

1 **A candidate culture-dependent form in apes, nut-cracking, can be individually learnt by**
2 **naïve orangutans (*Pongo abelii*)**

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28 ***Abstract***

29 Several species of non-human apes have been suggested to rely on copying to acquire some of
30 their behavioural forms. One of the most cited examples – and UN-protected – is nut-cracking
31 in chimpanzees. However, copying might not be the most parsimonious explanation for nut-
32 cracking, considering the lack of evidence for spontaneous copying in this species. The zone
33 of latent solutions (ZLS) hypothesis argues instead that the behavioural form of nut-cracking
34 is individually learnt, whilst non-copying social learning fosters frequency differences across
35 populations. In order to differentiate between the copying and the ZLS hypothesis, four nut-
36 cracking-naïve orangutans ($M_{age}=16$; age range=10-19; 4F; at time of testing) were provided
37 with nuts and hammers but were not demonstrated the behaviour. Whilst the adults in the
38 group were able to open nuts with their teeth, one juvenile spontaneously expressed nut-
39 cracking with a wooden hammer. We therefore show that the behavioural form of nut-
40 cracking does not necessarily rely on copying in orangutans.

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57 *Introduction*

58 Once heralded as the main distinguishing feature of humans in the animal kingdom, it is now
59 known that several other species also possess the ability to use tools (Shumaker, Walkup,
60 Beck, & Burghardt, 2011). Of these species, non-human great apes (henceforth apes),
61 alongside New Caledonian crows (Kenward et al., 2011), demonstrate the most extensive
62 tool-use repertoires (van Schaik, Deaner, & Merrill, 1999). However, the actual mechanisms
63 behind the apes' acquisition of tool-use repertoires are still debated. The most common
64 approach in the current literature is one in which apes are argued to acquire some of their
65 behavioural forms through copying variants of social learning (e.g., imitation and/or
66 mechanisms such as object movement re-enactment; de Waal, 2001; Matsuzawa et al., 2008;
67 Whiten et al., 2001, 1999a). We refer to this view as the “copying hypothesis” throughout this
68 paper.

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70 Whilst the copying hypothesis is pervasive in the literature, the evidence for apes having the
71 ability to spontaneously acquire novel behavioural forms (actions) through copying is still
72 lacking. Indeed, unenculturated captive apes reliably fail to spontaneously copy actions in
73 controlled experimental settings (unenculturated apes are those that have not been human-
74 reared or exposed to long-term human contact and/or training; Henrich & Tennie, 2017; Clay
75 & Tennie, 2017; Tennie, Call, & Tomasello, 2012). Yet, some argue against findings from
76 experimental studies with captive apes, claiming that observational reports of *wild apes* (such
77 as wild chimpanzees) suggest that these animals can copy actions (e.g., Boesch, 1991;
78 Boesch, 2012). This question is difficult to test with wild apes, and so it remains a possibility.
79 Yet, it seems to be an unparsimonious possibility, especially considering that the only apes
80 that have, so far, been found to copy some actions (in a crude way) are human
81 trained/enculturated captive apes (Pope, Tagliatalata, Skiba, & Hopkins, 2018; Toth, Schick,
82 Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993). This would suggest instead that wild apes –
83 who do not have a background of either human training or enculturation - would be just as
84 unlikely to copy actions as unenculturated, untrained captive apes (see also Tennie, in press).
85 Indeed, neuroscience studies carried-out with enculturated/imitation-trained captive apes
86 found that extended exposure to humans and/or human training (with methods such as the
87 ‘do-as-I-do’ paradigm) demonstrably *changes* apes' brain structures in a way that only then
88 allows for some (rudimentary) action copying (Pope, Tagliatalata, Skiba, & Hopkins, 2018).

89 Overall, then, we may surmise that wild apes, alongside untrained/unenculturated captive
90 apes, most likely lack the ability to copy novel actions.

91 Despite these data, action copying is still often cited as the main mechanism behind ape, and
92 especially chimpanzee, behavioural forms. Some have even further claimed that (certain) ape
93 behaviours (such as tool-use behaviours) depend on copying social learning to be acquired by
94 naïve individuals (Boesch, 1991; Boesch, 2003; Luncz, Mundry, & Boesch, 2012a; Luncz &
95 Boesch, 2014; Lycett, Collard, & McGrew, 2007, 2010; Whiten, & Goodall, 2001; Whiten et
96 al., 1999b). If that were true, these behavioural forms would represent examples of so-called
97 culture-dependent forms (henceforth CDFs; Reindl, Apperly, Beck, & Tennie, 2017; Tennie
98 et al., in press) and, in principle, should only exist where they can be copied from others – i.e.
99 where cultural evolution has produced them.

100

101 *Nut-cracking in chimpanzees*

102 Some non-human primate species (henceforth: primates) include nuts in their diets. This is a
103 beneficial behaviour, as nuts represent an important source of calories and fat (Biro et al.,
104 2003). The encased condition of these nutrients, however, makes it often necessary that these
105 species use stone and/or wooden hammers to crack open the nuts against hard surfaces (e.g.,
106 chimpanzees, long-tailed macaques, and capuchins; Boesch & Boesch, 1990b; Gumert,
107 Kluck, & Malaivijitnond, 2009; Ottoni & Mannu, 2001). Perhaps the best studied example is
108 that of nut-cracking in chimpanzees (Biro et al., 2003; Boesch & Boesch, 1990b; Luncz &
109 Boesch, 2014; Luncz, Mundry, & Boesch, 2012b). Indeed, this behaviour has now been
110 selected for conservation by the United Nations Convention on the Conservation of Migratory
111 Species (CMS) body, emphasising how important this behaviour is considered to be, even by
112 organisations outside of academia (Picheta, 2020). This emphasis may be, at least in part,
113 because chimpanzee nut-cracking is often regarded as an ape CDF – supposedly maintained
114 by action copying (Boesch, 1991; Boesch, Marchesi, Marchesi, Fruth, & Joulian, 1994).

115

116 The claim of culture-dependency for nut-cracking in chimpanzees rests primarily on four
117 factors: 1) The presumed complexity of this behavioural form (and complexity is often
118 assumed to require copying; e.g., Byrne & Byrne, 1993; Whiten, 2017) 2) Observations that
119 the behaviour takes a long time to be expressed (Biro et al., 2003) 3) The presence of a
120 sensitive learning period in which the behaviour must develop (Biro et al., 2003) and 4)

121 Localised occurrences of nut-cracking across wild populations in Africa (McGrew & Tutin,
122 1978). We address these points further below.

123

124 Wild chimpanzees in the Taï Forest (Ivory Coast) and in Bossou (Guinea) use hammer tools
125 to access the kernels of several nut species - *Panda oleosa*, *Parinari excelsa*, *Saccoglottis*
126 *gabonensis*, *Coula edulis*, and *Detarium senegalensis* (Proffitt, Haslam, Mercader, Boesch, &
127 Luncz, 2018). The crux of the nut-cracking behavioural form in these chimpanzees (see also
128 Foucart et al., 2005) involves three steps: (1) Retrieving a nut from the surrounding area and
129 placing it on an anvil (e.g., a tree root or a stone), (2) Picking up a stone- or wooden hammer
130 (with one hand or both hands) and (3) Hitting the nut with the hammer (holding it with one or
131 both hands) until it is open and the inside kernel can be retrieved and consumed (Boesch &
132 Boesch, 1983; Carvalho et al., 2009). Sometimes more steps are described, such as the
133 transportation of the materials to the nut-cracking site (Carvalho, Biro, McGrew, &
134 Matsuzawa, 2009) and the stabilisation of the anvil on the ground (although this is a rare
135 behaviour; Carvalho, Biro, McGrew, & Matsuzawa, 2009). However, here we focus solely on
136 the tool-use aspect of the behaviour, and the crux of the copying claim for nut-cracking. This
137 multi-step approach has been regarded as a complex tool use behaviour (Meulman, Sanz,
138 Visalberghi, & van Schaik, 2012), because it is improbable that such a compound behaviour
139 is acquired in its entirety by chance, especially considering that it is only rewarded at the end
140 of the chain of actions (note that most of the other behavioural forms within the chimpanzee
141 tool-use repertoire only involve the manipulation of a single object (usually a stick) and only
142 one action (e.g., marrow picking; see Whiten et al., 2001 for an overview of chimpanzee
143 behaviours and their descriptions)). Moreover, the precision needed to crack open nuts
144 contributes to the complexity of the behaviour since (at least at the beginning) many attempts
145 will go unrewarded. However, behaviour complexity does not necessarily indicate the need
146 for copying forms of social learning (Byrne, 2007). For example, naïve weaver birds make
147 apparently complex nests, but are able to make these nests in the total *absence* of any variant
148 of social learning – including copying (Collias & Collias, 1964). Therefore, rather than
149 assuming a direct relationship between complexity and copying, all behaviours must instead
150 be empirically tested for their dependence on copying (as we do below).

151

152 Second, juvenile chimpanzees take a long time to acquire nut-cracking (Biro et al., 2003;
153 Boesch & Boesch, 1990). Some have claimed that during this period, juveniles acquire nut-

154 cracking by observing and then copying their mother’s actions (e.g., see Biro et al., 2003) and
155 that a repeated cycle of such observation and practice sessions is required before nut-cracking
156 can be expressed (e.g., what Whiten, 2017, 7795, describes as a “helical process of learning”).
157 In a similar interpretation, de Waal (2008) also claims that juvenile chimpanzees copy their
158 mothers via ‘Bonding and Identification-based Observational Learning’ (BIOL), where a
159 juvenile is copying the underlying actions – in order “to be like others” (de Waal, 2001, 231).
160 Yet, a lengthy learning period alone is not necessarily indicative of copying. Instead, it can be
161 also be explained by mere maturation processes, alongside an extended period of *individual*
162 learning (likely encouraged by non-copying variants of social learning, such as stimulus and
163 local enhancement; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004 and “peering”;
164 Corp & Byrne, 2002; Schuppli et al., 2016). For example, a naïve weaverbird in a baseline
165 condition took longer to make a species-typical nest than weaverbirds surrounded by active
166 nest makers (Colias & Colias, 1964). Yet, the fact remains that the naïve weaverbird
167 eventually made a nest which form was indistinguishable from the species-typical nest (Colias
168 & Colias, 1964). This example empirically demonstrates that long learning times do not
169 necessarily imply that copying is taking place.

