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Refocusing the Debate: Our Original Critiques of Koops et al. (2022) Still Stand

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Response to: Koops, K., Biro, D., Matsuzawa, T., McGrew, W., & Carvalho, S. (2023). Appropriate knowledge of wild chimpanzee behavior ('know-what') and field experimental protocols ('know-how') are essential prerequisites for testing the origins and spread of technological behavior. Response to "Unmotivated subjects cannot provide interpretable data and tasks with sensitive learning periods require appropriately aged subjects" by C. Tennie & J. Call. *Animal Behavior and Cognition*. *11*(2), 163-168.

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Abstract – Koops et al. (2022, 2023) claim that an experimental field study (Koops et al., 2022) provided valid evidence against a latent solution explanation for chimpanzee (*Pan troglodytes verus*) nut cracking know-how in the wild. In our previous response (Tennie & Call, 2023) we identified two major problems with this interpretation. First, Koops et al. (2022) study subjects were clearly unmotivated to access the intended food reward (nut kernels) – rendering the secondary question of whether they would use tools to crack the provided nuts to access these kernels a moot point. Second, only one of the subjects who came into contact with the experimental setup was within the chimpanzee most sensitive learning bracket to develop nut cracking (identified in previous field studies; Matsuzawa, 1994, 1996; Biro et al., 2003). We concluded that Koops et al.'s (2022) study failed to provide valid evidence against the zone of latent solution hypothesis as applied to chimpanzee nut cracking in the wild. In their reply, Koops et al. (2023) argued against both our critiques. Here, we refocus the debate, reiterate our arguments and provide further evidence that invalidate Koops et al. (2022) conclusion that "nut cracking falls outside" the zone of latent solutions of wild chimpanzees. We end with a call for more data.

Keywords – Nut cracking, Copying, Innovation, Latent Solution, Social learning, Culture, Experimental methods, Chimpanzee, Ape

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In our original commentary (Tennie & Call, 2023), we applauded Koops' et al. (2022) efforts to conduct latent solution tests in the wild. Recognizing that wild and captive populations could principally differ in their behavior and cognition, both field and captive experiments are necessary to make progress in addressing pressing questions such as the nature of chimpanzee cultures. However, we also pointed out two key limitations in Koops et al.'s (2022) study that invalidate their conclusion that "nut cracking falls outside" the zone of latent solutions of chimpanzees. Despite Koops' et al. (2023) response, our constructive criticisms still stand, and we have now been forced into the uncomfortable position of utilizing some of the authors' (some in the original paper and others that joined in the reply) arguments that they themselves had published in the past. Our concern is not just about how to properly test the Zone of Latent Solutions (ZLS) hypothesis in specific cases, but more generally, about the use of rigorous experimental methods to test hypotheses.

The first limitation was that Koops et al.'s (2022) sample did not include large enough numbers of appropriately aged subjects, i.e., those *inside* the age class that has been shown empirically in previous field studies to be most likely to initiate the development of nut cracking. In fact, Matsuzawa (1994, 1996) argued that there is a *critical period* in which nut cracking must be acquired, and that outside this period chimpanzees' ability to acquire nut cracking is compromised. If at least some chimpanzees in their sensitive age range were to spontaneously invent how to crack nuts (know-how) without having observed others do it, this would support a ZLS interpretation. In contrast, if a sufficient number of such youngsters were tested (Tennie & Call, 2023), and *none* of them did it, it would rule out the ZLS hypothesis as a valid explanation for wild chimpanzee nut cracking. As we noted in our original commentary, the Koops et al. (2022) study seems to have been underpowered because it only included *one* such youngster.

The importance of the critical period seems to have been somewhat softened over the years, with Biro et al. (2003) arguing for a "sensitive period", a term less restrictive[1] than the earlier term of "critical period" (see APA dictionary of Psychology). Some softening of the original position seems warranted given that subsequent studies have shown that, on rare occasions, older chimpanzees have acquired nut cracking (Matsuzawa, 2011). However, this does not alter the fact that appropriately aged *youngsters* still offer the most stringent test of the ZLS hypothesis, not least also because they display more varied and frequent object exploration than adults (e.g., Biro et al., 2003).

