Chimpanzees (*Pan troglodytes*) display limited behavioural flexibility when faced with a changing foraging task requiring tool use

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Behavioural flexibility, the ability to alter behaviour in response to environmental feedback, and to relinquish previously successful solutions to problems, is a crucial ability in allowing organisms to adapt to novel environments and environmental change; it is essential to cumulative cultural change. To explore this ability in chimpanzees, 18 individuals (*Pan troglodytes*) were presented with an artificial foraging task consisting of a tube partially filled with juice that could be reached by hand or retrieved using tool materials to hand. Effective solutions were then restricted in the second phase of the study by narrowing the diameter of the tube, necessitating the abandonment of previously successful solutions. Chimpanzees showed limited behavioural flexibility in comparison to some previous studies, increasing their use of effective techniques, but also continuing to attempt solutions that had been rendered ineffective. This adds to a literature reporting divergent evidence for flexibility (the ability to alter behaviour in response to environmental feedback, and to relinquish previously successful solutions to problems) versus conservatism (a reluctance or inability to explore or adopt novel solutions to problems when a solution is already known) in apes.

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Chimpanzees (*Pan troglodytes*) display limited behavioural flexibility when faced with a changing foraging task requiring tool use

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15 **Abstract**

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17 to relinquish previously successful solutions to problems, is a crucial ability in allowing

18 organisms to adapt to novel environments and environmental change; it is essential to

19 cumulative cultural change. To explore this ability in chimpanzees, 18 individuals (*Pan*

20 *troglodytes*) were presented with an artificial foraging task consisting of a tube partially filled

21 with juice that could be reached by hand or retrieved using tool materials to hand. Effective

22 solutions were then restricted in the second phase of the study by narrowing the diameter of the

23 tube, necessitating the abandonment of previously successful solutions. Chimpanzees showed

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25 effective techniques, but also continuing to attempt solutions that had been rendered ineffective.

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27 in response to environmental feedback, and to relinquish previously successful solutions to

28 problems) versus conservatism (a reluctance or inability to explore or adopt novel solutions to

29 problems when a solution is already known) in apes.

30

31   **Introduction**

32   Behavioural flexibility, the ability to alter behaviour based upon environmental feedback

33   and to inhibit previously successful behaviours, is an ability that allows organisms to adapt their

34   behaviour to suit changing or novel environments and supports problem solving by allowing

35   individuals to adapt their behaviour to success or failure at a problem (Sol, Timmermans &

36   Lefebvre 2002; Griffin & Guez 2014; Chow, Lea & Leaver 2016; Audet & Lefebvre 2017).

37   Behavioural flexibility can also describe the capacity for, and interest in, continuing to acquire

38   novel solutions to an unchanging problem for which a solution is already known (Lehner, Burkart

39   & van Schaik 2011), though most experimental explorations of behavioural flexibility incorporate

40   changes in task parameters (and therefore changes in environmental feedback). Behavioural

41   flexibility is thought to be a key ability supporting the evolution of cumulative culture (Dean et

42   al. 2014). With culture defined as "group-typical behaviour patterns shared by members of a

43   community that rely on socially learned and transmitted information" (Laland & Hoppitt 2003,

44   pp.151), cumulative culture is the process whereby these socially learnt behaviours are modified

45   and the modifications are retained, resulting in behaviours and technologies more complex than

46   an individual could invent within their lifetime (Tomasello 1994; Tennie, Call & Tomasello

47   2009). As cumulative culture relies upon the modification of known behaviours it necessitates

48   flexibility in both the process of innovation by some individuals, and in the acquisition by others

49   of the improved behaviours that result.

50   <u>Behavioural flexibility and cumulative culture</u>

51   Evidence for cumulative culture in our closest living relative, the chimpanzee, is limited and

52   controversial (Dean et al 2014; Whiten 2017), with Boesch (2003) highlighting three behaviours

53   observed in wild chimpanzees (nut-cracking incorporating additional stones to stabilise the anvil,

54   parasite manipulation in which parasites are placed on a leaf which is then folded and cut, and

55   well-digging incorporating the use of leaf-sponges to retrieve water from deep wells) as potential

56   evidence of cumulative culture, whilst Sanz, Call and Morgan (2009) describe apparent

57   improvements made to termite fishing tools by chimpanzees in the Goualougo Triangle, Republic

58   of Congo. However, such interpretations require assumptions to be made regarding the social

59   transmission of these behaviours, whether they represent greater complexity than that achievable

60   by an individual alone, and indeed whether they are the result of cumulative progressions rather

61 than unconnected innovations. With such limited evidence of cumulative culture in chimpanzees,

62 investigation of the abilities required to support cumulative culture is required. We suggest that

63 behavioural flexibility, along with innovation (defined by Reader and Laland (2003 pp14) as "A

64 process that results in new or modified learned behaviour and that introduces novel behavioural

65 variants into a population's repertoire") and social learning, should be considered and investigated

66 as a potential limiting factor for cumulative culture. Whilst innovation has been suggested to be a

67 component of behavioural flexibility (Lehner, Burkart & van Schaik 2011), we also consider the

68 acquisition of novel behaviours via social learning to constitute flexible behaviour (Wright,

69 Eberhard, Hobson, Avery & Russello 2010), and indeed the application of known behaviours to a

70 novel problem. Social learning, innovation and behavioural flexibility are expected to work in

71 concert to support cumulative culture – an individual innovates an improvement to a behaviour or

72 tradition, and this improvement is passed on via social learning to other group members. High-

73 fidelity social transmission is believed to be critical in supporting cumulative culture, as it

74 prevents backwards 'slippage' or the loss of modifications to behaviours (Lewis & Laland 2012;

75 Tennie et al. 2009)' however somewhat paradoxically, at least some individuals in a population

76 must also be capable of modifying behaviours, having acquired them via high-fidelity social

77 learning. As outlined by Charbonneau (2015), an ability to innovate entirely novel behaviours

78 'from scratch' alone is not sufficient to support cumulative culture, which instead requires an

79 ability to modify *known* behaviours. In order for both the modification to the behaviour to occur

80 on an individual level in the innovator, and then for other group members to adopt this alteration,

81 individuals in the community must be capable of flexibly altering their behaviour.

82 <u>Measuring behavioural flexibility</u>

83 Behavioural flexibility has been assessed at a species level via the proxy measure of innovation

84 frequency (for example, Lefebvre, Whittle, Lascaris & Finkelstein 1997; Lefebvre, Reader & Sol

85 2004, for avian comparisons), and innovation has been considered a component of behavioural

86 flexibility (Lehner, Burkart & van Schaik 2011; Audet & Lefebvre 2017). This makes the

87 assumption that behavioural flexibility leads to increased innovativeness, which may not always

88 be the case at either an individual or species level (Griffin, Guez, Lermite & Patience 2013;

89 Logan 2016). Behavioural flexibility in response to environmental change has been tested

90 directly in a range of species, both in the wild and captivity, frequently by employing

91 experimental paradigms in which animals must respond to a change in task parameters, such as

92 reversal learning (Bond, Kamil & Balda 2007; Boogert, Monceau & Lefebvre 2010; Manrique &

93   Call, 2015; Liu, Day, Summers & Burmeister 2016) or multi-access puzzle box tests (Auersperg,

94   von Bayern, Gajdon, Huber & Kacelnik 2011; Lehner, Burkart & van Schaik 2011; Manrique,

95   Völter & Call 2013; Richter, Hochner & Kuba 2016).

96   Both intra- and interspecific differences in flexibility have been found using these

97   experimental techniques. Individual differences in behavioural flexibility within species have

98   been shown in animals as diverse as octopuses, pigs and mice (Richter et al. 2016; Bolhuis,

99   Schouten, de Leeuw, Schrama & Wiegant 2004; Benus, Den Daas, Koolhaas & van Oortmerssen

100   1990), as well as in wild chimpanzees and sanctuary-housed orangutans (Gruber 2016). Such

101   inter-individual differences within species are perhaps not surprising, given potential differences

102   between individuals in terms of task motivation, cognitive ability, and personality (the latter

103   having been shown to impact performance on problem solving tasks in chimpanzees (Massen,

104   Antonides, Arnold, Bionda & Koski 2013)). In the context of cumulative culture, an

105   understanding of which individuals are most capable of behavioural flexibility, and investigation

106   of any other traits which might co-occur with behavioural flexibility on an individual level, may

107   allow predictions to be made regarding which individuals or demographics are likely to

108   contribute to the modification of behaviours in a population's repertoire.

