Testing the individual and social learning abilities of adult, captive and task-naïve 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 some types of social learning, with some researchers arguing, more specifically, 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 behind the behavioural form of nut-cracking. Despite this, the available data provides some evidence for the spontaneous acquisition of nut-cracking by chimpanzees (who were likely task-naïve when they individually developed the behaviour). The acquisition of nut-cracking in the rest of the group was then found to be at least facilitated by (unspecified) variants of social learning, the latter findings in line with both the hypothesis that copying social learning is required and the hypothesis that other (non-copying) social learning mechanisms are at play. Here we present the first study which (initially) focused 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 nut-cracking would emerge spontaneously. After the baseline condition (which was unsuccessful), we tested for the role(s) of social learning by providing social information in a step-wise fashion, culminating in a full action demonstration of nut-cracking (this last condition potentially allowed the observers to copy all actions underlying the behaviour). Despite the extensive opportunities to individually and/or socially learn nut-cracking, none of the chimpanzees tested here developed the behaviour in any of the conditions in our study. We conclude that this failure was the product of an 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 inside – but at the very edge of – chimpanzees' individual abilities, that may only be acquired when chimpanzees are still inside their sensitive learning period for it.

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Abstract

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 some types of social
learning, with some researchers arguing, more specifically, 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 behind the behavioural form of
nut-cracking. Despite this, the available data provides some evidence for the spontaneous
acquisition of nut-cracking by chimpanzees (who were likely task-naïve when they individually
developed the behaviour). The acquisition of nut-cracking in the rest of the group was then found
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(non-copying) social learning mechanisms are at play. Here we present the first study which
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cracking, none of the chimpanzees tested here developed the behaviour in any of the conditions
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cracking in chimpanzees. The possibility remains that nut-cracking is a behaviour inside – but at
the very edge of – chimpanzees' individual abilities, that may only be acquired when
chimpanzees are still inside their sensitive learning period for it.

Introduction

Humans have created a unique niche within the animal kingdom, one that (most likely) relies on an ability to transfer knowledge between and within generations, allowing our species to inhabit almost every environment on the planet. However, modern industrialised human society is so far removed from that of our ancestors, that it is difficult to understand how our cultural ability – or our cultural niche (Olding-Smee, Laland, & Feldman, 2003) – evolved. Therefore, the closest extant relatives of the *hominin* clade, non-human great apes (hereafter: apes), are often used as a phylogenetic proxy to help shed light on our own evolution.

Modern human culture may be unique in the animal kingdom (Tomasello, 1998) – at least in the technological domain (Tennie, Caldwell, & Dean, 2018). Thus, to allow for the study of culture *across* species, a more minimal (or soft) definition of culture is required. Here we follow the terminology recently suggested by Neadle, Allritz and Tennie (2017), in which a cultural trait is any behaviour that is at least influenced (including merely its frequency being facilitated or catalysed; Tennie, Call, & Tomasello, 2010) by social learning. Within this definition of culture, the social learning mechanisms at play can be any of the many proposed variants (for an overview, see Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). This minimal definition of culture allows for the identification of cultures that involve a range of social learning variants, including ones that rely on the copying of behaviour directly (often called imitation, see, e.g., Whiten & Ham, 1992). Crucially, the minimal definition of culture also encompasses many examples of behavioural forms that can come about without requiring social learning. Behaviours that instead *rely* on social learning are 'culture dependent traits' (henceforth CDTs; Reindl, Apperly, Beck, & Tennie, 2017; Tennie, Caldwell, & Dean, 2018). Some animal cultures may be culture dependent (e.g., whale song is a candidate culture dependent trait (CDT); Tennie et al., 2018), but whether any animal tool use qualifies as CDT is a matter of considerable debate (Galef, 1992; Kendal, 2008; Tennie, Call, & Tomasello, 2009). In the human case, technology has often evolved to the point that no naïve individual, on their own, could reinnovate the behaviour leading to and using that technology, from scratch – within their own lifetime (Galef, 1992; Tomasello, Kruger, & Ratner, 1993), making many modern human traits CDTs.

Amongst non-human animals (hereafter: animals), chimpanzees (*Pan troglodytes*) are, for now, the 'most cultural' species – at least in terms of (known) numbers of cultural traits (Whiten et al., 1999) – where a mere increase in sheer number of cultural traits is known as accumulation (Dean, Vale, Laland, Flynn, & Kendal, 2014). However, accumulation (numbers of traits) should not be confused with *cumulation*, i.e. the cultural change of the traits themselves along transmission pertaining to cumulative culture (Dean et al., 2014). Only the latter is the result of the 'ratchet effect' (Tomasello et al., 1993), which underlies cumulative culture (Boyd & Richerson, 1996) – and is responsible for the special product of cumulative culture: CDTs (Reindl et al., 2017). Therefore, whilst chimpanzees' number of cultural traits is impressive, for those concerned with human cultural evolution, the presence or absence of CDTs in chimpanzees is of particular interest.

CDTs are not always more complex than other cultural traits (though they may be; Reindl et al., 2017), yet trait complexity can serve as a rough first guide to identify at least some candidate CDTs – namely those who may have ratcheted up in complexity via cultural transmission (Tennie et al., 2018). However, complexity is both hard to define and to measure. Complexity can be defined in several ways and can be depicted using stepwise flow-diagrams (sensu Byrne, Corp, & Byrne, 2001) or "cognigrams" (Haidle, 2012). It can refer to the number of parts within a final artefact/behaviour (techno-units; Oswalt, 1976), the goals and sub goals of an action

100 (Read & Andersson, 2019), the manual dexterity of an action (Foucart et al., 2005) and the
101 number of "rules" necessary to describe the behaviour (Sirianni, Mundry, & Boesch, 2015),
102 amongst other metrics (see Vaesen & Houkes, 2017 for further discussion of complexity).
103 Indeed, even seemingly highly complex behaviours may not require cultural transmission
104 (Byrne, 2007). For example, naïve bower birds can make their elaborate nests without requiring
105 any cultural transmission of knowledge (therefore nest-making in these birds is not a CDT;
106 compare Collias & Collias, 1984).
107 Regarding chimpanzee culture, nut-cracking is regarded as one of the most complex behaviours
108 expressed by any wild apes, as it requires a high level of dexterity (Foucart et al., 2005), and
109 involves several tools in several steps that need to be followed in a specific sequential order to
110 produce the desired effect (Biro et al., 2003; Boesch, Bombjaková, Meier, & Mundry, 2019;
111 Inoue-Nakamura & Matsuzawa, 1997; Read & Andersson, 2019). Furthermore, nut-cracking is
112 rare across wild communities, (so far) only being documented in two geographically separate
113 populations: two communities in West Africa (Bossou, Guinea and Taï Forest, Côte d'Ivoire
114 Whiten et al., 2001) and one in Ebo Forest, Cameroon (Morgan & Abwe, 2006).
115 The behavioural form of nut-cracking itself consists of the following four sequential steps[1]: 1.
116 Place nut on anvil, 2. Pick up hammer (unless already picked up) 3. Lift hammer up, 4.
117 Drop/push the hammer onto nut (all may be repeated). The number of steps alongside with the
118 manual dexterity and use of multiple objects in conjunction is required for this behaviour,
119 suggests that nut-cracking is most likely a complex behaviour for chimpanzees.
120 Perhaps due to this apparent complexity, nut-cracking is often assumed to be culturally
121 transmitted (Boesch & Boesch-Achermann, 2000; Lycett, Collard, & McGrew, 2007, 2010),
122 with some researchers arguing that action copying (or imitation) must be the mechanism
123 responsible for its acquisition. For example, Boesch (1996) claims that chimpanzees learn how
124 to crack nuts "by individual and social learning, *including imitation*" (Boesch, 1996, p. 418,
125 emphasis added), Biro et al (2003, p. 220) further argue that when nut-cracking "infant
126 chimpanzees are driven not by a motivation for food but to produce a *copy of the mother's*
127 *actions*" [emphasis added]. Others agree, claiming that nut-cracking (alongside other chimpanzee
128 traits) are difficult to explain "by social learning processes simpler than imitation" (Whiten et al.,
129 1999, p. 685). More recently, similar claims have been made that chimpanzees rely on mother to
130 infant "*teaching*" to acquire the skills required to crack nuts at a rate consistent with that of
131 others within their community (Boesch et al., 2019). In conclusion, the behaviours underpinning
132 nut-cracking have been argued to require social learning (in particular action copying and/or
133 unspecified variants of teaching). Therefore, it has been assumed that nut-cracking is outside of
134 naïve chimpanzees' individual learning abilities, which would make nut-cracking a CDT (sensu
135 Reindl et al., 2017). This is a clear claim that can be tested. If nut-cracking requires social

