbühler K, 2009. Wild chimpanzees rely on
459 cultural knowledge to solve an experimental honey acquisition task. Current Biology 19:1806-1810.

460 Gruber T, Poisot T, Zuberbühler K, Hoppitt W, Hobaiter C, 2015a. The spread of a novel behaviour in wild
461 chimpanzees: New insights into the ape cultural mind. Communicative & Integrative Biology
462 8:e1017164.

463 Gruber T, Potts K, Krupenye C, Byrne M-R, Mackworth-Young C, McGrew WC, Reynolds V, Zuberbühler
464 K, 2012. The influence of ecology on chimpanzee cultural behaviour: A case study of five Ugandan
465 chimpanzee communities. Journal of Comparative Psychology 126:446-457.

466 Gruber T, Reynolds V, Zuberbühler K, 2010. The knowns and unknowns of chimpanzee culture.
467 Communicative and Integrative Biology 3:1-3.

468 Gruber T, Zuberbühler K, Clément F, van Schaik CP, 2015b. Apes have culture but may not know that they
469 do. Frontiers in Psychology 6:91. doi: 10.3389/fpsyg.2015.00091.

470 Gruber T, Zuberbühler K, Neumann C, 2016. Travel fosters tool use in wild chimpanzees.
471 eLife:10.7554/eLife.16371.

472 Hobaiter C, Poisot T, Zuberbühler K, Hoppitt W, Gruber T, 2014. Social network analysis shows direct
473 evidence for social transmission of tool use in wild chimpanzees. PLOS Biology 12:e1001960.

474 Hoyt RW, Opstad PK, Haugen A-H, DeLany JP, Cymerman A, Friedl KE, 2006. Negative energy balance in
475 male and female rangers: effects of 7 d of sustained exercise and food deprivation. The American
476 Journal of Clinical Nutrition 83:1068-1075. doi: 10.1093/ajcn/83.5.1068.

477 Janmaat KRL, Byrne RW, Zuberbühler K, 2006. Evidence for a spatial memory of fruiting states of
478 rainforest trees in wild mangabeys. Animal Behaviour 72:797-807.

479 Janmaat KRL, Chapman CA, Meijer R, Zuberbühler K, 2012. The use of fruiting synchronicity by foraging
480 mangabey monkeys: a 'simple tool' to find fruit. Animal Cognition 15:83-96.

481 Koops K, McGrew WC, Matsuzawa T, 2013. Ecology of culture: Do environmental factors influence
482 foraging tool use in wild chimpanzees (*Pan troglodytes verus*)? Animal Behaviour 85:175-185.

483 Koops K, Visalberghi E, van Schaik CP, 2014. The ecology of primate material culture. Biol Letters
484 10:20140508.

485 Kummer H, Goodall J, 1985. Conditions of innovative behaviour in primates. Phil Trans Roy Soc Lond B
486 308:203-214.

487 Laland KN, Reader SM, 1999. Foraging innovation in the guppy. Animal Behaviour 57:331-340.

488 Lamon N, Neumann C, Gier J, Zuberbühler K, Gruber T, 2018. Wild chimpanzees select tool material based
489 on efficiency and knowledge. Proceedings of the Royal Society B: Biological Sciences.

490 Lamon N, Neumann C, Gruber T, Zuberbühler K, 2017. Kin-based cultural transmission of tool use in wild
491 chimpanzees. Science Advances 3:e1602750.

492 Lee PC, Moura ACA, 2015. Necessity, unpredictability and opportunity: an exploration of ecological and
493 social drivers of behavioural innovation. In: A. B. Kaufman, Kaufman JC, editors. Animal Creativity
494 and Innovation London: Elsevier. p. 317-329.

495 Marshall AJ, Wrangham RW, 2007. Evolutionary consequences of fallback foods. International Journal of
496 Primatology 28:1219–1235.

497 Matsumoto-Oda A, 2002. Behavioral seasonality in Mahale chimpanzees. Primates 43:103-117.

498 McLennan MR, 2015. Is honey a fallback food for wild chimpanzees or just a sweet treat? American journal
499 of physical anthropology 158:685-695.

500 Morand-Ferron J, Cole EF, Rawles JE, Quinn JL, 2011. Who are the innovators? A field experiment with 2

501 passerine species. Behavioral Ecology 22:1241-1248.

502 Moscovice LR, Issa MH, Petrzekova KJ, Keuler NS, Snowdon CT, Huffman MA, 2007. Fruit availability,
503 chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. American Journal of
504 Primatology 69:487-502.

505 Murray CM, Eberly LE, Pusey AE, 2006. Foraging strategies as a function of season and rank among wild
506 female chimpanzees (*Pan troglodytes*). Behavioral Ecology 17:1020-1028.