109   In addition, interspecific differences in behavioural flexibility have been demonstrated in

110   both corvids and great apes (Bond et al. 2007; Manrique et al. 2013), and investigation of these

111   interspecific differences allows exploration of hypotheses regarding the evolution of behavioural

112   flexibility. Bond et al. (2007) argue that behavioural flexibility may be more apparent in species

113   with highly complex social systems, in order to cope with rapidly fluctuating social contexts, and

114   found that pinyon jays, a highly social species, had lower error rates on a serial reversal learning

115   tasks than Clark's nutcrackers (a relatively solitary species with specialised spatial memory

116   supporting caching behaviour) and western scrub jays (a generalist species in terms of both

117   ecology and social behaviour). Continued investigation of species' abilities to behave flexibly

118   will allow investigation of the evolutionary pressures which lead to high behavioural flexibility,

119   and will also allow investigation of other cognitive abilities which may co-evolve with

120   behavioural flexibility. For example, it has also been shown that pinyon jays outperform Clark's

121   nutcrackers on social learning tasks (Templeton, Kamil & Balda 1999). Given that a suite of

122   abilities is likely required to support cumulative culture (Dean et al 2014), an understanding of

123   why component abilities may emerge, and whether they share common evolutionary origins, is

124   likely to enhance our understanding of the evolution of cumulative culture.

125   Observation of the tool preferences of wild tool-using species also provides some

126   indication of the flexibility of such species. Examination of the tool preferences of wild New

127 Caledonian crows found strong, persistent local preferences in terms of the plant species from

128 which their hook-tools are manufactured (St Clair et al 2016), despite access to alternative plants

129 which are preferred at another, nearby study site. This may indicate some level of individual

130 conservatism (a reluctance to explore alternative solutions) in this species' tool manufacture,

131 though the authors also point out that it shows that crows at one study site have either switched

132 from a previous tool material, or acquired hooked stick tool-use relatively recently. Both

133 scenarios would reflect flexibility, both on the part of initial innovators and any individuals which

134 may have socially acquired this alternative behaviour. Study of individual crows' tool

135 manufacture indicates multiple bending techniques and adjustments during manufacture, that

136 would seem to indicate flexibility (Rutz et al 2016; Klump, Sugasawa, St Clair & Rutz 2015).

137 Wild chimpanzees have been observed to modify their tool-use behaviours, with an individual in

138 Bossou being observed firstly applying a tool and technique generally used for ant-dipping on the

139 ground to ant-fishing in trees, and later using tools of a length better suited to ant-fishing in trees

140 (Yamamoto, Yamakoshi, Humle & Matsuzawa 2008). Wild chimpanzees have also been observed

141 to socially learn novel tool behaviours, such as crafting sponges from moss rather than leaves

142 (Hobaiter, Poisot, Zuberbühler, Hoppitt & Gruber 2014). These observations of wild behaviour

143 provide some insight into chimpanzees' capacity for behavioural flexibility.

144 <u>Chimpanzees – behaviourally flexible or conservative?</u>

145 In several studies chimpanzees have been reported to be conservative, rather than flexible, in

146 their approach to artificial foraging tasks, continuing to use a habitual solution despite the

147 prospect of gaining a greater reward via behavioural change (Marshall-Pescini & Whiten 2008)

148 or the habitual solution being made impossible or unrewarding (Bonnie et al. 2012; Hrubesch et

149 al. 2009). Behavioural conservatism has also been reported in wild chimpanzees, with Gruber et

150 al (2009) finding that two dfferent communities relied upon their respective habitual tool

151 behaviours when faced with a novel artificial honey-dipping task, in one community failing to

152 acquire the useful tool behaviour used by the other community even when scaffolded towards it

153 (Gruber et al 2011; Gruber 2016). Similarly, Cardoso and Ottoni (2016) found that providing two

154 communities of wild bearded capuchin monkeys with a dipping task resulted in only the group

155 that already habitually used probing tools solving the task, again despite efforts to scaffold the

156 non-probe-using group towards this behaviour. Chimpanzees may also continue to perform

157 behaviours when these behaviours are no longer necessary, for example, continuing to avoid a

158 non-functional trap in the inverted trap-tube problem (Povinelli 2000; though see also Mulcahy &

159 Call 2006), although it should be noted that in paradigms in which continuing this behaviour is

160 equally rewarding as ceasing to avoid the trap, adult humans also continue to avoid non-

161 functional traps (Silva, Page & Silva 2005).Related to these findings of apparent conservatism or

162 lack of flexibility in chimpanzees is the concept of 'functional fixedness': the inability to invent a

163 novel use for a tool with which the animal already has experience (Hanus, Mendes, Tennie & Call

164 2011; Brosnan & Hopper 2014). Hanus et al (2011) found that captive chimpanzees were more

165 likely to solve the 'floating peanut' experiment (in which water must be added to a tube in order

166 to raise a floating peanut to a level at which it can be reached) when a novel water dispenser was

167 added to their enclosure. The authors suggest that the old dispenser had a fixed function for the

168 animals which prevented them from discovering it as a potential task solution.

169 By contrast, other recent studies have implied that under certain conditions, great apes

170 may be capable of flexibly altering their behaviour in response to a changing task (Lehner et al.

171 2011; Yamamoto, Humle & Tanaka 2013; Manrique et al. 2013; Davis et al. 2016; Vale et al.

172 2017). In the studies of both Lehner et al. (2011), and Manrique et al. (2013), in order to

173 successfully retrieve a reward, great apes had to not only flexibly alter their behaviour in

174 response to changing tasks, but also develop novel methods of solving the foraging tasks with

175 which they were presented. Lehner et al. (2011) found that orangutans were capable of inventing

176 novel solutions to a task in which juice could be retrieved from a tube by dipping tool materials

177 into the tube. When the width of the tube was narrowed, orangutans flexibly altered their

178 behaviour, abandoning previously successful solutions and inventing novel solutions, some of

179 which the authors argue are cumulative improvements upon previous solutions. It should be

180 noted that although novel solutions were not experimentally seeded in the Lehner et al. study

181 (2011), orangutans were tested under group conditions, and so potentially had access to social

182 information. In a study testing all four nonhuman species of great ape, in which subjects were

183 tested individually (eliminating the possibility of social learning) Manrique et al. (2013) found

184 that all species, with the exception of orangutans, were able to abandon previous solutions and

185 invent novel solutions to a non-tool-based artificial foraging task in which solutions were

186 rendered obsolete over time.

187 Studies have also shown that chimpanzees are able to social acquire more efficient or

188 more rewarding solutions to problems, having already mastered a less efficient solution.

189 Yamamoto et al. (2013) found that chimpanzees provided with a task in which juice could be

190 retrieved from within a tube via a small hole were capable of swapping from an inefficient

191   'dipping' technique to a more efficient 'straw-sucking' technique following observation of a

192   conspecific employing the more efficient technique, while Vale et al. (2017) found that following

193   the removal of simple tools that could be used to acquire juice in a dipping task, chimpanzees

194   began to use complex tools that required modification (unscrewing a valve so a tube could be

195   used as a 'straw' to suck up juice). Davis et al. (2016) found that chimpanzees were able to

196   relinquish a highly inefficient task solution in favour of a more efficient solution when provided

197   with demonstrations of the efficient solution by a conspecific or human demonstrator. The

198   authors of the latter study argue that such flexibility may be more apparent in situations in which

199   there is a large difference in efficiency between two technique options (with a relatively highly

200   inefficient solution more likely to be relinquished). This may suggest chimpanzees use a 'copy-if-

201   dissatisfied' strategy when given the opportunity to socially acquire more efficient solutions to

202   problems (Laland 2004). If so, behavioural flexibility in such studies may be apparent only when

203   the original solution is rendered highly inefficient and unsatisfying. The findings of Lehner et al.

204   (2011) and Manrique et al. (2013) may, in light of this, imply that great apes also employ an

205   'explore-if-dissatisfied' strategy when given the opportunity to achieve improved solutions to

206   problems without the benefit of an existing competent model.

207   **Study aims**

208   We aimed to investigate the capability of chimpanzees to alter their behaviour in response to an

209   artificial foraging task in which viable solutions became restricted as time progressed, using a

210   liquid-retrieval task comparable to that used by Lehner et al. (2011) with orangutans.

211   <u>Behavioural flexibility</u>

212   Chimpanzees were presented with the task as a group, and therefore had access to both

213   individual and social information about the task and potential solutions. This means that

214   individuals were not limited to what they themselves could invent in terms of task solutions,

215   which we believe provides a more ecologically valid measure of behavioural flexibility, as this

216   has been defined in the past as the continued acquisition of new solutions through either

217   innovation or social learning (Lehner et al 2011). If chimpanzees are able to respond flexibly to

218   changes in task conditions (as shown by Manrique et al. 2013), we would predict individuals to

219   increase their use of techniques which remain effective, and to decrease their use of techniques

220   which have been rendered ineffective, in the face of task restrictions. Alternatively, if

221   chimpanzees are behaviourally inflexible, we predict the continued use of ineffective techniques

222   and no increase in the use of effective techniques.

