Testing the individual and social learning abilities of task-naïve captive chimpanzees (*Pan troglodytes sp.*) in a nut-cracking task

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Nut-cracking is often cited as one of the most complex behaviours observed in wild chimpanzees. However, the cognitive mechanisms behind its acquisition are still debated. The current null hypothesis is that the form of nut-cracking behaviour relies on variants of social learning, with some researchers arguing, more precisely, that copying variants of social learning mechanisms are necessary. However, to date, very few experiments have directly investigated the potentially sufficient role of individual learning in explaining the behavioural form of nut-cracking. Despite this, the available data provides some evidence for the spontaneous acquisition of nut-cracking by chimpanzees; later group acquisition was then found to be at least facilitated by (unspecified) variants of social learning. The latter findings in line with both suggested hypotheses, i.e., that copying social learning is required and that other (non-copying) social learning mechanisms are at play. Here we present the first study which focused (initially) on the role of individual learning for the acquisition of the nut-cracking behavioural form in chimpanzees. We tested task-naïve chimpanzees (N=13) with an extended baseline condition to examine whether the behaviour would emerge spontaneously. After the baseline condition (which was unsuccessful), we tested for the role of social learning by providing social information in a step-wise fashion, culminating in a full action demonstration of nut-cracking by a human demonstrator (this last condition made it possible for the observers to copy all actions underlying the behaviour). Despite the opportunities to individually and/or socially learn nut-cracking, none of the chimpanzees tested here cracked nuts using tools in any of the conditions in our study. We conclude that this failure was the product of interplay of factors, including behavioural conservatism and the existence of a potential sensitive learning period for nut-cracking in chimpanzees. The possibility remains that nut-cracking

is a behaviour that chimpanzees can individually learn. However, this behaviour might only be acquired when chimpanzees are still inside their sensitive learning period, also when ecological and developmental conditions allow for it. The possibility also remains that nut-cracking is an example of a culture dependent trait in non-human great apes. Recommendations for future research projects to address this question are considered.

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29 **Abstract**

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31 chimpanzees. However, the cognitive mechanisms behind its acquisition are still debated. The

32 current null hypothesis is that the form of nut-cracking behaviour relies on variants of social

33 learning, with some researchers arguing, more precisely, that copying variants of social learning

34 mechanisms are necessary. However, to date, very few experiments have directly investigated

35 the potentially sufficient role of individual learning in explaining the behavioural form of nut-

36 cracking. Despite this, the available data provides some evidence for the spontaneous acquisition

37 of nut-cracking by chimpanzees; later group acquisition was then found to be at least facilitated

38 by (unspecified) variants of social learning. The latter findings in line with both suggested

39 hypotheses, i.e., that copying social learning is required and that other (non-copying) social

40 learning mechanisms are at play. Here we present the first study which focused (initially) on the

41 role of individual learning for the acquisition of the nut-cracking behavioural form in

42 chimpanzees. We tested task-naïve chimpanzees (N=13) with an extended baseline condition to

43 examine whether the behaviour would emerge spontaneously. After the baseline condition

44 (which was unsuccessful), we tested for the role of social learning by providing social

45 information in a step-wise fashion, culminating in a full action demonstration of nut-cracking by

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48 cracking, none of the chimpanzees tested here cracked nuts using tools in any of the conditions

49 in our study. We conclude that this failure was the product of interplay of factors, including

50 behavioural conservatism and the existence of a potential sensitive learning period for nut-

51 cracking in chimpanzees. The possibility remains that nut-cracking is a behaviour that

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55 of a culture dependent trait in non-human great apes. Recommendations for future research

56 projects to address this question are considered.

Introduction

58 **Introduction**

59 Humans have created a unique niche within the animal kingdom, one that (most likely)

60 relies on an ability to transfer knowledge between and within generations, allowing our species

61 to inhabit almost every environment on the planet. However, modern industrialised human

62 society is so far removed from that of our ancestors, that it is difficult to understand how our

63 cultural ability – or our cultural niche (Odling-Smee, Laland, & Feldman, 2003) – evolved.

64 Therefore, the closest extant relatives of the *hominin* clade, non-human great apes (hereafter:

65 apes), are often used as a phylogenetic proxy to help shed light on our own evolution.

66 Modern human culture may be unique in the animal kingdom (Tomasello, 1998) – at

67 least in the technological domain (Tennie, Caldwell, & Dean, 2018). Thus, to allow for the study

68 of culture *across* species, a more minimal (or soft) definition of culture is required. Here we

69 follow the terminology suggested recently by Neadle, Allritz and Tennie (2017), in which a

70 cultural trait is any behaviour that is at least influenced (including merely its frequency being

71 facilitated or catalysed; Tennie, Call, & Tomasello, 2010) by social learning. Within this

72 definition of culture, the social learning mechanisms at play can be any of the many proposed

73 variants (for an overview, see Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). This

74 minimal definition of culture allows for the identification of cultures that involve a range of

75 social learning variants, including ones that rely on the copying of behaviour directly (often

76 called imitation, see, e.g., Whiten & Ham, 1992). Crucially, the minimal definition of culture

77 also encompasses examples of behavioural forms that can emerge without requiring social

78 learning. Instead, behaviours that *rely* on (i.e., cannot occur in the absence of) copying variants

79 of social learning are 'culture dependent traits' (henceforth CDTs; see Reindl, Apperly, Beck, &

80 Tennie, 2017; Tennie, Caldwell, & Dean, 2018). Some animal cultures may be culture dependent

81 (e.g., whale song is a candidate CDT; Tennie et al., 2018), but whether any animal tool use

82   qualifies as CDT is a matter of considerable debate (Galef, 1992; Kendal, 2008; Tennie, Call, &

83   Tomasello, 2009). In the human case, technology has often evolved to the point that no naïve

84   individual could reinnovate the behaviour on their own within their lifetime (Galef, 1992;

85   Tomasello, Kruger, & Ratner, 1993), making many modern human traits CDTs and indeed

86   examples of cumulative culture (Boyd & Richerson, 1996) .

87   Amongst non-human animals (hereafter: animals), chimpanzees (*Pan troglodytes*) are,

88   for now, the 'most cultural' species – at least in terms of (known) numbers of cultural traits

89   (Whiten et al., 1999) – where a mere increase in sheer number of cultural traits is known as

90   accumulation (Dean, Vale, Laland, Flynn, & Kendal, 2014). However, accumulation (numbers of

91   traits) should not be confused with *cumulation*, i.e. the cultural change of the traits themselves

92   along transmission pertaining to cumulative culture (Dean et al., 2014). Only the latter is the

93   result of the 'ratchet effect' (Tomasello et al., 1993), which underlies cumulative culture (Boyd

94   & Richerson, 1996) – and is responsible for the special product of cumulative culture: CDTs

95   (Reindl et al., 2017). Therefore, whilst chimpanzees' number of cultural traits is impressive, for

96   those concerned with human cultural evolution, the presence or absence of CDTs in chimpanzees

97   is of particular interest.

98   Regarding chimpanzee culture, nut-cracking is considered one of the most complex

99   behaviours expressed by any wild apes. Complexity can refer to the number of parts within a

100   final artefact/behaviour (techno-units; Oswalt, 1976), the goals and sub goals of an action (Read

101   & Andersson, 2019), the manual dexterity of an action (Foucart et al., 2005) and the number of

102   "rules" necessary to describe the behaviour (Sirianni, Mundry, & Boesch, 2015), amongst other

103   metrics (see Vaesen & Houkes, 2017 for further discussion of complexity). Nut-cracking

104   requires a high level of dexterity (Foucart et al., 2005) and involves several tools in various steps

105   that need to be followed in a specific sequential order to produce the desired effect (Biro et al.,

106   2003; Boesch, Bombjaková, Meier, & Mundry, 2019; Inoue-Nakamura & Matsuzawa, 1997;

107   Read & Andersson, 2019); thus, it can be considered a complex behavioural form. Furthermore,

108   nut-cracking is rare across wild communities, (so far) only being documented in two

109   geographically separate populations: two communities in West Africa (Bossou, Guinea and Taï

110   Forest, Côte d'Ivoire Whiten et al., 2001) and one in Ebo Forest, Cameroon (Morgan & Abwe,

111   2006; although note that these data are based on indirect evidence and should be treated with

112   some degree of caution).

113   The number of steps alongside with the manual dexterity and use of multiple objects

114   required for this behaviour suggests that nut-cracking is most likely a complex behaviour for

115   chimpanzees. The basic behavioural form of nut-cracking consists of the following four

116   sequential steps, though note that other steps might occur:

117   1. Place nut on anvil

118   2. Pick up hammer (unless already picked up)

119   3. Lift hammer up

120   4. Drop/push the hammer onto nut (all may be repeated).

121   Perhaps due to this apparent complexity, nut-cracking is often assumed to be culturally

122   transmitted (Boesch & Boesch-Achermann, 2000; Lycett, Collard, & McGrew, 2007, 2010),

123   with some researchers arguing that action copying (or imitation) must be the mechanism

124   responsible for its acquisition. For example, Boesch (1996) claims that chimpanzees learn how to

125   crack nuts "by individual and social learning, *including imitation*" (Boesch, 1996, p. 418,

126   emphasis added), Biro et al (2003, p. 220) further argue that when nut-cracking "infant

127   chimpanzees are driven not by a motivation for food but to produce a *copy of the mother's*

128   *actions*" [emphasis added]. More generally, others agree, claiming that nut-cracking (alongside

129   other chimpanzee traits) are difficult to explain "by social learning processes simpler than

130   imitation" (Whiten et al., 1999, p. 685). More recently, similar claims have been made that

131   chimpanzees rely on mother to infant "*teaching*" to acquire the skills required to crack nuts at a

132   rate consistent with that of others within their community (Boesch et al., 2019). Some have

133   further argued that young wild chimpanzees engage with this process during a so-called

134   'sensitive learning period' between the ages of approx. 3.5 years and 10 years (Inoue-Nakamura

135   & Matsuzawa, 1997; Matsuzawa, 1994; Biro et al., 2003).