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[1] Prior to each of these steps occurring the individual must: 1. Identify the nut as a potential source of food 2.
Identify the hammer as a potential tool – weight might be an important factor here (Schrauf, Call, Fuwa, & Hirata,
2012). 3. Identify that a hard surface – whether this be a portable anvil or a tree root for example – must be used in
order to crack the nut. It may also be required that the individual transports some of these objects to bring them
together (Boesch & Boesch, 1984), potentially suggesting some form of future planning. We did not include these
actions in the experimental set-up as, although they are important for the behaviour as a whole, the culture-
dependency claim focuses primarily on the tool-use aspect of the behaviour (i.e., using a stone or wooden hammer
and an anvil to crack the nut). Furthermore, it is likely that the knowledge that nuts are edible is socially facilitated
(through non-copying forms of social learning such as stimulus and/or local enhancement). Therefore, here we focus
only on the crux of the behaviour: the tool-use aspect (see also Bandini & Tennie, 2017 for further explanation of
this method).

learning (if it is indeed a CDT), it should re-appear when a naïve chimpanzee has access to a
model nut cracker to observe. This would provide evidence for the view that social learning is
sufficient for nut-cracking to occur. However, to determine whether social learning is actually
necessary, it has to be tested whether nut-cracking can occur even in the absence of social
learning. If nut-cracking is a CDT, then it should not re-appear in such a (baseline) condition.
In its purest form, the Zone of Latent Solutions (ZLS) hypothesis (Tennie et al., 2009) posits that
all non-human great ape 'cultural' behaviours can be reinnovated (defined by Bandini & Tennie,
2017) by naïve apes[2]. In line with this and regarding nut-cracking, Hayashi, Mizuno and
Matsuzawa (2005) suggested that nut-cracking could potentially be individually reinnovated by
chimpanzees. Some field reports support these views. For example, a report of nut-cracking in
Cameroon (Morgan & Abwe, 2006) passes the 'information barrier' of the N'Zo-Sassandra
River (McGrew, Ham, White, Tutin, & Fernandez, 1997); this can be regarded as the outcome of
a natural quasi-latent solution test (sensu Bandini & Tennie, 2018), as this pattern strongly
suggests that that nut-cracking was (re-)innovated in two, culturally separate, wild communities
(Tennie et al., 2009, p. 2406). If all underlying steps of the nut-cracking behaviour are also found
to be reinnovated by a naïve, captive, chimpanzee in a culturally separate "island" of individuals
(Tennie, Braun, Premo, & McPherron, 2016; Tomasello, 1999) then the behaviour would (by
definition) cease to be a putative example of an animal CDT. If support were found for the ZLS
hypothesis, it would determine that chimpanzees are capable of individually learning all four of
the steps underpinning nut-cracking, demonstrating that social learning is not *required* for the
behavioural form (these steps in succession) to emerge. Just like for other chimpanzee
behaviours, including the accumulated number of cultural traits (Tennie et al., 2009, in press)
other, non-copying variants of social learning would then suffice to explain the cultural patterns
of nut-cracking in the wild by way of increasing and stabilising latent solution frequencies
instead (see above; Tennie et al. in press).
Therefore, here we test two competing hypotheses: chimpanzee nut-cracking as a culture
dependent trait (the "CDT hypothesis") versus chimpanzee nut-cracking as a behaviour that can
be individually learned (re-innovated; Bandini & Tennie, 2017), but whose expression may
nevertheless be facilitated by non-copying variants of social learning (the "ZLS hypothesis",
compare Tennie et al., 2009; in press).
Due to the fact that the two hypotheses are differentiated by the presence or absence of
observational necessity of nut-cracking behaviour, a test for the requirement of these
opportunities necessitates, as a logical starting point, the absence of all such observational
opportunities in the subjects. By testing captive apes, it is possible to control for their past
observational and individual experiences with target behavioural forms through keeper reports,
therefore ensuring that subjects are truly naïve to the trait. The only requirement is that subjects
are provided with the necessary raw materials[3] to be able to show the behavioural pattern (just as
may have occurred for the first (re-)innovations in each group in the wild, where all materials
could have been close by due to chance). Latent solutions (LS) tests (Bandini & Tennie, 2017;

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[2] Also known as the 'ZLS-Only' hypothesis for apes (Reindl, Bandini, & Tennie, 2018)
[3] In a wild population the raw material selection may be influenced by social learning of various non-copying
variants (e.g. via stimulus enhancement). However, the form of the behaviour is not as that would require copying
variants of social learning (both wood and stone anvils hold the nut and both wood and stone hammer are hammered
with), therefore the *form* of the behavior would be considered to be reinnovated if it comes about in naïve
individuals, even if material selection is different. And so, in the case of nut-cracking, wild chimpanzees may choose
the raw material type as a function of social learning but the expression of the behavioural form of nut-cracking can
still be a product of individual learning.

175 Tennie & Hedwig, 2009), allow for the examination of the role of individual learning in the
176 reinnovation of a behavioural trait that is claimed to be culture dependent – when the raw
177 material provided. The focus of the test is therefore whether the trait itself, here the behavioural
178 form – requires social learning – in line with the focus on culture dependent traits. It is important
179 to note here that whilst raw material selection may be influenced by non-copying variants of
180 social learning; the form of the behaviour is not (according to the ZLS hypothesis). For example,
181 in the case of nut-cracking, wooden or stone anvils are used in the wild to keep the nut in place
182 and wooden or stone hammers are used to crack it. Whether stone or wood is used, the form of
183 the behaviour is the same, and only material selection has changed – it is possible then that
184 individual learning is responsible for the form, whereas social learning, at least non-copying
185 variants, is responsible for material selection (Tennie et al. 2009).
186 Thus far, various chimpanzee behavioural traits, previously assumed to be culture dependent,
187 have already been reinnovated by naïve, captive subjects in latent solution tests (Bandini &
188 Tennie, 2017, 2019; Menzel, Fowler, Tennie, & Call, 2013; Motes-Rodrigo et al., 2019; Neadle
189 et al., 2017; Tennie et al., 2009; Tennie, Hedwig, Call, & Tomasello, 2008). These behaviours
190 ('latent solutions'; Tennie et al., 2009), were reinnovated without requiring any observation (or
191 teaching). This does not, however, mean that social learning does not play any role in the
192 innovation likelihood of these behavioural forms. Indeed, several forms of social learning (the
193 specific mechanism was not directly tested for in the studies mentioned above) greatly facilitate
194 the innovation likelihood of the behaviour in both captive and wild chimpanzees (therefore
195 affecting the observed frequencies of behaviours within and across populations; Tennie et al. in
196 press; Bandini & Tennie, 2017, 2019).
197 In the current study, we tested both the CDT and the ZLS hypothesis predictions for nut-
198 cracking. In 2010, Tennie et al. hypothesised that nut-cracking would be within the chimpanzee
199 ZLS, but that it may simply have a relatively low baseline probability of reinnovation (i.e., it is at
200 the at the very edge of the chimpanzee ZLS). We were able to test both hypothesis by applying
201 the extended latent solutions testing methodology (Bandini & Tennie, 2018). This method first
202 starts by testing for the reinnovation of the target behavioural form (here nut-cracking) in
203 completely naïve chimpanzees (we ensured naivety by asking keepers of the animals' previous
204 experiences of the behaviour) subjects (a pure island test) – thus testing the ZLS hypothesis. If
205 the behaviour does not appear in this baseline, subjects are then provided with incremental levels
206 of social learning information. The particular methodology followed in this study (Bandini &
207 Tennie, 2018) allows for the examination of the role of individual learning (initial baseline test),
208 then subsequently for end-state emulation, goal emulation and finally action copying (imitation)
209 in the emergence of the target trait.