223   If chimpanzees follow an 'explore if dissatisfied' strategy, we would predict the emergence of

224   novel techniques following the imposition of task restrictions, whilst a 'copy if dissatisfied'

225   strategy would result in the acquisition of effective techniques by individuals other than the

226   technique's innovator following the imposition of task restrictions.

227   <u>Subgroups and the impact of developmental conditions</u>

228   Chimpanzees were studied in Edinburgh Zoo, which houses a single community that originates

229   from two separate subgroups; long-term residents of the zoo ('Edinburgh' chimpanzees), and

230   others introduced in 2010 ('Beekse Bergen' chimpanzees). These subgroups are now well

231   integrated socially (Schel et al. 2012; Watson et al. 2015) but have differing life histories, with

232   the Beekse Bergen subgroup coming from a laboratory and first living in a zoo environment from

233   2007. This may be anticipated to impact their problem-solving abilities, with chimpanzees raised

234   in more restricted environments potentially possessing more limited problem-solving skills

235   (Morimura & Mori 2010; Brent, Bloomsmith & Fisher 1995; Vlamings, Hare & Call 2010), so

236   this study also considers the impact of subgroup membership upon task performance. The

237   subgroup with a history of laboratory-housing were predicted to perform more poorly on the task

238   than long-term zoo residents.

239   <u>Scaffolding towards an effective solution</u>

240   Previous experimental studies of chimpanzees and capuchin monkeys (chimpanzees: Gruber et al

241   2011; capuchins: Cardoso & Ottoni 2016) have found that scaffolding in this manner has no

242   effect, however, learning through exposure to the artefacts of others' tool use is hypothesised to

243   aid in the development of tool behaviour in wild populations (Tennie et al. 2009). By providing

244   chimpanzees with limited exposure to scaffolding towards a novel tool technique in the final

245   phase of our study, we examined whether chimpanzees could acquire novel tool behaviour

246   through exposure to favourable affordances in the form of an effective tool material correctly

247   inserted into the task, as might occur in the wild where proficient tool-users leave tools in place

248   that novices may discover.

249 **Methods**

250 <u>Ethical approval</u>

251 The study received ethical approval from the University of St Andrews Animal Welfare and
252 Ethics Committee, and was approved by the Budongo Trail Research Committee. Research was
253 conducted in accordance with the guidelines of the Association for the Study of Animal
254 Behaviour.

255 <u>Subjects and study site</u>

256 Subjects were 18 chimpanzees housed as one group in the Budongo Trail facility at Edinburgh
257 Zoo (see Table 1 for details). The group is composed of two 'subgroups', long-term residents of
258 the zoo ('Edinburgh' chimpanzees), and others introduced in 2010 ('Beekse Bergen'
259 chimpanzees), each numbering nine individuals. The chimpanzees lived in three interconnecting
260 indoor enclosures measuring 120m^2 each and one outdoor enclosure measuring 1832m^2, along
261 with two research 'pods' (two connected rooms measuring 26.5m^2 in total) provided for cognitive
262 research. Chimpanzees were fed six to eight scatter feeds throughout the day at random times and
263 locations, with water available *ad libitum* throughout the facility. The research pods were
264 accessible via overhead tunnels from the chimpanzees' indoor enclosures, and activity within the
265 pods could not be viewed by chimpanzees outside the pods. Our task was presented in one of
266 these research pods, and chimpanzees had access to both pods during testing. Chimpanzees in the
267 second research pod during testing had limited visual access to the task through an open slide
268 door separating the pods, while individuals in the primary pod (in which the task was presented)
269 generally had good visual access to the task. A maximum of seven chimpanzees were recorded as
270 present in the primary pod during testing, with space for further individuals in the second pod. All
271 chimpanzees had previous experience with artificial foraging tasks involving tool use, having
272 been provided with the 'Panpipes' task (in which a stick tool is used to retrieve a grape from
273 within the apparatus, see Whiten, Horner and de Waal (2005) for details of the apparatus) and a
274 food-raking task in which plastic stick tools could be used to retrieve out-of-reach rewards (see
275 Price, Lambeth, Schapiro and Whiten (2009) for a similar task) (V West, unpublished master's
276 thesis; R Harrison, unpublished master's thesis). In addition, chimpanzees had previous
277 experience using a touchscreen device in the research pods (Wallace et al 2017).

278 [Insert Table 1 here]

279 <u>Apparatus</u>

280 Echoing the study of Lehner et al. (2011), we provided the chimpanzees with an artificial

281 foraging task in which dilute Ribena juice could be retrieved from within transparent

282 polycarbonate tubes, using either provided tool materials or hands. The task had two stages, for

283 which two widths of tube were provided. The first ('wide') tube measured 30cm tall with a 10cm

284 inner diameter (see Figure 1), and the second ('narrow') tube measured 30cm tall with a 5cm

285 inner diameter. These tubes were presented in the research pods, bolted to a polycarbonate screen

286 facing into the pod, and could be filled and emptied by the experimenter through holes in the

287 screen. Alongside the tubes, chimpanzees were provided with a selection of tool materials

288 comprising plain sticks (rigid sticks measuring approximately 40-50cm), straw bedding material,

289 strips of cloth and 'wood wool'/'excelsior' (fine wood slivers typically provided as bedding

290 material). Leafy sticks (a selection of browse generally provided to the chimpanzees by care staff

291 for nesting and feeding, primarily eucalyptus – these leafy sticks were flexible and measured

292 approximately 40-80cm) were available in the chimpanzees' enclosure throughout testing, and

293 were placed in the research pod along with the other tool materials from the fifth hour of testing

294 onwards. Chimpanzees were familiar with all tool materials, as straw, cloth, wood wool and

295 browse were generally provided as nesting material, and sticks were readily available in their

296 outdoor enclosure. All tool materials were placed into the research pods before chimpanzees were

297 given access.

298 <u>Procedure</u>

299 The apparatus was presented during twice-daily research sessions facilitated by Edinburgh Zoo

300 staff. These sessions lasted for 45-60 minutes. In the first stage of the study ('Wide Tube' phase),

301 chimpanzees were provided with the wide tube, filled with diluted sugar free Ribena to a depth of

302 around 7cm. This was presented alongside the aforementioned selection of tool materials, and in

303 the 'Wide Tube' phase the juice could also be reached by hand. All provided tool materials could

304 potentially be used to successfully retrieve juice from the task. The tube was baited with juice for

305 ten sessions, each lasting between 45 and 60 minutes, with juice added by the experimenter to

306 ensure a reward was present for the duration of each session. The tube was emptied of liquid by

307 the researcher through a valve at the base at the end of each session, as removing the

308 chimpanzees from the research pods was logistically unfeasible, and so the juice reward was

309   removed in order to discourage further interaction with the tube outside of the twice-daily

310   research session.

311   In the second stage of the study ('Narrow Tube' phase), chimpanzees were presented with

312   the narrow tube, filled with juice to a depth of 7cm, along with the same selection of tool

313   materials. Again, chimpanzees had access to the baited tube for ten 45-60 minute sessions. The

314   narrow tube prevented chimpanzees from inserting their hands into the tube to gain juice, and

315   also rendered attempts made using rigid, leafless sticks relatively unsuccessful, due to the ledge

316   surrounding the panel to which the tube was attached. This ledge meant that rigid sticks inserted

317   into the tube frequently hit the back of the tube and could be inserted no further, preventing them

318   from reaching the juice. Leafy sticks remained functional. Absorbent materials (straw, cloth, and

319   wood wool) could no longer be inserted and retrieved by hand.

320   In the third stage of testing ('Narrow Scaffolded' phase), chimpanzees were again

321   presented with the narrow tube for ten 45-60 minute sessions, but at the start of each day of

322   testing, prior to the chimpanzees having access to the research pods, a leafy stick was inserted

323   into the tube, with its leaves in the juice. As multiple sessions were conducted on some testing

324   days, with no access to the research pods to re-insert the stick following the start of the first

325   session each day, this provided four sessions which began with a stick already inserted. Only the

326   first individual to interact with the task on these four sessions encountered this scaffolding,

327   however their interactions with the scaffolding and their subsequent interactions with the task

328   could be observed by other group members.

329   In the course of testing, on 12 occasions two sessions occurred on the same day, and due

330   to the impossibility of removing chimpanzees from the research pods between sessions,

331   chimpanzees had access to the empty tube and remaining tool materials for approximately one

332   hour between sessions. It was not possible to document any attempts made during this time.

