RESEARCH ARTICLE

Naïve orangutans (*Pongo abelii* and *Pongo pygmaeus*) individually acquire nut-cracking using hammer tools

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Abstract

Nut-cracking with hammer tools (henceforth: nut-cracking) has been argued to be one of the most complex tool-use behaviors observed in nonhuman animals. So far, only chimpanzees, capuchins, and macaques have been observed using tools to crack nuts in the wild (Boesch and Boesch, 1990; Gumert et al., 2009; Mannu and Ottoni, 2009). However, the learning mechanisms behind this behavior, and the extent of nut-cracking in other primate species are still unknown. The aim of this study was two-fold. First, we investigated whether another great ape species would develop nut-cracking when provided with all the tools and appropriate conditions to do so. Second, we examined the mechanisms behind the emergence of nut-cracking by testing a naïve sample. Orangutans (*Pongo abelii* and *Pongo pygmaeus*) have the second most extensive tool-use repertoire among the great apes (after chimpanzees) and show flexible problem-solving capacities. Orangutans have not been observed cracking nuts in the wild, however, perhaps because their arboreal habits provide limited opportunities for nut-cracking. Therefore, orangutans are a valid candidate species for the investigation of the development of this behavior. Four nut-cracking-naïve orangutans at Leipzig zoo (*P. abelii*; M_{age} = 16; age range = 10–19; 4F; at the time of testing) were provided with nuts and hammers but were not demonstrated the nut-cracking behavioral form. Additionally, we report data from a previously unpublished study by one of the authors (Martina Funk) with eight orangutans housed at Zürich zoo (six *P. abelii* and two *P. pygmaeus*; M_{age} = 14; age range = 2–30; 5F; at the time of testing) that followed a similar testing paradigm. Out of the twelve orangutans tested, at least four individuals, one from Leipzig (*P. abelii*) and three from Zürich (*P. abelii* and *P. pygmaeus*), spontaneously expressed nut-cracking using wooden hammers. These results demonstrate that nut-cracking can emerge in orangutans through individual learning and certain types of non-copying social learning.

KEYWORDS
individual learning, nut-cracking, orangutan, social learning, tool-use

1 | INTRODUCTION

Of all nonhuman animal species, great apes, alongside New Caledonian crows (e.g., Kenward et al., 2011), currently demonstrate the most extensive tool-use repertoire and potentially the most "complex" tool-use behaviors (van Schaik et al., 1999). Within the great apes, nut-cracking using hammer tools (henceforth: nut-cracking) by chimpanzees is one of the most cited examples (Boesch, 1991; Lonsdorf, 2013). Complex tool-use has been defined as: *"tool-use variants that include at least two tool elements (for example, hammer and anvil), flexibility in manufacture or use (that is, tool properties are adjusted to the task at hand), and that skills are acquired in part by social learning"* (Meulman et al., 2012, p. 58). The claimed complexity of chimpanzee nut-cracking, therefore, partly rests on the idea that copying social learning drives this behavior. Although we will discuss this assumption in further detail in the following section, below we provide definitions for the main social learning mechanisms discussed in this paper.

The animal social learning field is rife with terminology and mechanisms (for an overview of these terms, see Whiten, 2021; Whiten et al., 2004). However, throughout this paper, we will mainly be referring to two categories of social learning: copying and non-copying social learning mechanisms (Tennie, Bandini, et al., 2020). Copying social learning (henceforth: copying) refers to social learning mechanisms that can transmit the actual form of a behavior and/or artifact (where form is defined as *"the specific action [and/or artifact] component(s) and organization of a behavior"*; Bandini & Tennie, 2020, p. 2). This category of social learning, therefore, transmits "know-how" and includes mechanisms such as imitation and some types of emulation (Bandini & Tennie, 2020; Tennie, Bandini, et al., 2020). On the other hand, non-copying social learning mechanisms are those that have social effects, but these effects do not involve the transmission of the form of a behavior and/or artifact. Instead, non-copying social learning mechanisms catalyze and regulate the frequency of the acquisition of a behavior/artifact, for example by increasing an individual's motivation to interact with or manipulate a certain object (stimulus enhancement; or "know-what") or to attend to a certain location (local enhancement; or "know-where" see Bandini et al., 2020).

1.1 | Nut-cracking in primates

Nut-cracking has (so far) only been observed in chimpanzees, long-tailed macaques, and capuchins (Boesch & Boesch, 1990; Gumert et al., 2009; Ottoni & Mannu, 2001). The best-studied example is that of chimpanzee nut-cracking (Biro et al., 2003; Boesch & Boesch, 1990; Luncz & Boesch, 2014; Luncz et al., 2012). 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 et al., 2018). The crux of the nut-cracking behavioral form in 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 a wooden hammer and (3) hitting the nut with the hammer (holding it with one or both hands) until its shell is cracked 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 et al., 2009) and the stabilization of the anvil on the ground (although this is a rare behavior; Carvalho et al., 2009). This multi-step, compound behavior is unlikely to be 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 behavioral forms within the chimpanzee tool-use repertoire involve the manipulation of a single object (usually a stick) and include the performance of a single action type (e.g., marrow picking; see Whiten et al., 2001 for an overview of chimpanzee behaviors and their descriptions). Furthermore, the precision required to crack open hard nuts contributes to the overall difficulty of nut-cracking and the improbability that it is acquired by chance, since (at least at the beginning), many attempts will go unrewarded (Biro et al., 2003). All this has contributed to nut-cracking being regarded as a complex tool-use behavior, often assumed to be driven and maintained by action copying (Boesch, 1991; Boesch et al., 1994), although this assumption is heavily debated (e.g., see Neadle et al., 2020). Furthermore, chimpanzee nut-cracking has recently been selected for conservation by the United Nations Convention on the Conservation of Migratory Species (CMS) body, demonstrating how important this behavior is considered to be (Picheta, 2020).