210 Materials & Methods

211 Subjects

212 The subjects were 13 chimpanzees (M_{age} = 31.08; SD = 1; female = 9, male = 4; *Pan troglodytes*
213 *sp.*). All subjects lived within a single group, except for one individual (C13), that, due to group
214 transfers within the zoological institution throughout the duration of this study, was introduced
215 into the group before the start of the second condition (therefore C13 did not participate in the
216 baseline condition). The subjects were housed in two enclosures throughout the course of the
217 study; between 13th June 2017 and April 2018 subjects were housed in the "conversion"
218 enclosure, from April 2018 until the end of the study subjects were housed in the "Eden"
219 enclosure. Both enclosures consisted of two indoor areas and an outdoor area (two smaller areas
220 in the case of conversion), with separate management areas (away from the observation of

221 visitors). Subjects could be observed through glass panes in all public areas and mesh in
222 management areas, observations used in this study were obtained from both. Within the main
223 enclosures, subjects had access to enrichment devices, such as climbing frames/ropes, hanging
224 feeders and nesting baskets. Other enrichment devices are regularly provided by keepers.
225
226   TABLE 1 ABOUT HERE
227
228 **Prior experience questionnaire**
229 In order to exclude any possible influence of social learning on the results of this study, keepers
230 filled out questionnaires and were interviewed (designed and distributed by EB at the zoological
231 institution) about prior tool use behaviour. The use of this questionnaire was approved by the
232 University of Birmingham STEM ethical review committee (ERN_17-1729). The section of the
233 questionnaire relevant to this study can be found in S1. The questionnaire asks keepers to
234 provide details on behaviours relating to "*Using one object to bang on, or hit, another: usually,*
235 *this means the use of a hard object to bang on or hit another, often hard, object. This may be*
236 *with the aim to crack or break open the latter object, or to remove a substrate. Here, we are*
237 *interested in any hammer-like behaviours, regardless of the objects involved*". This definition
238 encompasses nut-cracking and similar actions, such as hammering behaviours. No instances of
239 nut-cracking were reported in the questionnaire; however, a keeper described how one individual
240 (C6; female; age 9) used a stone to tap on the glass of the outdoor enclosure. All but one keeper
241 reported that the chimpanzees were frequently witnessed using their teeth to crack nuts[4].
242 **Ethical statement**
243 All participation in this study was voluntary, and subjects were allowed to leave the testing area
244 at any point throughout the session. Subjects' usual feeding and cleaning routines were followed,
245 minimising disruption to the animals. The experimental phase of this study was ethically
246 reviewed and approved by the University of Birmingham AWERB committee (UOB 31213) and
247 by an internal committee at the testing location, following guidelines provided by SSSMZP,
248 EAZA, BIAZA, WAZA on animal welfare and research in zoological institutions; this study also
249 received a letter of support from BIAZA. This study adhered to legal requirements of the UK,
250 where the research was carried out, and adhered to the ASP principles for the Ethical Treatment
251 of Primates.
252 **Motivation tests**
253 This phase took place between 13th June 2017 and 27th September. Prior to starting experimental
254 testing, it was important to ensure that the subjects were sufficiently interested and motivated to
255 access the novel food reward (macadamia nuts) used in this study. To motivate the chimpanzees
256 to try the nut kernels when first presented, the first stage involved a trusted individual (a keeper
257 that has worked with the subjects for more than five years) first eating a different familiar food in
258 front of the subjects (here we used dried raisins and berries). The keeper attracted the subject's
259 attention by calling their name, and then ate a single item of the familiar food (i.e., one raisin) in
260 view of them. This process was repeated until each individual had observed the consumption; in
261 a group context. The subjects were then provided with the same food and were required to eat it
262 before moving onto the next step, as this food was familiar this occurred in every case. The next
263 stage was to introduce the *novel* food (macadamia nut kernels already without their shells). The
264 same keeper ate a single macadamia kernel in the same way as with the familiar foods. Again,

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[4] However, note that these chimpanzees had never been provided with shelled macadamia nuts – these are the
hardest commercially available nut.

265 each individual was given a demonstration (sometimes groups of individuals could watch
266 together as subjects were not separated during this part of testing). Once each individual had
267 observed the consumption of the nuts at least once, they were provided with a macadamia kernel,
268 again within a group context. This process was designed to increase the likelihood that the
269 subjects would eat the novel food (sensu Visalberghi, Yamakoshi, Hirata, & Matsuzawa, 2002) –
270 as the trusted keeper ate and introduced edible and safe food, ensuring that the chimpanzees
271 would be motivated to get inside the macadamia nuts to eat the kernels. We required at least half
272 the chimpanzees to eat the novel nuts before starting testing, this was to ensure that the
273 preference testing did not go on for too long, as these tests were carried out within a group
274 context, it was likely that lower ranking individuals would never be allowed access to the nut
275 kernels.

Test conditions

277 Each trial was video recorded, this started when the subjects were given access to the testing
278 apparatus. This time was chosen as it complimented the daily routine of the keepers and animals
279 (it was the period of time between the first morning feed and afternoon feed) whilst providing the
280 maximum texting time possible. The timings changed once the chimpanzees moved enclosure as
281 the keepers were able to provide the afternoon feed without needing to move the subjects outside
282 the testing area. Average trial length before the move was 3 hours ($n = 8$), after the move it was 5
283 hours 41 minutes ($n = 12$). Overall, there was a total of 92 hours and 18 minutes observation
284 time ($M_{trial\ length} = 4$ hours 37 minutes). The experimenter (DN) was present throughout each trial.
285 This study used a stepwise design, where each condition (see Figure 1) was followed by the next
286 in the event that the behaviour was not expressed in the first condition after five trials. For
287 example, the "End state" condition was only implemented in the event that the behaviour was not
288 reinnovated in the "Baseline" condition. Testing ended once the subjects had received 5 trials
289 with full action demonstrations.

<p style="text-align:center">FIGURE 1 ABOUT HERE</p>

291
292 In all of the conditions, behaviours were first live coded. If, after live coding, any attempts at
293 nut-cracking had been identified then these would have been coded from videos and then second
294 coded for reliability analysis. Here we defined nut-cracking in terms of tool use, therefore, to
295 qualify as nut-cracking, the subject needed to use an object as a hammer to attempt to break open
296 the nut, whilst resting the nut on another hard surface (the anvil). Video recordings were
297 focussed on the experimental hammer and anvil set up, described below, however DN was
298 present at all times to observe any behaviours which might have occurred outside of the camera
299 frame.

Materials

301 The same apparatus set up was used in all conditions, and any changes to these conditions are
302 noted in the relevant section. To set up the apparatus, DN entered the outdoor enclosure and
303 secured a large wooden log (50cm tall x 40cm diameter; that would serve as an "anvil") to an
304 upright portion of the climbing frame (which had a horizontal crossbeam, to ensure that the anvil
305 could not be removed; see Figure 2). The anvil was secured to the upright climbing frame using
306 two 1m long, 8mm thick, PVC coated, steel rope passed through two (12mm diameter) holes
307 drilled through the anvil (located ¼ and ¾ of the way down the log). Both ends of the rope had a
308 loop (secured by five 'clips' at each point, 'clips' used two, 8mm, nuts and bolts (tightened using
309 an electric drill), which was too large to pass through the hole in the anvil, and a steel padlock

310 attached the two ends. Two of these securing attachments were used as a failsafe measure (see
311 Figure 2).
312   FIGURE 2 ABOUT HERE
313