136   However, other research has suggested that migratory primates, outside the estimated

137   sensitive learning period, can still engage with and adopt behaviours – perhaps in keeping with

138   their new groups. Most relevant here, Luncz, Mundry and Boesch (2012) describe how migrant

139   female chimpanzees adapt their hammer choice during nut-cracking to conform to that of their

140   new group. The migrating females were beyond the age of sexual maturity, and so outside their

141   sensitive learning period. The fact that these individuals can modify their behaviour in this way,

142   suggests that the possibility remains for individuals outside of the sensitive learning period to

143   adopt the full behavioural form. This said, these findings are not evidence of the behavioural

144   form of nut-cracking emerging for the first time, instead are evidence of behaviours being

145   adapted and therefore whilst interesting might not represent a strong argument against the notion

146   of a sensitive learning period.

147   In conclusion, the behaviours underpinning nut-cracking have been argued to require

148   social learning (in particular action copying and/or unspecified variants of teaching). Therefore,

149   it has been assumed that nut-cracking is outside of naïve chimpanzees' individual learning

150   abilities, which would make nut-cracking a CDT (sensu Reindl et al., 2017). This is a clear claim

151 that can be tested. If nut-cracking requires social learning (if it is indeed a CDT), it should re-

152 appear when a naïve chimpanzee has access to a model nut cracker to observe. This would

153 provide evidence for the view that social learning is required for nut-cracking to occur. However,

154 the absence of data should not be considered as evidence itself; accordingly, the lack of evidence

155 for nut-cracking even at the end of this study should only be considered as an indication that it

156 might not be a CDT rather than concrete evidence for it, such a result would need replicating in

157 another population before confident assumptions can be made from the data. Indeed, it is

158 possible that environmental, social or individual factors might influence the likelihood of

159 expression (*sensu* Tennie et al., 2009). However, if nut-cracking does occur in a baseline

160 condition in this naïve population, this *would* constitute evidence that naïve chimpanzees have

161 the capacity to reinnovate nut-cracking in the absence of social learning (i.e. it is within the

162 species' ZLS).

163   In one formulation, the Zone of Latent Solutions (ZLS) hypothesis (Tennie et al., 2009)

164 posits that all non-human great ape 'cultural' behaviours can be reinnovated (defined by Bandini

165 & Tennie, 2017) by naïve apes. This specific case has been termed as the 'ZLS-Only' hypothesis

166 (Reindl, Bandini & Tennie, 2018). In line with this, Hayashi, Mizuno and Matsuzawa (2005)

167 suggested that nut-cracking could potentially be individually reinnovated by chimpanzees. Some

168 field reports support these views; for example, a report of nut-cracking in Cameroon (Morgan &

169 Abwe, 2006) passes the 'information barrier' of the N'Zo-Sassandra River (McGrew, Ham,

170 White, Tutin, & Fernandez, 1997). This report can be regarded as the outcome of a natural quasi-

171 latent solution test (sensu Bandini & Tennie, 2018), as this pattern strongly suggests that that

172 nut-cracking was (re-)innovated in two, culturally separate, wild communities (Tennie et al.,

173   2009, p. 2406). Though, again, these results should be considered in the light of the fact that they

174   are supported by second hand reports, sounds in the forest and finding of tools.

175   If all underlying steps of the nut-cracking behaviour are also found to be reinnovated by a

176   naïve, captive, chimpanzee in a culturally separate "island" of individuals (Tennie, Braun,

177   Premo, & McPherron, 2016; Tomasello, 1999) then the behaviour would (by definition) cease to

178   be a putative example of an animal CDT. This would support the ZLS hypothesis and would

179   suggest that chimpanzees are capable, in principle, of individually learning the basic behaviour

180   form underpinning nut-cracking; demonstrating that social learning is not *required* for this to

181   occur. Importantly, it should be noted that social learning is likely to play a role in the process of

182   chimpanzees understanding that nuts are a food source and, in addition, that they can be

183   considered a 'safe' food (Hopper, Schapiro, Lambeth, & Brosnan, 2011). Although this process

184   is important for the frequency of nut-cracking within and across populations, our study is

185   concerned with the mechanisms underlying tool-use aspect of the behavioural form of nut-

186   cracking.

187   Therefore, here we test two competing hypotheses: chimpanzee nut-cracking as a culture

188   dependent trait (the "CDT hypothesis") versus chimpanzee nut-cracking as a behaviour that can

189   be individually learned (re-innovated; Bandini & Tennie, 2017), but whose expression may

190   nevertheless be facilitated by non-copying variants of social learning (the "ZLS hypothesis",

191   compare Tennie et al., 2009; in press). Simply, the ZLS hypothesis posits that nut-cracking

192   should emerge in a 'baseline' condition, i.e., without requiring social learning. Contrastingly, the

193   CDT hypothesis argues that copying variants of social learning are necessary for the emergence

194   of nut-cracking in a naïve sample.

195   Thus far, various chimpanzee behavioural traits, previously assumed to be culture

196   dependent, have been reinnovated by naïve, captive subjects in latent solution tests (Bandini &

197   Tennie, 2017, 2019; Menzel, Fowler, Tennie, & Call, 2013; Motes-Rodrigo et al., 2019; Neadle

198   et al., 2017; Tennie et al., 2009; Tennie, Hedwig, Call, & Tomasello, 2008). These behaviours

199   ('latent solutions'; Tennie et al., 2009), were reinnovated without requiring any observation (or

200   teaching). This does not, however, mean that social learning does not play any role in the

201   innovation likelihood of these behavioural forms. Indeed, several variants of non-copying social

202   learning (the specific mechanism was not directly tested in the studies mentioned above) greatly

203   facilitate the innovation likelihood of the behaviour in both captive and wild chimpanzees

204   (therefore affecting the observed frequencies of behaviours within and across populations;

205   Tennie et al., in press; Bandini & Tennie, 2017, 2019).

206   In the current study, we tested both the CDT and the ZLS hypothesis predictions for nut-

207   cracking. In 2010, Tennie et al. hypothesised that nut-cracking would be within the chimpanzee

208   ZLS, but that it may simply have a relatively low baseline probability of reinnovation (i.e., it is at

209   the very edge of the chimpanzee ZLS). We were able to test both hypothesis by applying the

210   extended latent solutions testing methodology (first described in Bandini & Tennie, 2018). This

211   method first starts by testing for the reinnovation of the target behavioural form (here nut-

212   cracking) in completely naïve chimpanzees (we ensured naivety by asking keepers of the

213   animals' previous experiences of the behaviour) – thus testing the ZLS hypothesis. If the

214   behaviour does not appear in this baseline, subjects are then provided with incremental levels of

215   social learning information. The particular methodology followed in this study allows for the

216   examination of the role of individual learning (initial baseline test), then subsequently for end-

217 state emulation, goal emulation and finally action copying (imitation) in the emergence of the

218 target trait.

219

Materials & Methods

221 **Subjects**

222 The subjects were 13 chimpanzees (M_{age} = 31.08; SD = 1; female = 9, male = 4; See

223 Table 1; *Pan troglodytes sp.).* All subjects lived within a single group and comprised the entirety

224 of that group, except for one individual (C13), which, due to group transfers within the

225 zoological institution throughout the duration of this study, was introduced into the group before

226 the start of the second condition (therefore C13 did not participate in the baseline condition).

227 Subjects were provided with scatter feeds, consisting primarily of vegetables with some fruit in

228 the morning (approx. 10am) and again in the afternoon (approx. 3pm). The subjects were housed

229 in two enclosures throughout the course of the study; between June 2017 and April 2018 subjects

230 were housed in the "conversion" enclosure, from April 2018 until the end of the study subjects

231 were housed in the "Eden" enclosure. Both enclosures consisted of two indoor areas and an

232 outdoor area (two smaller areas in the case of conversion), with separate management areas

233 (away from the observation of visitors). Subjects could be observed through glass panes in all

234 public areas and mesh in management areas, observations used in this study were obtained from

235 both. Within the main enclosures, subjects had access to enrichment devices, such as climbing

236 frames/ropes, hanging feeders and nesting baskets. Other enrichment devices are regularly

237 provided by keepers.

238

239 TABLE 1 ABOUT HERE

240

241 **Prior experience questionnaire**

242   In order to exclude any possible influence of social learning on the results of this study,

243 keepers filled out questionnaires and were interviewed (designed and distributed by EB at the

244 zoological institution) about prior tool use behaviour. The use of this questionnaire was approved

245 by the University of Birmingham STEM ethical review committee (ERN_17-1729). The section

246 of the questionnaire relevant to this study can be found in S1. The questionnaire asks keepers to

247 provide details on behaviours relating to "*Using one object to bang on, or hit, another: usually,*

248 *this means the use of a hard object to bang on or hit another, often hard, object. This may be*

249 *with the aim to crack or break open the latter object, or to remove a substrate. Here, we are*

250 *interested in any hammer-like behaviours, regardless of the objects involved*". This definition

251 encompasses nut-cracking and similar actions, such as hammering behaviours. No instances of

252 nut-cracking were reported in the questionnaire; however, a keeper described how one individual

253 (C6; female; age 9) used a stone to tap on the glass of the outdoor enclosure. All but one keeper

254 reported that the chimpanzees were frequently witnessed using their teeth to crack nuts, although

255 they have never been provided with shelled macadamia nuts.