507 N'guessan AK, Ortmann S, Boesch C, 2009. Daily energy balance and protein gain among *Pan troglodytes*
508 *verus* in the Taï National Park, Côte d'Ivoire. International journal of primatology 30:481-496.

509 Plasqui G, Westerterp KR, 2004. Seasonal Variation in Total Energy Expenditure and Physical Activity in
510 Dutch Young Adults. Obesity Research 12:688-694. doi: doi:10.1038/oby.2004.80.

511 Pontzer H, 2017. The crown joules: energetics, ecology, and evolution in humans and other primates.
512 Evolutionary Anthropology: Issues, News, and Reviews 26:12-24. doi: doi:10.1002/evan.21513.

513 Pruett JD, Bertolani P, 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses
514 associated with living in a savanna-mosaic environment: implications for hominin adaptations to
515 open habitats. PaleoAnthropology:252–262. doi: 10.4207/PA.2009.ART33.

516 Ramsey G, Bastian ML, van Schaik C, 2007. Animal innovation defined and operationalized. Behavioral and
517 Brain Sciences 30:393-407.

518 Reader SM, Laland KN, 2001. Primate innovation: Sex, age and social rank differences. International
519 Journal of Primatology 22:787-805.

520 Reader SM, Morand-Ferron J, Flynn E, 2016. Animal and human innovation: novel problems and novel
521 solutions. Philosophical Transactions of the Royal Society of London B: Biological Sciences 371.
522 doi: 10.1098/rstb.2015.0182.

523 Reynolds V, 2005. The chimpanzees of the Budongo forest: Ecology, behaviour and conservation. Oxford:
524 Oxford University Press.

525 Rutz C, St Clair JJH, 2012. The evolutionary origins and ecological context of tool use in New Caledonian
526 crows. Behavioural Processes 89:153-165. doi: <http://dx.doi.org/10.1016/j.beproc.2011.11.005>.

527 Sanz CM, Morgan DB, 2013. Ecological and social correlates of chimpanzee tool use. Philosophical
528 Transactions of the Royal Society of London B: Biological Sciences 368. doi:
529 10.1098/rstb.2012.0416.

530 Snaith TV, Chapman CA, 2008. Red colobus monkeys display alternative behavioral responses to the costs
531 of scramble competition. *Behavioral Ecology* 19:1289-1296. doi: 10.1093/beheco/arn076.

532 Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L, 2005. Big brains, enhanced cognition, and
533 response of birds to novel environments. *Proceedings of the National Academy of Sciences of the*
534 *United States of America* 102:5460-5465.

535 Sol D, Griffin AS, Bartomeus I, 2012. Consumer and motor innovation in the common myna: the role of
536 motivation and emotional responses. *Animal Behaviour* 83:179- 188.

537 Sommer V, Buba U, Jesus G, Pascual-Garrido A, 2012. Till the last drop. Honey gathering in Nigerian
538 chimpanzees. *Ecotropica* 18:55-64.

539 Ungar PS, 2007. *Evolution of the human diet: the known, the unknown, and the unknowable*. Oxford:
540 Oxford University Press.

541 van Schaik CP, van Noordwijk MA, de Boer RJ, 1983. The effect of group size on time budgets and social
542 behaviour in wild long-tailed macaques. *Behav Ecol Sociobiol* 13:173-181.

543 Wartmann FM, Purves RS, van Schaik C, 2010. Modelling ranging behaviour of female orang-utans: a case
544 study in Tuanan, Central Kalimantan, Indonesia. *Primates* 51:119-130.

545 Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW,
546 Boesch C, 1999. Cultures in chimpanzees. *Nature* 399:682-685.

547 Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM, 2009. Emulation, imitation, over-imitation and the
548 scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B:*
549 *Biological Sciences* 364:2417-2428.

550 Wrangham RW, Conklin NL, Chapman CA, Hunt KD, 1991. The Significance of fibrous foods for Kibale
551 Forest chimpanzees. *Philosophical Transactions of the Royal Society B: Biological Sciences*
552 334:171-178.

553 Yamagiwa J, Basabose AK, 2009. Fallback foods and dietary partitioning among Pan and Gorilla. *American*
554 *Journal of Physical Anthropology* 140:739-750.

555 Yamakoshi G, 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible
556 implications for ecological importance of tool use. *American Journal of Physical Anthropology*
557 106:283-295.

558

559 **Figure legends**

560

561 **Figure 1. Components of the experimental device supplying liquid honey by tool use.** **a)** Lower
562 part of the log with cavity carved out to fit a plastic receptacle containing liquid honey; **b)** tool-
563 retaining mechanism of the receptacle: a metal spring (relaxed) was coiled around a cone-shaped
564 stick, whose wide ($> 1\text{cm}$) end prevented removal through the 1cm hole in the lid. During each trial
565 the receptacle was filled with liquid honey to a depth of 10 cm; **c)** receptacle with closed lid and
566 protruding stick; the metal spring inside the receptacle slightly compressed; **d)** receptacle inserted
567 into the artificial cavity of the log; **e)** experimental log completely assembled. As soon as a subject
568 pulled the stick out of the receptacle honey became accessible at its lower end ($\sim 3\text{ cm}$). As soon as
569 a subject released the stick it retracted back into the cavity by the mechanical force of the
570 compressed spring, replenishing it for another round of manipulation.