Even more importantly, the second limitation was about motivation, more specifically, we argued that the tested population of chimpanzees did not regard the newly introduced nuts (*Coula edulis*) as edible. We based this on two findings. First, Koops et al. (2022) reported that even when chimpanzees encountered cracked nuts – with their kernels exposed – they did not eat them. If subjects are not motivated to consume the food provided in a task, one cannot expect them to work in any way to access it. Simply put, tests of unmotivated subjects are invalid. Interestingly, in their classical study of nut cracking with re-introduced chimpanzees in a Liberian island, Hannah and McGrew (1987) precisely made this point when they stated that "motivation thus seems to be important for the development of tool-use" (p. 43). Koops et al. (2022, 2023) do not adhere to this basic tenet of experimental design.

Second, Biro et al. (2003) introduced Coula nuts to the Mt. Nimba chimpanzee community that regularly cracked and consumed oil-palm nuts (but not Coula nuts). Note that these data, collected in January 1993, were initially reported by Matsuzawa (1994). Except for an older female ("Yo") who cracked open Coula immediately after their introduction[2], during the initial study period none of the chimpanzees in that community incorporated Coula nuts to their diet even though those chimpanzees already knew how to crack open oil-palm nuts. Their reluctance to incorporate Coula was therefore probably *not* a question of failing to learn *how to extract kernels*, which is the focus of the ZLS hypothesis here, but a question of a lack of interest in the newly introduced food[3]. This idea is further reinforced by the behavior of two youngsters, aged 6 and 6 and a half years, who "cracked the nuts and sniffed the kernel and chewed and spat it out" (Matsuzawa, 1994, p. 364). Thus, most Mt. Nimba chimpanzees either did not consider Coula nuts as edible (and seeing "Yo" eating them did not help either, at least initially), or they considered them as potentially edible, but their conservatism might have curtailed their dietary choices. In any case, this initial failure to incorporate a new nut species to a chimpanzee population's diet is consistent with the lack of nut-eating reported by Koops et al. (2022).

Two other things are worth noting. First, youngsters in Biro et al. (2003) showed more general interest in Coula than adults (except for the older female mentioned earlier). This further reinforces the idea that youngsters are the most valid test subjects to rule out the ZLS hypothesis (see also Kummer & Goodall, 1985). Second, after *several years* of exposure to Coula nuts the tested community of chimpanzees *did*

[1] Note however that Biro et al. (2003) used both the terms "critical period" and "sensitive period", interchangeably. Also note that Biro et al. (2003) still wrote "We have identified a sensitive period in acquisition between the ages of 3 and 5 years [...] *If not learnt by the end of this period, the skill will not be acquired*" (p. 216; emphasis added).

[2] The authors suspected this subject had exploited Coula nuts in the past, in the previous population she lived in.

[3] This statement should be entirely uncontroversial. Indeed, Biro et al. 2003 clearly agreed with this interpretation. They wrote: "our experiments dealt *not with the introduction of an entirely novel behaviour* into the community, but the adaptation of an existing tool-using skill *to novel target items*" (p. 222; emphasis added)

incorporate Coula nuts to their diet (and even came to prefer Coula). This is an important piece of data because it highlights that Koops et al.'s (2022) study may not have been long enough to motivate the chimpanzees to eat (and then potentially spontaneously use tools to crack open) the nuts.

When one highlights the limitations of a study, we think that it is a good practice, in the spirit of constructive criticism, to offer potential solutions to those limitations. This is what we tried to do when we proposed using nuts partially filled with honey as a motivating food item (Tennie & Call, 2023). Our idea was received with overt hostility and even dubbed as ethically questionable by Koops et al. (2023). We suggested honey because it is a naturally occurring substance that is often consumed by chimpanzees across the African continent and – importantly – that has already been used (successfully) by chimpanzee fieldworkers to carry out experiments in the wild (Gruber et al., 2009). In any case, this minor point[4] –- should not deflect from the more serious limitations of an inadequate sample and the lack of motivational prerequisites to truly test the ZLS hypothesis for wild chimpanzee nut cracking know-how.