256 **Ethical statement**

257   All participation in this study was voluntary, and subjects were allowed to leave the

258 testing area at any point throughout the session. Subjects' usual feeding and cleaning routines

259 were followed, minimising disruption to the animals. The experimental phase of this study was

260 ethically reviewed and approved by the University of Birmingham Animal Welfare and Ethical

261 Review Body (UOB 31213) and Twycross Zoo Research Committee (TZR-2017- 013),

262 following guidelines provided by SSSMZP, EAZA, BIAZA, WAZA on animal welfare and

263 research in zoological institutions; this study also received a letter of support from BIAZA. This

264   study adhered to legal requirements of the UK, where the research was carried out, and adhered

265   to the ASP principles for the Ethical Treatment of Primates.

266   **Motivation tests**

267   This phase took place between 13th June 2017 and 27th September. Prior to starting

268   experimental testing, it was important to ensure that the subjects were sufficiently interested and

269   motivated to access the novel food reward (macadamia nuts) used in this study. To motivate the

270   chimpanzees to try the nut kernels when first presented, the first stage involved a trusted

271   individual (a keeper that has worked with the subjects for more than five years) first eating a

272   different familiar food in front of the subjects (here we used dried raisins and berries). The

273   keeper attracted a subject's attention by calling their name, and then ate a single item of the

274   familiar food (i.e., one raisin) in view of them. This process was repeated until each individual

275   had observed the consumption in a group context. The subjects were then provided with the same

276   food and required to eat it before moving onto the next step. As this food was familiar, this

277   occurred in every case. The next stage was to introduce the *novel* food (macadamia nut kernels

278   already without their shells). The same keeper ate a single macadamia kernel in the same way as

279   with the familiar foods. Again, each individual was given a demonstration (sometimes groups of

280   individuals could watch together as subjects were not separated during this part of testing). Once

281   each individual had observed the consumption of the nuts at least once, they were provided with

282   a macadamia kernel, again within a group context. This process was designed to increase the

283   likelihood that the subjects would consume the novel food, as prior research has shown that

284   captive chimpanzees can vary substantially in their acceptance of novel food sources

285   (Visalberghi, Yamakoshi, Hirata, & Matsuzawa, 2002). Despite the neophobia reported by

286   Visalberghi et al. (2002), we chose to replicate their 'trusted' human demonstrator condition in

287   an attempt to maximise the likelihood that the subjects would consume the macadamia nuts. In

288   addition to this, the 'motivation tests' were used to ensure that the nuts were palatable to the

289   subjects; therefore, should they have succeeded in cracking a nut, they would be sufficiently

290   motivated to continue doing so. Equally, during the demonstration conditions (see below) the

291   nuts provided might then serve as a suitable motivator to encourage the chimpanzees to attempt

292   to reinnovate or copy the behaviour. We required at least half the chimpanzees to eat the novel

293   nuts before starting testing, this was to ensure that the motivation testing did not go on for too

294   long, as these tests were carried out within a group context, it was likely that lower ranking

295   individuals would never be allowed access to the nut kernels.

296   **Test conditions**

297   Each trial was video recorded, starting when the subjects were given access to the testing

298   apparatus. The study took place between the morning and afternoon feeds; this time was chosen

299   as it complemented the daily routine of the keepers and animals whilst providing the maximum

300   testing time possible. The timings changed once the chimpanzees moved enclosure as the

301   keepers were able to provide the afternoon feed without needing to move the subjects outside the

302   testing area. Average trial length before the move was 3 hours ($n = 8$), after the move it was 5

303   hours 41 minutes ($n = 12$). Overall, there was a total of 92 hours and 18 minutes observation

304   time ($M_{trial\ length} = 4$ hours 37 minutes). The experimenter (DN) was present throughout each trial.

305   This study used a stepwise design, where each condition (see Figure 1) was followed by

306   the next in the event that the behaviour was not expressed in the first condition after five trials.

307   For example, the "End state" condition was only implemented in the event that the behaviour

308   was not reinnovated in the "Baseline" condition. Testing ended once the subjects had received 5

309   trials with full action demonstrations.

310   FIGURE 1 ABOUT HERE

311

312   In all of the conditions, behaviours were first live coded. If, during live coding, any

313   attempts at nut-cracking were identified then these were checked against videos and then second

314   coded for reliability analysis. Here we defined nut-cracking in terms of tool use, therefore, to

315   qualify as nut-cracking, the subject needed to use an object as a hammer to attempt to break open

316   the nut, whilst resting the nut on another hard surface (the anvil). Video recordings were

317   focussed on the experimental hammer and anvil set up (described below), however DN was

318   present at all times to observe any behaviours that might have occurred outside of the camera

319   frame.

320   **Materials**

321   The same apparatus set up was used in all conditions, and any changes to these conditions

322   are noted in the relevant section. To set up the apparatus, DN entered the outdoor enclosure and

323   secured a large wooden log (50cm tall x 40cm approx. diameter; that would serve as an "anvil")

324   to an upright portion of the climbing frame (which had a horizontal crossbeam, to ensure that the

325   anvil could not be removed; see Figure 2). The anvil was secured to the upright climbing frame

326   using two 1m long, 8mm thick, PVC coated, steel rope passed through two (12mm diameter)

327   holes drilled through the anvil (located ¼ and ¾ of the way down the log). Both ends of the rope

328   had a loop (secured by five 'clips' at each point, 'clips' used two, 8mm, nuts and bolts (tightened

329   using an electric drill), which was too large to pass through the hole in the anvil, and a steel

330   padlock attached the two ends. Two of these securing attachments were used as a failsafe

331   measure (see Figure 2).

332   FIGURE 2 ABOUT HERE

333

334   A wooden "hammer" was also attached to this structure (wooden, rather than stone,

335   hammers were chosen as they were more secure in their attachment to the rope). The hammer

336   consisted of a 30cm long x 15cm diameter log – approx. weight 2.5 kg – with a 12mm hole

337   drilled through half way along (see Figure 2). Hammer length was chosen based on the

338   descriptions of hammers used in wild populations to crack coula nuts (20-80cm long; Boesch &

339   Boesch, 1983). Our diameter was chosen to be larger than these wild hammers (4-10cm in the

340   wild; Boesch & Boesch, 1983) in the interest of safety being more likely to remain attached to

341   the securing attachment (see below). As a result of this increased diameter the hammers were

342   slightly heavier than the majority of those used in wild populations (77% of which were less than

343   2kg; however, our hammers were still within the 2-4kg larger range described in wild

344   populations; Boesch & Boesch, 1983).

345   The hammer was attached to the anvil's own securing attachment by creating a looped

346   end in another (1.5m) length of the same steel rope; the loop was passed onto the top securing

347   attachment (of the anvil) and the loose end was secured to the hammer (by passing the loose end

348   through the drilled hole and then securing with another five clips). The hammer was then moved

349   less than 1m from the anvil (see Figure 3).

350

351   FIGURE 3 ABOUT HERE

352

353   The keepers then scattered three macadamia nuts (in their shell) per individual (i.e., 3

354   nuts x 13 individuals = 39 nuts) throughout the enclosure, avoiding a 2m radius around the

355   hammer and anvil set-up. The macadamia nuts were distributed at the same time as a regular

356   scatter feed – just prior to the subjects being released into the outdoor enclosure. The unshelled

357   weight of the nuts (around 1g average across 10 measurements) was taken from the

358   chimpanzees' usual allowance of nuts for the week (this was to maintain the dietary health of the

359   subjects, at the testing institution's request). Once the attachments had been checked by DN and

360   at least one keeper, all humans exited the enclosure and the chimpanzees were allowed in the

361   enclosure. Just prior to the chimpanzees being allowed access, video cameras (SONY HDR-

362   CX330e), set at two points framing the apparatus (to better capture various angles), on tripods,

363   were set to record. DN was also present to live code relevant behaviours (see Table 2) that

364   occurred outside of the frame of the fixed cameras.

365   **Baseline condition**

366   This test condition took place between 15th October 2017 and 30th November 2017.

367

368   FIGURE 4 ABOUT HERE

369

370   In order to examine whether the subjects would individually reinnovate the target nut-

371   cracking behaviour, it was necessary to test subjects without providing any social information

372   beforehand. All sessions began between 10 am and 12 noon, when keepers provided the

373   chimpanzees' scatter feed (mainly consisting of vegetables and fruit). All sessions were

374   conducted in the "Outdoor 1" section of the enclosure (see Figure 4); however, subjects had

375   access to both indoor areas throughout the session.

376   **End state condition**

377   This phase of the study was completed between 15th January 2018 and 18th May 2018.

378   However, after the first two trials (15th January 2018 and 17th January 2018) the weather

379   conditions at the testing institution became so harsh that the subjects would often refuse to leave

380   the indoor enclosure. Thus, testing was paused until 14th May 2018, after which the final three

381   trials were completed on the 14th, 16th & 18th May. Between testing in January and May subjects

382   were moved from "Conversion" (their previous enclosure) to a new enclosure: "Eden" (see

383   Figure 5); subjects were therefore given one month after moving to the new enclosure to settle in

384   before testing resumed.

