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Unmotivated Subjects Cannot Provide Interpretable Data and Tasks with Sensitive Learning Periods Require Appropriately Aged Subjects:
A Commentary on Koops et al. (2022) "Field experiments find no evidence that chimpanzee nut cracking can be independently innovated"

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Abstract – In a recent paper in *Nature Human Behaviour*, Koops et al. (2022) argued that unlike most other chimpanzee "know-how", nut-cracking falls outside the zone of latent solutions (ZLS). Their conclusion is based on an experiment in which the authors placed nuts and hammers in an area frequented by a wild population of chimpanzees (*Pan troglodytes verus*) naïve to nut-cracking. Although some of these chimpanzees came into proximity with the provisioned materials, they did not develop nut-cracking. Koops et al. concluded that chimpanzee nut-cracking know-how requires a model to copy – and does not represent a latent solution. We applaud Koops et al.'s efforts to test for the mechanisms that drive nut-cracking in wild chimpanzees, but we argue that their results are inconclusive because the chimpanzees lacked the required test motivation – there was no willingness to eat the nuts, even when their kernels were already exposed. Additionally, most individuals fell outside the age range most likely to foster nut-cracking innovation. For these reasons, Koops et al.'s study outcome is uninterpretable. The question whether nut-cracking is or is not a latent solution in chimpanzees therefore awaits further empirical testing on motivated subjects within adequate age ranges.

Keywords – Test motivation, Sensitive learning period, Nut-cracking, Zone of latent solutions, Innovation, Social learning

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The question of whether non-human ape (henceforth ape) culture is principally similar to human culture remains contentious. In a recent paper, Koops et al. (2022) agreed with us (e.g., Tennie et al., 2009, 2020), that most chimpanzee know-how is different from most human know-how because the former, but not the latter, mainly consists of latent solutions. However, Koops et al. claim to have found evidence that, in rare cases, chimpanzees show copying-dependent know-how, i.e., know-how that goes beyond the level of a latent solution.

Latent solutions are behavioral and/or artefact forms whose underlying know-how can be spontaneously innovated by ecologically relevant individuals (here: not trained or enculturated by another species) in the absence of cultural access (Tennie et al., 2009, 2020). This is in stark contrast to most (but not all; Reindl et al., 2016) human know-how today. Most human know-how is "supra-individual" – as

such, it prototypically depends on, among other things, at least three factors: the cultural evolution of the know-how in the past, the ability to copy such culturally evolved know-how, and cultural access to this culturally evolved know-how (Tennie et al. 2009, 2020). The total number of such "supra-individual," or copying-dependent, know-how reaches in the billions in humans today – yet, recent estimations of this number in apes overlap with zero and do not exceed single digits (Motes-Rodrigo & Tennie, 2021). Against this background, Koops et al. (2022) claim to have found reliable evidence for copying-dependent know-how in chimpanzees would have important consequences, if valid. Here we argue that their claim is invalid – due to motivational and sample selection limitations.

In previous work we proposed that non-human great ape know-how is at least largely, but perhaps even fully, restricted to latent solutions (e.g., Tennie et al., 2009, 2020) – a view with implications for the types of culture that pre-modern hominins might have possessed (e.g., Snyder et al., 2022). While they agree with the weak version of our claim, Koops et al. (2022) reject its strong version. They disagree that chimpanzee cultures may be fully restricted to latent solutions. Logically, even a single case of supra-individual know-how copying in (ecologically-relevant) apes would refute the strong version of the zone of latent solutions (ZLS) claim. Consequently, Koops et al. set out to empirically test this latter possibility with regards to whether one particular type of know-how (nut-cracking using hammers) is outside of the chimpanzee ZLS, and thus must be copied to be acquired. To examine this question, Koops et al. provided a population of wild chimpanzees, which has not been observed to crack nuts before, with nuts and hammers placed in proximity to each other. Up to 19 chimpanzees from this group came into contact with these materials – briefly – but none started cracking nuts with the provided hammers. Koops et al. interpret their findings as providing support for the view that: "nut-cracking falls outside the ZLS of chimpanzees and may thus qualify as a culture-dependent trait and, as such, possibly an outcome of cumulative culture" (Koops et al., 2022). If valid, these data would refute the strong version of the ZLS claim for chimpanzees.

Here, we challenge this interpretation because of two major methodological shortcomings. First, the chimpanzees in Koops et al.'s (2022) study proved to be unsuitable test subjects due to a clear lack of motivation to participate in the study in the intended way. The chimpanzees did not show any interest in eating the nuts – including in the pre-opened palm nuts – rendering this population an invalid sample. Second, even if these subjects had been motivated, the ages of all but one subject clearly fell outside of the known sensitive age range for chimpanzee nut-cracking development (Biro et al., 2003). The question whether nut-cracking can be re-innovated by chimpanzees in the absence of cultural models therefore remains open.