One last point before closing. Contrary to what some investigators maintain, the ZLS is testable and falsifiable. One of us has been testing it for years in captive settings (reviews in Tennie et al. 2020a,b) – supplemented most recently, in two different and complementary ways, also with tests using wild ape data patterns (Acerbi et al., 2022, Motes-Rodrigo & Tennie, 2021). Encouraging is also the implication in the original Koops et al. (2022) study – but also in the introduction of another recent study by ape fieldworkers (Boesch et al., 2020) – that the ZLS hypothesis already parsimoniously describes *captive* ape data patterns. The prospect of adding field experiments to test the ZLS hypothesis in the specific case of wild chimpanzee nut cracking remains appealing. Here, as Koops et al. (2023) make very clear, fieldworkers rather literally hold the keys to experimental work with wild apes. The question is: will they dare to open the gates all the way? Rivers of ink flowing from opposite sides into the public arena are far less likely than solid data – from valid tests – to settle such matters. A valid test for wild chimpanzee nut cracking requires sufficient motivation but also sufficient numbers – at least 16 (Bandini & Tennie, 2018) – of appropriate subjects (i.e., those *inside* the empirically reported sensitive age range). Even with all these pre requisites in place, each of these subjects needs to be tested for enough time (at least one year; see supplementary material).

Summary

Koops et al.'s (2023) target – to refute the two major criticisms we raised in an earlier reply – fail under scrutiny. The original study by Koops et al. (2022) therefore continues to suffer from not one, but two critical problems (Tennie & Call, 2023): a lack of appropriately aged subjects and a lack of necessary test motivation. Contra to the claims of Koops et al. (2022, 2023), the study they discuss found evidence *neither for nor against* the view that nut cracking know-how can be independently re-innovated by wild chimpanzees. This question therefore remains open – and requires additional tests (see also Bandini et al. in prep.).

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[4] As these issues are likely only of interest to highly specialized readers, we decided that we keep our current piece (re-)focused on the main issues at hand (hence also our title). A note for these specialized readers: there is a detailed reply to these other points contained in the supplementary material accompanying this piece.

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Supplementary Material to "Refocusing the debate: our original critiques of Koops et al. (2022) still stand" by Tennie and Call.

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Abstract – Both in our previous response (Tennie & Call 2023) and in the current main manuscript (above) we identified two major problems with the interpretation of Koops et al. (2022, 2023). Concentrating on the main data and arguments, we concluded that the original study (Koops et al. 2022) failed to provide valid evidence against the latent solution approach for nutcracking know-how in chimpanzees. However, Koops et al. (2023) also claim to contain data and arguments in addition to those we have responded to. This supplementary material examines these additional points. We conclude that none have the power to change our original conclusion. This reinforces the view that Koops et al. (2022) produced invalid claims regarding chimpanzee nutcracking innovatibility.

"Since no testing was performed without prior observation of a model, it remains a possibility that the emergence of nut cracking would have occurred spontaneously"
Hayashi et al. (2004)

Latent solutions consist of behavioral and/or artefact forms for which the underlying know-*how* has a realistic chance of innovation by suitable subjects (unenculturated, untrained – and naive) in suitable conditions – such as with access to raw materials, sufficient motivation etc. (e.g. Tennie et al. 2020a). In response to Tennie and Call (2023) Koops et al. (2023) defend an earlier claim (Koops et al. 2022) that denies the possibility of chimpanzee nutcracking know-how being an instance of a latent solution.