571

572 **Figure 2. Time frame for estimating travel effort and feeding behaviour.** The experiment
573 consisted of two-day focal animal follows, terminated by the presentation of the apparatus on day 2.
574 Individuals were left in the evening after they have built their nests and were thus assumed to have
575 remained stationary overnight (i.e. from 18:00 to 07:00 local time the following day). Presentation
576 of the apparatus on day 2 varied depending on the opportunities to run an experimental trial.

577

578 **Figure 3. Photographs of two successful stick-based interaction sequences with the apparatus.**

579 Top panel: Adult female KU (left) pulls the stick maximally out of the device with her right hand
580 and licks the honey from the stick's lower end. KU then repeated this behaviour one more time, all
581 the time observed by her offspring KH (middle) and KS (right), who had already engaged with the
582 device before. Bottom panel: Juvenile KB pulls the stick maximally out of the device with her
583 mouth and then, with her right hand, and licks honey from the stick's lower end (no repetition).

584

585 **Figure 4. Relationship between estimated travel effort (a) and estimated feeding effort (b)**
586 **with subsequent engagement time with the device.** Note that two individuals are represented
587 more than once (KC (triangle) = 2 data points; KB (squares) = 3 data points). However, rank
588 correlation tests in all possible combinations revealed a similarly positive correlation between
589 estimated travel distance and device engagement time even if KB and KC were only entered once
590 (N = 6; rho ranging between 0.71 and 0.89; see supplemental table S5). The same was the case for
591 the negative correlation between estimated feeding time and device engagement time (N = 6; rho
592 ranging between -0.14 and -0.89; supplemental table S5).

593

594 **Figure 5. Estimated travel effort (a) and feeding effort (b) in trials with and without stick**
595 **interactions.**

596

597 **Figure 6. Ecological model of the role of ‘necessity’ and ‘opportunity’ in the emergence of**
598 **foraging-related behavioural innovations and tool use. 1) Individual innovation.** Unusually
599 severe food shortages or prolonged periods of food stress cause difficulties for individuals to meet
600 their nutritional requirements (‘necessity’) and, as a consequence increase motivation to explore
601 their surroundings for alternative food resources (‘opportunity’). Unfavourable energy balances
602 further increase subjects’ attention and motivation to access previously inaccessible, high-value
603 foods, which is likely to lead to behavioural innovations. **2) Social transmission of the behaviour.**
604 If a behaviour innovation is advantageous it is likely to spread to other community members
605 through social learning and become part of the community’s cultural repertoire. **3) Maintenance or**
606 **disappearance of the behaviour.** Variation in ecological necessity (availability of alternative food
607 options to meet nutritional requirements) and opportunity (availability of tool-accessed resource and
608 tool material as well as social opportunity to witness a behaviour being demonstrated) will shape
609 tool use exhibition and maintenance in the community.

610

611 **Table and Table legend**

Table 1. Experimental trials with estimated feeding and travel history

612

<i>Date</i>	<i>Focal</i>	<i>Travel</i>	<i>Feeding</i>	<i>Device</i>	<i>Stick</i>	<i>Honey</i>	<i>Stick</i>	<i>Foraging</i>
		<i>Distance</i>	<i>Effort</i>	<i>Engage</i>	<i>Touch</i>	<i>Comb</i>	<i>Interaction</i>	<i>Success</i>
21.01.	NT	3371	5.0	32	18	All	1	0
23.01.	KC	3072	6.9	26	5	All	1	0
03.02.	KB	3130	6.0	8	2	All	1	0
06.03.	KB	4079	1.8	50	45	All	1	1
12.04.	KC	2815	11.0	0	0	All	0	0
12.04.	KX	977	6.4	1	0	Nca	0	0
19.05.	KB	2285	6.0	0	0	None	0	0
28.05.	KU	4337	6.2	41	31	Nca	1	1
31.05.	OK	3498	7.3	12	12	All	1	0

613

614 **Travel distance** (m) = estimated travel effort in metres; **Feeding Effort** (h) = estimated feeding

615 effort in hours; **Device Engage** (s) = total device engagement time in seconds (incl. stick

616 interaction); **Stick Touch** (s) = stick touching in seconds; **Honey Comb** = combs taken and fed on

617 (all; none; nca = no combs available); **Stick Interaction** = stick interaction (1 = yes; 0 = no),

618 **Foraging Success** = Honey retrieved with the stick (1 = yes; 0 = no).