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171 Third, observations of wild juvenile chimpanzees suggest that the acquisition period of nut-
172 cracking may occur within a sensitive learning period, most likely when chimpanzees are
173 between the ages of three and five years old (Inoue-Nakamura & Matsuzawa, 1997). If the
174 behaviour is not acquired within this sensitive learning period, chimpanzees will seemingly
175 never develop the behaviour (Biro et al., 2003b). This seems to also be the case for nut-
176 cracking in other primates, such as long-tailed macaques (Tan, 2017). But, again, the mere
177 presence of a sensitive learning period in and of itself does not pinpoint what type of learning
178 must occur inside it. Indeed, sensitive learning periods do not, a priori, demonstrate that
179 learners must copy the behavioural form. It may equally be that juveniles must simply be in
180 this sensitive learning period in order to individually develop the behavioural form (see also
181 Ratcliffe, Boag, Shackleton, Weisman, & Weary, 1994).

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183 Lastly, the N’Zo-Sassandra river in Ivory Coast has been argued to be a ‘cultural boundary’
184 between the nut-cracking West African chimpanzees and the East African chimpanzees (who
185 do not show this behaviour), despite having nuts and tool materials available in their
186 environment (McGrew, Ham, White, Tutin, & Fernandez, 1997). Some researchers have

187 argued that these regional differences must be due to chimpanzees needing to copy the
188 behavioural form of nut-cracking from other, knowledgeable, chimpanzees, and that, in the
189 absence of demonstrators, they cannot acquire the behaviour. This copying hypothesis is
190 inherently suitable to logically explain the observed differences. If copying of the behavioural
191 form is required, and copying cannot occur across a river, then that would indeed render all
192 chimpanzees east of the river incapable of nut-cracking (Boesch, Marchesi, Marchesi, Fruth,
193 & Joulian, 1994). However, potentially contrary to this argument, Morgan & Abwe (2006)
194 reported evidence (albeit indirect) of chimpanzees in Cameroon (approx. 1700 km east of the
195 N’Zo-Sassandra river) also showing the behavioural form of nut-cracking. The full
196 behavioural form must therefore have been individually acquired by at least one chimpanzee
197 in Cameroon (as copying the behaviour from nut-cracking populations in the west is likewise
198 impossible). Therefore, the case of chimpanzee nut-cracking in Cameroon can be seen as the
199 outcome of a “natural baseline experiment” of nut-cracking – similar to Collias and Collias’
200 (1964) baseline experiment on weaverbird nest making. As in Collias and Collias’s (1964)
201 study, the reappearance of the behavioural form in the absence of copying opportunities from
202 one place to another leaves only the logical conclusion that copying is not strictly necessary.
203 However, it is important to note that some have called into question the Cameroon data, as
204 this data is not (yet) based on direct observation (Whiten, 2015).

205

206 Therefore, overall, the validity of the copying hypothesis for the behavioural form of nut-
207 cracking in chimpanzees is questionable. A potentially more parsimonious approach is
208 provided by the zone of latent solutions hypothesis (ZLS; Tennie, Call, & Tomasello, 2009).
209 The ZLS hypothesis argues for individual reinnovation of behavioural forms aided by non-
210 copying forms of social learning, across species. According to this hypothesis, the
211 behavioural form of chimpanzee nut-cracking is not copied, but individually derived. There
212 are many ways in which this individual learning may work. To give just one example, the
213 difficulty of learning individually such a complex behaviour may be overcome by individuals
214 having a general predisposition to explore and manipulate objects plus some cognitive
215 capacities like good spatial memory (that allows to locate the needed materials), inhibitory
216 control (that allows to delay a reward), planning abilities and working memory (that allow to
217 chain steps towards a goal- and some understanding of the physical affordances of objects),
218 and of object relations (that can aid in the selection of appropriate materials and actions to
219 process the materials). As a result, such subjects should be able to solve problems in a flexible
220 way. Indeed, when nut-cracking, wild chimpanzees use different types of anvils (stationary

221 and non-stationary) and in some cases detached stones are used as anvils (these differences
222 have also been used by some to claim that nut-cracking is a CDF; Boesch & Boesch-
223 Achermann, 2000). The ZLS hypothesis also suggests that the observed differences in nut-
224 cracking activity across chimpanzee populations are fostered by non-copying social learning
225 mechanisms (widespread in the animal kingdom) on the likelihood of reinnovation once a
226 population already contains individuals who have innovated the behavioural form. This then
227 can lead to a frequency increase and maintenance of the behavioural forms in question in
228 some populations but not in others. Ape innovation catalyses ape reinnovation – provided the
229 behavioural form is currently useful to individuals in the affected populations (Tennie et al.,
230 in press). The overall result of this process can sometimes lead to important differences in the
231 relative frequencies (from 0 to 1) of behavioural forms between populations – i.e. ape
232 cultures. However, these cultures are not created or maintained by copying, instead they are
233 created and maintained by socially *mediated* reinnovations (SMR; Bandini & Tennie, 2019,
234 2017). That is, according to the ZLS account, social learning plays a role (even a large role)
235 but copying variants of social learning are excluded, which is justified by the absence of
236 evidence for spontaneous copying in apes (see above). Given that (non-copying) social
237 learning plays some role, the affected ape behaviours are only cultural in a minimal sense of
238 the word (see Neadle, Allritz, & Tennie, 2017). Importantly, the ape ZLS hypothesis predicts
239 successful reinnovation of behavioural forms by naïve ape subjects provided the right
240 conditions and in the absence of any copying opportunities. This prediction holds true in a
241 fast-growing experimental literature detailing successful individual acquisitions of various
242 wild-type behavioural forms (including tool use) across various species of naïve, captive great
243 apes (Allritz, Tennie, & Call, 2013; Bandini & Tennie, 2017; 2019; Bandini & Harrison, in
244 press; Menzel, Fowler, Tennie, & Call, 2013; Neadle, Allritz, & Tennie, 2017; Tennie,
245 Hedwig, Call, & Tomasello, 2008). Therefore, the ape ZLS hypothesis has growing support,
246 but whether it can also explain the behavioural form of nut-cracking is still an open question.

247

248 Previous studies on the acquisition of the behavioural form of nut-cracking by captive
249 chimpanzees either did not include the necessary baseline condition -where copying the
250 behaviour is not possible- or only did very few, and often short, baseline sessions of which
251 details were not specified (Hayashi, Mizuno, & Matsuzawa, 2005; Hirata, Morimura, &
252 Houki, 2009; Marshall-Pescini & Whiten, 2008; Sumita, Kitahara-Frisch, & Norikoshi, 1985;
253 although see Neadle et al., (2020) for a different approach). Even when the wild form of nut-
254 cracking *did* appear in naïve subjects, the logical conclusion that copying is not necessary was

255 not considered, and instead it was assumed that successful subjects culturally carried over the
256 behaviour from earlier observations (e.g., Marshall-Pescini & Whiten, 2008). Therefore, the
257 debate behind the learning processes required for nut-cracking in chimpanzees, and other
258 primates, continues.

259

260 Chimpanzee nut-cracking is a rare behaviour and therefore it is a particularly interesting case
261 study to assess whether ape culture is based on copying, similarly to human culture (as
262 suggested by, e.g., de Waal & Ferrari, 2010 and Whiten et al., 1999) or whether it rests
263 primarily on non-copying social learning in which behavioural patterns at a population level
264 develop and are maintained via SMR (Bandini & Tennie, 2017). Analogous to the logic of the
265 weaverbird nest-making experiment (Colias & Colias, 1964), a clear way to answer this
266 question is to experimentally test each behavioural form that has been argued to be a CDF (for
267 example, as listed by Robbins et al., 2016; Santorelli, Schaffner, & Aureli, 2011; van Schaik
268 & Pradhan, 2003; Whiten et al., 1999). Here we follow this approach for the behavioural form
269 of nut-cracking (see also Neadle et al., 2020), by testing whether the behavioural form of nut-
270 cracking can emerge in the absence of copying opportunities.

271

272 *Latent solutions testing methodology*

273 Tennie & Hedwig (2009) describe the ‘latent solutions’ (LS) testing methodology. This
274 methodology allows for the role of individual learning in the acquisition of a target
275 behavioural form. All the ecological materials of the target behavioural form, but no
276 demonstrations, are provided to naïve subjects, who have never seen, or been trained in, the
277 target behaviour before. Subjects should be so-called ‘ecologically-representative’
278 individuals, i.e. unenculturated captive animals who live in social groups (Henrich & Tennie,
279 2017). If the target behavioural form emerges under these conditions, then, logically, it can be
280 concluded that copying is not *required* for the form of behaviour to emerge. If the behaviour
281 does not emerge in this baseline condition, then it could be that some variant of social
282 learning is necessary for the behaviour to be acquired (for these cases, Bandini & Tennie,
283 2018 provide an extended LS testing methodology that allows for the level and variant of
284 social learning required (if any) to be identified), *or* that other factors, such as sensitive
285 periods, or opportunities to practice or motivation levels, play a role (Bandini & Tennie,
286 2018; Neadle et al., 2020). Past LS studies have demonstrated that multiple target behavioural
287 forms – including tool use behavioural forms – can be individually acquired by primates (see

288 above). Furthermore, it was also shown that different species may sometimes overlap in their
289 latent solution repertoires (Allritz et al., 2013; Bandini & Tennie, 2019, 2017; Menzel et al.,
290 2013; Neadle et al., 2017; Reindl, Beck, Apperly, & Tennie, 2016; Tennie et al., 2008).