In our main manuscript (see above) we refine and reiterate our two main critiques of the original study (Koops et al. 2022) – which both still stand in the light of Koops et al. (2023). In doing so, we concentrated on the main data and main arguments raised by Koops et al. (2022, 2023). This however leaves some claims by Koops et al. (2023) unaddressed. First are those claims and arguments by Koops et al. (2023) that are not relevant to the main issue at hand – namely as to whether chimpanzee nutcracking know-how is or is not a latent solution[5]. This supplementary text will not engage with those arguments. Second are claims and arguments by Koops et al. (2023) that could potentially be relevant to the issue at hand. This supplementary will engage with the additional claims and arguments from this second category only.

"We have identified a sensitive period in acquisition between the ages of 3 and 5 years [...] If not learnt by the end of this period, the skill will not be acquired"
Biro et al. (2003)

In 2003, Biro and colleagues published an analysis of an impressive 16-year dataset on the development of nutcracking in wild chimpanzees. This analysis "highlighted the importance of a *critical period for learning* (3–5 years of age)" (Biro et al. 2003; italics added). This is the *field-based*, empirically observed "sensitive age" range for learning how to crack nuts in chimpanzees. In our previous reply (Tennie & Call 2023) and in our main text (above), we simply applied this sensitive age-range to Koops et al.s' (2022) own field data.

Koops et al. (2023) do not accept this field-based conclusion[6]. First, they conflate the difference between the originally described sensitive age period – which related specifically to learning to crack nuts

[5] For example, Koops et al.'s (2023) negative sentiments towards theory/terminology development, their call for an apparently unidirectional learning pathway from field research to captive work or their (implied) claim of unity-of-thought among all ape field researchers.

[6] This is surprising especially considering that Biro (and other original authors of Biro et al. 2003) joined the reply of Koops et al. (2023).

at all – versus the length of time it took those chimpanzees who already learned this to then hone their skill (an additional 5 to 11 years; Biro et al. 2003). Consequently, Koops et al. (2022, 2023) aim to *include* this very different, secondary age range into the sensitive age range. Such confounding is clearly unwarranted, given the data and conclusion of Biro et al. (2003) for two separate age ranges. Conflating these age ranges would therefore artificially increase the number of potentially valid test subjects beyond warranted numbers. Instead, what matters for the inclusion of potential test subjects is the sensitive age range only – i.e. the age at which the skill is learned *at all*. This is indeed how we calculated numbers of potential test subjects of Koops et al. (2022) in our original reanalysis – finding these numbers inadequately low (Tennie & Call, 2023).

Koops et al. (2023) additionally question the usability of Biro et al.'s (2003) – field-based – sensitive age range for claims regarding what might be called a chimpanzee nutcracking innovation age range. Koops et al. (2023) hypothesize: "the learning window can be seen as a result of channels of social transmission closing, rather than as a consequence of a lack of ability to learn". Note that the learning window is defined by Biro et al. (2003) by a (near) absence of initiation of nutcracking know-how development outside of it. As such, the existence of the learning window in chimpanzee nutcracking is consistent both with a ZLS *and* a non-ZLS approach. Given this equifinality, this critique put forward by Koops et al. (2023) is unsuitable to decide between these two possibilities[7].

The remainders of Koops et al. (2023) critiques of the sensitive age range fall into two categories: captive and field work. Regarding captive work, Koops et al. (2023) first point to positive outcomes of social learning studies in captive chimpanzees generally. However, nobody disputes that chimpanzees – like all apes (and many other animals) – learn socially in the wild and in captivity; the relevant dispute instead concerns whether they are spontaneously able to copy supraindividual know-how[8], i.e. *know-how that is outside their ZLS*[9].