385

386   FIGURE 5 ABOUT HERE

387

388   In this condition, we placed three macadamia nuts, shells and kernels, which had been

389   split in half (see Figure 6) on top of the anvil (in the "Conversion" enclosure this was in

390   "Outdoor 1" and in "Eden" this was in "Habitat 1"). This condition was designed to specifically

391   trigger stimulus/local enhancement (defined as when an animal's attention is drawn to an

392   object/location as a result of some change in the environment). In this condition, we drew a

393   subject's attention to the anvil and hammer (and the nuts) by adding the cracked nuts on top of

394   the anvil.

395

396   FIGURE 6 ABOUT HERE

397

398   This condition was carried-out as the chimpanzees failed to individually reinnovate the

399   nut-cracking behaviour in the baseline condition and followed the exact same protocol as the

400   individual learning condition, described above. During the design process the study originally

401   included an extra condition between the "Baseline" and "End state" conditions, called "Local

402   Enhancement". In this condition it would have been made clear to the subjects that a kernel is

403   inside the macadamia nut and therefore that it constitutes a food source by shaving half of the nut

404   shell away to reveal the kernel inside (see Bandini and Tennie, 2018). However, some of the

405   chimpanzees in this study cracked the shells of the macadamia nuts with their teeth and

406   subsequently consumed the kernels (see Figure 7), rendering this condition unnecessary. This

407   was unexpected as Boesch and Boesch (1983) state that they never observed a wild chimpanzee

408   cracking coula nuts with its teeth; macadamia nuts (as used in this study) have a break strain of

409   between 1800-4000N (Schüler, Speck, Bührig-Polaczek, & Fleck, 2014), which is comparable to

410   coula nuts and substantially less than required for panda nuts (Boesch, Bombjaková, Boyette, &

411   Meier, 2017).

412

413   FIGURE 7 ABOUT HERE

414

415   **Ghost condition**

416   This phase of the study was completed between 19th July 2018 and 10th August 2018. The

417   ghost condition involved a significant increase in the level of social information provided to the

418   subjects. In this condition, the hammer and anvil set-up were still present inside the enclosure,

419   along with three macadamia nuts per individual (scattered throughout "Eden Habitat 2") and a

420   further three nuts (this time whole and uncracked nuts, inside the shell was provided) placed on

421   top of the anvil. Additionally, a replica of the equipment inside the enclosure (i.e., a hammer and

422   anvil set up) was placed outside the enclosure, visible through the mesh near the subjects'

423   sleeping area (see Figures 8 & 9); DN was also present, standing to the left of the anvil.

424

425   FIGURE 8 ABOUT HERE

426

427   A reel of clear fishing line (0.65mm diameter; 18kg break strain) was attached to the

428   hammer and passed through a section of mesh, allowing the hammer to be raised (between 80

429   and 50cm) above the anvil, via a pulley-like system (see Figure 9). A keeper steadied the

430   hammer before dropping it onto the nut, thus increasing the likelihood of the hammer cracking

431   the nut in the shortest possible time. Once the subject was clearly attending the apparatus (a

432   subject's attention was gained by calling their names), the hammer was dropped onto a nut

433   (which was placed in a groove in the centre of the anvil), cracking the nut open- this did not

434   always occur first time and may have required multiple attempts. A keeper then approached the

435   anvil and gave the subject who watched the demonstration the cracked nut. The device was then

436   rebaited with a new nut in the centre of the anvil. This procedure was repeated for a further 29

437   nuts (equalling a total of 30 demonstrations; with the exception of trial 4, where the line broke,

438   meaning that the trial was halted after 17 demonstrations). Subjects had access to the testing

439   apparatus during the course of the ghost trials. One camera was used to record the subjects'

440   interactions with the test apparatus, whilst the other was used to record subjects observing the

441   ghost demonstrations; chest mounted GoPro (Hero5 Session) cameras were also used to record

442   demonstrations and attention from the demonstrator's perspective. In both this condition and the

443   Full Action Demonstration condition, observing subjects were considered to be those in the

444   enclosure immediately in front of the demonstration area (far left sleeping area in Figure 8)

445   oriented towards the apparatus/demonstrator (i.e., not with their back turned).

446

447   FIGURE 9 ABOUT HERE

448

449   The ghost condition (inspired by Hopper, Lambeth, Schapiro, & Whiten, 2008) fulfils the

450   primary stipulation of learning by emulation (Tomasello et al., 1993); i.e., the learner should not

451   copy the motor patterns of the demonstrator. In this ghost condition, the motor patterns required

452   for nut-cracking were not demonstrated, making it impossible for the chimpanzees to copy the

453   actions (Heyes, 1994). Thus, if the behaviour were to occur following this condition, it could be

454   inferred that the results of the actions were replicated rather than the actions themselves (Hopper,

455   2010; Whiten et al., 2004).

456   **Full action demonstration condition (human demonstrator)**

457   This phase of the study was completed between 16th August 2018 and 6th September

458   2018. The full action demonstration condition was the first one that allowed for the possibility of

459   action copying. In this condition, DN was positioned outside the enclosure (in the same location

460   as the ghost condition). An anvil was placed in the same location as in the ghost condition (see

461   Figure 8), with a hammer placed 1m from the anvil (both pieces of wood were identical to those

462   in the subjects' enclosure). The researcher then attracted a subject's attention by calling their

463   name and proceeded to crack a nut, on top of the anvil, using the hammer. Note, it was not

464   possible to exclude the fact that multiple subjects may attend to the call of one individual –

465   subjects attending to a demonstration were coded from videos. The experimenter used the

466   hammer in a vertical manner, in the same orientation to the hammer in Figure 9 (see Figure 10),

467   raising it to eye level and then hitting down onto the nut, resulting in the nut breaking open. The

468   orientation of the hammer was used to attempt to control for hammer orientation between the

469   ghost and full action demonstration trials. Once cracked, the kernel was provided to the subject

470   by a keeper (see Figure 10D) and the device rebaited with another nut. A total of 30 nuts were

471   cracked using this procedure in each trial; a nut was not cracked until DN considered that the

472   target subject was attending to the demonstration. A maximum of 30 nuts was used based on

473   advice from keepers that not all subjects would attend to, or even approach, the demonstrations

474   (therefore, for all subjects to observe, trials could have continued indefinitely which would have

475   been unfeasible).

476

477   FIGURE 10 ABOUT HERE

478

479   **Coding/analysis of behaviours**

480   *Coding procedure*

481   Trials were live coded using the ethogram in Table 2. Following live coding a formal

482   coding procedure from video was followed. DN coded each trial in turn and a second coder

483   (MT), naïve to the hypothesis of this study, second coded 100% of the behaviours identified

484   (N=31) along with an equal number of "dummy" clips where a subject was in the frame but DN

485   did not identify a behaviour occurring to test for inter-rater reliability (acceptable Kappa would

486   be 0.6; Cohen, 1968; calculted using R package "irr" v.0.84.1; Gamer, Lemon, Fellows, & Singh,

487   2019). Note that the behaviours in Table 2 rely on the previous behaviour in order for them to be

488   coded; e.g., if the subject picked up the hammer without first placing a nut on the anvil then the

489   hammer behaviour would not be coded. This was to attempt to parse hammer centred

490   play/exploration from attempts at nut-cracking.

491

492   TABLE 2 ABOUT HERE

493

494   *Analyses*

495   After a behaviour has been reinnovated, social facilitation cannot be excluded as a

496   potential reason for the behaviour's continued emergence in other group members (Bandini &

497   Tennie, 2018; Tennie & Hedwig, 2009). Given an N of 1, it is not possible to perform inferential

498   statistics on acquisition times or rates between individuals. However, descriptive statistics were

499   used. All descriptive statistics were produced using R v.3.5.2 (R Core Team, 2013).

500   **Results**

501 **Motivation test**

502   During the motivation test, seven subjects (54% of sample; C3, C7, C9, C8, C5, C12 &

503   C13) consumed at least one macadamia nut provided by the keeper, leading to the conclusion

504   that macadamia nuts palatable to most of subjects included in this study (although note that

505   dominance hierarchies/individual personality characteristics may have interfered with certain

506   individual's ability/motivation to access the nuts).

507 **Reliability analysis**

508   The results of a Cohen's Kappa analysis revealed a strong level of agreement between

509   coders ($\kappa = .85$, $p<.001$).

510 **Attempts at nut-cracking**

511   None of the individuals in this study attempted to crack open the nuts using a tool in any

512   of the conditions described above. As there was never any evidence of nut-cracking, or

513   approximations of it, all conditions were completed (as explained in the methods section).

514   *Attempts recorded within the ethogram*

515   The coding procedure identified the following behaviours from the ethogram: place ($n =$

516   26; first occurring during baseline condition trial 2 but distributed across baseline ($n = 7$), end

517   state ($n = 15$) and ghost ($n = 4$) conditions), hold ($n = 1$; occurring during baseline condition trial

518   2), stamp ($n = 2$; occurring during baseline condition trial 2) and throw ($n = 2$; occurring during

519   baseline condition trial 2). Recordings of "place" were identified in C5 ($n = 7$), C6 ($n = 18$) and

520   C7 ($n = 1$) across all conditions apart from full demonstration. In only one instance did a "hold"

521   event follow "place", this concerned C6 during baseline condition trial 2; who was also the only

522   individual to "stamp" on or "throw" the nuts. It is unclear whether throwing was an active effort

523   to break the nut or simply an act of frustration/play as it did not appear that the throws were

524 aimed at any hard surface, nor were there ever attempts to retrieve the nuts afterwards by the

525 throwers.