291
292 The aim of the current study was to examine the acquisition of the behavioural form of nut-
293 cracking following the LS testing methodology. This has already been successfully carried-
294 out in the past. For example, naïve, captive, capuchins have already been tested (and two
295 individuals spontaneously started cracking nuts, without any social learning necessary;
296 Visalberghi, 1987a). Given that successful cases of reinnovation of capuchin and chimpanzee
297 nut-cracking may be dismissed on the (often remote) possibility that the behavioural form has
298 been culturally carried over from the wild, different primate species must be tested for the
299 spontaneous reinnovation of the behavioural form of nut-cracking. Observations of gorillas
300 and bonobos cracking nuts in sanctuaries have been reported (Wrangham, 2006) – though the
301 exact circumstances of innovation remain unclear. We decided to test reinnovation of the
302 behavioural form of nut-cracking in another ape species: orangutans. After chimpanzees,
303 orangutans use tools most often in the wild, but they have not (perhaps not yet) been reported
304 to crack nuts in the wild (Fox, van Schaik, Sitompul, & Wright, 2004; Parker & Gibson,
305 1977) – making them ideal test cases. Furthermore, inferences are often made from the
306 behaviour of chimpanzees to early hominins and even modern humans (due to our close
307 phylogenetic ties; Haslam et al., 2009), and if such comparisons and the resulting inferences
308 are valid, then similar inferences should hold also between ape species. For these reasons we
309 decided to test for the spontaneous ability of orangutans to develop the nut-cracking
310 behavioural form.

311
312 Four naïve captive orangutans ($M_{age}=16$; age range=10-19; 4F; at time of testing) were
313 provided with all the raw materials necessary for nut-cracking (nuts, wooden hammers,
314 cracking locations), but they were not provided with any information or demonstrations on
315 *how* to crack nuts – they never had access to the behavioural form of nut-cracking. This was
316 to test whether orangutans could individually and spontaneously acquire this behavioural
317 form of nut-cracking - without copying variants of social learning. The naivety of the
318 orangutans with regard to nut-cracking behaviour was confirmed by the keepers, who assured
319 us that the subjects had never been shown, or exposed to, the target nut-cracking behavioural
320 form prior to testing.

321 **Results**

322 *Reliability testing*

323 Cohen's kappa was run to assess the reliability of the coded data. We did not expect to find a
324 very high reliability due to the fact that the data was collected in the orangutans' management
325 areas (due to the testing facilities requirements), which are dark and often did not allow for a
326 clear view from the filming platform. Regardless, in terms of the general coding of the
327 ethogram, and the individuals that showed the behaviours, a moderate (Cohen, 1968)
328 agreement was found ($k=0.60$; although note that an individual substantial agreement ($k=0.80$)
329 was found for the specific anvil on floor and hammer on floor behaviours). For the number of
330 successes and time spent with the nuts in the mouth, a moderate ($k=0.51$) was found.

331

332 *Experimental results*

333 Table 1 presents the behaviours coded, descriptions of the behaviours, how many individuals
334 attempted the various behaviours, the first trial in which these were observed, in which
335 experimental conditions they were observed, whether or not they allowed opening nuts and
336 the percentage of times each method resulted in successfully cracking open a nut (see
337 supplementary for video clips of the most common behaviours observed). In the baseline
338 condition, the juvenile individual, PD (F, 10 years old at time of testing, parent-reared and
339 born at the testing institution; see Table 3), successfully cracked nuts by using the large
340 wooden anvil-block as a hammer-tool (see also Table 2). When, in the locked-anvil condition,
341 the large anvil-block was fixed to the ground, this same subject cracked nuts by using the
342 wooden hammers (see supplementary videos) – i.e. she reinvented the behavioural form of
343 nut-cracking. No other individual in the study demonstrated the nut-cracking behaviour with a
344 tool. Instead, the other (all adult) subjects opened the nuts with their teeth (*bite*, see Tables 1
345 & 2). This *bite* behaviour of adults continued even after the demonstration condition, in which
346 the adults had the opportunity to observe PD cracking nuts using the target behaviour. The
347 adult subjects spent between 56%-93% of the time in all trials with unopened nuts in their
348 mouths (this excludes PD, who only spent between 15%-43% of trials), thus suggesting that
349 the adults were motivated to open the nuts. Indeed, the adults used primarily the *bite* method,
350 followed by the only other method they used: *hit with hand* (see more below).

351

352

353 *Table 1: Ethogram of methods directed towards the nuts by subjects across all conditions*

Method	Description	Number of subjects & name	First trial in which the behaviour was observed	Condition in which the method was observed	Successful for opening nuts	Percentage of total successes
Bite	The subject inserts the nut in its mouth, and presses the nut between its teeth	All subjects	1 st trial baseline	All conditions	Yes	69%
Hit with Hand	The subject hits the nut with its hand against a hard surface	2 (PD & DK)	1 st trial baseline	All conditions	No	N/A
Step	The subject hits the nut with its foot against a hard surface	2 (PD & PI)	1 st trial baseline	Only baseline condition	No	N/A
Anvil on Floor	The subject tilts the anvil and either drops it or rolls it on the nut that is on the floor	1 (PD)	2 nd trial baseline	Only baseline condition	Yes	90%
Hammer on Floor	The subject lifts the hammer and drops it on the nut which is on the floor	1 (PD)	1 st trial locked anvil	Only locked anvil condition	Yes	95%

354

355 *Baseline condition*

356 The *bite* method was the first method attempted in the baseline, and the one used most often
357 (*bite* was attempted in 100% 20/20 of the trials), followed by *hit with hand* (30%; 6/20), *anvil*
358 *on floor* (20%; 4/20) and *step* (51%; 3/20). All subjects attempted to open at least some nuts
359 with their mouth, feet or hands in most trials, whereas only PD used the *anvil on floor*
360 method, in 80% of PD's individual trials (from the 2nd trial of the baseline). Of these methods,
361 only the *bite* and *anvil on floor* led to successful kernel access. The adult females accessed an
362 average of 4.4 out of 5 nut kernels per trial using the *bite* method (and were successful from
363 the first trial). PD also tried to open nuts first with the mouth in her first trial, but failed to
364 open them. However, in the first to third trials, PD tilted the large wooden block, placed a nut
365 under the block, and then dropped it on the nut. By using this method (*anvil on floor*), PD
366 successfully opened six nuts overall (the remaining nuts stayed unopened, as PD then reverted

367 to attempting the *bite* methodology unsuccessfully). In the fourth trial, PD successfully
368 cracked one nut with her mouth but failed to open more nuts with either the *bite* or *anvil on*
369 *floor* techniques. These data suggest that PD was relatively incapable of cracking open the
370 nuts with her teeth (perhaps as, due to her young age, she did not possess enough force to
371 crack through the shell). In the last trial, PD opened all five nuts using the *anvil on floor*
372 method, and used only this method throughout the trial.

373

374 *Anvil-locked condition (note: only PD was tested)*

375 This condition (4 trials) was carried out to examine whether PD would be able to change from
376 her technique of using the large wooden block (which had been devised as an anvil) to using
377 the smaller wooden pieces provided (which were designed to resemble the hammers used by
378 wild chimpanzees). From the first trial, PD used the wooden hammers to perform the target
379 nut-cracking behaviour, albeit ignoring the large block as an anvil. Instead, PD placed nuts on
380 the floor (which was sufficiently hard), and then used the wooden hammer to forcibly hit the
381 nut until it opened (i.e., *hammer on floor*, which occurred in in 75%; 3/4 trials). Only one
382 other nut-cracking method was recorded in this condition: *bite* (which occurred in the one
383 remaining trial). PD cracked 19 of 20 nuts using the *hammer on floor* method and no nuts
384 using the *bite* method.

385

386 *Demonstration condition*

387 Despite being provided with live demonstrations from PD of the target nut-cracking
388 behaviour in the demonstration condition (15 trials in total), none of the adult females
389 subsequently used any of the provided tools to open nuts. All adults continued to crack the
390 nuts using their teeth or by trying to open the nuts (unsuccessfully) using the *hit with hand*
391 method (*bite* 100%, 15/15 of the trials; *hit with hand* 13%, 2/15 of the trials). All the nuts that
392 were opened in the demonstration condition were opened with the *bite* behaviour. In a single
393 trial of the demonstration condition one nut remained unopened, despite the use of the *bite*
394 method.

395

Table 2: Count and percentage of each method used per individual per condition and trial

396

Condition	Subject	Number of trials	Number of trials in which Bite was observed	%	Number of trials in which Hit with Hand was observed	%	Number of trials in which Step was observed	%	Number of trials in which Anvil on Floor was observed	%	Number of trials in which Hammer on Floor was observed	%
Baseline	DK	5	5	100%	3	60%	0	0%	0	0%	0	0%
Baseline	DJ	5	5	100%	0	0%	0	0%	0	0%	0	0%
Baseline	PD	5	5	100%	3	60%	2	40%	4	80%	0	0%
Baseline	PI	5	5	100%	0	0%	1	20%	0	0%	0	0%
Baseline Total		20	20	100%	6	30%	3	15%	4	20%	0	0%
Anvil Locked	PD	4	0	0%	0	0%	0	0%	0	0%	4	100%
Anvil Locked Total		4	0	0%	0	0%	0	0%	0	0%	4	100%
Social	DK	5	5	100%	0	0%	0	0%	0	0%	0	0%
Social	DJ	5	5	100%	2	40%	0	0%	0	0%	0	0%
Social	PI	5	5	100%	0	0%	0	0%	0	0%	0	0%
Social Total		15	15	100%	2	13%	0	0%	0	0%	0	0%

397 **Discussion**

398 One naïve, juvenile, unenculturated, captive orangutan spontaneously showed the behavioural
399 form of chimpanzee nut-cracking – she cracked nuts using a wooden hammer as a tool
400 (Boesch et al., 1994). This finding suggests that naïve orangutans possess the individual
401 ability to express the wild chimpanzee behavioural form of nut-cracking, and that it does not
402 require behaviour copying to be expressed in this species.