Koops et al. (2023) then claim more specifically that social learning studies with captive chimpanzees "have shown that non-nutcrackers may learn to crack nuts [...] even if they are well beyond the so-called sensitive learning period". First, note that Koops et al. (2022, 2023) here endorse captive studies (and direct comparisons of field and captive data), despite their earlier claims that consider field data superior[10]. Second, their appraisal of captive *social learning* nutcracking studies *that support their hypothesi*s is markedly different to their treatment of studies that instead favour a ZLS account. The latter are either not mentioned at all (Koops et al. 2023) or alternative interpretations of such findings are highlighted (Koops et al. 2022). Regarding the latter, Koops et al. (2022) argue that "zoo-housed orangutans were reported to have individually innovated nut cracking [...] *which may have been (in part) due to their experiences in captivity* [...] *and past interactions with humans*" [italics added]. Note that, where captive studies support their preferred hypothesis any potential effects of past "experiences" or "interactions" with humans are no longer mentioned as viable alternative explanations. This is particularly problematic as all of the captive chimpanzee nutcracking social learning studies cited by Koops et al. (2023) as evidence in favour for their view contained subjects with *extensive "human-interaction" backgrounds*: The original innovator in Hannah & McGrew (1987) has most likely been a human pet. In Hayashi et al. (cited by some as 2004), *all* tested chimpanzees were enculturated. Finally, the most impressive subject in Hirata et al. (2009; "Mizuki") had been hand-reared by humans.

If selectively ignoring rearing backgrounds was permissible, then the evidence from captive studies would be that nut-cracking *is* a latent solution for chimpanzees (e.g., see positive baseline performances in

[7] The existence of this learning window constrains *both* the ZLS and the non-ZLS account. This is why we have called for a focus on subjects whose ages fall inside this window when testing for the innovatibility of nutcracking know-how in chimpanzees (Tennie & Call 2023).

[8] Note that Koops et al. (2023) asked us for more details on this choice of terminology; these can be found in Tennie (2023).

[9] Note for example that the chimpanzee social learning study first cited by Koops et al. (i.e., Whiten et al. 2005) *failed* to show this type of social learning, simply because both techniques to access rewards implemented in this study can clearly be individually innovated by chimpanzees – these techniques therefore reside instead *in* their ZLS (Tennie et al. 2020b).

[10] In 2022, Koops et al. had additionally claimed that captive studies lack general ecological validity, e.g. because they supposedly test "simplified versions" of the target behavior, and because captive chimpanzees "may be more predisposed towards exploration" in general.

Marshall-Pescini and Whiten 2008; Hirata et al., 2009). In this vein, even Whiten (2015) claims that nutcracking know-how *has* been reinnovated by a captive chimpanzee[11]. However, because such a one-sided approach is clearly not permissible, we concluded instead in Tennie & Call (2023) that whether nut-cracking is or is not a latent solution in chimpanzees remains open.

So far, this question is more clearly answered in different primates. For example, the orangutan study dismissed by Koops et al., (2022) actually *controlled* for previous "experiences" *and* "interactions". The subjects tested were unenculturated. Moreover, their keepers reported that the innovators were naive with regard to nutcracking know-how. When – like here – these factors have been controlled for, they simply become unparsimonious as alternative explanations – contra Koops et al. (2022) – especially when they would have to explain how nutcracking know-how emerged not just in one, but across culturally independent populations[12].

Koops et al. (2023) continue with their critique of Biro et al. (2003) sensitive learning age in wild chimpanzees by seemingly claiming that merely *visiting or exploring – or even looking at* – nuts should count as evidence against a sensitive age period. This is a surprising statement and clearly in contrast to the sensitive age range described by Biro et al. (2003), which was instead concretely about learning *how to crack nuts*. Second, Koops et al. (2023) point to cases in the wild in which adult chimpanzees supposedly learned "a new nut-cracking technique". However, the novelty in the cited case (Luncz et al., 2012) was not about technique (know-how), but about hammer raw material choice (a type of know-*what*[13]). Third, Koops et al. 2023 also argue that *other* types of chimpanzee tool use do not seem to have a sensitive age range. Yet, what matters is whether chimpanzee *nutcracking* has a sensitive learning age window (it has; Biro et al., 2003, see also above). Finally, Koops et al. (2023) describe a scenario in which a chimpanzee nutcracking sensitive period could be maladaptive. Sensitive age ranges can be maladaptive, yes – but that possibility does not negate their existence, as clearly evidenced by Biro et al. (2003).