Alternative techniques

527 Anecdotally, the majority of subjects (if not all) were witnessed, at least once, attempting

528 to crack the nuts with their teeth (with some individuals succeeding; see Figure 7). Male

529 chimpanzees ($n = 4$) were the only individuals observed (by DN) successfully accessing the nut

530 kernel using this method. The teeth cracking technique was first observed in the baseline

531 condition and persisted throughout the study. These behaviours were not captured on the main

532 videos as the cameras were facing the apparatus throughout the trial (to ensure that any attempts

533 at using the apparatus to crack the nuts were captured), also some subjects were not visible

534 throughout; therefore, any attempt to quantify these behaviours would be inaccurate as it would

535 likely present only part of the actual series of events.

Observers Ghost and Full Action Demonstration Conditions

537 Occasionally the identity of the observer could not be ascertained from video footage; in

538 these cases, the individuals were not included in the calculations below. Furthermore, as

539 participation in the study was voluntary, and subjects were free to approach and interact with the

540 testing apparatus whenever they chose, not all subjects observed all the demonstrations provided.

541 Some subjects ($n = 2$; C5 & C11) never observed the demonstrations in either condition; whilst

542 other subjects never observed demonstrations in the ghost ($n = 3$; C5, C13 & C11) or full

543 demonstration conditions ($n = 4$; C5, C11, C1, C10). Overall, 77% of subjects ($n=10$) were

544 coded as observers in the ghost condition and 69% of subjects ($n=9$) were coded as observers the

545 full demonstration condition; there was an average of 2.48 observers per ghost demonstration

546 and 2.99 observers per full demonstration.

547 **Discussion**

548   We found no evidence of nut-cracking with a tool, or any approximation at this, at any

549   point during the course of this study. Thus, our sample of 13 naïve chimpanzees failed to

550   reinnovate or socially learn the behavioural form of nut-cracking. At first, it would seem our

551   findings support the CDT hypothesis, in that nut-cracking behaviour was not reinnovated in our

552   initial baseline condition. However, our study also consisted of various social learning test

553   conditions – including one that demonstrated the necessary action patterns for nut-cracking to the

554   chimpanzees. This condition allowed for the possibility of action copying being a requirement of

555   the behaviour, as has recently been claimed (Estienne, Cohen, Wittig, & Boesch, 2019). Even so,

556   nut-cracking was not acquired by the subjects. Therefore, our study does not provide conclusive

557   evidence for either the CDT or the ZLS hypothesis. Below we discuss three possible

558   explanations for our null result and the general disparity in studies of chimpanzee nut-cracking.

559   **Conspecific models**

560   The findings of this study raise the question as to why some chimpanzee populations in

561   the wild regularly crack nuts (on average 270 nuts per day for as long as 2 hours 15 minutes in

562   Taï Forest; Boesch & Boesch-Achermann, 2000) whereas captive chimpanzees (in this sample

563   and others; Funk, 1985) seem to rather consistently fail to acquire the behaviour, even after

564   demonstrations. A first possibility for the disparity between wild and captive data is that nut-

565   cracking is indeed a CDT and requires the learner to imitate a conspecific demonstrator (Boesch,

566   1996). In this study we used human demonstrators, which may not have been considered 'good'

567   enough models for the chimpanzees. Indeed, some research has shown that chimpanzees are

568   more proficient social learners from conspecific models as compared to videos or human models

569   (Hopper, Lambeth, Schapiro, & Whiten, 2015). However, in contrast, others have instead

570   claimed that it is possible for chimpanzees to "learn" nut-cracking from human demonstrators

571   (see findings of Ross, Milstein, Calcutt, & Lonsdorf, 2010 but also review of other related

572 studies Table 3 (p. 230) of Ross et al. 2010). Concurrently, other studies have found that, even

573 with conspecific demonstrators, sometimes captive chimpanzees fail to acquire complex

574 behaviours such as nut-cracking (Funk, 1985) or behaviours which strictly require imitation

575 (Clay & Tennie, 2018; Tennie, Call, & Tomasello, 2012; Tomasello et al., 1997). Although it

576 might have been interesting to observe the chimpanzees' reaction to a conspecific demonstrator

577 in this study, we did not have the resources to train a chimpanzee to act as a demonstrator, but

578 we encourage interested researchers who do have the resources to replicate this study, and

579 include a conspecific demonstrator to observe whether this affects the findings presented here.

580 **Behavioural flexibility**

581 An alternative explanation for the fact that nut-cracking did not emerge in this study is

582 that the chimpanzees were hindered by their lack of behavioural flexibility, a commonly

583 recorded phenomenon in chimpanzees (e.g., Harrison & Whiten, 2018). The chimpanzees in the

584 current study seemed to become fixated on one solution to open the nuts: i.e., the use of their

585 teeth. The chimpanzees may have relied on this technique due to their pre-existing knowledge on

586 how to crack softer-shelled nuts (such as peanuts and walnuts), which they are often provided

587 during their feeds at the testing institution. These nuts are easily cracked open by apes using

588 teeth (DN; personal observation, keeper reports and see also Visalberghi et al., 2008 for

589 measurements on the required force for different types of nuts). The heuristic (Marsh, 2002) in

590 this case may be that nuts (in general) *can* be opened with teeth – and indeed our macadamia

591 nuts were no exception. Chimpanzees have been shown to be reluctant to display behavioural

592 flexibility in abandoning a previously successful solution (see Harrison & Whiten, 2018;

593 Hrubesch, Preuschoft, & van Schaik, 2009; but see also Manrique, Völter, & Call, 2013). Thus,

594 it is possible that the first individual to successfully crack a nut with the use of teeth (see Figure

595 7), facilitated this behaviour within the group and/or that other individuals independently

596   converged on this method, and then the subjects were unable to innovate a new method, even if

597   cracking the nuts with a tool would have been mechanistically easier/more efficient (this

598   possibility is also in line with cultural founder effects; Tennie et al., 2009).

599   **Sensitive learning period**

600   Based on the literature, the most likely explanation for the findings in this study is that

601   the chimpanzees may have simply been outside of their sensitive learning period for nut-

602   cracking. Previous studies on nut-cracking in wild chimpanzees have reported that before 3.5

603   years, juvenile chimpanzees are unable to express the full nut-cracking behavioural form (Inoue-

604   Nakamura & Matsuzawa, 1997; Matsuzawa, 1994). However, juvenile chimpanzees (as young as

605   1.5 years old) that had been exposed to the materials required for nut-cracking at various

606   ages/developmental stages were able to perform the basic actions of the behaviour (put, hold, hit

607   and eat), but not combine them in the required order to perform the full nut-cracking behaviour

608   (Inoue-Nakamura & Matsuzawa, 1997). Indeed, recent research in wild chimpanzees shows an

609   exponential increase in nut-cracking between 5 and 6 years of age, though the first signs were

610   observed in 3-4-year-old individuals (Estienne et al., 2019) in line with the concept of maturation

611   (Corp & Byrne, 2002). This finding suggests a certain level of developmental prowess required

612   to express nut-cracking, perhaps somewhere between maturation effects of the body and the

613   brain.

614   In addition to this lower age limit for the acquisition of nut-cracking, there also appears to

615   be an upper limit (more relevant for the current study). A 13 year longitudinal study by Biro et

616   al., (2003) found that wild chimpanzees who did not learn the basic nut-cracking skills before

617   five years old seemed unable to acquire the behaviour later on in adulthood (a similar case has

618   been documented recently for stone tool-use in long-tailed macaques; Tan, 2017). The subjects

619   tested in the current study were all outside of the hypothesised sensitive learning period for nut-

620   cracking, as the youngest subject in our sample was already 10 years old at the time of testing.

621   The youngest individual however was the only subject to display the "hold" behaviour (stage two

622   of four) in the behavioural form of nut-cracking. Our findings, coupled with those described here

623   suggest that a sensitive learning period may be a decisive factor for whether a chimpanzee will

624   start to crack nuts or not (leaving open the question how this is learned, i.e. whether it is a CDT

625   or a latent solution).

626   Given the fact that wild chimpanzees engage in an extended process of acquisition before

627   expressing nut-cracking (Matsuzawa et al., 2008), we suggest that future work considers

628   applying an even longer study time than the one employed here. It is possible that chimpanzees

629   may then individually, or socially, learn the behaviour. The social learning oppertunities here

630   provided comparativley more demonstrations than related studies (5 trials with 30 nuts per

631   demonstration in our study versus 5 trials with 5 nuts per demonstration by Marshall-Pescini &

632   Whiten; 2008). Even so, the social learning opportunities that we present here were fewer

633   compared to the wild; in wild populations that express the behaviour, individuals have more and

634   longer (and perhaps also more varied) opportunities to observe nut-cracking. Equally, given the

635   potential importance of a sensitive learning period in explaining the emergence patterns of

636   chimpanzee nut-cracking (discussed in this section) we suggest that the next logical test of this

637   behaviour should aim to test younger chimpanzees between the ages of 3 and 10 years (Ross et

638   al., 2010 suggest between ages 3-7); either way, these individuals should once again be selected

639   from populations that have not been observed previously to crack nuts.

640   Though we used a within-subject design throughout our result-dependent design, we

641   would reccomend that (wherever feasible) a between-subject design be used in future tests (one

642   group for each of the conditions). By doing the latter, it is possible to control for and measure the

643 time of exposure required for chimpanzees to express nut-cracking, and it would exclude

644 potential carry-over effects. However, this project would likely be an overly large undertaking

645 for any one research group, so therefore may be better suited to large scale colaborative projects

646 (e.g., the ManyPrimates project).

