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

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Abstract

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

Introduction

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

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

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

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

Nut-cracking in chimpanzees

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Latent solutions testing methodology

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

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

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

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

Results

Reliability testing

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

Experimental results

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

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	1st trial baseline	All conditions	Yes	69%
Hit with Hand	The subject hits the nut with its hand against a hard surface	2 (PD & DK)	1st trial baseline	All conditions	No	N/A
Step	The subject hits the nut with its foot against a hard surface	2 (PD & PI)	1st 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)	2nd 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)	1st trial locked anvil	Only locked anvil condition	Yes	95%

Baseline condition

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

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

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

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

Demonstration condition

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

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

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%

Discussion

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

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

Previous studies

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

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

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

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

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

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

Nut-cracking in other primates

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

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

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

Conclusion

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

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)	*Pongo abelii*	F	31/01/1989	Dresden, DE	Parent
Padana (PD)	*Pongo abelii*	F	18/11/1997	Leipzig, DE	Parent
Pini (PI)	*Pongo abelii*	F	30/06/1988	Leipzig, DE	Parent
Dunja (DJ)	*Pongo abelii*	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

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

Baseline condition

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

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

Locked-anvil condition

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

Demonstration condition

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

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

Reinnovation standards

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

Data collection and reliability

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

Ethics

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

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