Here and in the main text we had to defend the chimpanzee sensitive age range interpretation against some of the original authors who introduced it. Note that, to the best of our knowledge, these authors have never published a correction of their original sensitive age range account. Indeed, we see no reason to deviate from their original claim of this sensitive age range – also not after reading Koops et al. (2023). Our original critique – that only one single subject was even potentially valid, due to the existence of a sensitive age range in this task in chimpanzees – therefore still stands (compare Tennie & Call 2023).

"Motivation thus seems to be important for the development of tool-use."
Hannah & McGrew (1987)

In any experiment that uses food as a reward, motivation for that food becomes a necessary pre-requisite for valid testing. If the tested population does not even try to eat any of the intended rewards, different food must be tried altogether *or* the original food must be made palatable to the local population (perhaps by (temporarily) adding other food known to be palatable). This logic should be entirely uncontroversial, *regardless* of the specific terminology used to describe this necessary test pre-requirement (i.e. contra Koops et al. 2023).

As we argued in our previous reply (Tennie & Call 2023) and as we argue again in our main text (above), the nuts (their kernels, to be more precise) intended to be a reward in Koops et al. (2022) were not treated as such by the population of chimpanzees. Subjects did not even eat these kernels when they were no longer encased in the nut-shells (Koops et al. 2022, Experiment 3). This is a problem that is far from

[11] Whiten (2015) called this a "true innovation" (albeit the actions of the innovator were ultimately unsuccessful in cracking open the nuts).
[12] It is also noteworthy that these orangutans – orangutans who innovated nutcracking know-how – were clearly motivated to eat the nuts provided.
[13] ...whose social learning in chimpanzees is not in dispute, compare Henrich and Tennie (2018).

new in animal cognition research at large, and it is also not a problem new to ape nutcracking research[14]. All this can only mean that Koops et al. (2022) was a failed study with regards to its main aim.

Koops et al. (2023) do not accept this logic, yet fail to provide valid reasons for their refusal to accept it. Instead, they list several facts that are irrelevant to the issue at hand: They remind the readers that one chimpanzee in Koops et al. (2022) tasted one nut's *outer fruit layer*. This is irrelevant, not least as the fruit layer does not afford cracking. They point out that other chimpanzee populations do eat nut kernels. This is not in dispute, but it is irrelevant to the question of whether their intended subjects ate nut kernels (which they did not). They state that nuts would be good foodstuff for these chimpanzees, if they had ingested them. This may be, but they did not ingest them, and this failure to ingest matters here. They highlight that the chimpanzees they intended to test remained unmotivated in nut kernels independent of local fruit availability. This is interesting for other reasons, but the fact remained that their intended tests subjects failed at test motivation. Finally, they claim that the ZLS approach had not earlier specified that subjects must be motivated. Even if this were true (which it is not, see footnote 14), this would not matter. Test motivation would remain key.

> "*First*, one has to discover that nuts are edible [i.e. know-*what*(-to-eat)], [...] *Second*, one has to learn a highly complex tool use technique [i.e. know-*how*(-to-crack-nuts)]."
> (Koops et al. 2023; text and italics added)

It is encouraging to see that Koops et al. (2022, 2023) generally agree with the theoretical distinction between types of information that may be relevant in activities such as chimpanzee nutcracking (e.g., know-what and know-how). There is clearly at least partial agreement between our positions in that, without target know-*what* in place, one cannot expect target know-*how* (see section quote above).

However, Koops et al. (2023) claim that a "*combined* difficulty" of having to learn the know-what *and* the know-how in chimpanzee nutcracking "may well be what places nut cracking *outside the chimpanzee ZLS*" (italics added). This is an incorrect representation of the ZLS account. Latent solutions are defined *specifically* by *whether their know-how* is beyond the realistic power of an individual of a target species to innovate. As we laid out in detail elsewhere, a local lack of indirect pathways (e.g. here, lacking know-*what*-to-eat) *can* prevent the know-how from being expressed – but this does not mean that the know-*how* could not be expressed in the absence of know-how models (Tennie et al. 2020a, but see also Tennie & Call 2023), provided sufficient motivation etc.