Conclusions

648   Although no chimpanzees in this study demonstrated nut-cracking using tools, two

649 geographically separate populations in the wild have seemingly converged on the same method

650 for cracking nuts using tools (West Africa; Whiten et al., 2001 and Cameroon; Morgan & Abwe,

651 2006). As these populations do not have access to each other, logically they must have

652 independently reinnovated nut-cracking (Byrne, 2007). However, the data from Cameroon is

653 based on procured nut cracking tools and auditory assumptions and so are an inference rather

654 than direct observations. It is possible that these tools were actually from modern human nut-

655 crackers and may not be considered evidence of chimpanzee nut-cracking in multiple

656 populations. Thus, to date, there is only concrete evidence of one culturally independent wild

657 population expressing nut-cracking. As the data from this study and wild data do not

658 unequivocally support either the ZLS or the CDT hypothesis, both remain in contention.

659   In addition to the wild data and that presented here, one chimpanzee in an experimental

660 study spontaneously reinnovated nut-cracking when provided with all the materials (Marshall-

661 Pescini & Whiten, 2008). The individual (Mawa) acquired the nut-cracking behaviour seemingly

662 without requiring any copying variants of social learning (Marshall-Pescini & Whiten, 2008).

663 However, Marshall-Pescini & Whiten (2008) fail to note the importance of these findings, by

664 assuming, based on the speed of acquisition, that "Mawa" had prior experience of nut-cracking.

665 It is worthy of note however that unlike this study and that of Funk (1985), no claim was made

666 about the naivety of the subjects. Indeed, Mawa was kept as a pet prior to residing at the

667   sanctuary where Marshall-Pescini and Whiten (2008) carried-out their study. Mawa arrived at

668   the sanctuary when he was approx. three years old with wounds from a rope where he was tied

669   up (Ferdowsian et al., 2011). As a result of this potential enculturation, or at the very least

670   deprivation, these data should be treated with caution; indeed, the generalisability of such

671   individuals to wild chimpanzees is questionable (Henrich & Tennie, 2017).

672   Excavations of chimpanzee nut-cracking sites suggest that the basic behavioural form

673   has remained constant for at least 4,000 years, and likely even longer (Mercader et al., 2007).

674   Similarly, excavations of capuchin nut-cracking sites have demonstrated that their nut-cracking

675   form has remained the same for 3,000 years, with only the tools (hammerstones) changing in

676   shape over time (Falótico, Proffitt, Ottoni, Staff, & Haslam, 2019). Indeed, if the behavioural

677   form of nut-cracking were being copied between individuals, we would expect to see some

678   changes to its form over time due to copying error alone (see Eerkens & Lipo, 2005). Lastly,

679   other extant species of primates also crack nuts using tools in the wild (long tailed macaques,

680   Gumert & Malaivijitnond, 2013; capuchins, Ottoni & Mannu, 2001), and some have even been

681   found to do so spontaneously in captivity without requiring social learning (e.g., nut-cracking is

682   a latent solution in capuchins: Visalberghi, 1987). Whilst other primate species being able to

683   spontaneously crack nuts is not evidence of a phylogenetic link; it does suggest that the

684   possibility that nut-cracking is a latent solution in chimpanzees remains. Therefore, social

685   learning may not be fully responsible for the emergence of nut-cracking in chimpanzees

686   (especially given the results of the current study, in which the chimpanzees did not acquire the

687   behaviour even after full demonstrations were provided). We acknowledge that the chimpanzees

688   in this study were captive and therefore are not subject to the same ecological pressures as their

689   wild conspecifics; that is, they would have less 'necessity' to reinnovate the behaviour (Fox,

690   Sitompul & van Schaik, 1999). Therefore, (parts of) this study could perhaps be replicated in a

691   wild sample, naïve to nut-cracking.

692   Therefore, the results of this study do not support nut-cracking as the first evidence of a

693   CDT in chimpanzees (see also Byrne, 2007), yet they also do not fully support nut-cracking as a

694   latent solution in chimpanzees. Instead, we conclude that the behaviour may not have emerged

695   here due to interplay of factors, including a certain level of behavioural conservatism and,

696   crucially, the fact that all the subjects were already out of their sensitive learning periods for nut-

697   cracking. We believe it is unlikely that our use of human demonstrators was the reason for the

698   failure of all our subjects to express nut-cracking, given the results of previous studies, discussed

699   above. Accordingly, we propose that future studies should adopt the methodology presented

700   here, but test unenculturated infant/juvenile chimpanzees, naïve to nut-cracking *and* to opening

701   nuts with their teeth, to remove the confounds of the sensitive learning periods and conservatism

702   (ideally tested in isolation in order to increase effective sample size). Under these conditions, it is

703   plausible that some naïve chimpanzees will reinnovate nut-cracking. Yet, on the other hand,

704   given the extended trial-and-error learning process that young wild chimpanzees engage in

705   (Matsuzawa et al., 2008) it is possible that under the relatively short term test conditions, the full

706   form of nut-cracking may still fail to emerge spontaneously, although some of the pre-requisite

707   steps to the behaviours may still develop.

708   So far, the current state of knowledge does not support the view that nut-cracking *has* to

709   be reliant on social learning as it has potentially been reinnovated in two culturally distinct

710   populations, therefore, it seems unlikely that it is a CDT. However, it is also possible that even

711   chimpanzees within their sensitive learning period would continue to fail to individually acquire

712   the skills required to crack nuts and therefore could be considered a CDT. The data at hand

713   suggest that the behavioural form of nut-cracking may only be acquired through an interplay of

714   ecological and developmental factors, i.e., chimpanzees must be in a location with appropriate

715   nuts and tool materials, during or before, their sensitive learning period. Therefore, it remains

716   possible that nut-cracking is within the species level ZLS of chimpanzees. Despite this, not all

717   individuals may realise this potential within their lifetime if they were not exposed to the

718   required ecological conditions or individual prerequisites (note that these were termed by Tennie

719   et al. (2009) as the "right" conditions that may be required). It is yet to be determined whether

720   nut-cracking's acquisition is best described as being due to, and requiring, social learning

721   (culture-dependent) or is due to socially mediated reinnovation (latent solution). Further research

722   should consider the importance of the ecological factors explored here in addressing this

723   question.

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734

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Subject demographic information

Note that subject names are anonymised for the purpose of the study – these codes were kept consistent throughout the study. Subject C13 is displayed in italics as she was only included in the study after *the baseline condition.*

ID	DoB	Sex	Rearing
C1	30/04/1976	Female	Hand
C2	09/06/1982	Male	Hand
C3	25/10/1986	Male	Hand
C4	18/08/1990	Female	Hand
C5	28/12/1990	Male	Hand
C6	10/08/2007	Female	Parent
C7	25/05/1995	Female	Hand
C8	17/06/1977	Female	Undetermined
C9	20/02/1988	Female	Hand
C10	01/01/1965	Female	Undetermined
C11	14/12/1971	Female	Undetermined
C12	05/12/2003	Male	Parent
C13	*27/12/1982*	*Female*	*Parent*

Coding ethogram used during the live coding procedure.

This was added to throughout live coding as behaviours of interest were observed. This ethogram was provided to the second coder for reliability coding.

Behaviour	Description
Place nut	The subject places one/several nuts on the surface of the anvil. This is also coded if the subject drops the nut onto the anvil. The nut *may* roll off the anvil after being "placed" this is acceptable as it is likely due to the nut's shape and the angle of the anvil's surface.
Hold hammer	The subject picks up the hammer – with the nut on the anvil, by holding the wood itself or the securing attachment.
Raise hammer	The subject lifts the hammer above the nut – this may be at/below/above head height for the subject.
Drop hammer	The subject brings the hammer down onto the nut, which must be resting on the anvil. The hammer can be dropped or held in the hand the entire time. This behaviour can be repeated until the nut is cracked. The behaviour is coded each time the behaviour occurs – i.e., each time the nut is struck.
Eat nut	The subject takes the kernel of the, now broken nut and eats it. Note, this must have followed cracking of the nut by the subject.
Stamp	The subject uses their foot to stamp on the nut, which has been placed on the anvil.
Throw	The subject, whilst sitting on the anvil, throws the nut in any direction.

Figure 1

Decision tree depiction of the result dependent conditions.

If, at any stage, evidence of the behaviour was encountered then testing would cease, and the resultant learning mechanism will be attributed to the emergence of the behaviour. Each condition is continued for five trials before moving onto the next condition.