314 A wooden "hammer" was also attached to this structure (wooden, rather than stone, hammers
315 were chosen as they were more secure in their attachment to the rope). The hammer consisted of
316 a 30cm long x 15cm diameter log – approx. weight 2.5 kg – with a 12mm hole drilled through
317 half way along (see Figure 2). The hammer was attached to the anvil's own securing attachment
318 by creating another looped end in another (1.5m) length of the same steel rope; the loop was
319 passed onto the top securing attachment (of the anvil) and the loose end was secured to the
320 hammer (by passing the loose end through the drilled hole and then securing with another five
321 clips). The hammer was then moved less than 1m from the anvil (see Figure 3).
322

323   FIGURE 3 ABOUT HERE
324

325 The keepers then scattered three macadamia nuts (in their shell) per individual (i.e., 3 nuts x 13
326 individuals = 39 nuts) throughout the enclosure, avoiding a 2m radius around the hammer and
327 anvil set-up. The macadamia nuts were distributed at the same time as a regular scatter feed –
328 just prior to the subjects being released into the outdoor enclosure. The unshelled weight of the
329 nuts (around 1g average across 10 measurements) was taken from the chimpanzees' usual
330 allowance of nuts for the week (this was to maintain the dietary health of the subjects, at the
331 testing institution's request). Once the attachments had been checked by DN and at least one
332 keeper, all humans exited the enclosure and the chimpanzees were allowed in the enclosure. Just
333 prior to the chimpanzees being allowed access, video cameras (SONY HDR-CX330e), set at two
334 points framing the apparatus (to better capture various angles), on tripods, were set to record. DN
335 was also present to live code relevant behaviours (see above) that occurred outside of the frame
336 of the fixed cameras.
337 **Baseline condition**
338 This test condition took place between 15th October 2017 and 30th November 2017.
339

340   FIGURE 4 ABOUT HERE
341

342 In order to examine whether the subjects would individually reinnovate the target nut-cracking
343 behaviour, it was necessary to test subjects without providing any social information beforehand.
344 All sessions began between 10 am and 12 noon, when keepers provided the chimpanzees' scatter
345 feed (mainly consisting of vegetables and fruit). All sessions were conducted in the "Outdoor 1"
346 section of the enclosure (see Figure 1); however, subjects had access to both indoor areas
347 throughout the session.
348 **End state condition**
349 This phase of the study was completed between 15th January 2018 and 18th May 2018. However,
350 after the first two trials (15th January 2018 and 17th January 2018) the weather conditions at the
351 testing institution became so harsh that the subjects would often refuse to leave the indoor
352 enclosure. Thus, testing was paused until 14th May 2018, after which the final three trials were
353 completed on the14th, 16th & 18th May. Between testing in January and May subjects were
354 moved from "Conversion" (their previous enclosure) to a new enclosure: "Eden"; subjects were
355 therefore given one month after moving to the new enclosure to settle in before testing resumed.

356
357   FIGURE 5 ABOUT HERE
358
359 In this condition, we placed three macadamia nuts, shells and kernels, which had been split in
360 half (see Figure 6) on top of the anvil (in the "Conversion" enclosure this was in "Outdoor 1"
361 and in "Eden" this was in "Habitat 1"). This condition was designed to specifically trigger
362 stimulus/local enhancement (Thorpe, 1963); stimulus/local enhancement can be defined as when
363 an animal's attention is drawn to an object/location as a result of some change in the
364 environment. In this condition, we drew the subject's attention to the anvil and hammer (and the
365 nuts) by adding the cracked nuts on top of the anvil.
366
367   FIGURE 6 ABOUT HERE
368
369 This condition was carried-out as the chimpanzees failed to individually reinnovate the nut-
370 cracking behaviour in the baseline condition and followed the exact same protocol as the
371 individual learning condition, described above. During the design process the study originally
372 included an extra condition between the "Baseline" and "End state" conditions, called "Local
373 Enhancement". In this condition it would have been made clear to the subjects that a kernel is
374 inside the macadamia nut and therefore that it constitutes a food source by shaving half of the nut
375 shell away to reveal the kernel inside (see Bandini and Tennie, 2018). However, some of the
376 chimpanzees in this study cracked the shells of the macadamia nuts with their teeth and
377 subsequently consumed the kernels (see Figure 7), rendering this condition unnecessary.
378
379   FIGURE 7 ABOUT HERE
380
381 **Ghost condition**
382 This phase of the study was completed between 19th July 2018 and 10th August 2018. The ghost
383 condition involved a significant increase in the level of social information provided to the
384 subjects. In this condition, the hammer and anvil set-up were still present inside the enclosure,
385 along with three macadamia nuts per individual (scattered throughout "Eden Habitat 2") and a
386 further three nuts (this time whole, uncracked nut, inside the shell was provided) placed on top of
387 the anvil. Additionally, a replica of the equipment inside the enclosure (i.e., a hammer and anvil
388 set up) was placed outside the enclosure, visible through the mesh near the subjects' sleeping
389 area (see Figures 8 & 9); DN was also present, standing to the left of the anvil.
390
391   FIGURE 8 ABOUT HERE
392
393 A reel of clear fishing line (0.65mm diameter; 40lbs break strain) was attached to the hammer
394 and passed through a section of mesh, allowing the hammer to be raised (between 80 and 50cm)
395 above the anvil[5], via a pulley-like system (see Figure 9). Once the subject was clearly attending
396 the apparatus (the subjects' attention was gained by calling their names), the hammer was
397 dropped onto a nut (which was placed in a groove in the centre of the anvil), cracking the nut

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[5] A keeper was required to steady the hammer prior to it dropping, this was to ensure the hammer fell on the nut, therefore cracking it.

398   open[6]. A keeper then approached the anvil and gave the subject who watched the demonstration
399   the cracked nut. The device was then rebaited with a new nut in the centre of the anvil. This
400   procedure was repeated for a further 29 nuts (equalling a total of 30 demonstrations[7]). Subjects
401   had access to the testing apparatus during the course of the ghost trials. One camera was used to
402   record the subjects' interactions with the test apparatus, whilst the other was used to record
403   subject's observing the ghost demonstrations[8]. In both this condition and the Full Action
404   Demonstration condition observing subjects were considered to be those in the enclosure
405   immediately in front of the demonstration area (far left sleeping area in Figure 8) oriented
406   towards the apparatus/demonstrator (i.e., not with their back turned).
407
408   FIGURE 9 ABOUT HERE
409
410   This ghost condition (inspired by Hopper, Lambeth, Schapiro, & Whiten, 2008) fulfils the
411   primary stipulation of learning by emulation (Tomasello et al., 1993); i.e., the learner should not
412   copy the motor patterns of the demonstrator (otherwise the patterns may be better attributed to
413   object movement re-enactment or imitation; see Whiten, Horner, Litchfield, & Marshall-Pescini,
414   2004 for discussion of this distinction). In this ghost condition, the motor patterns required for
415   nut-cracking were not demonstrated, making it impossible for the chimpanzees to copy the
416   actions (Heyes, 1994). Thus, if the behaviour were to occur following this condition, it could be
417   inferred that the results of the actions were replicated rather than the actions themselves (Hopper,
418   2010; Whiten et al., 2004).
419   **Full action demonstration condition (human demonstrator)**
420   This phase of the study was completed between 16th August 2018 and 6th September 2018. The
421   full action demonstration condition was the first condition that for the first time allowed for the
422   possibility of action copying. In this condition DN was positioned outside the enclosure (in the
423   same location as the ghost condition). An anvil was placed in the same location as in the ghost
424   condition (see Figure 8), with a hammer placed 1m from the anvil (both pieces of wood were
425   identical to those in the subject's enclosure). The researcher then attracted a subjects' attention
426   by calling their name and proceeded to crack a nut, on top of the anvil, using the hammer. Note,
427   it was not possible to exclude the fact that multiple subjects may attend to the call of one
428   individual – subjects attending to a demonstration were coded from videos. The experimenter
429   used the hammer in a vertical manner[9], in the same orientation to the hammer in Figure 9 (see
430   Figure 10), raising it to eye level and then hitting down onto the nut, resulting in the nut breaking
431   open. The kernel was then provided to the subject by a keeper (see Figure 10D) and the device
432   rebaited with another nut. A total of 30 nuts were cracked using this procedure in each trial; a nut
433   was not cracked until DN considered that the target subject was attending to the demonstration.
434   A maximum of 30 nuts was used based on advice from keepers that not all subjects would attend
435   to, or even approach, the demonstrations; therefore, trials could have continued indefinitely and
436   would have quickly become unfeasible.
437

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[6] Sometimes the nut did not break the first time, in such cases, several drops of the hammer were required.