1.2 | Acquisition of nut-cracking in chimpanzees

Juvenile chimpanzees take a long time to acquire nut-cracking (Biro et al., 2003; Boesch & Boesch, 1990) and observations of wild juvenile chimpanzees suggest that the acquisition of this behavior may only occur within a sensitive learning period, most likely when chimpanzees are between the ages of 3 and 5 years old (Inoue-Nakamura & Matsuzawa, 1997). Chimpanzees that do not acquire the nut-cracking behavior within this sensitive learning period, do not seem to develop it later in life either (Biro et al., 2003). A sensitive learning window seems to also be present for nut-cracking in other primates, such as long-tailed macaques (Tan, 2017).

It has been proposed that juvenile chimpanzees 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 observation and practice sessions is required before nut-cracking can be expressed (e.g., what Whiten, 2017, p. 7795, describes as a "helical process of learning"). It has also been suggested that juvenile chimpanzees copy their mothers' nut-cracking via "Bonding and Identification-based Observational Learning" (BIOL), where a juvenile is socially motivated to copy actions in order "to be like others" (De Waal, 2008, p. 231).

Yet, the existence of a sensitive learning window and a lengthy learning period alone is not necessarily indicative of copying.

Learning periods can be explained by maturation processes and, within these windows, extended periods of individual learning may also occur (likely encouraged or guided by non-copying variants of social learning, such as stimulus and local enhancement; Whiten et al., 2004 and "peering"; Corp & Byrne, 2002; Schuppli et al., 2016). As nut-cracking is a multi-step process, the learning period may indeed be longer than for other behaviors.

Furthermore, conclusive evidence for (unenculturated, untrained) apes possessing the ability to copy actions is still lacking. Although enculturated and/or trained apes have demonstrated an ability to copy actions (this type of training seems to change the individuals' brain structures to allow for action copying; Hecht et al., 2013; Pope et al., 2017), experimental paradigms aimed at identifying this ability in unenculturated, untrained chimpanzees have so far been unsuccessful – at least when the task was to copy novel actions (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997). Therefore, while further studies should be carried out on this ability in different ape species, the current state of knowledge suggests that alternative explanations to those based primarily on copying should be explored.

1.3 | The zone of latent solutions hypothesis

One alternative approach towards explaining the acquisition of nut-cracking in primates is provided by the zone of latent solutions hypothesis (ZLS; Tennie et al., 2009; see Tennie, Bandini, et al., 2020 for more information on the term "ZLS"). The ZLS hypothesis argues that behavioral forms are acquired in many species via a catalytic interplay between individual learning and non-copying variants of social learning (Tennie et al., 2009; see also Fragaszy & Visalberghi, 2001; Galef, 1992; Tomasello, 1994, 1999). According to this hypothesis, the behavioral form of primate nut-cracking might not be copied but individually derived. The ZLS hypothesis also suggests that the observed differences in nut-cracking activity across chimpanzee populations are fostered by non-copying social learning mechanisms (such as local and/or stimulus enhancement), which increase the likelihood of reinnovation once a population already contains individuals who have innovated the behavioral form. This can then lead to a frequency increase and maintenance of the behavioral forms in question in some populations but not in others, creating the cultural patterns that have been observed across several animal species (as also discussed by Fragaszy & Visalberghi, 2001; Galef, 1992).

The ZLS hypothesis, therefore, predicts successful reinnovation of behavioral forms by naïve apes, provided the right conditions (e.g., access to the necessary raw material) and motivation to perform the behavior (Tennie, Hopper, et al., 2020). Moreover, in contrast to the copying hypothesis, the ZLS hypothesis predicts reinnovation to be possible in the absence of copying opportunities. This last prediction has been met several times for behaviors other than nut-cracking in apes, as demonstrated by a growing experimental literature detailing successful individual acquisitions of wild-type behavioral forms in various species of naïve, captive great apes (Allritz et al., 2013;

Bandini & Harrison, 2020; Bandini & Tennie, 2017, 2019, 2020; Menzel et al., 2013; Neadle et al., 2017; Tennie et al., 2008). Therefore, the ZLS hypothesis has growing support, but whether it can also explain the behavioral form of ape nut-cracking is still an open question (see also Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020 for further discussion).

To examine the role of copying mechanisms in the acquisition of a tool-use behavioral form, all the ecological materials of the target behavior, but no demonstrations, are provided to subjects (Bandini et al., 2020; Hopper et al., 2015; Tennie & Hedwig, 2009). For this methodology to be valid, subjects must be naïve (i.e., they must have never seen, or been trained in the target behavior before), as well as 'ecologically representative (i.e., they must be unenculturated, untrained, and undeprived subjects; Henrich & Tennie, 2017). If the target behavioral form emerges under these circumstances, then it can be concluded that copying is not needed for the form of this behavior to emerge (see also Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020). If the behavior does not emerge in any subject in this baseline condition, then it could be that some variant of copying—including action copying—is necessary for the behavior to be acquired (for these cases, Bandini & Tennie, 2018; Bandini et al., 2020 provide an extended testing methodology that allows for the level and variant of social learning required to be identified), or that other factors, such as low motivation levels, sensitive learning periods, limited opportunities to practice, pre-existing experience (Hanus et al., 2011), and quality of captive conditions or wild environmental conditions may have played a role (Bandini & Tennie, 2018; Neadle et al., 2020).