Baseline Condition

No evidence after 5 trials

End state

No evidence after 5 trials

Ghost Condition

No evidence after 5 trials

Demonstration

Individual Learning

"End state" emulation

Goal emulation

Imitation
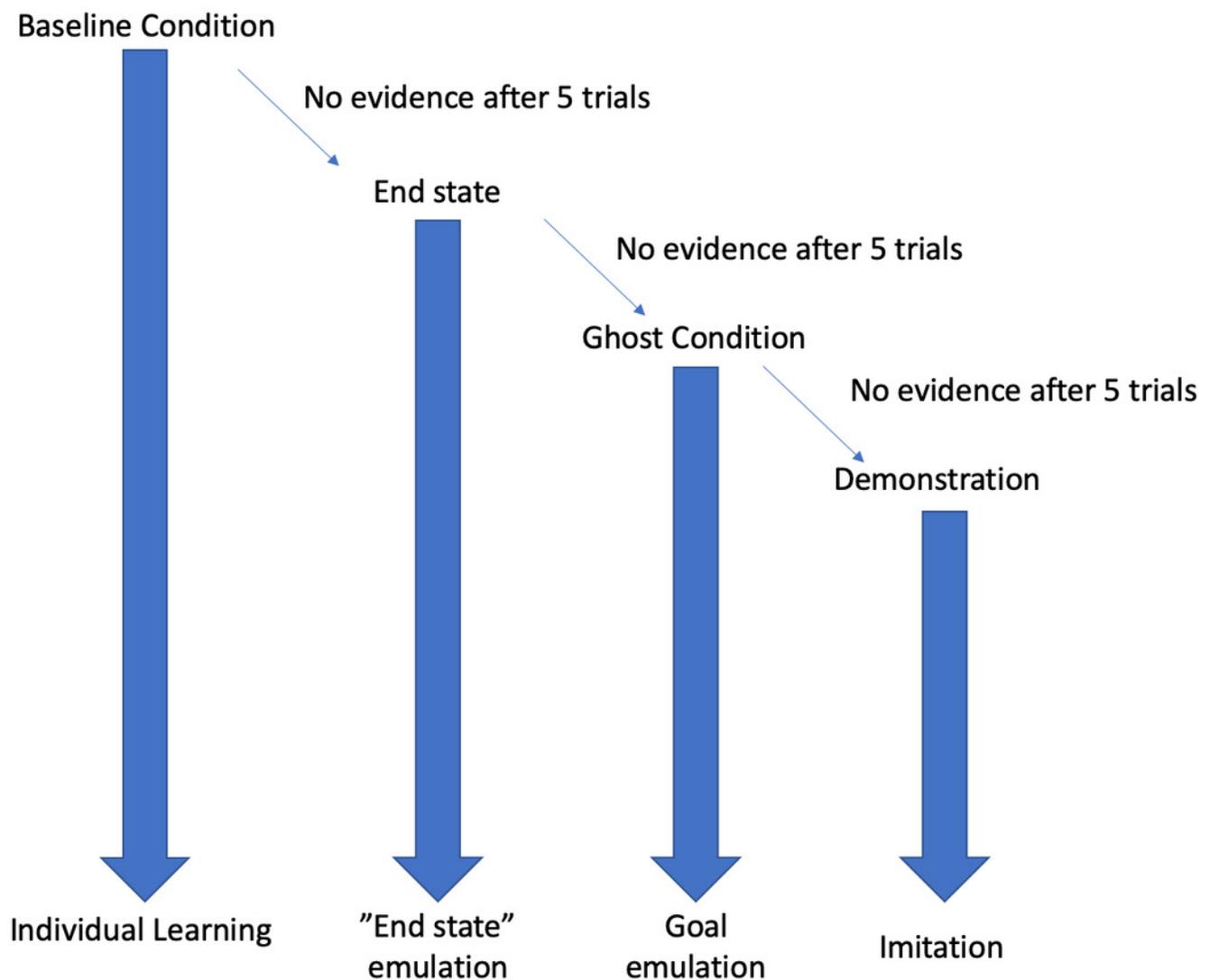
Figure 2

Securing attachment of the hammer.

Note how there are several 'clips' to act as a failsafe.

Figure 3

Hammer and anvil set up within the subjects ' enclosure.

Note, the two securing attachments are passed through separate holes within the anvil and the hammer is less than 1m from the anvil (this was ensured by the length of the securing attachment of the hammer to the anvil).

Figure 4

Experimental set up for baseline condition in "conversion"

Note, the same set up was used for the first two trials of the "end-state" condition, prior to the enclosure move (see below).
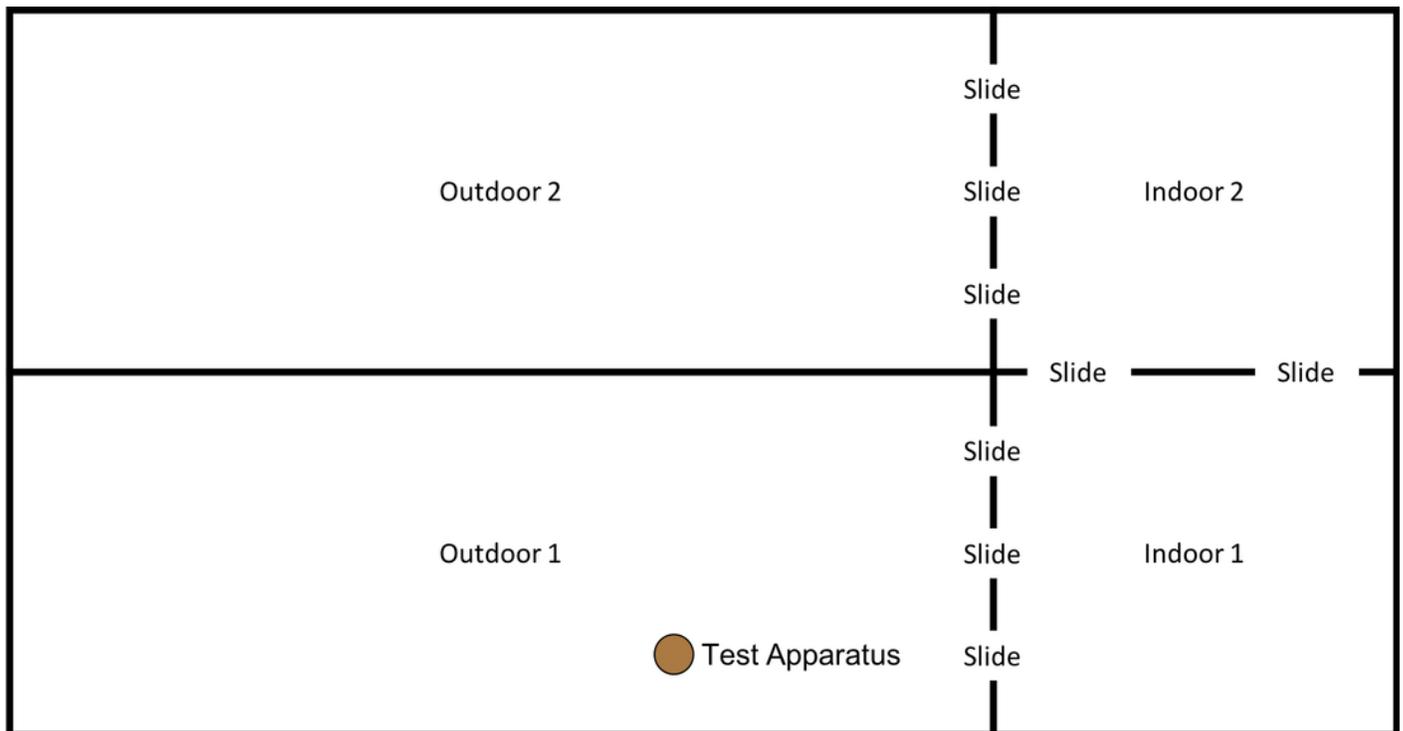
Figure 5

Experimental set up for "end-state" condition in "Eden".

Note, subjects had access to the entirety of this enclosure throughout these trials, however, the outdoor section of the enclosure was still under construction.
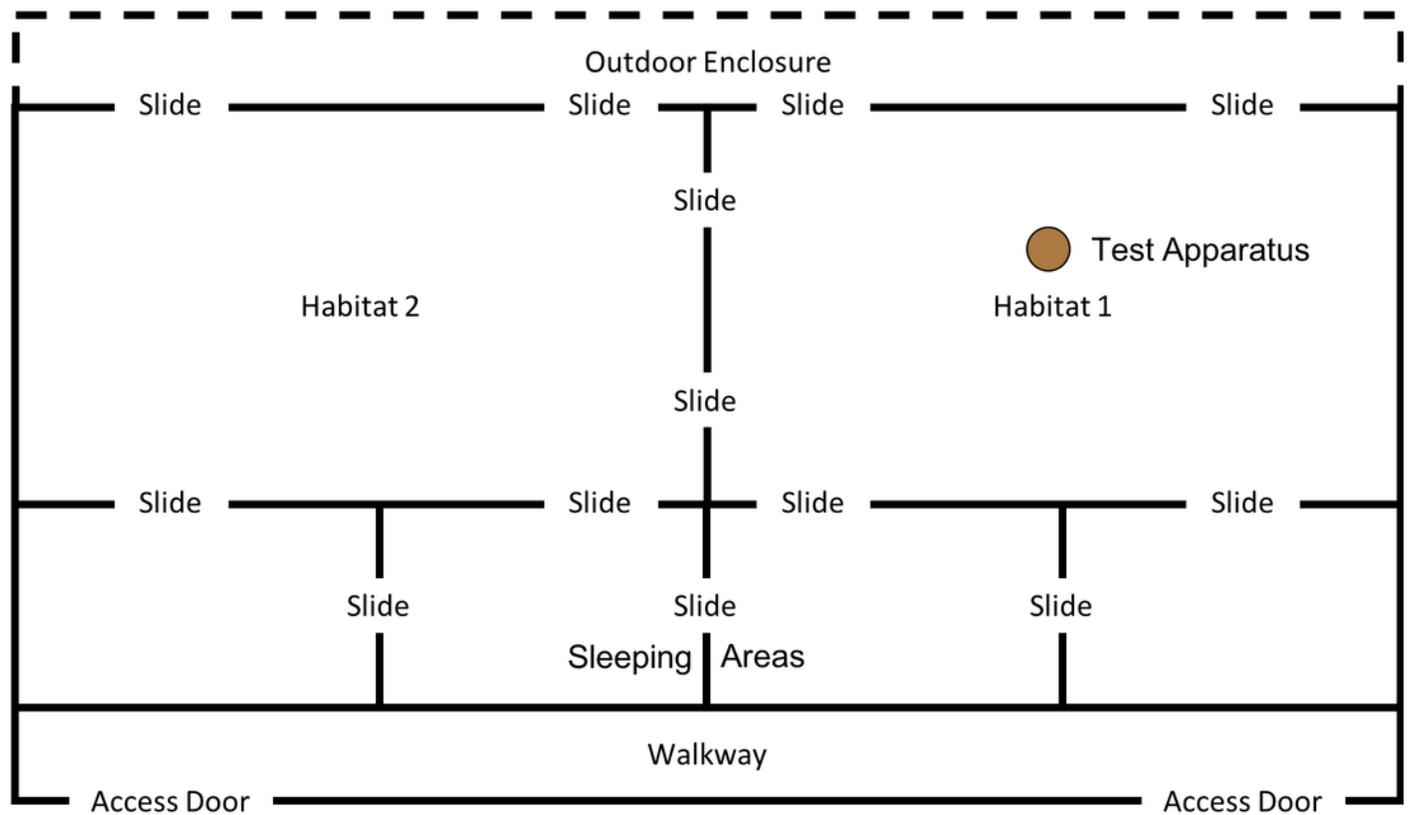
Figure 6

Macadamia nut placement and state for end-state condition.