[7] With the exception of trial 4 – where an equipment malfunction (the fishing line broke) – forced the trial to end after 17 nuts had been cracked.

[8] In addition, a GoPro (Hero Session 5) camera was used to record the ghost demonstrations from the viewpoint of the demonstrator.

[9] This orientation was chosen to control for the position of the hammer between the ghost and full demonstration conditions.

438   FIGURE 10 ABOUT HERE
439
440 **Coding/analysis of behaviours**
441 *Coding procedure*
442 Trials were live coded using the ethogram in Table 2. Following live coding a formal coding
443 procedure from video was followed. DN coded each trial in turn and a second coder (MT), naïve
444 to the hypothesis of this study, second coded 100% of the behaviours identified (N=31) along
445 with an equal number of "dummy" clips where a subject was in the frame but DN did not
446 identify a behaviour occurring to test for inter-rater reliability (acceptable Kappa would be 0.6;
447 Cohen, 1968; calculted using R package "irr" v.0.84.1; Gamer, Lemon, Fellows, & Singh, 2019).
448 Note that the behaviours in Table 2 rely on the previous behaviour in order for them to be coded;
449 e.g., if the subject picked up the hammer without first placing a nut on the anvil then the hammer
450 behaviour would not be coded. This was to attempt to parse hammer centred play/exploration
451 from attempts at nut-cracking.
452
453   TABLE 2 ABOUT HERE
454
455 *Analyses*
456 After a single reinnovation of the behaviour social facilitation cannot be excluded as a potential
457 reason for the behaviour's continued emergence (Bandini & Tennie, 2018; Tennie & Hedwig,
458 2009). Given an N of 1, it is not possible to perform inferential statistics on acquisition times or
459 rates between individuals. However, descriptive statistics were used. All descriptive statistics
460 were produced using R v.3.5.2 (R Core Team, 2013).
461 # Results
462 **Motivation test**
463 During the motivation test, seven subjects[10] (54% of sample) consumed at least one macadamia
464 nut provided by the keeper, leading to the conclusion that macadamia nuts were a) palatable and
465 b) desirable to most of subjects included in this study (although note that dominance
466 hierarchies/individual personality characteristics may have interfered with certain individual's
467 ability/motivation to access the nuts).
468 **Reliability analysis**
469 The results of a Cohen's Kappa analysis revealed a strong level of agreement between coders (κ
470 = .85, p<.001).
471 **Attempts at nut-cracking**
472 None of the individuals in this study attempted to crack open the nuts using a tool in any of the
473 conditions described above; as there was never any evidence of nut-cracking, or approximations
474 of it, all conditions were completed (as explained in the methods section).
475 *Attempts recorded within the ethogram*
476 The coding procedure identified the following behaviours from the ethogram: place ($n = 26$),
477 hold ($n = 1$), stamp ($n = 2$) and throw ($n = 2$). Recordings of "place" were identified in C5 ($n = 7$), C6 ($n = 18$) and C7 ($n = 1$). In only one instance did a "hold" event follow "place", this
479 concerned C6; who was also the only individual to "stamp" on or "throw" the nuts. It is unclear
480 whether throwing was an active effort to break the nut or simply an act of frustration/play as it

[10] C3, C7, C9, C8, C5, C12 & C13.

481 did not appear that the throws were aimed at any hard surface, nor were there ever attempts to
482 retrieve the nuts afterwards by the throwers.
483 *Alternative techniques*
484 Anecdotally, the majority of subjects (if not all) were witnessed, at least once, attempting to
485 crack the nuts with their teeth (with some individuals succeeding; see Figure 7). Male
486 chimpanzees ($n = 4$) were the only individuals observed (by DN) successfully accessing the nut
487 kernel using this method. The teeth cracking technique was first observed in the baseline
488 condition and persisted throughout the study. These behaviours were not captured on the main
489 videos as the cameras were facing the apparatus throughout the trial (to ensure that any attempts
490 at using the apparatus to crack the nuts were captured), also some subjects were not visible
491 throughout; therefore, any attempt to quantify these behaviours would be inaccurate as it would
492 likely present only part of the actual series of events.
493 *Observers Ghost and Full Action Demonstration Conditions*
494 Occasionally the identity of the observer could not be ascertained from video footage; in these
495 cases, the individuals were not included in the calculations below. Furthermore, as participation
496 in the study was voluntary, and subjects were free to approach and interact with the testing
497 apparatus whenever they chose, not all subjects observed all the demonstrations provided. Some
498 subjects ($n = 2$; C5 & C11) never observed the demonstrations in either condition; whilst other
499 subjects never observed demonstrations in the ghost ($n = 3$; C5, C13 & C11) or full
500 demonstration conditions ($n = 4$; C5, C11, C1, C10). However, 77% of subjects ($n=13$) were
501 coded as observers in the ghost condition and 69% ($n=13$) were coded as observers the full
502 demonstration condition; there was an average of 2.48 observers per ghost demonstration[11] and
503 2.99 observers per full demonstration.
504 **Discussion**
505 We found no evidence of nut-cracking with a tool, or any approximation at this, at any point
506 during the course of this study. Thus, our sample of 13 naïve chimpanzees failed to reinnovate as
507 well as socially learn the behavioural form of nut-cracking. At first, it would seem our findings
508 support the CDT hypothesis, in that nut-cracking behaviour was not reinnovated in our initial
509 baseline condition. However, our study also contained various social learning test conditions –
510 including one that demonstrated the necessary action patterns for nut-cracking to the
511 chimpanzees. This condition allowed for the possibility of action copying being a requirement of
512 the behaviour, as has recently been claimed (Estienne, Cohen, Wittig, & Boesch, 2019). Even so,
513 nut-cracking was not acquired by the subjects. Therefore, our study does not provide conclusive
514 evidence for either the CDT or the ZLS hypothesis. Below we discuss three possible
515 explanations for our null result and the general disparity in studies of chimpanzee nut-cracking.
516 **Conspecific models**
517 The findings of this study raise the question as to why some chimpanzee populations in the wild
518 regularly crack nuts (on average 270 nuts per day for as long as 2 hours 15 minutes in Taï Forest;
519 Boesch & Boesch-Achermann, 2000) whereas captive chimpanzees (in this sample and others;
520 Funk, 1985) seem to rather consistently fail to acquire the behaviour, even after demonstrations.
521 A first possibility for the disparity between wild and captive data is that nut-cracking is indeed a
522 CDT and requires the learner to imitate a conspecific demonstrator (Boesch, 1996). In this study

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[11] Note, a demonstration in the ghost condition was defined as a single drop of the hammer onto the nut – regardless
of whether the nut broken. However, in the full demonstration condition a demonstration was the successful
breaking of the nut – this was because repeated strikes of the hammer on the nut were often required for the human
demonstrator – where in the ghost condition a single "on-target" strike was sufficient.

523 we used human demonstrators, which may not have been considered 'good' enough models for
524 the chimpanzees. Indeed, some research has shown that chimpanzees are more proficient social
525 learners from conspecific models as compared to videos or human models (Hopper, Lambeth,
526 Schapiro, & Whiten, 2015). However, in contrast, others have instead claimed that it is possible
527 for chimpanzees to "learn" nut-cracking from human demonstrators (see findings of Ross,
528 Milstein, Calcutt, & Lonsdorf, 2010 but also review of other related studies Table 3 (p. 230) of
529 Ross et al. 2010). Concurrently, other studies have found that, even with conspecific
530 demonstrators, sometimes captive chimpanzees fail to acquire complex behaviours such as nut-
531 cracking (Funk, 1985) or behaviours which strictly require imitation (Clay & Tennie, 2018;
532 Tennie, Call, & Tomasello, 2012; Tomasello et al., 1997). Although it might have been
533 interesting to observe the chimpanzees' reaction to a conspecific demonstrator in this study, we
534 did not have the resources nor the possibility to train a chimpanzee to show the behaviour to act
535 as a demonstrator, but we encourage interested researchers who do have the resources and the
536 chance to replicate this study, and include a conspecific demonstrator to observe whether this
537 affects the findings presented here.