1.4 | Aims of the current study

Apart from the observations of chimpanzee nut-cracking, anecdotal reports exist of gorillas and bonobos cracking nuts in sanctuaries (Wrangham & Peterson, 1996), although the exact circumstances of these observations remain unclear. Orangutans, despite having the second most extensive tool-use repertoire in the wild after chimpanzees, have not (perhaps not yet) been reported to crack nuts using tools (Fox et al., 2004; Meulman & van Schaik, 2013; Parker & Gibson, 1977). Orangutans' tool-use repertoire includes extractive foraging tool use and, similarly to chimpanzees, demonstrate intra- and interpopulation variation in their behavior (van Schaik & Knott, 2001). Moreover, there are some reports of orangutans using sticks to "hammer" open termite or bee nests (Fox et al., 1999). However, these behaviors are not fully comparable to chimpanzee nut-cracking as they generally involve thin sticks (while chimpanzee wooden hammers are usually thicker and/or heavier than the sticks they use for other tool-use behaviors) and the hammering action used by orangutans is unlikely to carry enough force to break an object as sturdy as an encased nut (Fox et al., 1999). Therefore, orangutans present a promising candidate to acquire nut-cracking, whilst remaining naïve to this form of hammering behavior.

Four naïve captive orangutans housed at Leipzig zoo (M_{age} = 16; age range=10–19; 4F; at the time of testing) were provided with the raw materials necessary for nut-cracking (nuts, wooden hammers, cracking locations), but no information or demonstrations on *how* to crack nuts. Although no direct claims have been made on the mechanisms required to develop nut-cracking in orangutans (as this behavior has not yet been observed outside of the current study), copying social learning has been suggested for the acquisition of nut-cracking in chimpanzees, as well as for other "complex" behaviors in several primate species (e.g., Biro et al., 2003; Byrne & Russon, 1998; de Waal, 2008; Whiten et al., 1999; and see references within Matthews et al., 2010). The baseline condition used in this study allowed us to test whether orangutans could individually acquire the behavioral form of nut-cracking without having access to a model to copy (and without training). This paradigm further allowed us to test, more generally, whether the acquisition of a seemingly complex behavior in apes is mainly based on copying (in which case the prediction would be that no orangutan would innovate the behavior) or on individual learning and non-copying social learning (in which case some orangutans should innovate nut-cracking). After conducting this study, it was brought to the authors' attention that an unpublished thesis contained a similar study with orangutans, carried out by Martina Funk (one of the co-authors of the current manuscript) between 1983 and 1984. In this study, eight naïve captive orangutans housed at Zürich zoo (six *Pongo abelii* and two *Pongo pygmaeus*; M_{age} = 14; age range =2–30; 5F; at the time of testing) were tested following a similar baseline paradigm as that used in our study. The methods and findings from this previous, unpublished, study are also described here. For the sake of clarity, we will refer to the Leipzig study and the Zürich study respectively.

2 | LEIPZIG STUDY

2.1 | Methods

2.1.1 | Ethical approval

All subjects were housed in 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) and 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. This study was noninvasive 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). Furthermore, this study complied with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

2.1.2 | Subjects

The research was carried out at the Wolfgang Köhler Primate Research Center (WKPRC), Leipzig, Germany, in 2007. Four orangutans (M_{age} = 16; age range = 10–19; 4F; at the time of testing) participated in the study (see the demographic information in Table 1; all subjects were born (except for DK) and raised at the testing institution). The keepers confirmed that none of the individuals in this study had prior experience with macadamia nuts. Hazelnuts and walnuts, however, had occasionally been provided by the keepers. Yet, the orangutans either opened them with their teeth or, occasionally, by hitting them with their hand against a hard surface. Crucially, none of the orangutans at the WKPRC had ever been observed using a *tool* for nut-cracking before this study. Indeed, heavy objects that could potentially be used as hammers (such as stones or wooden stumps) are not allowed inside the enclosures of the WKPRC for health and safety reasons, and therefore the subjects can confidently be assumed to have been naïve to the target behavior before this study.

2.1.3 | Procedure

We implemented three conditions sequentially (see Table 2): The first condition was a baseline in which subjects could only acquire the nut-cracking behavior individually, as no information on the actions required for the behavior was provided (note that whilst copying social learning mechanisms were excluded in this condition, non-copying social learning mechanisms were intentionally not excluded, see more information on this below and in Bandini et al., 2020). The second condition was another baseline, which we called the locked-anvil condition, that guaranteed that

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

TABLE 1 Demographic information on the subjects included in the Leipzig zoo study

TABLE 2 Table showing the number of conditions, sessions, and role of each subject from the Leipzig zoo study

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

Abbreviations: DJ, Dunja; DK, Dokana; PD, Padana; PI, Pini.

the object provided as an anvil could *only* be used as an anvil and not as a hammer (see below). The third condition was a demonstration condition, in which subjects could potentially learn the nut-cracking behavior through social learning (of any variant) after observing a conspecific model (PD; age 10 at the time of testing). Subjects were tested separately with no visual or acoustic access to each other. Although the sub-adult (PD) was tested alone, the adult females were tested together with their dependent offspring (however, no data were analyzed from the offspring as they were too young at the time of testing to attempt the task).