403

404 Although naïve to nut-cracking with a tool, PD and all the other subjects in this study did
405 have prior experience with nuts, and therefore knew that force could be applied to the shells
406 of the nuts to access the kernel inside. However, they only had experience with walnuts and
407 hazelnuts, and these types of nuts can be opened relatively easily by using the teeth - even by
408 juvenile orangutans such as PD. This, and the lack of suitable tool materials prior to our
409 study, may explain, at least in part, why none of the subjects in this study had ever been
410 observed using tools to crack nuts. Therefore, we can confidently state that PD *spontaneously*
411 reinnovated nut-cracking in our study, without requiring behaviour copying. Although none
412 of the other subjects in the study acquired the behavioural form of nut-cracking (there was no
413 need for them to do so either), the fact that we found reinnovation of nut-cracking behaviour
414 in one subject already fulfils the single-case ZLS standard (Bandini & Tennie, 2017 and see
415 methods section) allowing nut-cracking to be categorised as a latent solution for orangutans.

416

417 *Previous studies*

418 Our conclusion is further validated by an unpublished study that was performed between 1983
419 and 1984 at Zürich Zoo, Switzerland, (supervised by the late Hans Kummer) which we
420 accessed after the current study was completed (courtesy of C. Boesch). In this study, Martina
421 Funk carried-out a baseline test, similar to the one used in the present study, to test whether
422 orangutans (chimpanzees were also tested, but contrarily to the orangutans, none of the
423 chimpanzee subjects opened the nuts with hammers, therefore we will not discuss the
424 chimpanzees further here) would spontaneously crack various species of nuts with a wooden
425 hammer (the hammer provided by Funk was 25cm long and 8-10cm diameter; the hammer
426 provided in our own study was 30cm long and 50cm in diameter). The subjects were given
427 coconuts, peanuts, and coula nuts. No moveable anvils were provided, but subjects had access
428 to hard surfaces that could be used as anvils. According to the keepers at the time, all test

429 subjects were naïve to the behavioural form of nut-cracking before testing. Both Sumatran
430 orangutans (n=6) and Bornean orangutans (n=2) were tested. Sumatra subjects were provided
431 with approximately five coula nuts and a wooden hammer per trial, whilst the Bornean
432 orangutans only received one coula nut. Trials lasted an hour, after which the keepers
433 removed nuts and hammers from the enclosure. Similarly to our study, the orangutans in
434 Funk's (1985) study immediately proceeded to try to open the coula nuts with their teeth.
435 However, unlike our macadamia nuts, this proved difficult, likely because coula nuts are
436 harder to open than macadamia nuts (coula nuts require 2.8kn to be opened, while macadamia
437 nuts which require 2.2kn; Visalberghi et al., 2008). Indeed, across all subjects in Funk's
438 (1985) study, (including the chimpanzees) only 32 coula nuts (of 223 coula nuts) were opened
439 by subjects without tools. Most importantly, just like in our study, Funk (1985) also found
440 that the naïve orangutans she tested were able to spontaneously and individually acquire the
441 behavioural form of nut-cracking: indeed, seven of the eight orangutans tested at least
442 attempted the nut-cracking behaviour (using the hammer). Four of the seven orangutans that
443 showed nut-cracking did so repeatedly and, out of these four, three orangutans successfully
444 opened coula nuts with the wooden hammer ("Rosa", "Radja" and "Timor"). For all
445 successful orangutans who demonstrated the nut-cracking behaviour, Funk (1985) concluded
446 that they logically must have acquired this behavioural form independently – that they must
447 have reinvented it – as these three subjects could not have observed the behavioural form
448 first in the other subjects. Our study alone, and in conjunction with Funk's (1985) study,
449 demonstrate that the behavioural form of nut-cracking does not require behaviour copying to
450 be acquired by orangutans.

451

452 *Candidate mechanisms behind nut-cracking in orangutans*

453 The findings of the current study and the one carried out by Funk (1985) suggest that nut-
454 cracking does not require copying variants of social learning. We are not suggesting, though,
455 that nut-cracking is a hard-wired behaviour in orangutans. Although the ZLS hypothesis can
456 also include such cases, it includes others as well; that is, 'latent solutions' is an umbrella
457 term that subsumes behaviours spanning from highly genetically-determined behaviours to
458 more learning-dependent behaviours, with the exception of copying-dependent behaviours
459 (Tennie et al., in press). In the case of orangutan nut-cracking, we indeed have several reasons
460 to believe that more than instinct is at play. Firstly, despite long-term field studies with wild
461 orangutans, they have not (yet) been observed to crack nuts (e.g., Krützen, Willems, &

462 van Schaik, 2011). Secondly, not all the orangutans in our, or Funk's (1985) study, acquired
463 the behaviour within the time frame given (although we acknowledge that motivation plays a
464 role as well). Lastly, the orangutan in our study, and Funks' subjects that demonstrated the
465 target behaviour, showed flexibility in their approach to the problem at hand – indeed, PD
466 attempted several different methods to access the kernels before arriving at the target
467 behavioural form of nut-cracking; even after discovering the target behaviour, PD did not then
468 use it in every trial and, perhaps most importantly, PD proved able to crack open nuts with a
469 variety of tool use styles.

470

471 Therefore, if strong genetic predispositions and reliance on copying forms of social learning
472 are excluded as explanations for the acquisition of this behaviour, a plausible alternative
473 candidate mechanism is individual learning. All apes demonstrate impressive abilities for
474 such type of learning (see Tomasello & Call 1997; Whiten & Mesoudi, 2008 for an overview
475 of these studies). Whilst these individual learning abilities probably involve some genetic
476 predispositions, they also rely on cognitive skills that allow for considerable behavioural
477 flexibility, including finding different solutions to a given problem. One example of this
478 flexibility is PD's performance in this study. In the baseline, before the locked-anvil
479 condition, PD used the provided large wooden block to crack open nuts, already
480 demonstrating a similar tool use to wild chimpanzee nut-cracking, but using a different tool
481 and action. PD might have initially preferred to use the large block instead of the small
482 wooden hammers as, although the former required more effort when being *lifted* due to its
483 large weight (approx. 50kg vs. 2.4kg), it did not require the application of hitting force and
484 speed to crack the nut, but could simply be part-lifted and/or rolled, and then dropped on top
485 of the nuts. Moreover, the large block may have been easier to manipulate since its larger
486 width required less precision when aiming to hit the nut than a hammer does. Once the large
487 block was rendered inaccessible in the locked-anvil condition, however, PD flexibly switched
488 her approach and used a hammer, demonstrating the target behavioural form of nut-cracking,
489 similar to that observed in some wild chimpanzee populations (Biro et al., 2003; Boesch et al.,
490 1994; Luncz & Boesch, 2014; Luncz et al., 2012b). In brief, individual learning, alongside
491 some genetic predispositions, non-copying social learning, and enhanced cognitive capacities
492 that allow flexibility in the search for solutions to problems, may drive the acquisition of nut-
493 cracking in orangutans.

494 *Potential explanations for the lack of reinnovation of the target behaviour by the adult*
495 *orangutans*

496

497 None of the adult orangutans in our study used tools to crack nuts. These subjects were
498 immediately and consistently successful in cracking open the nuts with their teeth, and
499 continued doing so even after they were exposed to five trials of live demonstrations of nut-
500 cracking with a tool by PD. One explanation for the absence of this behaviour in these
501 subjects could be precisely the fact that, as we observed, the adults were strong enough to bite
502 through the shells of the nuts (note that, although macadamia nuts are hard, orangutans have a
503 remarkable bite strength; Daegling, 2007), which might have rendered the use of a tool
504 superfluous for them. On the other hand, the sub-adult PD attempted to bite nuts in the first
505 trial but failed, most likely because she had not yet developed the same jaw strength as the
506 adults in the group. Therefore, PD may have been the only test subject motivated to find
507 alternative methods to biting in order to access the kernels, including the use of tools to open
508 the nuts. According to this explanation, if even harder nuts had been provided, rendering the
509 bite methodology impossible, the adults in the group might have also spontaneously acquired
510 the target tool-use behaviour. Indeed, note that no clear age differences were found in the
511 orangutans that acquired the behaviour in Funk's (1985) study, suggesting that the
512 orangutans' inability to crack hard nuts with their teeth in that study led them to explore tool-
513 based solutions. Alternatively, or in addition, it might be that age differences in inhibitory
514 control and functional fixedness (Albiach-Serrano, Guillén-Salazar & Call, 2007; Amici,
515 Aureli, & Call, 2008; Parrish et al., 2014) encouraged PD to explore new solutions to the
516 problem at hand while preventing the adults in our study from finding the same solution.

517

518 In any case, the fact that the adults in the group did not acquire the behaviour even after
519 multiple social demonstrations is not without precedence. Indeed, several studies across
520 species have reported similar findings: if a behaviour is not (re)innovated by an individual in
521 a baseline condition, social learning (of any type) will also sometimes fail to release the
522 behaviour as well (e.g., Anderson, 1985; Bandini & Tennie, 2018; Menzel, Davenport, &
523 Rogers, 1970; Tebbich, Taborsky, Fessl, & Blomqvist, 2001; Visalberghi, 1987b; Tennie et
524 al., 2009).