333   [insert Figure 1 here]

334   <u>Data collection and coding</u>

335   Sessions were recorded using a Sony Handycam DCR-SX21 camera. This recorded chimpanzees'

336   responses to the task, while the experimenter narrated chimpanzees' actions as well as the identity

337   and presence of other individuals in the research pod. The video and narration were later coded

338   together. The chimpanzee identity, tool material choice (hand, plain stick, wood wool, straw, or

339   leafy stick), action (dip, retrieve, squash, drop), and success of individuals attempting the task

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340   were coded for each attempt. The presence of other individuals in the research pod was also

341   coded for each attempt. Techniques were then classified as 'Always effective' and 'Partially

342   effective' (Table 2), based upon their potential efficacy in narrow tube conditions. A second

343   coder, blind to the experimental hypotheses, coded 50 randomly selected attempts for tool

344   material, technique (as listed in Table 2), and success. Inter-observer reliability was calculated

345   using Cohen's Kappa, revealing agreement for all variables (tool material $K = 0.90$, technique K

346    $= 0.87$, success $K = 0.95$).

347   Data analysis

348   Data were analysed in R (version 3.2.2, R Core Team 2015) and RStudio (version

349   0.99.893, RStudio Team, 2015) using a generalised linear mixed model with a Laplace

350   approximation (GLMM), using the function glmer in the R statistics package lme4 (Bates,

351   Maechler & Bolker 2012). Analysing binomial data using GLMM is recommended by Jaeger

352   (2008) and Bolker et al. (2009). The impact of predictor variables upon the number of 'Always

353   effective vs 'Partially effective' technique attempts in the 'Wide Tube' and 'Narrow Tube' phases

354   was assessed for all individuals that made attempts in both the 'Wide' and 'Narrow' tube phases

355   (N=10).

356   A full random slope model was fitted (for discussion on the benefits of fitting random

357   slopes as well as random intercepts, see Schielzeth & Forstmeier 2009). The full model contained

358   fixed effects for Phase ('Wide Tube' vs 'Narrow Tube') and Subgroup (Edinburgh vs Beekse

359   Bergen), along with an interaction between the two and a random intercept and slope by Phase

360   for each Individual (N=10). This full model was compared with a null model including only the

361   random intercept and slope by Phase for each Individual. Both models were fitted using a

362   binomial error structure due to the binary nature of the response variable (Effectiveness) and a

363   logit link function. A likelihood ratio test comparing the full and null models indicated that the

364   full model was a significantly better fit ($\chi^2 = 8.65$, $df = 3$, $p = .0343$; dAIC = 2.7).

365   **Results**

366   Sixteen of the eighteen chimpanzees interacted with the task during at least one of the

367   three phases of testing (see Table 1 for frequency of participation for all individuals) In addition,

368   sixteen of eighteen individuals were present in the research pod during another individual's

369   attempt at the task on at least one occasion (with only Cindy and Liberius never having the

370   opportunity to observe others at the task). Ten individuals attempted the task in both the 'Wide

371   Tube' and 'Narrow Tube' phases. Seven individuals participated in all three phases (see Table 1).

372   A total of 3,022 attempts were made across the three phases and 30 hours of testing. Seven

373   techniques were used to successfully solve the task (see Table 2). Six of these techniques

374   emerged in the 'Wide Tube' phase (and four of these six within the first testing session), with the

375   remaining technique emerging in the 'Narrow Tube' phase. No novel techniques were observed in

376   the 'Narrow Scaffolded' phase. Techniques involving the use of hands only and the use of plain,

377   rigid sticks emerged first, within the first testing session. The use of leafy sticks emerged after

378   several hours of exposure to the task (Table 2). Only one novel technique (*wood wool retrieve)*

379   emerged in the 'Narrow Tube' phase, though some individuals performed techniques in this phase

380   that were novel to them (though not novel to the group, and so potentially acquired socially)

381   (Table 3).

382   <u>Behavioural flexibility</u>

383   In order to examine behavioural flexibility in the chimpanzees' response to the task

384   restrictions imposed by the transition from the 'Wide Tube' to 'Narrow Tube' phase, the

385   techniques described above were categorised as 'Always effective' or 'Partially effective'

386   according to their potential efficacy across phases (see Table 2). Note that all techniques (see

387   Table 2) were effective in the 'Wide Tube' phase, in which there were few constraints upon

388   potential solutions.

389   Techniques involving the insertion of a hand into the tube (ie. *hand dip*) were classified as

390   'Partially effective', as insertion of the hand into the tube was made impossible by the width of

391   the tube in the 'Narrow Tube' phase, though this technique could be successfully used in the

392   'Wide Tube' phases. Techniques reliant upon the insertion of a plain, rigid stick into the tube were

393   also classified as 'Partially effective', as the overhang of the task presentation window was such

394   that these sticks could frequently no longer be inserted into the tube in the 'Narrow Tube' phase.

395   Short rigid sticks could still successfully be dropped into the tube and retrieved by hand, and so

396   the technique *stick drop* is categorised as 'Always effective'. For further discussion of this

397   classification, see Supplemental Article S1.

398   Comparison of the use of 'Partially effective' and 'Always effective' techniques in the

399   'Wide Tube' and 'Narrow Tube' phases indicates the extent to which chimpanzees altered their

400   behaviour in response to the change in task, and the extent to which they were able to set aside

401   techniques that had been rendered impossible by the change in tube width. An increase in the use

402   of 'Always effective' techniques in the 'Narrow Tube' phase compared with the 'Wide Tube'

403   phase would indicate a flexible response to the task changes. The 'Narrow Scaffolded' phase is

404   not included in these analyses, in order to exclude the possibility of the scaffolding impacting

405   observed flexibility.

406   [insert Table 2 here]

407   [insert Figure 2 here]

408   The ten individuals that took part in both 'Wide' and 'Narrow' tube phases used 'Always

409   effective' techniques for 58 of 1527 attempts in the 'Wide Tube' phase, increasing to 514 of 1250

410   attempts in the 'Narrow Tube' phase. On average, each individual used 'Always effective'

411   techniques for a mean of 8.7% (SD = 15.6) attempts in the 'Wide Tube' phase, increasing to a

412   mean of 24.2%% (SD = 19.4) of attempts in the 'Narrow Tube' phase (see Figure 2). Individual

413   preferences in terms of specific techniques for the 10 individuals that took part in both 'Wide'

414   and 'Narrow' tube phases are shown in Table 3.

415   [insert Table 3 here]

416   The full model (see Table 4) indicates that use of 'Always effective' tool techniques increased

417   significantly in the 'Narrow Tube' phase ($b = 2.93$, $p = .0013$); in the 'Narrow Tube' phase,

418   chimpanzees were 18.67 (Wald 95% CI [3.16, 110.47]) times more likely to use an 'Always

419   effective' technique than in the 'Wide Tube' phase. This indicates a significant increase in

420   'Always effective' technique use in the 'Narrow tube' phase, and as we present a binomial

421   GLMM, and each attempt made could only be 'Always effective' or 'Partially effective', an

422   equivalent significant decrease in the use of 'Partially effective' techniques.

423   There was no significant effect of Subgroup ($b = 1.57$, $p = .1631$) upon the likelihood of an

424   individual using 'Always effective' techniques in either Phase, and no significant interaction

425   between Phase and Subgroup ($b = -1.57$, $p = .2387$), indicating that the two Subgroups did not

426   respond significantly differently to the change in Phase. A likelihood ratio test indicated no

427   significant difference between this full model (including the impact of Subgroup and an

428   interaction with Phase) and a reduced model including only Phase ($\chi^2 = 1.52$, $df = 2$, $p = .4676$;

429   dAIC = 2.4), and so we present the full model with all predictors here.

430   [insert Table 4 here]

431   "Narrow Scaffolded" phase

432   Four individuals (Kindia, Edith, Frek, and Pearl) encountered the task with the scaffolded leafy

433   stick solution in place. Of these individuals, only two (Edith and Pearl) put the leaves in their

434   mouths to retrieve the reward. Frek and Kindia instead discarded the branch without retrieving

435   any reward from it. These four individuals (Kindia, Edith, Frek, and Pearl) who encountered the

436   leafy stick solution first-hand did not use the leafy stick solution (dipping the top, leafy part of

437   the branch in, rather than the bare, stick end). It therefore appears that scaffolding the behaviour

438   in this limited manner did not provide sufficient information for these chimpanzees to acquire a

439   novel 'Always effective' solution to the task.

440   **Discussion**

441   In this study, chimpanzees were found to be capable of responding with some flexibility to a

442   changing task. However, although individuals significantly increased their use of 'Always

443   effective' techniques in the 'Narrow Tube' phase, no individual that made more than one attempt

444   used 'Always effective' techniques for a majority of their attempts. This indicates that

445   chimpanzees' behavioural flexibility was limited by an inability to relinquish the previously

446   successful solutions used in the 'Wide Tube' phase, which continued to comprise at least 50% of

447   all individuals' attempts. Scaffolding provided to four individuals in an attempt to facilitate use of

448   an 'Always effective' technique in the final 'Narrow Scaffolded' phase did not result in the use of

449   this novel technique by this limited subsample of chimpanzees. Membership of subgroups with

450   differential experiential histories did not have a significant impact upon use of 'Always effective'

451   techniques. The principal issues addressed by the study are discussed in turn below.