2.1.4 | Baseline condition

During each of five baseline sessions, 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 et al., 2012), two smaller wooden blocks (the wooden hammers; height 55 cm, diameter 8 cm, approximate weight 2.4 kg each) and five macadamia nuts (see Figure 1). The materials were scattered evenly on the floor in the testing room, which was emptied of any other objects before 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. Sessions lasted a maximum of 20 min 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 session and discarded. A video camera was used to record the subjects' behavior. For each subject, the between-session interval was at least 24 h. As no training or demonstrations of nut-cracking were provided before or during this condition, copying social learning was excluded from this condition. However, by placing the materials necessary for the behavioral form (nuts, hammer, and anvil) within an empty enclosure, some types of non-copying social learning, such as stimulus or local enhancement could have increased the likelihood of acquisition of nut-cracking in the orangutans. This is by design and does not affect any conclusions regarding the role of copying that can be derived

FIGURE 1 Photograph of the testing apparatus with the anvil, wooden hammers, and macadamia nuts in the Leipzig Zoo study

from this study. That is, just like in wild apes, non-copying social learning mechanisms may have played a role here (for a more in-depth discussion on this point, see Bandini et al., 2020).

2.1.5 | Locked-anvil condition

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

2.1.6 | Demonstration condition

After the baseline and locked-anvil conditions, the three orangutans that did not develop nut-cracking in the baseline condition participated in five subsequent demonstration condition sessions. Before each session, PD, who had reliably developed nut-cracking in the previous phases, served as a demonstrator, cracking (and eating) five macadamia nuts

using wooden hammers. Subjects, who during the demonstration had access to two wooden hammers and a fixed anvil (but not yet to nuts), could observe PD's performance from an adjacent cage. As soon as the subject had observed at least one successful nut-cracking event by PD (coded when the subject had its head oriented towards the demonstrator and its eyes were open during a successful nut-cracking bout by PD), five macadamia nuts were placed into the subject's enclosure and the session started. The demonstrations by PD 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).

2.1.7 | Data collection and reliability

We live- and video-coded subjects' behavior directed towards the macadamia nuts (see Tables 3 and 4). Two second coders, who were not familiar with the aims and results of the study, watched all the videos and coded the same categories as the original coder to assess inter-rater reliability. One coded the ethogram of behaviors, and how often each individual practiced each method, whilst the other coded the number of successes in opening the nuts with each technique and the time spent by subjects with a nut in their mouth. A Cohen's kappa coefficient was calculated to assess the inter-rater reliability of both sets of data. All data are available in OSF (see: https://osf.io/43fbr/?view_only=fd9290ce18b542c7a43a102f600ab22d).

2.2 | Reliability testing results

A Cohen's kappa was run to assess the reliability of the coded data. We did not expect to find a very high interobserver reliability for some of the behaviors, as the data were collected in the orangutans' management areas (due to the testing facilities requirements), which were dark and often did not allow for a clear view from the filming platform (also because subjects moved dynamically and often blocked the camera angles with their bodies). Despite this, there was a moderate agreement ($k = 0.60$; Cohen, 1968) in the general coding of the ethogram, and a substantial agreement ($k = 0.80$) was found for the main variables of the study (i.e., the anvil on the floor and the hammer on floor nut-cracking techniques). Therefore, whilst we acknowledge that the reliability scores are lower than ideal for some additional behaviors coded in the ethogram, the main behavioral outcome (nut-cracking) was reliably coded. The overarching aim of this study was to examine whether nut-cracking with a tool would develop in naïve orangutans, and these observations received a substantial agreement across coders ($k = 0.80$).

2.3 | Results

Table 3 presents the behaviors coded, their descriptions, how many individuals performed each behavior, the first session in which the behaviors were observed, in which experimental conditions they were

TABLE 3 Ethogram of behaviors directed towards the nuts by subjects in the Leipzig zoo study alongside information on who performed the behavior and whether they were successful in opening the nuts, across all conditions

Behavior	Description	Number of subjects & name	First session in which the behavior was observed	Condition in which the behavior was observed	Successful for opening nuts	Percentage of success per individual
Bite	The subject inserts the nut in its mouth	5 (all subjects)	1st session baseline	All conditions	Yes	DK: 100% DJ: 100% PD: 11% PI: 100%
Hit with hand	The subject hits the nut with its hand against a hard surface	2 (PD and DK)	1st session baseline	All conditions	No	N/A
Step	The subject hits the nut with its foot against a hard surface	2 (PD and PI)	1st session 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 session baseline	Only baseline condition	Yes	PD: 75%
Hammer on floor	The subject lifts the hammer and hits the nut which is on the floor	1 (PD)	1st session locked anvil	Only locked anvil condition	Yes	PD: 100%

Abbreviations: DJ, Dunja; DK, Dokana; PD, Padana; PI, Pini.