525

526

527 *Nut-cracking in other primates*

528

529 So far, capuchins (*Cebus apella*, *Cebus capucinus imitator*, *Sapajus libidinosus*),
530 chimpanzees (*Pan troglodytes*), long-tailed macaques (*Macaca fascicularis aurea*) and
531 humans (*Homo sapiens*) have all been observed using tools to crack nuts (Barrett et al., 2018;
532 Boesch et al., 1994; Haslam, Cardoso, Visalberghi, & Frigaszy, 2014; Luncz et al., 2017;
533 Morgan & Abwe, 2006; Ottoni & Mannu, 2001; Parker & Gibson, 1977; Pfungst, 1912). The
534 data on nut-cracking across primate species suggests that this behaviour may have also been
535 present in the last common ancestor between modern human and great apes (Neadle et al.,
536 2002). Furthermore, so far, two captive capuchins, one orangutan (in this study), and (at least)
537 three further orangutans (Funk 1985) have clearly demonstrated an ability to spontaneously
538 and individually acquire the behavioural form of nut-cracking in the absence of copying.

539

540 Given the results mentioned above, and the potential occurrence of nut-cracking in more than
541 one wild population of chimpanzees (see introduction), it seems possible that the form of nut-
542 cracking could be individually learnt by chimpanzees as well (see also Byrne, 2007, 579, who
543 claims that behaviours such as chimpanzee nut-cracking “*are not difficult for chimpanzees to*
544 *invent, and that invention has occurred independently at many sites*”). One question that
545 remains open, then, is why some chimpanzee populations do not crack nuts with tools, even if
546 they have all the materials required for the behaviour. One possible explanation is that
547 different populations often experience different ecological conditions. For example,
548 chimpanzees living in areas with scarce easily-available food might be more encouraged to
549 explore alternative food sources (like nuts) than chimpanzees living in areas with abundant
550 easily-available food. Similarly, chimpanzees living in areas with more competitors, or
551 predators, might be less prone to explore new foraging activities that (usually) require staying
552 on the ground (like nut-cracking). Furthermore, even if currently sharing similar
553 environments, different chimpanzee populations may have lived in different environments in
554 the past. . For example, a period of food scarcity in one area might have encouraged the
555 chimpanzees living there to explore alternative available food sources, thus increasing the
556 probability that more individuals in these populations would develop nut-cracking (see also
557 Haslam, 2014 who further argues that “opportunity” and “relative profitability” drove the
558 emergence of nut-cracking in some populations of chimpanzees). This situation would
559 increase other group members’ exposure to nuts and nut-cracking materials and would

560 therefore enhance both their motivation and opportunities to individually reinnovate the nut-
561 cracking behaviour (via individual learning and non-copying mechanisms such as local and
562 stimulus enhancement; see Zentall, 2003 for definitions). Given the catalysing effect of non-
563 copying social learning, the behaviour would as a result seem to “spread” in the affected
564 populations. Once nut-cracking has been established in these populations, similar learning and
565 preservation mechanisms would later enable the behaviour to also be maintained until present
566 time (see also McGrew, Ham, White, Tutin, & Fernandez, 1997) -even if, as mentioned
567 above, the ecological conditions changed and became similar to those experienced by
568 populations of non-nut-cracking chimpanzees.

569

570 *Conclusion*

571 The results of our study (especially in conjunction with Funk, 1985) demonstrate that
572 individual learning (probably aided by several factors, such as genetic predispositions and
573 cognitive capacities that allow to find solutions to problems flexibly) is sufficient for the
574 acquisition of the behavioural form of nut-cracking in orangutans. Thus, this study adds
575 another behaviour to the growing list of primate tool-use and social behavioural forms that
576 have been found to be culture-*independent* forms (the authors are very grateful to C. Schuppli
577 for suggesting this term), i.e. latent solutions (e.g., Allritz et al., 2013; Bandini & Tennie,
578 2017; 2019; Menzel et al., 2013; Neadle et al., 2017; Reindl & Tennie, 2018; Tennie et al.,
579 2008). Although this study did not find evidence for (non-copying) social learning increasing
580 the frequency of target behaviour (as the older orangutans may have been fixed in their
581 alternative, successful method of cracking open the nuts with their teeth), it is likely that,
582 similar to other ape behaviours, non-copying variants of social learning can increase and
583 stabilise the frequency of nut-cracking within populations – at least when these mechanisms
584 apply across generations (see also discussion in Moore, 2013). Therefore, the behavioural
585 form of nut-cracking could, in principle, become another example of a SMR (Bandini &
586 Tennie, 2017; 2019), for orangutans. Indeed, it is possible that orangutans may one day be
587 found to express (or have expressed) nut-cracking behaviour in the wild - as a latent solution.

588

589

590

591

592 *Methods*

593 *Subjects*

594 Research was carried out at the Wolfgang Köhler Primate Research Center (WKPRC),
595 Leipzig, Germany. Four orangutans ($M_{age}=16$; age range=10-19; 4F; at time of testing)
596 participated in the study (see the demographic information in Table 3 below; all subjects were
597 born (except for DK) and raised at the testing institution). The keepers confirmed that none of
598 the individuals in this study had prior experience with macadamia nuts. Hazelnuts and
599 walnuts, however, had occasionally been provided by the keepers. Yet, the orangutans either
600 opened these with their teeth or, occasionally, by hitting them with their hand against a hard
601 surface. Crucially, none of the orangutans at the WKPRC had ever been observed using a *tool*
602 for nut-cracking before this study. Indeed, heavy objects that could potentially be used as
603 hammers (such as stones or wooden stumps) are not allowed inside the enclosures of the
604 WKPRC, for health and safety reasons, and therefore the subjects can confidently be assumed
605 to have been naïve to the target behaviour prior to this study. This study strictly adhered to the
606 legal requirements of the country in which it was carried-out.

607

608 *Table 3: Demographic information on the subjects included in this study*

Name	Species	Sex	Date of birth	Place of birth	Breeding
Dokana (DK)	<i>Pongo abelii</i>	F	31/01/1989	Dresden, DE	Parent
Padana (PD)	<i>Pongo abelii</i>	F	18/11/1997	Leipzig, DE	Parent
Pini (PI)	<i>Pongo abelii</i>	F	30/06/1988	Leipzig, DE	Parent
Dunja (DJ)	<i>Pongo abelii</i>	F	19/04/1990	Leipzig, DE	Hand

609

610 *Procedure*

611 We implemented three conditions sequentially (see also Table 4): The first condition was a
612 baseline, in which subjects could only acquire the nut-cracking behaviour individually, as no
613 information on the actions required for the behaviour were provided. The second condition
614 was another baseline, which we called locked-anvil condition, that guaranteed that the object
615 provided as an anvil could *only* be used as an anvil and not as a hammer (see below). The
616 third condition was a demonstration condition, in which subjects could potentially learn nut-
617 cracking behaviour through social learning (of any variant) after observing a conspecific (PD)
618 model. Subjects were tested separately with no visual or acoustic access to each other. While

619 the sub-adult (PD; age 10 at the time of testing) was tested alone, the adult females were
620 tested together with their dependent offspring (however no data was analysed from the
621 behaviour of the offspring as they were too young at the time of testing to attempt the task).

622

623 *Baseline condition*

624 During each of five baseline trials, subjects had access to one large wooden block (the anvil;
625 height 30 cm, diameter 50 cm, approximate weight 50 kg) with 5 depressions (diameter 2.5
626 cm) carved into the top side to facilitate the placement of the nuts, mirroring similar
627 depressions of anvils in the wild (e.g., Carvalho et al., 2009; Luncz, Mundry, & Boesch,
628 2012b), two smaller wooden blocks (the wooden hammers; height 30 cm, diameter 50 cm,
629 approximate weight 2.4 kg each) and five macadamia nuts (see figure 1 below). The materials
630 were scattered evenly on the floor in the testing room, which was emptied of any other objects
631 prior to the test to avoid distractions, within approx. one square meter. The subjects were not
632 allowed to enter the room until all the materials were in place. Trials lasted a maximum of
633 twenty minutes but were discontinued earlier if the subjects had successfully opened all the
634 nuts. The shells of the opened nuts and any nuts that the subjects did not open were retrieved
635 after each trial and discarded. A video camera and live-coding were used to record the
636 subjects' behaviour. For each subject, the between-trial interval was at least 24 hours.

637



638

639 *Figure 1: Photograph of the testing apparatus with the anvil, wooden hammers and*
640 *macadamia nuts.*

641

642 *Locked-anvil condition*

643 After the baseline condition, the single successful subject (PD, see the results section)
644 participated in four additional trials that were similar to the initial baseline trials but with the
645 anvil fixed on the ground (by being pressed down with a sliding door). This way, we
646 encouraged the subject to explore other options to crack open the nuts (as in the baseline the
647 subject used an anvil-dropping and rolling technique to crack the nuts).

648

649 *Demonstration condition*

650 After the baseline and locked-anvil conditions, the remaining three orangutans, which did not
651 demonstrate the target nut-cracking behaviour in the baseline condition, participated in five
652 subsequent demonstration condition trials (15 trials in total). Before each trial, PD, who had
653 reliably started the nut-cracking behaviour in the previous phases, served as a demonstrator,
654 cracking five macadamia nuts. The subject, who had access to two hammers and a fixed anvil,
655 could observe PD's performance from an adjacent cage. As soon as the subject had observed
656 at least one successful nut-cracking bout (coded when the subject had its head oriented
657 towards the demonstrator and its eyes were open during a successful nut-cracking bout by the
658 demonstrator), five macadamia nuts were placed into the subject's enclosure and the trial
659 started. The demonstrations continued even after the nuts were placed in the enclosure. The
660 rest of the testing procedure remained the same as in the baseline condition (see above).