(A) Macadamia nuts, sawn in half (with kernels left whole) for the end-state emulation condition. (B) Nuts placed atop the anvil as described in text.
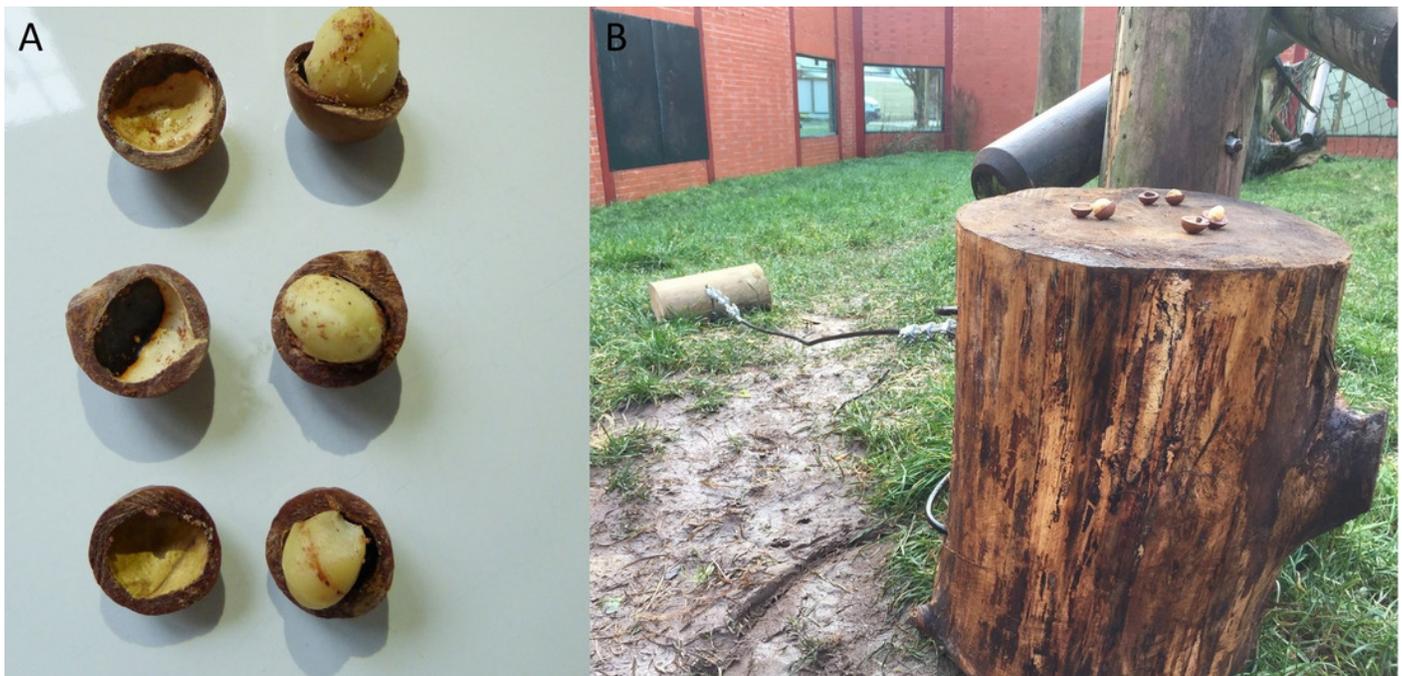
Figure 7

Adult male chimpanzee (C5) cracking a macadamia nut with his teeth, then eating the kernel.

(A) C5 biting the nut in an attempt to break it; (B) C5 consuming the kernel from the now broken shell

Figure 8

Experimental set up for "Ghost" condition in "Eden".

Note, subjects had access to the entirety of this enclosure throughout these trials including *the outdoor enclosure.*
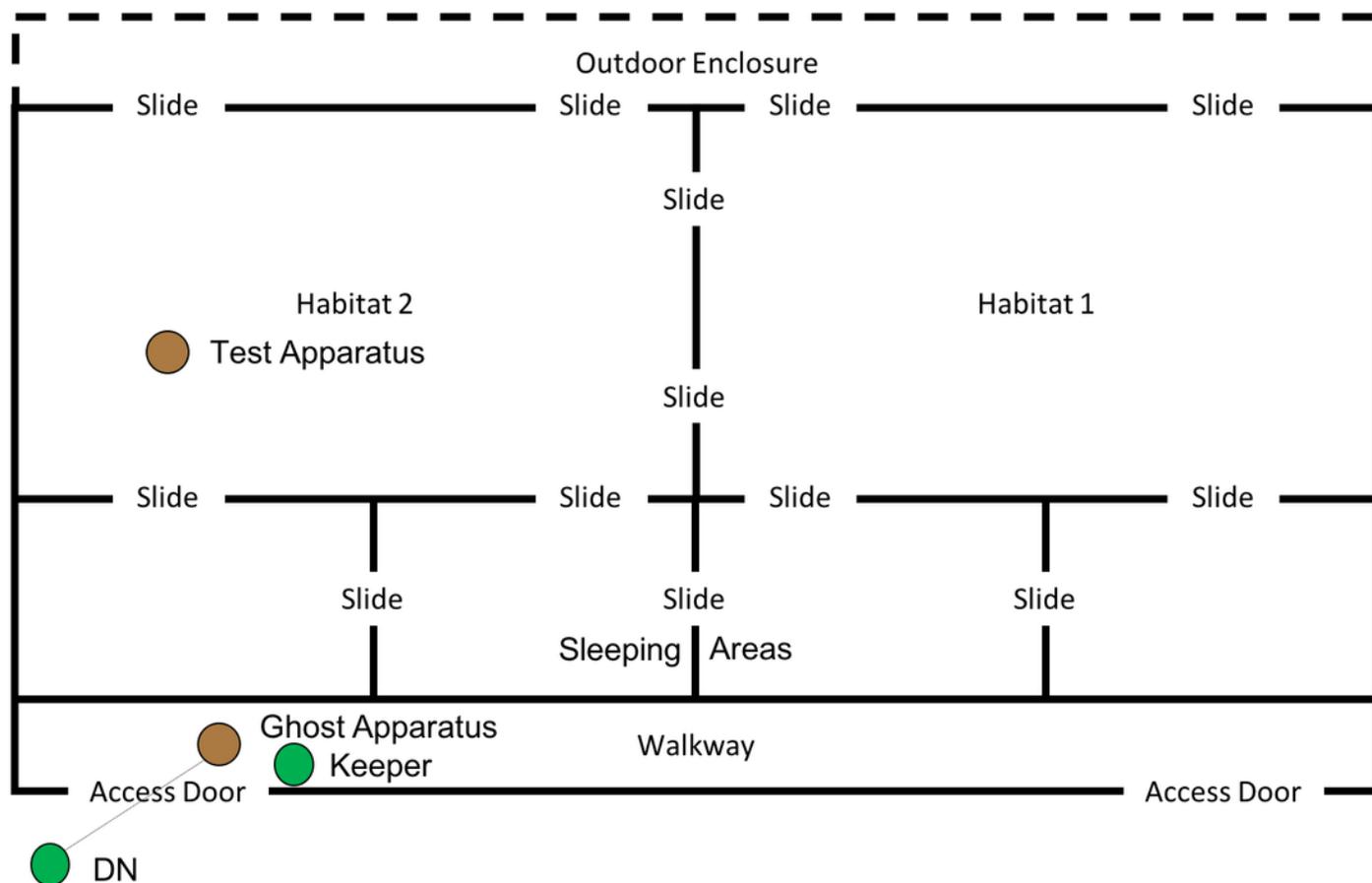
Figure 9

Experimental set up of "Ghost Condition" apparatus.

Note, the hammer is suspended by fishing line, and a single nut is in the centre of the anvil.

Figure 10

DN performing full nut-cracking action demonstrations

(A) subjects' attention was gained by calling their given name; (B) hammer was to eye-level and (C) brought down on the nut as many times as required until it cracked; (D) the cracked nut (both shell and kernel) are provided to the target subject by a keeper. Subject in this demonstration was the female (C9) to the left of DN – holding onto the mesh in panels A-C; keeper rolled the nut to C9 in panel D (hand feeding, even by keepers, is not permitted at the testing institution).