TABLE 4 Count and percentage of each behavior directed towards the nuts per individual per condition and sessions in the Leipzig zoo study

Condition	Subject	Number of sessions undertaken	Number and % of sessions in which bite was observed (%)		Number and % of sessions in which hit with hand was observed		Number and % of sessions in which step was observed (%)		Number and % of sessions in which anvil on floor was observed (%)		Number and % of sessions in which hammer on floor was observed (%)	
Baseline	DK	5	5	100	3	60	0	0	0	0	0	0
	DJ	5	5	100	0	0	0	0	0	0	0	0
	PD	5	5	100	3	60	2	40	4	80	0	0
	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	4	100	2	50	0	0	0	0	4	100
Anvil locked Total		4	4	100	2	50	0	0	0	0	4	100
Social demonstration	DK	5	5	100	0	0	0	0	0	0	0	0
	DJ	5	5	100	2	40	0	0	0	0	0	0
	PI	5	5	100	0	0	0	0	0	0	0	0
Social demonstration Total		15	15	100	2	13	0	0	0	0	0	0

Abbreviations: DJ, Dunja; DK, Dokana; PD, Padana; PI, Pini.

observed, whether or not they allowed opening nuts at all, and the percentage of times each behavior resulted in successfully cracking open a nut for each subject (see the supplementary material for video clips of the most common behaviors observed). Table 4 presents the number and percentage of sessions in which each behavior was observed for each subject and condition. In the baseline condition, the juvenile individual, PD (F, 10 years old at the time of testing, mother-reared and born at the testing institution; see Table 1), successfully cracked nuts by using the large wooden block (originally conceived as an anvil) as a hammer–tool (see Table 3). When, in the locked-anvil condition, the large wooden block was fixed to the ground and therefore could no longer be used as a hammer, this same subject cracked nuts by using the small wooden blocks (originally conceived as hammers; see the supplementary videos), thus showing similar behavior to chimpanzee nut-cracking (see Figure 2). No other individual in the study performed the nut-cracking behavior with a tool. Instead, the other (all adult) subjects opened the nuts with their teeth (bite, see Tables 3 and 4). The bite behavior continued even after the demonstration condition, in which the adults had the opportunity to observe PD cracking nuts with a hammer. Indeed, the adults used primarily the bite method, followed by the only other method they used, which was unsuccessful: hit with hand (see more below).

2.3.1 | Baseline condition

The bite method was the first method attempted in the baseline by all individuals, and the one used in a higher number of sessions in this

FIGURE 2 Photograph of Padana (PD) cracking nuts with a hammer tool in the Leipzig Zoo study (photo taken after this study was conducted)

phase (bite was attempted in 20/20 [100%] of the sessions, followed by hit with hand [6/20, 30%], anvil on floor [4/20, 20%] and step [3/20, 15%]). All subjects attempted to open at least some nuts with their mouth, feet or hands in most sessions, whereas only PD used the anvil on floor method, in 4/5, 80% of her sessions (from the 2nd session of the baseline, after 25 min of testing). 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 session using the bite method (and were successful from the first session). PD also tried to open nuts first with the mouth in her first

TABLE 5 Demographic information on the subjects included in the Zürich zoo study

Name	Species	Testinggroup	Sex	Date of birth	Place of birth	Breeding
Rosa (RS)	*Pongo pygmaeus*	1	F	1958	Wild Caught	Parent
Adam (AD)	*Pongo pygmaeus*	1	M	1953	Wild Caught	Parent
Pongo (PG)	*Pongo abelii*	2	M	1961	Wild Caught	Parent
Lea (LA)	*Pongo abelii*	2	F	22/08/1967	Zürich, CH	Hand
Farida (FA)	*Pongo abelii*	3	F	3/5/1979	Zürich, CH	Hand/ parent
Hantu (HU)	*Pongo abelii*	2	M	3/5/1981	Zürich, CH	Parent
Radja (RJ)	*Pongo abelii*	3	F	19/1/1973	Zürich, CH	Parent
Timor (TR)	*Pongo abelii*	2	F	23/11/1973	Basel, CH	Parent

session but failed to open them. In the second and third sessions, 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 session, 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. In the last session, PD opened all five nuts using the anvil on floor method.

2.3.2 | Anvil-locked condition (note: Only PD was tested)

This condition (4 sessions) was carried out to examine whether PD would be able to change from using the large wooden block (which had been originally devised as an anvil) as a hammer to using the smaller wooden blocks (designed to resemble the hammers used by wild chimpanzees) as a hammer. From the first session (after 11 min 45 s), PD used the wooden hammers to perform the nut-cracking behavior, albeit ignoring the large block as an anvil. Instead, PD placed the nuts on the floor (which was sufficiently hard), and then used the wooden hammer to forcibly hit the nut until it opened. PD performed the hammer on floor technique in all sessions. Other than hammer on floor, only bite and hit with hand were recorded in this condition. PD cracked 19 of 20 nuts using the hammer on floor method and no nuts using the bite and the hit with hand methods.

2.3.3 | Demonstration condition

Despite being provided with live demonstrations from PD of the target nut-cracking behavior, none of the adult females subsequently used any of the provided tools to open nuts in this condition. All adults continued to crack the nuts using their teeth or tried (unsuccessfully) to open them using the hit with hand method (bite

100%, 15/15 of the sessions; hit with hand 13%, 2/15 of the sessions). All the nuts that were opened in the demonstration condition were opened with the bite behavior.

3 | ZÜRICH STUDY

3.1 | Methods

3.1.1 | Ethical approval

No specific ethical protocols were required when this study was carried out (in the 1980s). However, the experiments were non-invasive, and were designed alongside the zookeepers to ensure the well-being of the animals. The study strictly adhered to the legal requirements of Switzerland and complied with the American Society of Primatologists Principles or the Ethical Treatment of Nonhuman Primates. All subjects were housed in 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. The research was conducted in the subjects' familiar environment and any kind of stress to the animals was avoided.