452   Behavioural flexibility

453   Chimpanzees did typically alter their behaviour in response to the change in task, using

454   significantly more 'Always effective' techniques in the 'Narrow Tube' phase. However, no

455   individual that made more than one attempt used 'Always effective' techniques for a majority of

456   their attempts, in contrast with the findings of Manrique et al. (2013) in whose study chimpanzees

457   successfully used an effective solution for the majority of attempts in the appropriate condition.

458   Using a very similar task to the current study, Lehner et al. (2011) found that orangutans

459   preferentially used efficient methods when task constraints rendered their previous preferences

460   inefficient. Similarly, Davis et al. (2016) found that most chimpanzees used a novel, efficient

461   solution for the majority of attempts when the efficiency of their previously known solution

462   became very low, though this extent of switching was only observed in groups with a trained

463   demonstrator using the efficient solution or with human demonstrations provided: in 'non-

464   seeded' groups, only one individual switched to the efficient solution, but then used it for the

465 majority of attempts. These comparisons with previous research indicate that whilst chimpanzees

466 in this study showed behavioural flexibility (altered their behaviour), the flexibility was limited in

467 comparison to several previous studies, thus concurring with some other previous studies of

468 chimpanzees (Marshall-Pescini & Whiten 2008; Bonnie et al. 2012; Hrubesch et al. 2009). The

469 finding also concurs to some extent with experimental studies of wild chimpanzees which have

470 shown that individuals approach novel problems with culturally-informed known behaviours,

471 which may limit the extent to which individuals perceive the affordances of alternative tools

472 (Gruber et al. 2009, 2011). However, evidence from wild observations also shows that

473 chimpanzees are capable of modifying tool behaviour (Yamamoto et al. 2008), and using novel

474 materials to achieve known forms of tool use (Hobaiter et al. 2014), both of which indicate some

475 level of behavioural flexibility in individual wild chimpanzees.

476   Regarding the 'explore-if-dissatisfied' strategy discussed previously, we found that only

477 one novel technique emerged following the imposition of task constraints (see Table 2), and this

478 technique was used successfully only once. This would seem to indicate that chimpanzees in the

479 current study did not respond to the task changes by exploring the possibility of novel solutions,

480 but rather altered the extent to which they employed known solutions. Three individuals (Louis,

481 Emma and Edith) used a technique which was novel to them in the 'Narrow Tube' phase for a

482 considerable proportion of their attempts (see Table 3). The technique in question (*leafy stick dip*)

483 was not novel on a group level, and so this may be the result of observational learning (perhaps

484 indicating a 'copy-if-dissatisfied' strategy).

485   The relatively limited flexibility found in the current study could be due to differences in

486 task demands between the present study and others reporting more flexibility. One possible

487 explanation for the difference in the apparent level of flexibility seen in this study compared with

488 Davis et al. (2016) is the presence in the Davis et al. (2016) study of social information provided

489 by a trained, competent model. The scaffolding in the final 'Narrow Scaffolded' phase aside,

490 chimpanzees were not provided with trained conspecific demonstrators or human demonstrations

491 to offer social information about 'Always effective' techniques. Had the chimpanzees in this

492 study entirely failed to discover 'Always effective' techniques, this lack of experimentally-

493 provided social information would be a plausible explanation for the relatively diminished

494 behavioural flexibility observed. However, the majority of individuals tested used 'Always

495 effective' techniques in the 'Narrow Tube' phase, and indeed had access to social information in

496 the form of others using 'Always effective' techniques, indicating that they were not limited by a

497   lack of knowledge of the existence of such techniques, but rather failed to employ them as

498   frequently as they used 'Partially effective' techniques.

499   As in the current study, apes in Manrique et al. (2013) and Lehner et al. (2011) had to

500   discover more efficient solutions to the provided tasks without additional information from

501   experimenters (though in both Lehner et al. (2011) and the current study, apes were tested in a

502   group context and thus had access to any social information conspecifics provided). Though three

503   individuals did use an 'Always effective' technique that was novel to them in the 'Narrow Tube'

504   phase (Table 3), indicating a capacity for acquisition of novel behaviours via either social or

505   individual learning in response to the change in task, only three of the seven observed solutions

506   (*leafy stick dip*, *leaf squash,* and *stick drop*) were 'Always effective' in the 'Narrow Tube' phase.

507   This limited range of available solutions may have restricted chimpanzees' ability to respond

508   flexibly to the change in task. In comparison, orangutans in the Lehner et al. (2011) study

509   exhibited six effective solutions in 'Restricted Condition 1' (analogous to our 'Narrow Tube'

510   phase) and so had knowledge of a wider range of potential solutions that could be usefully

511   applied to the narrow tube. Comparison of the range of solutions discovered by chimpanzees in

512   the current study with the range of solutions observed by Tonooka, Tomonaga and Matsuzawa

513   (1997) in response to a task similar to the 'Wide Tube' phase of our study may indicate that

514   chimpanzees in our study were somewhat limited in their exploration of the task, with Tonooka et

515   al. (1997) observing 16 different solutions in comparison to only seven solutions seen in the

516   current study. Although chimpanzees in Tonooka et al. (1997) had access to a wider range of tool

517   materials, which, rather than a lack of exploration, may account for the discrepancy in the

518   number of solutions observed in their study and the current study, there were tool materials

519   available to chimpanzees in our study (namely *cloth* and *wood wool*) that were never used in the

520   'Wide Tube' phase, when there were few limitations to the efficacy of solutions.

521   The fact that chimpanzees in our study did not explore the potential of absorbent materials

522   as tool solutions to the task could suggest a role for 'functional fixedness' (Hanus et al. 2011) in

523   limiting their exploration of the task. While the chimpanzees are familiar with these absorbent

524   materials, they are primarily used as nesting material. The chimpanzees may therefore have

525   struggled to perceive them as having an alternative use. This does not appear to have constrained

526   the chimpanzees' use of leafy sticks as tools (despite such browse often also being used as nesting

527   material), though their reluctance to use the leaves of these sticks to dip with may also reflect a

528   level of 'functional fixedness', as only the stick portion of such leafy sticks appeared to be

529   considered functional by the chimpanzees.

530   In contrast to the current study, the tasks provided by Manrique et al. (2013) and Davis et

531 al. (2016) did not require the use of tools, and were solvable by hand. Tasks requiring tool use are

532 typically more challenging than those requiring purely manual actions, with the inclusion of tool

533 use more challenging for causal cognition (Seed, Call, Emery & Clayton 2009; Völter & Call

534 2014). The necessity of tool-use in the latter conditions of this study ('Narrow Tube' phases) may

535 therefore have impeded behavioural flexibility, perhaps by confounding the chimpanzees'

536 comprehension of the efficacy of their solutions, or impeding the acquisition of further 'Always

537 effective' solutions via social or asocial means.

538 <u>The Impact of Scaffolding</u>

539 The limited exposure to scaffolding provided to four chimpanzees in the third and final phase of

540 this study did not lead to the acquisition of novel techniques by any individual. This scaffolding

541 (providing the task with a leafy stick already inserted) aimed to approximate a form of

542 information chimpanzees have access to in the wild – the products and debris of other

543 chimpanzees' tool use, hypothesised to be a facilitator of learning local techniques by Tennie et

544 al. (2009) (eg. "…nut crackers and termite fishers leave their tools and detritus behind, and in the

545 right place, which makes the learning of their offspring and others much easier", pp.2406). This

546 information in the form of residual, enduring artefacts has been argued to facilitate technical

547 activities in New Caledonian crows, bearded capuchins, Japanese macaques and chimpanzees

548 (New Caledonian crows: Holzaider, Hunt & Gray 2009; bearded capuchins and chimpanzees:

549 Fragaszy et al. 2013; Japanese macaques: Lecca, Gunst & Hoffman 2010), although we are not

550 aware of any direct experimental evidence for such hypothesised effects.