Relatedly, Koops et al. (2023) claim that these two types of knowledge (know-what and know-how) cannot ever be separated. As shown below, this is not true. Yet, even if one were to assume this claim to be true, note that this would then go against Koops et al.s´ own position, as it would mean that the relative likelihood of the two competing positions (nutcracking being a latent solution *or* supraindividual know-how) simply cannot be tested in the way that Koops et al. (2022) claimed that they did. It is therefore essential for progress – for testability – that these types of knowledge *can* principally be separated.

Is a separation of know-what and know-how (or other types of knowledge) "practically possible" or not? Koops et al. (2023) claim that it is not. They claim that that this cannot happen: "for an embedded resource in an ecologically-valid setting"[15]. One therefore needs to ask if the separation can happen after all (ideally with two prerequisites (embedded resource; eco-valid setting) simultaneously fulfilled).

Note that Koops et al. (2022) used an "embedded resource" (i.e. here: nuts in their shells) *and* that they themselves state that the study of Koops et al. (2022) has been "ecologically valid". Recall also that Koops et al., (2022) did separate the different types of knowledge; they did so by providing the chimpanzees with kernels already removed from their shells – in the absence of nutcracking demonstrations. This clearly provided an opportunity for learning know-what-to-eat in the absence of information on the know-how of

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[14] Tennie & Hedwig (2009) describe valid requirements for chimpanzee nutcracking reinnovation studies as follows: "provide such naive captive chimpanzees with all the necessary material (i.e. closed nuts, hammers & anvils) *and make also sure they like the nut kernels ("motivation check").* " [italics added]. See also Tennie et al. (2020a) for a similar point.

[15] Instead, such separation attempts are even interpreted by Koops et al. (2023) as human "coaxing". We see many issues with this view. Here, we will however focus on determining whether the separation can happen at all.

how to crack nuts. Therefore, the original study of Koops et al. (2022) fulfilled both prerequisites listed by Koops et al. (2022), while successfully separating these two knowledge types[16]. Koops et al. (2023) claim that separation of these types of knowledge is impossible is therefore untrue.

Outlook

As we have shown, the question of whether chimpanzee nutcracking is or is not a latent solution remains open – and requires additional tests on a sufficient number of valid subjects under controlled conditions. What would an ideal test look like? Regarding tests in the wild, as in Koops et al. (2022), populations of wild western chimpanzees (*Pan troglodytes verus*) – if nut-cracking-naive at start of test[17] – should be targeted. Again as in Koops et al. (2022) these populations should be regularly provided with appropriate tools and nuts (know-where and know-what). Based on Biro et al.s´ (2003) findings, Coula nuts would indeed likely be best[18]. Yet, in contrast to Koops et al. (2022) in the pre-test phase sufficient numbers of target subjects must develop a robust interest *both* in the test setup[19] *and* in consuming the provided nuts' kernels. To (hopefully) induce this, ready-to-eat nut kernels should be intermixed with uncracked nuts from the start[20] (similar to Experiment 3 in Koops et al. 2022); other methods may or may not be used to induce the pre-requisite food motivation (e.g., Tennie & Call 2023). As we highlighted before (Tennie & Call 2023), valid target subjects should be restricted to those that have been empirically shown to be most likely to initiate development of nut cracking know-how; i.e., juveniles between the ages of 3-5 years (see Biro et al., 2003)[21]. Only when *such* juveniles *continuously* show the required food and test motivation can they enter the test phase. Given the shortness of the sensitive time window, the theoretical maximum length of this test phase for each subject is two (to maybe three) years; reachable if target subjects show the necessary pre-test motivation by the time they turn three. However, this motivation may not always appear fast enough, or subjects' ages may already be beyond this point when the experiment is set up. Therefore, for such practical reasons, the minimum test phase duration likely needs to be relaxed (but *no less* than to one full year of test phase per subject; see our main text above). As for target behavior, note that these juveniles do not instantaneously develop full-blown, fully honed nut cracking in wild social learning settings (e.g., Biro et al. 2003). Therefore, the operationalized *target behavior*[22] to look out for will have to be instead whether these juveniles enter on the reported developmental trajectory of nut cracking[23]. A valid test is one in which all these conditions and pre-requisites have been met. Given all the above is met, if at least one