538 **Behavioural flexibility**
539 An alternative explanation for the fact that nut-cracking did not emerge in this study is that the
540 chimpanzees were hindered by their lack of behavioural flexibility, a commonly recorded
541 phenomenon in chimpanzees (e.g., Harrison & Whiten, 2018). The chimpanzees in the current
542 study seemed to become fixated on one solution to open the nuts: i.e., the use of their teeth. The
543 chimpanzees may have relied on this technique due to their pre-existing knowledge on how to
544 crack softer-shelled nuts (such as peanuts and walnuts), which they are often provided during
545 their feeds at the testing institution. These nuts are easily cracked open by apes using teeth (DN;
546 personal observation, keeper reports and see also Visalberghi et al., 2008 for measurements on
547 the required force for different types of nuts). The heuristic (Marsh, 2002) in this case may be
548 that nuts (in general) *can* be opened with teeth – and indeed our Macadamias were no exception.
549 Chimpanzees have been shown to be reluctant to display behavioural flexibility in abandoning a
550 previously successful solution (see Harrison & Whiten, 2018; Hrubesch, Preuschoft, & van
551 Schaik, 2009; but see also Manrique, Völter, & Call, 2013). Thus, it is possible that the first
552 individual to successfully crack a nut with the use of teeth (see Figure 7), facilitated this
553 behaviour within the group and/or that other individuals independently converged on this
554 method, and then the subjects were unable to innovate a new method, even if cracking the nuts
555 with a tool would have been mechanistically easier/more efficient (this possibility is also in line
556 with the cultural founder effects; Tennie et al., 2009).

557 **Sensitive learning period**
558 Based on the literature, the most likely explanation for the findings in this study is that the
559 chimpanzees in this study may have simply been too old (outside their sensitive learning period
560 for this behaviour) to reinnovate nut-cracking. Previous studies on nut-cracking in wild
561 chimpanzees have reported that before 3.5 years, juvenile chimpanzees are unable to express the
562 full nut-cracking behavioural form (Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, 1994).
563 However, juvenile chimpanzees (as young as 1.5 years old) that had been exposed to the
564 materials required for nut-cracking at various ages/developmental stages were able to perform
565 the basic actions of the behaviour (put, hold, hit and eat), but not combine them in the required
566 order to perform the full nut-cracking behaviour (Inoue-Nakamura & Matsuzawa, 1997). Indeed,
567 recent research in wild chimpanzees shows an exponential increase in nut-cracking between 5
568 and 6 years of age, though the first signs were observed in 3-4-year-old individuals (Estienne et

569 al., 2019) in line with the concept of maturation (Corp & Byrne, 2002). This finding suggests a
570 certain level of developmental prowess required to express nut-cracking, perhaps somewhere
571 between maturation effects of the body and the brain.
572 In addition to this lower age limit for the acquisition of nut-cracking, there also appears to be an
573 upper limit (more relevant for the current study). A 13 year longitudinal study by Biro et al.,
574 (2003) found that wild chimpanzees who did not learn the basic nut-cracking skills before five
575 years old seemed unable to acquire the behaviour later on in adulthood (a similar case has been
576 documented recently for stone tool-use in long-tailed macaques; Tan, 2017). The subjects tested
577 in the current study were all outside of the hypothesised sensitive learning period for nut-
578 cracking, as the youngest subject in our sample was already 10 years old at the time of testing.
579 The youngest individual however was the only subject to display the "hold" behaviour (stage two
580 of four) in the behavioural form of nut-cracking. Our findings, coupled with those described here
581 suggest that a sensitive learning period may be a decisive factor for whether a chimpanzee will
582 start to crack nuts or not (leaving open the question how this is learned, i.e. whether it is a CDT
583 or a latent solution).
584
585 **Conclusions**
586 Although no chimpanzees in this study demonstrated nut-cracking behaviour, two geographically
587 separate populations in the wild have all converged on the same method for cracking nuts using
588 tools (West Africa; Whiten et al., 2001 and Cameroon; Morgan & Abwe, 2006). As these
589 populations do not have access to each other, logically they must have independently reinnovated
590 nut-cracking (Byrne, 2007). Furthermore, one chimpanzee in an experiential study has
591 spontaneously reinnovated nut-cracking when provided with all the materials (Marshall-Pescini
592 & Whiten, 2008). The individual (Mawa) acquired the nut-cracking behaviour seemingly without
593 requiring any copying forms of social learning (Marshall-Pescini & Whiten, 2008)[12]. However, it
594 is important to note that Mawa was kept as a pet prior to residing at the sanctuary where
595 Marshall-Pescini and Whiten (2008) carried-out their study. Mawa arrived at the sanctuary when
596 he was approx. three years old with wounds from a rope where he was tied up (Ferdowsian et al.,
597 2011). As a result of this potential enculturation, or at the very least deprivation, these data
598 should be treated with caution; indeed, the generalisability of such individuals to wild
599 chimpanzees is questionable (Henrich & Tennie, 2017).
600 This said, excavations of chimpanzee nut-cracking sites suggest that the basic behavioural form
601 has remained constant for at least 4,000 years, and likely even longer (Mercader et al., 2007).
602 Similarly, excavations of capuchin nut-cracking sites have demonstrated that their nut-cracking
603 form has remained the same for 3,000 years, with only the tools (hammerstones) changing in
604 shape over time (Falótico, Proffitt, Ottoni, Staff, & Haslam, 2019). Indeed, if the behavioural
605 form of nut-cracking were being copied between individuals, we would expect to see some
606 changes to its form over time due to copying error alone (see Eerkens & Lipo, 2005). Lastly,
607 other extant species of primates[13] also crack nuts using tools in the wild (long tailed macaques,

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[12] However, Marshall-Pescini & Whiten (2008) fail to note the importance of these findings, by assuming, based on
the speed of acquisition, that "Mawa" had prior experience of nut-cracking. It is worthy of note however that unlike
this study and that of Funk (1985) no claim of naivety of the subjects was made by either of the other studies and
therefore these results should be treated with caution.

[13] Also, there have been suggestions that, given the archeological record, it is likely that early hominins were
capable of, and indeed did, crack nuts using stone tools (Goren-Inbar, Sharon, Melamed, & Kislev, 2002). Although
some have claimed that our last common ancestor did not use tools to crack nuts (Haslam, 2014).

608 Gumert & Malaivijitnond, 2013; capuchins, Ottoni & Mannu, 2001), and some have even been
609 found to do so spontaneously in captivity without requiring social learning (e.g., nut-cracking is
610 a latent solution in capuchins: Visalberghi, 1987). Collectively, this data suggests that copying
611 forms of social learning are likely not or not fully responsible for the acquisition of nut-cracking
612 in chimpanzees (especially given the results of the current study, in which the chimpanzees did
613 not acquire the behaviour even after full demonstrations were provided).
614 Therefore, the results of this study do not support nut-cracking as the first evidence of a CDT in
615 chimpanzees (see also Byrne, 2007). Instead, the behaviour may not have emerged here due to
616 interplay of factors, including a certain level of behavioural conservatism and, crucially, the fact
617 that all the subjects were already out of their sensitive learning periods for nut-cracking. We
618 believe it is unlikely that our use of human demonstrators was in the reason for the failure of all
619 our subjects to express nut-cracking, given the results of previous studies, discussed above.
620 Accordingly, we propose that future studies should adopt the methodology presented here, but
621 test unencultured infant/juvenile chimpanzees, naïve to nut-cracking *and* to opening nuts with
622 their teeth, to remove the confounds of the sensitive learning periods and conservatism (ideally
623 tested in isolation in order to increase effective sample size). Under these conditions, it is
624 plausible that some naïve chimpanzees will reinnovate nut-cracking. Yet, on the other hand,
625 given the extended trial-and-error learning process that young chimpanzees engage in
626 (Matsuzawa et al., 2008) it is possible that under the relatively short term test conditions, the full
627 form of nut-cracking may still fail to emerge spontaneously, although some of the pre-requisite
628 steps to the behaviours may still develop. So far, the findings of this study, and others, do not
629 support the view that nut-cracking has to be reliant on social learning, i.e., it does not seem to be
630 a CDT. Therefore, it remains possible that nut-cracking, while inside the chimpanzees' ZLS, is at
631 the very brink of it. Additionally, it appears as if nut-cracking's behavioural form may only be
632 acquired through an interplay of ecological factors, i.e., chimpanzees must be in a location with
633 appropriate nuts and tool materials, during or before, their sensitive learning period.