3.1.2 | Subjects

The research was carried out at Zürich zoo, Switzerland, between 1983 and 1984 by MF. Eight orangutans were tested (6 *Pongo abelii* and two *P. pygmaeus*; M_{age} = 14; age range= 2–30; 5F; see the demographic information in Table 5). The keepers confirmed that none of the subjects had any previous experience with Coula nuts or Brazil nuts. However, the orangutans had occasionally been provided with walnuts and coconuts. Although the walnuts could be easily opened by biting, the coconuts were opened by hitting them against the hard floor or walls of the enclosure. Despite the potential utility of a tool

TABLE 6 Ethogram of behaviors directed towards the nuts observed in the Zürich study and whether they were successful in opening the nuts

Behavior	Description	Successful for opening nut?
Bite	The subject inserts the nut in its mouth and presses it between the teeth	Yes
Shake	The subject holds the nut in one or both hands and moves it back and forth quickly	No
Hit with hand/foot	The subject strikes the nut with either hands or feet, without using any tools	No
Press nut against teeth	After positioning the nut on the outer surface of the teeth, the subject presses it against the teeth either with the hands directly or by using a hard object such as the iron bars of the cage or wooden sticks	No
Scratch nut	The subject uses the nails to scratch the nut by damaging the surface of the shell	No
Rub nut	The subject moves the nut back and forth on a surface such as the ground or the walls	No
Beat against substrate	The subject holds the nut in one or both hands or feet and hits it against the floor or the walls or any other element in the enclosure	No
Press nut	The subject uses its weight or force on the nut without causing a sudden impact on the nut	No
Bounce nut	The subject throws or drops the nut onto the floor	No
Poke with branch	The subject pokes the shell of the nut with a branch	No
Wrapping nut	The subject wraps the nut with objects such as cardboard, wood wool or cotton bags	No
Hammering	The subject uses a hard object such as the wooden hammer to pound against the nut	Yes

to open the coconuts, the keepers had never observed the orangutans using hammer tools to open the coconuts and had never demonstrated the hammer technique to them—for these or any other nuts. The two *P. pygmaeus* were tested together, and the remaining subjects (all the *P. abelii*) were tested in two groups (see Table 5 for a list of individuals in each group). The groups did not have visual access to each other during the experiments.

3.1.3 | Procedure

A baseline condition was implemented, in which a wooden hammer (25 cm long, 8–10 cm in diameter) was provided alongside shelled Coula nuts, Brazil nuts, and coconuts. No demonstrations on how to use the hammers to crack the nuts were provided before or during testing—although note that as mentioned above for the Leipzig study, by design this condition allowed—and most likely led to—certain types of non-copying social learning, such as local and/or stimulus enhancement (see also Bandini et al., 2020). The two *P. pygmaeus* received one Coula nut for both individuals, five Brazil nuts each and one coconut each per session whilst the *P. abelii* received one Coula nut and one coconut each and five Brazil nuts each per session. Each subject received one wooden hammer. Initially, no anvils were provided, as there were already objects inside the enclosure that could be used as anvils, such as logs with indentations that were in the orangutans outside the enclosure. However, once it became clear that the *P. pygmaeus* preferred to manipulate the testing equipment in the indoor enclosure, an extra anvil location was created by

chiseling a hole into the concrete of the *P. pygmaeus'* indoor enclosure. The *P. abelii* were not provided with additional anvils (due to zoo management requirements, as their enclosure had just been renovated and they had more anvil-type objects that could be used). The nuts were scattered on the floor of the enclosure one hour before feeding. Following the testing protocols adopted at the time, once the testing session started, focal animals (defined as the ones that were currently holding a nut at the start of the session) were followed and observations reported at 10 s intervals. In the cases where more than one individual was manipulating a nut, all subjects were followed. However, this happened rarely, and a maximum of two individuals at a time manipulated a nut, making the combined focal follows manageable. Each session lasted one hour, and 15 sessions were carried out in total. Once a session ended, the keepers removed the hammers and the nuts from the enclosure. No video recording was made of the tests, as the video equipment was found to be too distracting to the subjects by the experimenter (MF). Observations were recorded by voice using a handheld tape recorder (unfortunately these tapes no longer exist).

4 | RESULTS

The orangutans were observed practicing several different techniques to open the nuts (see Table 6 for an ethogram of these behaviors). Three individuals, one in each group (PG, AD, and RJ), used the wooden hammer to crack open the Coula nuts in the first testing session. In the subsequent second to seventh testing sessions, seven out of the eight orangutans also demonstrated this hammering action

TABLE 7 Total number of nut manipulation and hammering bouts in the Zürich zoo study

Subject	Number of interactions with nuts	Number of hammering bouts	Number of hammering bouts before first success or at all if no success	Number of successes with hammering	Total number of successes	Proportion of hammering bouts in %
RS	41	390	3	30	37	57.5
AD	9	18	18	0	0	2.6
PG	24	1	1	0	11	0.1
LA	9	3	3	0	8	0.4
RJ	17	72	22	2	8	10.6
TR	16	192	13	4	7	28.3
FA	11	2	2	0	0	0.3
HU	8	0	0	0	0	0.0
All subjects	120	678	62	36	74	100

Abbreviations: AD, Adam; FA, Farida; HU, Hantu; LA, Lea; PG, Pongo; RJ, Radja; RS, Rosa; TR, Timor.

(see Table 7 for the number of interactions with nuts with the hammering method observed across subjects). Therefore, at least three individuals spontaneously acquired nut-cracking with a hammer without having any demonstrator available. The only individual who did not demonstrate nut-cracking with a hammer was the youngest subject (HU), who rolled or threw away the nuts at the start of each session and did not seem motivated to manipulate the nuts or the hammer. Although seven individuals attempted to crack nuts with the provided hammer, only three individuals (RS, RJ, and TR) were successful in opening the nuts with this method, potentially because only two individuals (RS and TR) used an anvil to stabilize the nut. Most individuals only used the hammer to crack the Coula nuts, as this was the only type of nut that required the hammer (both the Brazil nuts and the coconuts could be opened by biting or by hitting them against the floor or walls). However, two individuals (PG and RJ) also used the hammer on the coconut, of which only RJ was successful. PG was the only individual who was able to open the Coula nuts with his teeth from the first session and continued with this method for the duration of the study.