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672 *Table 4: Table showing the number of conditions, trials and role each subject was involved in*

Subject	Conditions participated in	Number of trials per condition	Role
DK	Baseline, Demonstration	Baseline: 5 Demonstration: 5	Subject
PD	Baseline, Locked-anvil, Demonstration	Baseline: 5 Locked-anvil: 4 Demonstration: 5	Subject Conspecific model in the demonstration condition
PI	Baseline, Demonstration	Baseline: 5 Demonstration: 5	Subject
DJ	Baseline, Demonstration	Baseline: 5 Demonstration: 5	Subject

673

674

675 *Reinnovation standards*

676 Bandini & Tennie, (2017) propose two standards to confidently categorise a behavioural form
677 as a latent solution if it appears in an LS test. The double-case ZLS standard is applied to
678 relatively simple animal tool-use behaviours, which usually require only one tool and one step
679 (such as most chimpanzee stick tool-use behaviours; Whiten et al., 1999) and therefore have a
680 higher likelihood (albeit still very unlikely) of appearing by chance through, for example, play
681 or display sessions (Bandini & Tennie, 2017). These behaviours require at least two
682 reinnovations by independent subjects before it can be confidently assumed that the behaviour
683 was acquired through individual learning (Bandini & Tennie, 2017). On the other hand, more
684 relatively complex behaviours, which involve more than one tool and usually a sequential set
685 of steps to achieve the final goal (such as chimpanzee nut-cracking, see above), are less likely
686 to emerge via chance. In these cases, the single-case ZLS standard is applied, and these
687 behaviours only require a single naïve individual to reinnovate them before they can be
688 confidently attributed to the species' ZLS (Bandini & Tennie, 2017). As nut-cracking is a
689 complex behaviour (see introduction), here we applied the single-case ZLS standard, and
690 therefore required a single case of spontaneous acquisition of the behaviour to categorise it as
691 a LS.

692

693

694

695 *Data collection and reliability*

696 We live and video coded the behaviour used by subjects to try to open the macadamia nuts
697 (see Tables 1 & 2). Two second coders, who were not familiar with the aims and results of the
698 study, watched the testing videos and coded the same categories as the original coder to assess
699 inter-rater reliability. One coded the ethogram of behaviours, and how often each individual
700 demonstrated the methods, whilst the other coded the number of successes and time spent
701 with a nut in the subject's mouth. A Cohens kappa was run to assess the inter-rater reliability
702 of both sets of data. All data is available in OSF (please see:
703 https://osf.io/43fbr/?view_only=fd9290ce18b542c7a43a102f600ab22d).

704

705 *Ethics*

706 In accordance with ethical recommendations, all subjects were housed in semi-natural indoor
707 and outdoor enclosures containing climbing structures and natural features. Subjects received
708 their regularly scheduled feedings and had access to enrichment devices and water *ad lib*.
709 Subjects were never food or water deprived for the purposes of this study. All research was
710 conducted in the subjects sleeping rooms. An internal committee of the Max Planck Institute
711 for Evolutionary Anthropology (director, research coordinator), the Leipzig zoo (head keeper,
712 curator, vet) granted ethical approval for this project. No medical, toxicological or
713 neurobiological research of any kind is conducted at the WKPRC. Research was non-invasive
714 and strictly adhered to the legal requirements of Germany. Animal husbandry and research
715 comply with the "EAZA Minimum Standards for the Accommodation and Care of Animals in
716 Zoos and Aquaria", the "WAZA Ethical Guidelines for the Conduct of Research on Animals
717 by Zoos and Aquariums" and the "Guidelines for the Treatment of Animals in Behavioral
718 Research and Teaching" of the Association for the Study of Animal Behavior (ASAB).

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755 **References cited**

- 756 Allritz, M., Tennie, C., & Call, J. (2013). Food washing and placer mining in captive great
757 apes. *Primates*, 54(4), 361–370. <https://doi.org/10.1007/s10329-013-0355-5>
- 758 Amici, F., Aureli, F., & Call, J. (2008). Fission-Fusion Dynamics, Behavioral Flexibility, and
759 Inhibitory Control in Primates. *Current Biology*, 18(18), 1415–1419.
760 <https://doi.org/10.1016/J.CUB.2008.08.020>
- 761 Anderson, J. R. (1985). Development of tool-use to obtain food in a captive group of *Macaca*
762 *tonkeana*. *Journal of Human Evolution*, 14(7), 637–645. [https://doi.org/10.1016/S0047-](https://doi.org/10.1016/S0047-2484(85)80072-5)
763 [2484\(85\)80072-5](https://doi.org/10.1016/S0047-2484(85)80072-5)
- 764 Bandini, E., & Tennie, C. (n.d.-a). Individual acquisition of ‘stick pounding’ behaviour by
765 naïve chimpanzees. *American Journal of Primatology*.
- 766 Bandini, E., & Tennie, C. (n.d.-b). Spontaneous Reoccurrence of “Scooping”, a Wild Tool-
767 Use Behaviour, in Naïve Chimpanzees. *In Review*.
- 768 Bandini, E., & Tennie, C. (2017). Spontaneous reoccurrence of “scooping”, a wild tool-use
769 behaviour, in naïve chimpanzees. *PeerJ*, 5, e3814. <https://doi.org/10.7717/peerj.3814>
- 770 Bandini, E., & Tennie, C. (2018). Naïve , captive long-tailed macaques (*Macaca fascicularis*
771 *fascicularis*) fail to individually and socially a tool-use behaviour.
- 772 Barrett, B. J., Monteza-Moreno, C. M., Dogandžić, T., Zwyns, N., Ibañez, A., & Crofoot, M.
773 C. (2018). Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus*
774 *capucinus*. *Royal Society Open Science*, 5(8), 181002.
- 775 Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T.
776 (n.d.). Cultural innovation and transmission of tool use in wild chimpanzees: evidence
777 from field experiments. *Animal Cognition*, 6(4), 213–223.
778 <https://doi.org/10.1007/s10071-003-0183-x>
- 779 Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T.
780 (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence
781 from field experiments. *Animal Cognition*, 6(4), 213–223.
782 <https://doi.org/10.1007/s10071-003-0183-x>
- 783 Boesch, Christophe. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, 41(3),
784 530–532. [https://doi.org/10.1016/S0003-3472\(05\)80857-7](https://doi.org/10.1016/S0003-3472(05)80857-7)
- 785 Boesch, Christophe;, Marchesi, P., Marchesi, N., Fruth, B., & Joulain, F. (1994). Is nut

- 786 cracking in wild chimpanzees a cultural behavior? *Journal of Human Evolution*, 26(4),
787 325–338. <https://doi.org/10.1006/jhev.1994.1020>
- 788 Boesch, Christophe., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai Forest :
789 behavioural ecology and evolution*. Oxford University Press. Retrieved from
790 [https://books.google.it/books?hl=en&lr=&id=6drtXIjIPZgC&oi=fnd&pg=PA1&dq=boesch-
791 ch+boesch-
792 achermann&ots=6HoEX92uim&sig=kf8C5HnfPRcvLmE0yFcQFcZKs9o#v=onepage&
793 q=boesch+boesch-achermann&f=false](https://books.google.it/books?hl=en&lr=&id=6drtXIjIPZgC&oi=fnd&pg=PA1&dq=boesch+boesch-achermann&ots=6HoEX92uim&sig=kf8C5HnfPRcvLmE0yFcQFcZKs9o#v=onepage&q=boesch+boesch-achermann&f=false)
- 794 Boesch, Christophe. (2003). Is culture a golden barrier between human and chimpanzee?
795 *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*,
796 12(2), 82–91.
- 797 Boesch, Christophe. (2012). *Wild cultures: a comparison between chimpanzee and human
798 cultures*. Cambridge University Press.
- 799 Boesch, Christophe, & Boesch, H. (1983). Optimisation of nut-cracking with natural hammers
800 by wild chimpanzees. *Behaviour*, 83(3–4), 265–286.
- 801 Boesch, Christophe, & Boesch, H. (1990a). Tool Use and Tool Making in Wild Chimpanzees.
802 *Folia Primatologica*, 54(1–2), 86–99. <https://doi.org/10.1159/000156428>
- 803 Boesch, Christophe, & Boesch, H. (1990b). Tool Use and Tool Making in Wild Chimpanzees.
804 *Folia Primatol*, 54(1–2), 86–99. <https://doi.org/10.1159/000156428>
- 805 Byrne, R. W. (2007). Culture in great apes: using intricate complexity in feeding skills to
806 trace the evolutionary origin of human technical prowess. *Philosophical Transactions of
807 the Royal Society B: Biological Sciences*, 362(1480), 577–585.
- 808 Byrne, R. W., & Byrne, J. M. E. (1993). Complex leaf-gathering skills of mountain gorillas
809 (*Gorilla g. beringei*): Variability and standardization. *American Journal of Primatology*,
810 31(4), 241–261. <https://doi.org/10.1002/ajp.1350310402>
- 811 Carvalho, S., Biro, D., McGrew, W. C., & Matsuzawa, T. (2009). Tool-composite reuse in
812 wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological
813 evolution of early hominins? *Animal Cognition*, 12(S1), 103–114.
814 <https://doi.org/10.1007/s10071-009-0271-7>
- 815 Clay, Z., & Tennie, C. (2017). Is Overimitation a Uniquely Human Phenomenon? Insights
816 From Human Children as Compared to Bonobos. *Child Development*.