551   While we are cautious in our interpretation of our results regarding scaffolding, given that

552 only four individuals had very limited interaction with the scaffolding, more extensive efforts to

553 provide this kind of information in experimental settings have often proven unsuccessful in

554 encouraging the invention of novel behaviours. Wild bearded capuchin monkeys from a

555 population which does not habitually use probing tools, when presented with a dipping task with

556 stick probes already inserted, never acquired probing behaviour (Cardoso & Ottoni 2016). Using

557 a similar task to the current study, Gruber et al. (2009) found that two communities of wild

558 chimpanzees had distinct tool use preferences when extracting honey from a cavity, with one

559 community solving the task using a stick tool while the other solved it using their hands or leaf

560 sponges. Subsequently providing this task to the hand/leaf-sponge community with a stick tool

561 already inserted failed to elicit stick tool use (Gruber et al. 2011). The authors interpret this

562   finding as evidence of "cultural bias" towards existing traditions of tool use, which constrains

563   how individuals perceive and evaluate the affordances of their environment (Gruber et al. 2011),

564   but it may also be that presenting chimpanzees with scaffolded solutions in this manner (at least

565   when numbers of such presentations are limited, with the majority of chimpanzees in Gruber et

566   al's study receiving only one or two exposures) simply provides insufficient information to elicit

567   acquisition of novel tool use behaviours. Gruber et al. (2011) argue that such limited exposure

568   may be ecologically valid, and tests the hypothesis that novel tool behaviours will emerge in

569   direct response to favourable affordances (a situation which highlights the physical properties of

570   potential tool materials and indicates the potential relationship between tool and goal), but the

571   possibility remains that such limited exposure to scaffolding is insufficient to impact behaviour.

572   Similarly, experiments incorporating 'ghost conditions', in which the operational

573   affordances of a task are demonstrated without the presence of a demonstrator individual (e.g.

574   task components are moved by fine fishing line or similar), perhaps also corroborates the

575   insufficiency of such scaffolding. Hopper et al. (2007, 2015) found that demonstration of the

576   workings of a 'Panpipes' apparatus in such a ghost condition did not lead chimpanzees to

577   discover the solution to the task. The efficacy of such ghost demonstrations may be affected by

578   the complexity of the task (Hopper, Lambeth, Schapiro and Whiten 2008), with complex tool use

579   perhaps proving more challenging to learn via such demonstrations. The information provided by

580   these scaffolded conditions (as the current study, and Gruber et al. 2011) can also be argued to be

581   even more impoverished than that provided by ghost conditions as it does not incorporate

582   movement, and so may not demonstrate the affordances of a task to the same extent as moving

583   displays.

584   Providing further groups of chimpanzees with scaffolding approximating the artefacts of

585   other's tool use they might encounter in the wild, perhaps in the context of novel tool use tasks

586   for which no pre-existing cultural biases are likely to exist, could shed further light on the ability

587   of chimpanzees to learn novel behaviours from this sort of information, and indicate whether

588   chimpanzees are limited by cultural biases, by the relative poverty of the information provided by

589   scaffolding, or simply require more extensive exposure to scaffolding in order to acquire novel

590   behaviours.

591   Subgroup differences

592   Subgroup membership was found to have no significant effect on the likelihood of individuals

593   using 'Always effective' techniques in either the 'Wide' or 'Narrow' tube phase, with both groups

594 increasing their use of 'Always effective' techniques in the 'Narrow' tube phases. Previous

595 research has found that chimpanzees reared in captivity perform more poorly than wild-born

596 chimpanzees in tool-use tasks. Morimura and Mori (2010) found that captive-reared chimpanzees

597 were less likely to succeed than wild-born chimpanzees on a tool use task involving retrieving

598 juice from a bottle using a provided stick tool. Similarly, Brent et al. (1995) found that both

599 captive mother-reared and captive nursery-reared chimpanzees were less likely to succeed than

600 wild-born chimpanzees (in captivity) on a reaching tool task. Rearing history has also been found

601 to have an impact on nest-building, with wild-born chimpanzees in captivity spending more time

602 constructing and using nests than captive-born chimpanzees, and using more complex techniques

603 in their nest building, while within the captive-born chimpanzee sample, mother-reared

604 individuals spent more time than nursery-born individuals making and using nests (Videan 2006).

605 Some research indicates that housing can influence performance on cognitive tests, with

606 Vlamings, Hare and Call (2010) finding that sanctuary-housed chimpanzees and bonobos

607 outperform zoo-housed apes in a detour-reaching task testing inhibitory control. However,

608 Wobber and Hare (2011), using a subset of the Primate Cognition Test Battery (Herrmann et al

609 2007) found no impact of housing (zoo vs sanctuary) on the performance of mother-reared

610 chimpanzees on tests of social or physical cognition, but did find that mother-reared individuals

611 (regardless of housing) outperformed orphaned individuals on physical cognition tests – this

612 effect was due to improved performance on a tool properties task in which individuals chose

613 between a functional and non-functional tool. Similarly, Herrmann, Wobber and Call (2008)

614 found no difference in performance between zoo- and sanctuary-housed chimpanzees and

615 orangutans on a tool functionality choice task.

616   We did not find evidence of subgroup differences in the current study, though the

617 subgroups compared here were based upon the chimpanzees' housing history rather than their

618 rearing. Although only the Beekse Bergen group includes individuals hand-reared by humans,

619 and this is the most common rearing history for this subgroup (five of nine individuals), both

620 groups include both wild- and captive-born mother-reared individuals. Sample size precluded any

621 analysis based upon rearing history (with only three individuals categorised as wild-born, only

622 two of which participated in both the 'Wide' and 'Narrow Tube' phases of the task), and given the

623 difference in origin of the two groups (laboratory vs. zoo) it was thought a subgroup analysis

624 might capture any differences in performance related to early life experiences. It may be that,

625 between captive environments housing chimpanzees with mixed rearing histories, there is little

626 difference in performance to be found using artificial foraging tasks such as the current task.

627   However, further groups of chimpanzees in different captive facilities would have to be provided

628   with the task in order to test this. Examination of the impact of both housing and rearing histories

629   upon chimpanzee performance in experimental tasks is essential for a full understanding of

630   chimpanzee cognition (Boesch 2007).

631   <u>Limitations to the current study</u>

632   While some previous studies of chimpanzee and great ape behavioural flexibility have tested

633   individuals in isolation (Manrique & Call 2013, 2015; Marshall-Pescini & Whiten 2008), and this

634   approach allows for control over chimpanzees' access to social information about the task and the

635   avoidance of issues around task monopolization by dominant individuals, we note that many

636   previous studies have presented tasks in a group context (Lehner et al 2011; Davis et al. 2016;

637   Gruber et al. 2009, 2011). This may be due to the constraints of conducting research at captive

638   facilities (or, in the case of Gruber et al. (2009, 2011), in the wild), or be a methodological choice

639   in order to explore the social learning abilities of subjects (Davis et al. 2016). The open

640   presentation of the task in the current study to the group of chimpanzees prevents us from making

641   claims regarding the process by which novel behaviours emerged and spread in individuals

642   during the trials (whether this occurred via social learning or innovation). However, following

643   Lehner et al.'s (2011) definition of behavioural flexibility, as the continued acquisition of novel

644   techniques via either social or asocial learning, group testing in this manner allows flexibility to

645   be demonstrated through either form of learning.

646   This study focused upon a community of chimpanzees with particular life histories

647   (primarily captive born) and was also limited to adult chimpanzees, with no infants or juveniles

648   in the population. Previous research has shown that cognitive flexibility (measured by a simple

649   reversal task) follows a U-shaped curve in great apes, with optimum performance in terms of

650   error avoidance appearing to occur between seven and 27 years of age (Manrique & Call 2015),

651   and so the age of many individuals in the current study may have impaired their performance.

652   With a sample of only ten individuals providing data across the 'Wide' and 'Narrow Tube'

653   phases, analysis of age effects was not possible in the current study, but Manrique and Call's

654   (2015) findings demonstrate the importance of considering the impact of age upon cognitive

655   performance when possible. Whilst we found no effect of subgroup (laboratory vs. zoo) in our

656   sample, previous research has shown that rearing history may have an impact upon problem-

657   solving and tool-use behaviour (Wobber & Hare 2011; Brent et al. 1995; Morimura & Mori

658   2010), and again, due to insufficient sample size, it was not possible to make comparisons in our

659   dataset based upon rearing (as opposed to housing). Position in the dominance hierarchy could

660   also impact performance on an artificial foraging task such as that of the current study. Low

661   ranking individuals may be more likely to innovate novel behaviours (Reader & Laland 2001),

662   and in a group context, dominance may impact the likelihood of others acquiring a behaviour

663   from an individual via social learning (Horner, Proctor, Bonnie, Whiten & de Waal, 2010; Kendal

664   et al., 2015, though see also Watson et al., 2017). Future work would benefit from expanding the

665   sample to include a more diverse range of ages and rearing histories, in sufficient numbers to

666   enable an analysis of the potential effects of these and other factors which might influence

667   participation and performance upon artificial foraging tasks, such as position in the dominance

668   hierarchy.

669   <u>Conclusions</u>

670   Chimpanzees in this study did respond flexibly to a changing task, increasing their use of

671   'Always effective' techniques when task alterations rendered previously used solutions

672   unrewarding. However, no individual altered their behaviour to the extent of using 'Always

673   effective' solutions for a majority of attempts, indicating relatively limited behavioural flexibility

674   in comparison with some previous research (Davis et al. 2016; Manrique et al. 2013; Lehner et al.