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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
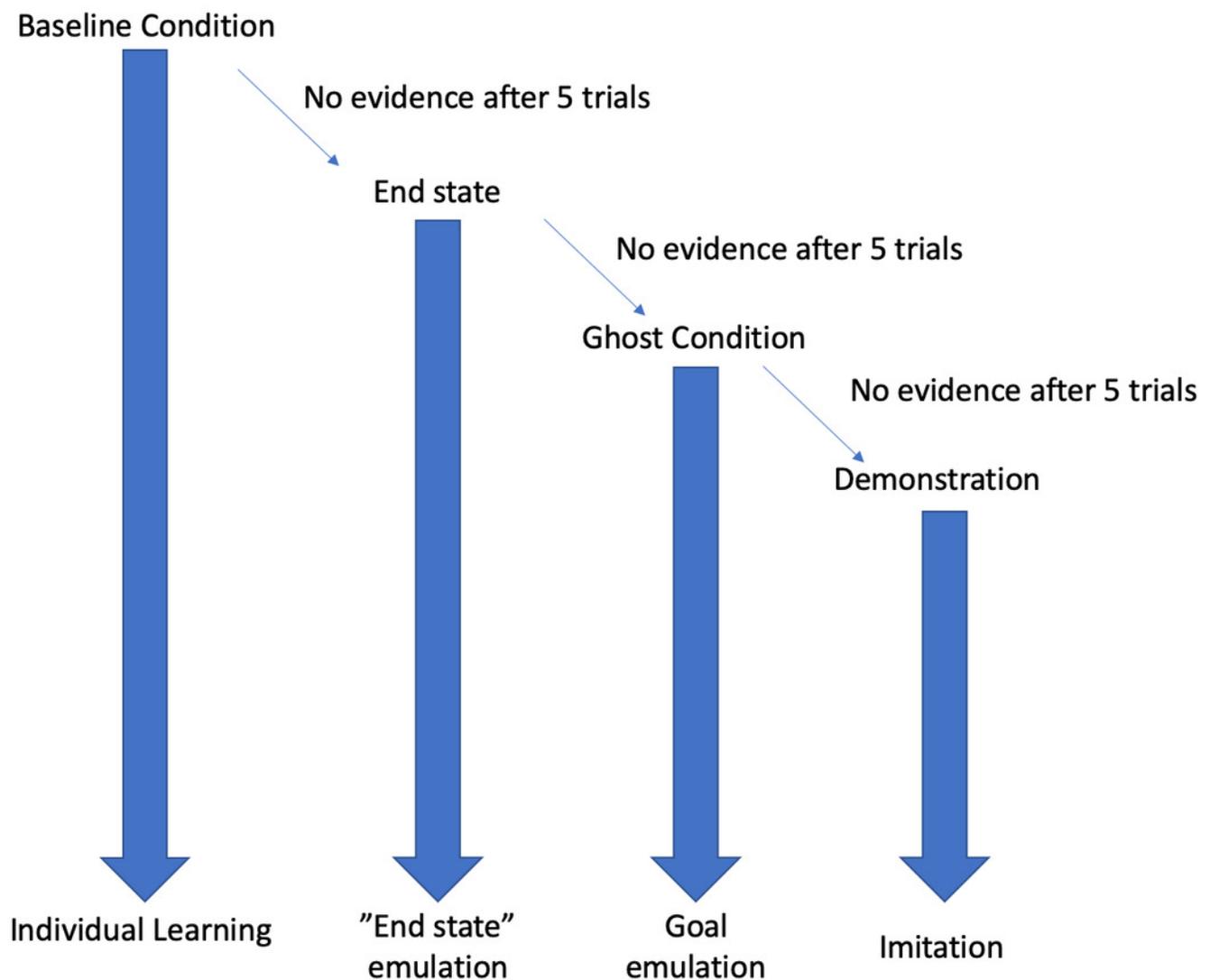
Figure 2

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 3

Securing attachment of the hammer.

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

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).
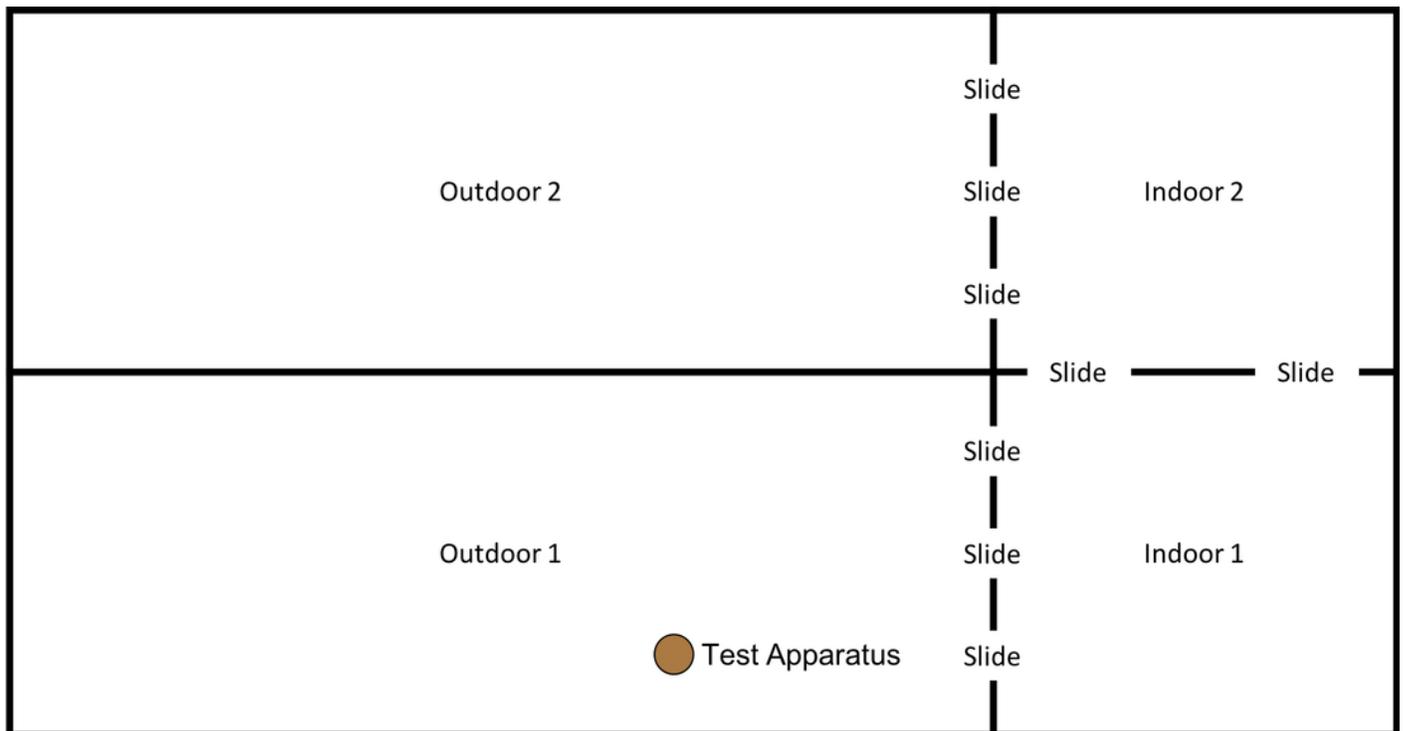
Figure 5