- 817 <https://doi.org/10.1111/cdev.12857>
- 818 Cohen, J. (1968). Weighted kappa: Nominal scale agreement provision for scaled
819 disagreement or partial credit. *Psychological Bulletin*, 70(4), 213–220.
820 <https://doi.org/10.1037/h0026256>
- 821 Collias, E. C., & Collias, N. E. (1964). The Development of Nest-Building Behavior in a
822 Weaverbird. *The Auk*, 81(1), 42–52. <https://doi.org/10.2307/4082609>
- 823 Corp, N., & Byrne, R. W. (2002). The ontogeny of manual skill in wild chimpanzees:
824 evidence from feeding on the fruit of *Saba florida*. *Behaviour*, 137–168.
- 825 Daegling, D. J. (2007). Morphometric estimation of torsional stiffness and strength in primate
826 mandibles. *American Journal of Physical Anthropology*, 132(2), 261–266.
827 <https://doi.org/10.1002/ajpa.20508>
- 828 De Waal, F. (2008). *The ape and the sushi master: Cultural reflections of a primatologist*.
829 Basic Books.
- 830 de Waal, F. B. M., & Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and
831 human cognition. *Trends in Cognitive Sciences*, 14(5), 201–207.
832 <https://doi.org/10.1016/j.tics.2010.03.003>
- 833 Foucart, J., Bril, B., Hirata, S., Monimura, N., Houki, C., Ueno, Y., & Matsuzawa, T. (2005).
834 A preliminary analysis of nut-cracking movements in a captive chimpanzee: adaptation
835 to the properties of tools and nuts. *Stone Knapping: The Necessary Conditions for a*
836 *Uniquely Hominin Behaviour*, 147–157.
- 837 Fox, E. A., van Schaik, C. P., Sitompul, A., & Wright, D. N. (2004). Intra-and
838 interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet:
839 Implications for the invention of tool use. *American Journal of Physical Anthropology*,
840 125(2), 162–174. <https://doi.org/10.1002/ajpa.10386>
- 841 Haslam, M. (2014). On the tool use behavior of the bonobo-chimpanzee last common
842 ancestor, and the origins of hominine stone tool use. *American Journal of Primatology*,
843 76(10), 910–918. <https://doi.org/10.1002/ajp.22284>
- 844 Haslam, M., Cardoso, R. M., Visalberghi, E., & Frigaszy, D. (2014). Stone Anvil Damage by
845 Wild Bearded Capuchins (*Sapajus libidinosus*) during Pounding Tool Use: A Field
846 Experiment. *PLoS ONE*, 9(11), e111273. <https://doi.org/10.1371/journal.pone.0111273>
- 847 Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., ...

- 848 Warren, R. (2009). Primate archaeology. *Nature*, *460*(7253), 339–344.
849 <https://doi.org/10.1038/nature08188>
- 850 Hayashi, M., Mizuno, Y., & Matsuzawa, T. (2005). How does stone-tool use emerge?
851 Introduction of stones and nuts to naive chimpanzees in captivity. *Primates*, *46*(2), 91–
852 102. <https://doi.org/10.1007/s10329-004-0110-z>
- 853 Hecht, E. E., Gutman, D. A., Preuss, T. M., Sanchez, M. M., Parr, L. A., & Rilling, J. K.
854 (2013). Process Versus Product in Social Learning: Comparative Diffusion Tensor
855 Imaging of Neural Systems for Action Execution–Observation Matching in Macaques,
856 Chimpanzees, and Humans. *Cerebral Cortex*, *23*(5), 1014–1024.
857 <https://doi.org/10.1093/cercor/bhs097>
- 858 Henrich, J., & Tennie, C. (2015). Cultural Evolution in Chimpanzees and Humans. *Working*
859 *Paper*, 1–31.
- 860 Hirata, S., Morimura, N., & Houki, C. (2009). How to crack nuts: acquisition process in
861 captive chimpanzees (*Pan troglodytes*) observing a model. *Animal Cognition*, *12*(S1),
862 87–101. <https://doi.org/10.1007/s10071-009-0275-3>
- 863 Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of Stone Tool Use by Wild
864 Chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*(2), 159–173.
- 865 Kenward, B., Schloegl, C., Rutz, C., Weir, A., Bugnyar, T., & Kacelnik, A. (2011). On the
866 evolutionary and ontogenetic origins of tool-oriented behaviour in New Caledonian
867 crows (*Corvus moneduloides*). *Biological Journal of the Linnean Society*, *102*(4), 870–
868 877. <https://doi.org/10.1111/j.1095-8312.2011.01613.x>
- 869 Krützen, M., Willems, E. P., & van Schaik, C. P. (2011). Culture and Geographic Variation in
870 Orangutan Behavior. *Current Biology*, *21*(21), 1808–1812.
871 <https://doi.org/10.1016/J.CUB.2011.09.017>
- 872 Lamal, P. A. (2002). The ape and the sushi master: Cultural reflections of a primatologist.
873 *Behavior Analyst*, *25*(2), 227–233.
- 874 Luncz, L. V., Mundry, R., & Boesch, C. (2012a). Evidence for Cultural Differences between
875 Neighboring Chimpanzee Communities. *Current Biology*, *22*(10), 922–926.
876 <https://doi.org/10.1016/J.CUB.2012.03.031>
- 877 Luncz, L. V., & Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee
878 communities maintain differences in cultural behavior despite frequent immigration of

- 879 adult females. *American Journal of Primatology*, 76(7), 649–657.
880 <https://doi.org/10.1002/ajp.22259>
- 881 Luncz, L. V., Mundry, R., & Boesch, C. (2012b). Evidence for cultural differences between
882 neighboring chimpanzee communities. *Current Biology*, 22(10), 922–926.
883 <https://doi.org/10.1016/j.cub.2012.03.031>
- 884 Luncz, L. V., Svensson, M. S., Haslam, M., Malaivijitnond, S., Proffitt, T., & Gumert, M.
885 (2017, August 29). Technological Response of Wild Macaques (*Macaca fascicularis*) to
886 Anthropogenic Change. *International Journal of Primatology*, pp. 1–9.
887 <https://doi.org/10.1007/s10764-017-9985-6>
- 888 Lycett, S. J., Collard, M., & McGrew, W. C. (2007). Phylogenetic analyses of behavior
889 support existence of culture among wild chimpanzees. *Proceedings of the National
890 Academy of Sciences of the United States of America*, 104(45), 17588–17592.
891 <https://doi.org/10.1073/pnas.0707930104>
- 892 Lycett, S. J., Collard, M., & McGrew, W. C. (2010). Are behavioral differences among wild
893 chimpanzee communities genetic or cultural? An assessment using tool-use data and
894 phylogenetic methods. *American Journal of Physical Anthropology*, 142(3), 461–467.
895 <https://doi.org/10.1002/ajpa.21249>
- 896 Marshall-Pescini, S., & Whiten, A. (2008). Social learning of nut-cracking behavior in East
897 African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *Journal of
898 Comparative Psychology*, 122(2), 186–194. <https://doi.org/10.1037/0735-7036.122.2.186>
- 899 Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G.
900 (2008). Emergence of Culture in Wild Chimpanzees: Education by Master-
901 Apprenticeship. In *Primate Origins of Human Cognition and Behavior* (pp. 557–574).
902 Tokyo: Springer Japan. https://doi.org/10.1007/978-4-431-09423-4_28
- 903 McGrew, W. C., Ham, R. M., White, L. J. T., Tutin, C. E. G., & Fernandez, M. (1997). Why
904 Don't Chimpanzees in Gabon Crack Nuts? *International Journal of Primatology*, 18(3),
905 353–374. <https://doi.org/10.1023/A:1026382316131>
- 906 McGrew, W. C., & Tutin, C. E. G. (1978). Evidence for a Social Custom in Wild
907 Chimpanzees? *Man*, 13(2), 234. <https://doi.org/10.2307/2800247>
- 908 Menzel, C., Fowler, A., Tennie, C., & Call, J. (2013). Leaf Surface Roughness Elicits Leaf
909 Swallowing Behavior in Captive Chimpanzees (*Pan troglodytes*) and Bonobos (*P.
910 paniscus*), but not in Gorillas (*Gorilla gorilla*) or Orangutans (*Pongo abelii*).

- 911 *International Journal of Primatology*, 34(3), 533–553. <https://doi.org/10.1007/s10764->
912 013-9679-7
- 913 Menzel, E. W., Davenport, R. K., & Rogers, C. M. (1970). The development of tool using in
914 wild-born and restriction-reared chimpanzees. *Folia Primatologica; International*
915 *Journal of Primatology*, 12(4), 273–283. <https://doi.org/10.1159/000155297>
- 916 Meulman, E. J. M., Sanz, C. M., Visalberghi, E., & van Schaik, C. P. (2012). The Role of
917 Terrestriality in Promoting Primate Technology. *Evolutionary Anthropology*, 21(2), 58–
918 68. <https://doi.org/10.1002/evan.21304>
- 919 Moore, R. (n.d.). Social learning and teaching in chimpanzees.
920 <https://doi.org/10.1007/s10539-013-9394-y>
- 921 Morgan, B. J., & Abwe, E. E. (2006). Chimpanzees use stone hammers in Cameroon. *Current*
922 *Biology : CB*, 16(16), R632-3. <https://doi.org/10.1016/j.cub.2006.07.045>
- 923 Neadle, D., Allritz, M., & Tennie, C. (2017). Food cleaning in gorillas: Social learning is a
924 possibility but not a necessity. *PLOS ONE*, 12(12), e0188866.
925 <https://doi.org/10.1371/journal.pone.0188866>
- 926 Ottoni, E. B., & Mannu, M. (2001). Semi-free ranging tufted capuchin monkeys (*Cebus*
927 *apella*) spontaneously use tools to crack open nuts. *International Journal of*
928 *Primatology*, 22(3), 347–358.
- 929 Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor
930 intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human*
931 *Evolution*, 6(7), 623–641. [https://doi.org/10.1016/S0047-2484\(77\)80135-8](https://doi.org/10.1016/S0047-2484(77)80135-8)
- 932 Parrish, A. E., Perdue, B. M., Stromberg, E. E., Bania, A. E., Evans, T. A., & Beran, M. J.
933 (2014). Delay of gratification by orangutans (*Pongo pygmaeus*) in the accumulation task.
934 *Journal of Comparative Psychology*, 128(2), 209.
- 935 Pfungst, O. (1912). Zur Psychologie der Affen. In *Bericht über den 5. Kongress für*
936 *experimentelle Psychologie* (pp. 200–205).
- 937 Pope, S., Tagliabata, J., Skiba, S., & Hopkins, W. D. (2017). Changes in fronto-parieto-
938 temporal connectivity following Do-As-I-Do imitation training in chimpanzees (*Pan*
939 *troglodytes*). <https://doi.org/none>
- 940 Proffitt, T., Haslam, M., Mercader, J. F., Boesch, C., & Luncz, L. V. (2018). Revisiting Panda
941 100, the first archaeological chimpanzee nut-cracking site. *Journal of Human Evolution*.