675   2011) and a tendency to continue to use previously rewarded behaviours. The relatively limited

676   flexibility observed here may be due to the complexity of the task, which required tool use. A

677   subset of chimpanzees did not acquire a more effective, novel, tool technique when provided with

678   a single instance of scaffolding towards the solution. However, this study focused upon a

679   community of chimpanzees with particular life histories (primarily captive-born) and was also

680   limited to adult chimpanzees, with no infants or juveniles in the population. Research has shown

681   that both rearing history and housing may impact great ape performance on cognitive tests,

682   perhaps especially those involving tool use, indicating that ideally, multiple groups of

683   chimpanzees from different environments and rearing histories should be considered when

684   studying behaviour and cognition. The current study is somewhat limited in this regard, though

685   no difference was found between the two subgroups (laboratory and zoo chimpanzees) included.

686   Future work would benefit from expanding the sample to include a more diverse range of ages

687   and backgrounds.

688   Research on behavioural flexibility in chimpanzees, both in the wild and in captivity,

689   using a variety of artificial foraging tasks, continues to provide divergent results, with some

690   studies indicating strong conservatism, while others find an ability to relinquish known solutions

691   in favour of more rewarding or efficient techniques. Further work must been done to investigate

692   what factors limit or encourage flexibility in great apes, with promising avenues for further study

693   being the relative complexity of the task (for example, the requirement for tool use versus tasks

694   which can be solved by hand), the disparity in efficacy between known and alternative techniques

695   (whether the established solutions become entirely unrewarded or simply less efficient or

696   rewarding than an alternative) and investigation of individual characteristics such as age or rank

697   which may promote or constrain behavioural flexibility.

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Figure 1

Image of the apparatus as presented to chimpanzees.

The 'wide' tube as presented to the chimpanzees within the research pod. The 'narrow' tube was presented in the same manner. The height of both tubes was 30cm, with the 'wide' tube diameter measuring 10cm and the 'narrow' tube diameter measuring 5cm.

Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.
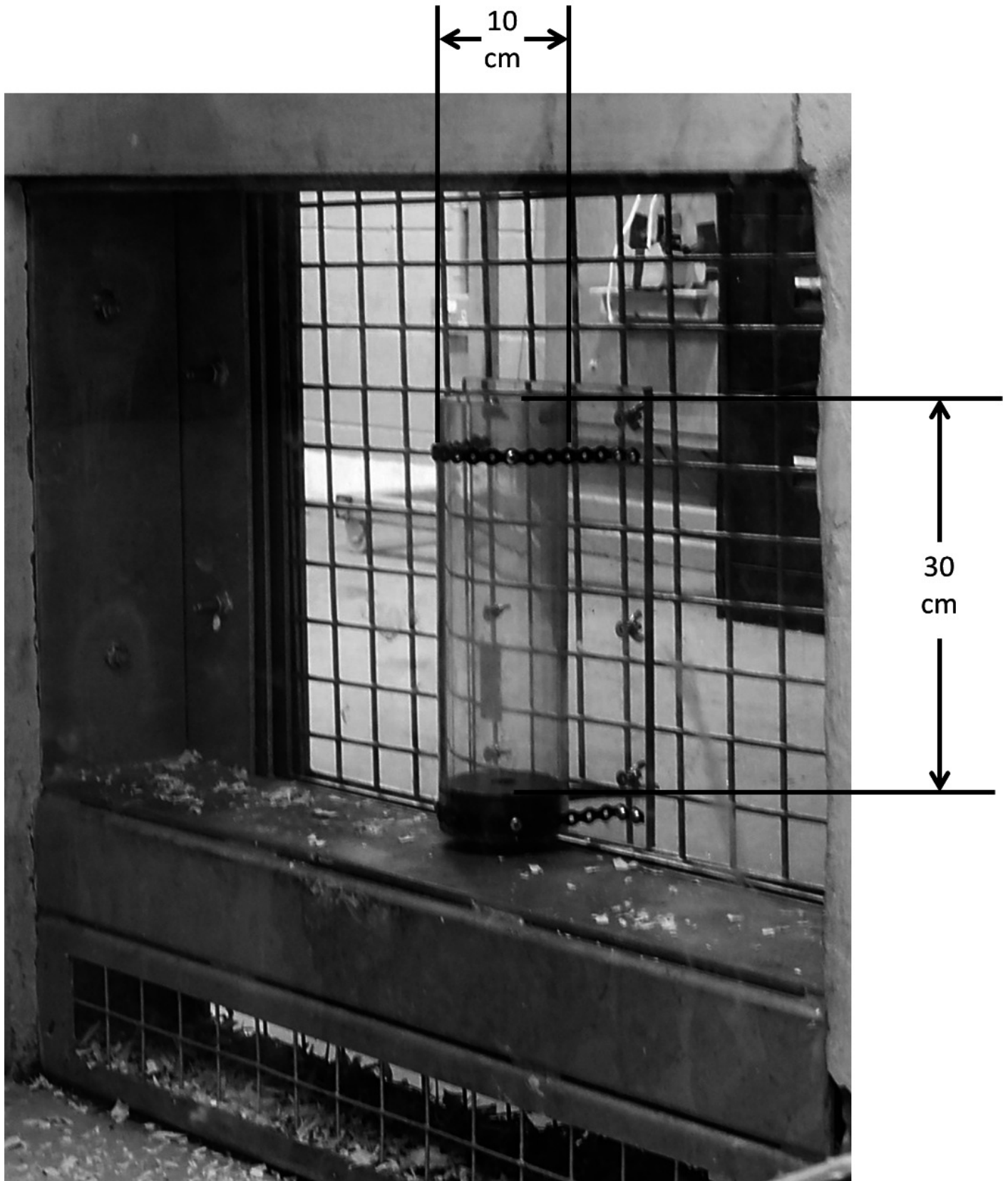
Figure 2

Proportion of attempts made using 'Always effective' techniques in the 'Wide' and 'Narrow' tube phases.

Proportion of attempts made using 'Always effective' techniques in 'Wide' vs 'Narrow' tube phases by the ten chimpanzees that took part in both phases. Individual chimpanzees' proportions are indicated by dots. Coloured horizontal bars show each subgroup's mean proportion. Black horizontal bars show overall mean proportion. Note that in the 'Narrow Tube' phase, the subgroup means and overall mean are the same.
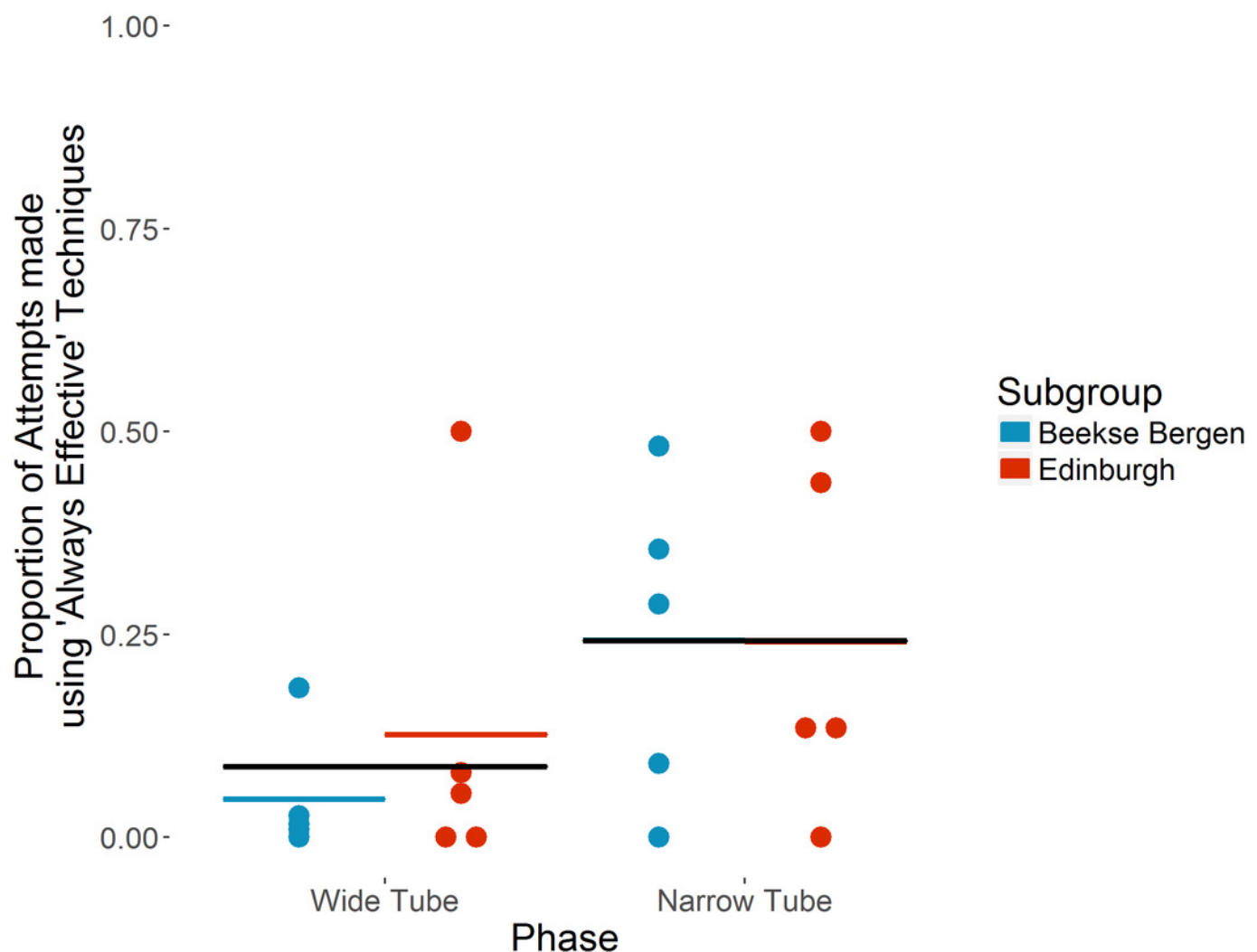
Table 1(on next page)