[16] None of the chimpanzees in Koops et al. (2022) who came into contact with the accessible kernels even tried to eat them. However, a failure to actually induce know-what(-to-eat), is not at all the same as a failure to separate know-what from know-how. The latter was indeed successfully done.

[17] Note that, once deemed nut-cracking-naive, no *ad hoc* change of this status, based on the outcome of testing, should be permissible. For these and other reasons, it is therefore best if such studies are done as Registered Reports.

[18] Practical considerations may make it necessary to use different nuts (all of which must of course be hard to crack). Here, as long as some populations of chimpanzees – anywhere – have eaten such nuts over extended periods of time, they should principally be suitable.

[19] Given the suspected demands of the specific task here, such interest should be measurable in hours or days, not in minutes (compare Motes Rodrigo & Tennie 2021b). Crucially, this must later prove to continue across the entire test phase.

[20] Depending on levels of interaction, the level of provisioning of pre-opened nuts might be adjusted or even faded out.

[21] Owing to somewhat different developmental speeds, captive studies would have to increase this range.

[22] Perhaps researchers will decide that *fully-honed nut cracking* know-how should be the target behavior instead. That is fine (even ideal), but then youngsters who have entered the (lengthy) developmental trajectory towards this would have to be continuously tested for much longer than the period described here (indeed, for as long as they continue to hone their nutcracking behavior).

[23] Note that if any chimpanzees access nut kernels from unopened nuts using *other* means (e.g., via using their teeth), this would likely prevent them developing nut cracking using hammers (due to well-known tendencies of conservatism in chimpanzees). This would likely prevent onlookers to develop hammer-use, too, for such occurrences would be expected to lead to a latent solution "cultural founder effect" for this alternative method (Tennie et al. 2009, compare also Tennie et al. 2020a). The entire affected population could then become invalid for testing the ZLS hypothesis for nutcracking know-how.

youngster[24] shows target behaviour, then the ZLS hypothesis for wild chimpanzee nutcracking should be accepted (Tennie et al. 2020a,b). However, if (likely across testing sites) at least 16 youngsters – calculated minimum power for a meaningful negative case (Bandini & Tennie 2018; see Tennie & Call 2023)[25] – *all fail* to develop target behavior, the ZLS hypothesis for wild chimpanzee nut cracking can be rejected (sensu Bandini & Tennie 2018).

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[24] If a *differently aged*, nutcracking know-how-naive individual spontaneously initiates nutcracking, then this would count as positive evidence for a ZLS interpretation, too. The reason why we do not focus on these cases is that such case are unexpected given earlier empirical findings from wild chimpanzees (Biro et al. 2003; see also above).

[25] Koops et al. (2023) accuse us of double standards – they cite Bandini et al. (2021) and Neadle et al. (2020) as two studies (from the Tennie lab) that failed to reach such a sample size. For the second study, this is clearly an unwarranted accusation – for, as a result of not reaching this necessary sample size, Neadle et al. (2020) *refrained* from concluding for or against any specific hypothesis based on their study. Regarding Bandini et al. (2021) the accusation may however be seen as partly justified, given their favoring of one hypothesis over another (though note that this manuscript tamed down its conclusions by frequent usage of terms such as that the data obtained "suggests" such-and-such and is "consistent with" etc). And so, in relation to Bandini et al. (2021) indeed we concur: it may still be that chimpanzees can spontaneously innovate early stone tool production and usage know-how after all (i.e., it may still be that this know-how resides inside their ZLS).

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