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.
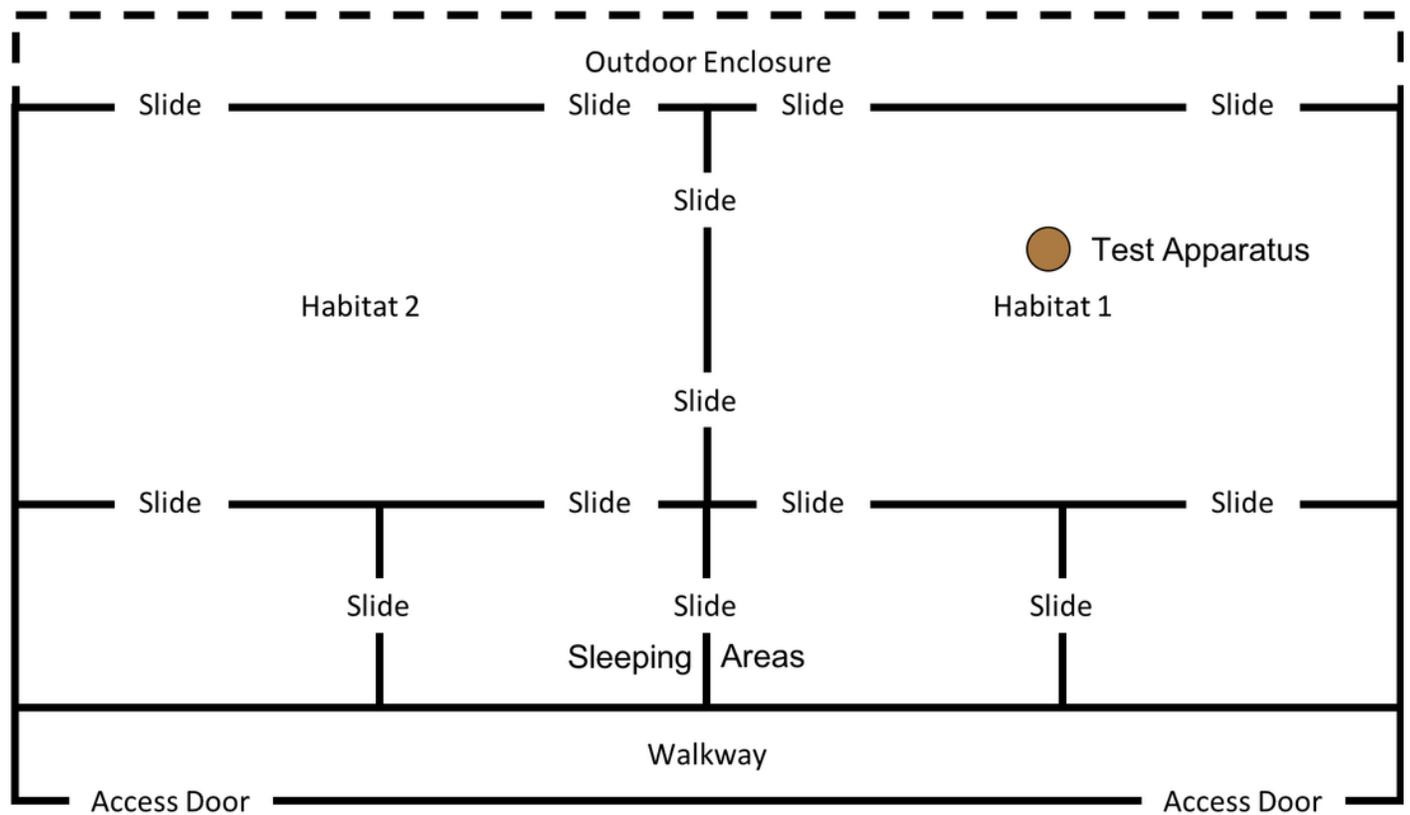
Figure 6

Macadamia nut placement and state for end-state condition.

(Left) Macadamia nuts, sawn in half (with kernels left whole) for the end-state emulation condition. (Right) 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.

(Left) C5 biting the nut in an attempt to break it; (Right) 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.*
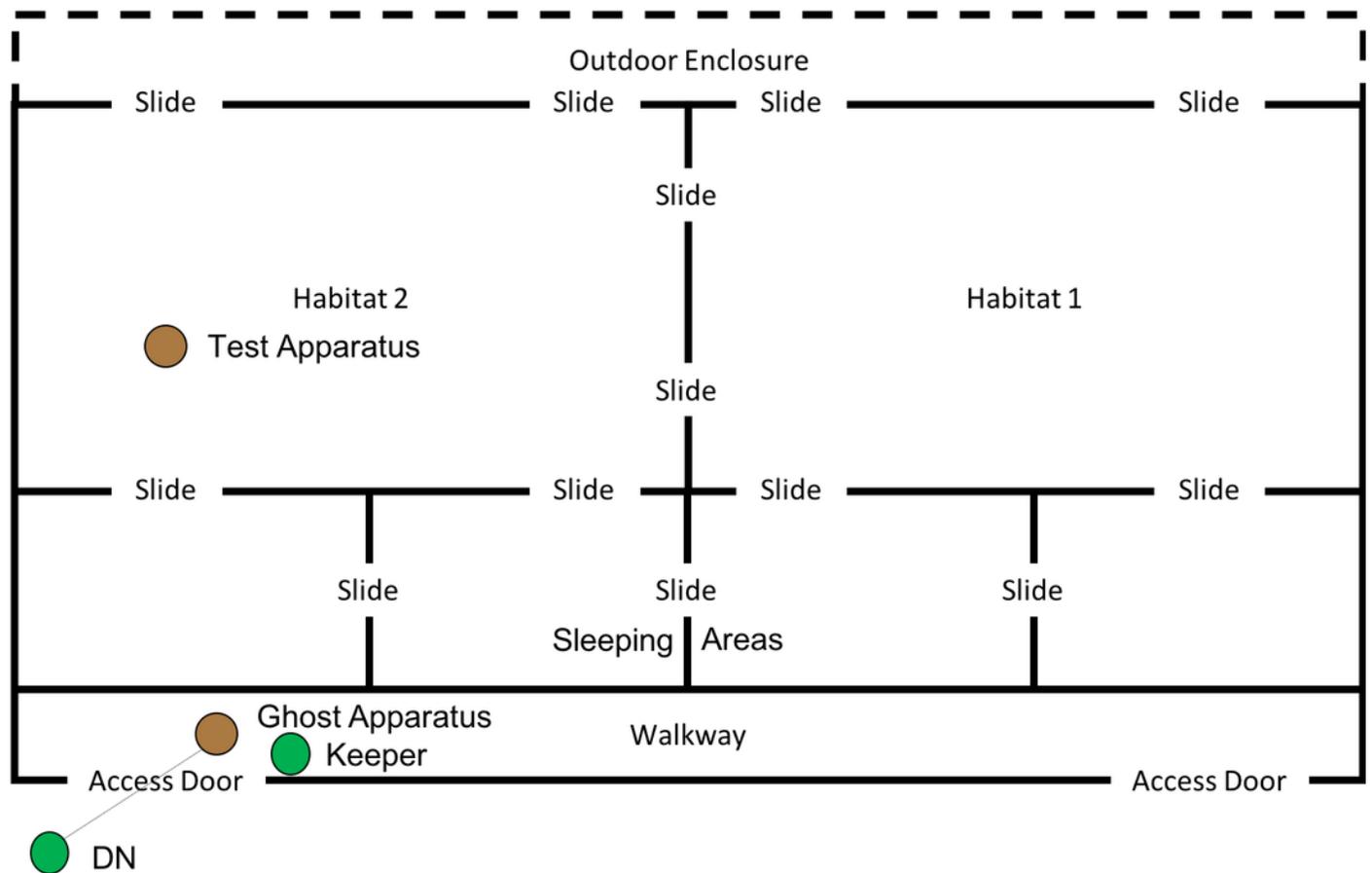
Figure 9

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).