Demographic and Rearing Information of the Chimpanzees with Level of Participation in Current Study

Table 1.

Demographic and Rearing Information of the Chimpanzees with Level of Participation in Current Study.

Subgroup	Individual	Sex	Year of birth (age at time of testing)	Origin (wild or captive born)	Rearing	Participation in current study (number of attempts)		
						Wide Tube	Narrow Tube	Narrow Scaffolded
Edinburgh	Qafzeh	M	1992 (22)	Captive	Mother	0	1	0
	Kindia	M	1997 (17)	Captive	Mother	14	4	1
	Liberius	M	1999 (15)	Captive	Mother	1	0	1
	David	M	1975 (39)	Captive	Mother	4	0	0
	Louis	M	1976 (38)	Wild		6	15	0
	Lucy	F	1976 (38)	Captive	Mother	11	2	0
	Kilimi	F	1993 (21)	Captive	Mother	175	103	87
	Cindy	F	1964 (50)	Wild		0	0	10
	Emma	F	1981 (33)	Captive	Mother	37	59	0
Beekse Bergen	Paul	M	1993 (21)	Captive	Hand-raised	0	0	0
	Pearl	F	1969 (45)	Wild		311	214	40
	Sofie	F	1981 (33)	Captive	Hand-raised	3	0	2
	Lianne	F	1989 (25)	Captive	Mother	0	0	0
	Heleen	F	1991 (23)	Captive	Mother	4	0	0
	Edith	F	1996 (18)	Captive	Mother	385	741	73
	Eva	F	1980 (34)	Captive	Hand-raised	311	21	4
	Frek	M	1993 (21)	Captive	Hand-raised	125	80	11
	Rene	M	1993 (21)	Captive	Hand-raised	152	11	3

Note: In addition to their own attempts, all individuals with the exception of Cindy and Liberius were present in the research pods during another individual's attempt on at least one occasion.

Table 2(on next page)

Techniques successfully used to solve the task

Note: Dashed horizontal line indicates transition between the 'Wide Tube' and 'Narrow Tube' phases.

Table 2.

Techniques successfully used to solve the task

Technique	Description	Latency to first successful use from start of first testing session	Effective in 'Wide Tube' phase?	Maintained efficacy in 'Narrow Tube' phase?	Effective in all phases?
Hand dip	Dip hand directly into juice	00:00:35	Yes	No	Partially effective
Stick dip	Stick is dipped directly into the juice	00:00:43	Yes	No	Partially effective
Stick retrieve	Stick already in tube removed with hand	00:23:38	Yes	No	Partially effective
Stick drop	Drop stick into tube then retrieve by hand	00:21:16	Yes	Yes	Always effective
Leafy stick dip	Dip stick end of a leafy branch directly into the juice (this differs from 'stick dip' only in the material) This technique remained Effective in Narrow tube phases due to the flexibility of the leafy sticks in comparison to standard sticks	02:47:23	Yes	Yes	Always effective
Leaf squash	A leafy branch is inserted stick first, and the leaves are then forced down into the tube into contact with the juice (*Note*: this technique was used successfully only once)	05:56:26	Yes	Yes	Always effective
Wood wool retrieve	Wood wool pushed part way into tube by a previous individual removed with hand (*Note*: this technique was used successfully only once)	11:43:12	Yes	No	Partially effective

Note: Dashed horizontal line indicates transition between the 'Wide Tube' and 'Narrow Tube' phases. The 'Narrow Tube'.phase began at 8:17:44 (the start of the 11th experimental session).

Table 3 (on next page)

The two most frequently used techniques of individuals that made attempts in both the 'Wide' and 'Narrow' tube phases.

The two most frequently used techniques of individuals that made attempts in both the 'Wide' and 'Narrow' tube phases. 'Always effective' techniques are shown in bold. An asterisk indicates that an individual used a technique for the first time within the 'Narrow' Tube phase (ie. that the technique was novel to them). Note: Percentages are rounded.

1 Table 3.

2 *The two most frequently used techniques of individuals that made attempts in both the 'Wide'*

3 *and 'Narrow' tube phases. 'Always effective' techniques are shown in bold. An asterisk indicates*

4 *that an individual used a technique for the first time within the 'Narrow' Tube phase (ie. that the*

5 *technique was novel to them).*

Subgroup	Individual	'Wide Tube' phase		'Narrow Tube' phase	
		1st preferred technique (no. of attempts; % of attempts)	2nd preferred technique (no. of attempts; % of attempts)	1st preferred technique (no. of attempts; % of attempts)	2nd preferred technique (no. of attempts; % of attempts)
Edinburgh	Kindia	Stick dip (6; 43%)	**Leafy stick dip** (6; 43%)	Stick dip (2; 50%)	**Leafy stick dip** (2; 50%)
	Louis	Stick dip (6; 100%)		Stick dip (13; 87%)	***Leafy stick dip** (2; 13%)
	Lucy	Stick dip (7; 64%)	Hand dip (4; 36%)	Stick dip (2; 100%)	
	Kilimi	Stick dip (127; 73%)	Hand dip (33; 19%)	Stick dip (49; 48%)	**Leafy stick dip** (44; 43%)
	Emma	Stick dip (19; 51%)	Hand dip (16; 43%)	Stick dip (38; 64%)	Hand dip (8; 14%) / ***Leafy stick dip** (8; 14%)
Beekse Bergen	Pearl	Hand dip (165; 53%)	Stick dip (134; 43%)	Stick dip (119; 56%)	**Leafy stick dip** (71; 33%)
	Edith	Stick dip (320; 83%)	Hand dip (64; 17%)	Stick dip (364; 49%)	***Leafy stick dip** (294; 40%)
	Eva	Stick dip (237; 76%)	Hand dip (61; 20%)	Stick dip (12; 57%)	Hand dip (5; 24%)
	Frek	Hand dip (74; 59%)	Stick dip (27; 22%)	Stick dip (40; 50%)	**Stick drop** (23; 29%)
	Rene	Hand dip (141; 93%)	Stick dip (7; 5%)	Hand dip (6; 55%)	Stick dip (3; 27%)

6 *Note:* Percentages are rounded.

7

Table 4(on next page)

Results of full model GLMM on the effects of Phase, Subgroup and an interaction between the two upon 'Always effective' technique use.

Table 4.

Results of full model GLMM on the effects of Phase, Subgroup and an interaction between the two, with random intercept and slope for Individual by Phase upon 'Always effective' technique use. Variance, standard deviation, and correlation for the random intercept and slope for Individual by Phase is provided.

Fixed effects	Estimate	[Wald 95% CI]	Std. Error	*z* value	*p* value	
Intercept (including 'Wide Tube' phase and Beekse Bergen subgroup)	-4.13	[-5.62, -2.64]	0.76			
Phase ('Narrow Tube')	2.93	[1.15, 4.70]	0.91	3.23	0.0013	**
Subgroup (Edinburgh)	1.57	[-0.63, 3.77]	1.12	1.40	0.1631	
Phase*Subgroup	-1.57	[-4.17, 1.04]	1.33	-1.18	0.2387	

Random effects	Variance			Std. Deviation	Correlation
Individual (Intercept)	2.46			1.57	
Slope by Phase	3.31			1.82	-0.87

**=$p < 0.01$