- 942 <https://doi.org/10.1016/J.JHEVOL.2018.04.016>
- 943 Ratcliffe, L., Boag, P., Shackleton, S., Weisman, R., & Weary, D. (1994). Sexual preferences
944 of female zebra finches: imprinting on beak colour. *Behaviour*, *128*(1–2), 15–24.
- 945 Reindl, E., Beck, S. R., Apperly, I. A., & Tennie, C. (2016). Young children spontaneously
946 invent wild great apes' tool-use behaviours. *Proceedings of the Royal Society B:
947 Biological Sciences*, *283*(1825), 20152402. <https://doi.org/10.1098/rspb.2015.2402>
- 948 Reindl, E., Apperly, I. A., Beck, S. R., & Tennie, C. (2017). Young children copy cumulative
949 technological design in the absence of action information. *Scientific Reports*, (April), 1–
950 11. <https://doi.org/10.1038/s41598-017-01715-2>
- 951 Reindl, Eva, & Tennie, C. (2018). Young children fail to generate an additive ratchet effect in
952 an open-ended construction task. *PLOS ONE*, *13*(6), e0197828.
953 <https://doi.org/10.1371/journal.pone.0197828>
- 954 Robbins, M. M., Ando, C., Fawcett, K. A., Grueter, C. C., Hedwig, D., Iwata, Y., ...
955 Yamagiwa, J. (2016). Behavioral Variation in Gorillas: Evidence of Potential Cultural
956 Traits. *PLOS ONE*, *11*(9), e0160483. <https://doi.org/10.1371/journal.pone.0160483>
- 957 Santorelli, C. J., Schaffner, C. M., & Aureli, F. (2011). Universal Behaviors as Candidate
958 Traditions in Wild Spider Monkeys. *PLoS ONE*, *6*(9), e24400.
959 <https://doi.org/10.1371/journal.pone.0024400>
- 960 Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., &
961 van Schaik, C. P. (2016). Observational social learning and socially induced practice of
962 routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98.
963 <https://doi.org/10.1016/J.ANBEHAV.2016.06.014>
- 964 Shumaker, R. W., Walkup, K. R., Beck, B. B., & Burghardt, G. M. (2011). *Animal Tool
965 Behavior: The Use and Manufacture of Tools by Animals*. Johns Hopkins University
966 Press. Retrieved from https://books.google.de/books?id=Dx7slq__udwC
- 967 Sumita, K., Kitahara-Frisch, J., & Norikoshi, K. (1985). The acquisition of stone-tool use in
968 captive chimpanzees. *Primates*, *26*(2), 168–181. <https://doi.org/10.1007/BF02382016>
- 969 Tan, A. W. Y. (2017). From play to proficiency: The ontogeny of stone-tool use in coastal-
970 foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-
971 action perspective. *Journal of Comparative Psychology*, *131*(2), 89–114.
972 <https://doi.org/10.1037/com0000068>

- 973 Tebbich, S., Taborsky, M., Fessl, B., & Blomqvist, D. (2001). Do woodpecker finches acquire
974 tool-use by social learning? *Proceedings of the Royal Society B: Biological Sciences*,
975 268(1482), 2189–2193. <https://doi.org/10.1098/rspb.2001.1738>
- 976 Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of
977 cumulative culture. *Philosophical Transactions of the Royal Society B: Biological*
978 *Sciences*, 364(1528), 2405–2415. <https://doi.org/10.1098/rstb.2009.0052>
- 979 Tennie, Claudio, Call, J., & Tomasello, M. (2012). Untrained Chimpanzees (*Pan troglodytes*
980 *schweinfurthii*) Fail to Imitate Novel Actions. *PLoS ONE*, 7(8), e41548.
981 <https://doi.org/10.1371/journal.pone.0041548>
- 982 Tennie, Claudio, & Hedwig, D. (2009). How latent solution experiments can help to study
983 differences between human culture and primate traditions. *Primateology: Theories,*
984 *Methods and Research*. Hauppauge, NY: Nova Science Publishers, 95–112.
- 985 Tennie, Claudio, Hedwig, D., Call, J., & Tomasello, M. (2008). An experimental study of
986 nettle feeding in captive gorillas. *American Journal of Primatology*, 70(6), 584–593.
987 <https://doi.org/10.1002/ajp.20532>
- 988 Toth, N., Schick, K. D., Savage-Rumbaugh, E. S., Sevcik, R. A., & Rumbaugh, D. M. (1993).
989 Pan the Tool-Maker: Investigations into the Stone Tool-Making and Tool-Using
990 Capabilities of a Bonobo (*Pan paniscus*). *Journal of Archaeological Science*, 20(1), 81–
991 91. <https://doi.org/10.1006/jasc.1993.1006>
- 992 van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in
993 primates: implications for the evolution of material culture. *Journal of Human Evolution*,
994 36(6), 719–741. <https://doi.org/10.1006/jhev.1999.0304>
- 995 van Schaik, C. P., & Pradhan, G. R. (2003). A model for tool-use traditions in primates:
996 Implications for the coevolution of culture and cognition. *Journal of Human Evolution*,
997 44(6), 645–664. [https://doi.org/10.1016/S0047-2484\(03\)00041-1](https://doi.org/10.1016/S0047-2484(03)00041-1)
- 998 Visalberghi, E., Sabbatini, G., Spagnoletti, N., Andrade, F. R. D., Ottoni, E., Izar, P., &
999 Fragaszy, D. (2008). Physical properties of palm fruits processed with tools by wild
1000 bearded capuchins (*Cebus libidinosus*). *American Journal of Primatology*, 70(8), 884–
1001 891. <https://doi.org/10.1002/ajp.20578>
- 1002 Visalberghi, Elisabetta. (1987a). Acquisition of Nut-Cracking Behaviour by 2 Capuchin
1003 Monkeys (<i>Cebus apella</i>). *Folia Primatologica*, 49(3–4), 168–181.
1004 <https://doi.org/10.1159/000156320>

- 1005 Visalberghi, Elisabetta. (1987b). Acquisition of nut-cracking behaviour by 2 capuchin
1006 monkeys (*Cebus apella*). *Folia Primatologica*, 49(3–4), 168–181.
1007 <https://doi.org/10.1159/000156320>
- 1008 Whiten, Andrew; Goodall, J. W. C. M. T. N. V. R. Y. S. C. E. G. T. R. W. W. and C. B.
1009 (2001). Charting Cultural Variation in Chimpanzees. *Behaviour*, 138(11), 1481–1516.
1010 <https://doi.org/10.1163/156853901317367717>
- 1011 Whiten, A. (2015). Experimental studies illuminate the cultural transmission of percussive
1012 technologies in Homo and Pan. *Philosophical Transactions of the Royal Society of*
1013 *London B: Biological Sciences*, 370(1682). Retrieved from
1014 <http://rspb.royalsocietypublishing.org/content/370/1682/20140359>
- 1015 Whiten, A. (2017). Culture extends the scope of evolutionary biology in the great apes.
1016 *Proceedings of the National Academy of Sciences*, 114(30), 7790–7797.
1017 <https://doi.org/10.1073/pnas.1620733114>
- 1018 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ... Boesch,
1019 C. (2001). Charting Cultural Variation in Chimpanzees. *Behaviour*, 138(11), 1481–1516.
- 1020 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ...
1021 Boesch, C. (1999a). Cultures in chimpanzees. *Nature*, 399(6737), 682–685.
1022 <https://doi.org/10.1038/21415>
- 1023 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ...
1024 Boesch, C. (1999b). Cultures in chimpanzees. *Nature*, 399(6737), 682–685.
1025 <https://doi.org/10.1038/21415>
- 1026 Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape?
1027 *Learning & Behavior*, 32(1), 36–52. <https://doi.org/10.3758/BF03196005>
- 1028 Whiten, A., & Mesoudi, A. (2008). Review. Establishing an experimental science of culture:
1029 animal social diffusion experiments. *Philosophical Transactions of the Royal Society of*
1030 *London. Series B, Biological Sciences*, 363(1509), 3477–3488.
1031 <https://doi.org/10.1098/rstb.2008.0134>
- 1032 Whiten, A., & van de Waal, E. (2017). Social learning, culture and the ‘socio-cultural brain’
1033 of human and non-human primates. *Neuroscience & Biobehavioral Reviews*, 82, 58–75.
1034 <https://doi.org/10.1016/J.NEUBIOREV.2016.12.018>
- 1035 Wrangham, R. W. (2006). Chimpanzees: The Culture-Zone Concept Becomes Untidy.

- 1036 *Current Biology*, 16(16), R634–R635. <https://doi.org/10.1016/J.CUB.2006.07.031>
- 1037 Zentall, T. R. (2003). Imitation by Animals. *Current Directions in Psychological Science*,
1038 12(3), 91–95. <https://doi.org/10.1111/1467-8721.01237>
- 1039
- 1040
- 1041
- 1042
- 1043
- 1044