5 | DISCUSSION

Four naïve, unencultured, untrained captive orangutans spontaneously cracked nuts using wooden hammers as a tool. This finding demonstrates that orangutans possess the individual ability to use a tool to crack nuts without copying opportunities. Although other (non-copying) variants of social learning such as local and/or stimulus enhancement are part of the experimental setup used in this study, these mechanisms influence the likelihood of the emergence of target behavioral forms, but cannot transmit these forms themselves.

As orangutans do not show nut-cracking in the wild, it is highly unlikely that any of the orangutans in the Leipzig and Zürich

studies had previously observed this behavior from wild, or wild-related, conspecifics. Furthermore, the subjects' training and enrichment and their relevant experiences in previous experiments were discussed in detail at both institutions with the keepers, who assured us that the subjects had never been trained or demonstrated how to crack nuts using tools. It is possible that the subjects had performed hammering actions without tools before this study, as this is a natural behavior within the orangutans' repertoire that may emerge in various contexts (e.g., when playing). However, the keepers confirmed that none of the subjects had been observed practicing the hammering action with a tool before testing. Although it is impossible to account for every minute of a subject's life, keepers at both zoological institutions are deeply involved in the research studies and enrichment programs implemented with their animals, which makes them the most reliable source of information about the animals' knowledge of behavioral forms. Therefore, based on all the information available from the wild and the testing facilities, we are confident in assuming that all the orangutans tested here were naïve to nut-cracking. This is not to say that the orangutans did not benefit from any previous experiences. Indeed, all the subjects had 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, which can be opened relatively easily by using the teeth—even by juvenile orangutans—and with coconuts, which can be opened by hitting them against a hard surface. In contrast, the Coula nuts provided in the Zürich study and the macadamia nuts provided in the Leipzig study require 2.8s and 2.2 kn to be opened, respectively (Visalberghi et al., 2008), which makes these alternative methods unviable. This, and the lack of suitable tool materials before our studies, may explain, at least in part, why none of the subjects in these studies had ever been observed using tools to crack nuts before.

5.1 | Candidate mechanisms behind nut-cracking in orangutans

The findings of both the Leipzig and the Zürich Zoo studies demonstrate that the *form* of nut-cracking can be acquired individually by orangutans. The behavior emerged in several culturally unconnected, unencultured, untrained, nut-cracking-naïve subjects after they were provided with the appropriate materials. These conditions, alongside a basic knowledge of the problem at hand (i.e., that shells often encase kernels, and that force can be applied to break them open) as well as motivation to perform the behavior (mainly to obtain and eat the kernel, although the exploration of new materials may have been motivating as well), were sufficient to elicit the development of nut-cracking in the orangutans.

We are not suggesting that nut-cracking is a hard-wired behavior, or instinct, in orangutans. Although the ZLS hypothesis can also (albeit rarely) include such cases, 'latent solutions' is an umbrella term that subsumes behaviors spanning from highly genetically predisposed behaviors to highly learning-dependent behaviors. Copying-dependent behaviors and/or artifacts are, however, excluded (Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020). In the case of orangutan nut-cracking, as in most other ape behaviors, there are several reasons to believe that more than instinct is at play. First, in contrast with the several orangutans that performed nut-cracking in our studies, long-term field studies with wild orangutans have not (yet) observed this behavior (e.g., Krützen et al., 2011). This may be due to a lack of need or motivation to crack open nuts, given that other foods and means to obtain them are available. Also, the arboreal habits of wild orangutans make percussive tool use harder, both to come up with and to carry out, compared to the primary terrestriality of primates such as chimpanzees (e.g., Fox et al., 1999). This suggests that nut-cracking is not (and is unlikely to have been) a critical behavior for the species' survival that may have been genetically fixed throughout evolution (although some of the general abilities required for nut-cracking, such as the manipulative tendency of the orangutans, their hand affordance and some of their cognitive capacities may be, at least in part, genetically determined). Second, there was variability in the performance of our study subjects. Despite experiencing the same conditions, not all the orangutans acquired the behavior within the time frame given, which seems indicative of different learning skills and opportunities (although individual differences in motivation may have played a role as well). Third, the orangutans in our studies demonstrated cognitive flexibility in their approach to the problem at hand. For example, PD attempted several different methods to access the kernels before performing the percussive nut-cracking and, even after discovering this behavior, she did not use it in every session. Perhaps most importantly, PD proved able to crack open nuts with a variety of tool-use techniques.

If both strong genetic predispositions and/or reliance on copying forms of social learning are excluded as explanations for the acquisition of nut-cracking by orangutans, a plausible alternative candidate mechanism is individual learning catalyzed by non-copying variants of social learning. All apes demonstrate an impressive ability for this type of learning (see Mesoudi & Whiten, 2008; Tomasello & Call, 1997 for an overview), alongside cognitive skills that allow for behavioral flexibility. One example of this flexibility is PD's performance in this study. In the baseline, PD used the provided large wooden block (originally devised as an anvil) to crack open nuts, demonstrating a tool-use behavior similar to that of wild chimpanzee nut-cracking in that it was percussive, but different in terms of the tool used (including size, weight, and shape). PD might have initially preferred to use the large block instead of the small blocks (which resembled the hammers that are typically used by wild chimpanzees) because, although the former required more effort when being lifted due to its large weight (approx. 50 vs. 2.4 kg), it did not require the application of hitting force and speed to crack the nut. 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 might have used her pre-existing knowledge of the task and properties of the materials to flexibly switch her approach and use the small wooden blocks as hammers, thus demonstrating a behavioral form of nut-cracking like that observed in some wild chimpanzee populations (Biro et al., 2003; Boesch et al., 1994; Luncz & Boesch, 2014; Luncz et al., 2012).

5.2 | Potential explanations for the lack of reinnovation of the target behavior by the remaining orangutans

None of the adult orangutans in the Leipzig zoo study used tools to crack macadamia nuts, and one (juvenile) individual in the Zürich Zoo never attempted to use a hammer on Coula nuts either. In the case of the Leipzig study, the adults were immediately and consistently successful in cracking open the nuts with their teeth and continued doing so even after they were exposed to five sessions of live demonstrations of nut-cracking with a tool by PD. One explanation for the absence of nut-cracking in these subjects could precisely be 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. Similarly, PG in the Zürich study was successful in opening the Coula nuts with the bite method and he persisted with this strategy (he only used the hammer on coconuts). In contrast, in the Leipzig study, the sub-adult PD attempted to bite nuts in the first session 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 in the Leipzig study motivated to find alternative methods to biting 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 acquired the tool-use behavior. This hypothesis is supported by the findings of the Zürich study in which the harder Coula nuts were provided and adult

orangutans were reported to acquire the behavior. Additionally, if a clearer cost had been associated with the bite methodology (e.g., a significantly reduced efficiency in opening the nuts, or tooth pain), it is possible that the adults would have been more motivated to explore alternative tool-based solutions (although note that one should not run a study with nuts that may cause pain for the subjects). Therefore, as the adults could consistently and (seemingly) painlessly open the nuts with their teeth, there was no obvious need to use tools to achieve the same end goal.

An alternative to the jaw/bite force explanation would be that age differences in inhibitory control (defined as the ability to stop a planned or ongoing thought or action; Carlson & Wang, 2007; see also Albiach-Serrano et al., 2007; Amici et al., 2008; Parrish et al., 2014) and functional fixedness (defined as "*the disinclination to use familiar objects or methods in novel ways*" Brosnan & Hopper, 2014, p. 2) encouraged PD to explore new solutions to the problem at hand while preventing the adults in the Leipzig study from finding alternative solutions. The fact that the only individual who did not attempt to use a hammer in the Zürich study (HU) was the youngest member of the group does not support this explanation, although it may have been that this subject simply lacked the motivation to manipulate or consume the nuts and/or lacked the strength to manipulate the hammer. Indeed, HU immediately rolled the nuts away when they were in his possession and did not attempt to retrieve them when other members of the group took them.

Finally, it could be that the adults in the Leipzig study did superficially attend to, but did not copy, PD's actions because she was a juvenile and therefore may not have been regarded as a salient or valid model (e.g., see Rendell et al., 2011), or that they were not exposed to PD's demonstrations during a potential critical learning period, which could have occurred earlier in their lifetimes. Although this is a possibility, the Zürich study shows that even with adult models, and whilst potentially being in a critical sensitive learning period, the subjects did not develop the nut-cracking behavior. Therefore, it does not seem that the age of the model and/or the observer played a decisive role in whether the behavior was copied or not. These findings, alongside the individual reinnovation of nut-cracking in several orangutans, render copying an unlikely driver for orangutan nut-cracking. Note also that, while we did not identify any sensitive learning period for this behavior, there is evidence that such periods are of importance for the development of chimpanzee nut-cracking (see introduction). A large-scale study of the individual innovative capacities of chimpanzees before, during, and after this sensitive learning period is still missing (Neadle et al., 2020).

6 | CONCLUSION

In this paper, we report percussive nut-cracking in orangutans for the first time. Collectively, our results suggest that individual learning is the main driver for the acquisition of nut-cracking in orangutans, alongside several factors including non-copying social learning, general genetic predispositions, and cognitive capacities that allow for finding solutions to problems in a flexible way. This study did not find evidence, however, for nut-cracking demonstrations increasing the frequency of the behavior in observer orangutans. Nevertheless, it is likely that, as with other ape behaviors, non-copying variants of social learning modulate and even stabilize the frequency of tool behaviors within orangutan populations—at least when these mechanisms apply across generations (see the discussion in Moore, 2013; Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020). Therefore, in future, the behavioral form of nut-cracking could, in principle, become another example of a "socially mediated reinnovation" (SMR; Bandini & Tennie, 2017, 2019) in orangutans. Indeed, it is possible that orangutans, like capuchins (Visalberghi, 1987), may one day be found to practice nut-cracking in the wild.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

AUTHOR CONTRIBUTIONS

Elisa Bandini: data curation (lead); formal analysis (lead); project administration (lead); writing original draft (lead); writing review & editing (lead). **Johannes Grossmann**: data curation (supporting); investigation (supporting); methodology (supporting). **Martina Funk**: investigation (lead). **Claudio Tennie**: conceptualization (lead); writing original draft (supporting); writing review & editing (equal).

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DATA AVAILABILITY STATEMENT

All data are available in OSF (please see: https://osf.io/43fbr/?view_only=fd9290ce18b542c7a43a102f600ab22d).

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