Nut-cracking Can Principally be Reinnovated

To non-specialists, the idea that nut-cracking might be individually reinnovated by even a single naive chimpanzee might sound far-fetched. Yet, there is an ongoing debate over whether any non-human ape (henceforth: ape) species ever culturally evolved any of their know-how beyond an individual's capabilities to innovate (the prototypical pathway to supra-individual know-how in the human case). If true, Koops et al.'s suggestion that chimpanzee nut-cracking is a case of supra-individual know-how would have major repercussions for our understanding of ape and human culture. Due to its far-reaching implications, and to the lack of positive evidence for this type of know-how copying in apes (reviewed in Tennie et al., 2020), such extraordinary claims require extraordinary data grounded in valid tests. This is particularly true for nut cracking, especially given the strong evidence for the individual innovation of nut-cracking know-how in other primate species (Bandini et al., 2021; Visalberghi, 1987) and given tentative – albeit still debatable – evidence that chimpanzees can innovate it, too (Hirata et al., 2009; Marshall-Pescini & Whiten, 2008; Morgan & Abwe, 2006).

Unmotivated Subjects Do Not Provide Interpretable Data

We agree that nut-cracking behavior is one of the best candidates for chimpanzee supra-individual know-how (Neadle et al., 2020). But an absence of clear cases of reinnovation – as in Koops et al. (2022)

– cannot be readily interpreted as evidence that a latent solution underpinning it is absent. Koops et al.'s study did not add relevant data to this debate as their experiment *lacked an essential prerequisite for a valid study*: test motivation. Simply put, the tested chimpanzees showed no signs that they even wanted to eat the provisioned nuts. This is not as surprising as it may at first seem to be.

Consuming nuts via nut cracking can improve primate diet quality (e.g., Izar et al., 2022). For this to happen, however, individuals must recognize nuts as safe, nutritious, and desirable food items – which is not a given. Being weary of novel food makes perfect sense, and therefore neither wild nor captive primate populations should be expected to accept any food that is novel *to them*. Indeed, during one of our early (unpublished) attempts at studying nut-cracking in captive chimpanzees (with A. Albiach-Serrano), we provided open Macadamia nuts – a novel food for the chimpanzee population we tested. This population failed to generate sufficient interest in consuming the nuts to render them valid test subjects (we were thus forced to abandon the study). In fact, some of the chimpanzees in that test population even spat the nut kernels out as soon as they tasted them. In sum, a lack of test motivation in studies that introduce food novel to the population is a potent threat to test validity. However, in studies that use locally novel food baits, a check for subject motivation is very simple: If subjects reliably consume the novel food, then the food-motivational pre-requirement for test validity is fulfilled. But if they do not, the test is clearly invalid. The chimpanzees in Koops et al.'s (2022) study exhibited a clear general disinterest in consuming the novel food (the provided nuts), evidenced by the fact that they never even *attempted* to eat the provisioned *nuts* (e.g., there were no cracking attempts even with their teeth). These chimpanzees did not attempt to eat the novel food even when – *and this is key* – they were given open nuts i.e., nuts which were already "ready to eat" (palm nuts, Experiment 3). Since this population was apparently uninterested in the provided nuts, there is no reason to think they would be motivated to develop the target nut-cracking know-how. Contrary to the authors' claims, a lack of motivation to eat provided food is thus not untestable in the wild ("we could not test their motivation"; Koops et al., 2022). Instead, it *was* tested by Koops et al., who found a clear absence of the necessary test motivation (see Experiment 3 in Koops et al.). For such reasons, other chimpanzee field experiments have made sure to provide food that was known to be valued by the test populations (e.g., honey; Gruber et al., 2009).

Unsurprisingly, subjects in cognitive tests are well-known to fail tests that use inefficient motivators, perhaps best evidenced by their sudden success once efficient motivators are used instead (e.g., Belger & Bräuer, 2018). Test motivation matters, not just to initially engage subjects with the task, but to entice persistence in the face of failure. Here, even when mere visits were included (i.e., visits without any contact to test materials), mean visit durations did not exceed five minutes in Koops et al.'s (2022) study (see Table 3 in that paper). Therefore, the average exploration time of each of the (up to) 19 chimpanzees that at least came into close proximity with the test materials was even shorter. Such short exploration bouts are insufficient for the innovation of a complex tool use behavior to occur (Motes-Rodrigo & Tennie, 2022) and are also further evidence for a lack of motivation. Lacking both the necessary pre-requisite test motivation and contact time, the observations of Koops et al. must be regarded as uninformative regarding the question of whether chimpanzees can or cannot re-innovate the know-how underlying nut-cracking behavior.

To Copy Knowledge Type A Does Not Have to Entail the Copying of Knowledge Type B

Koops et al. (2022) replicated the widely accepted finding that know-*what*-to-eat (e.g., nuts) is socially learnt in apes, and perhaps *must* be socially learnt (e.g., see Bastian et al., 2010). This finding is fully in line with the ZLS hypothesis – which is instead concerned with know-*how* (Tennie et al., 2009, 2020). However, we disagree with Koops et al.'s implication that the learning of such know-*what* entails that the know-*how* must be socially learned, too. Indeed, while chimpanzees copy know-what with relative ease, they fail to copy supra-individual know-how (reviewed in Tennie et al., 2020). Koops et al.'s test population was clearly unmotivated to develop any know-how in opening nuts (even to attempt using their teeth), and this was likely due to lacking the specific know-*what* culture of eating the provided nuts (see above). In summary, it does not matter what type of lack of knowledge leads to a lack of test motivation,

the resulting lack of motivation will invalidate any attempts of data interpretation with regards to other types of knowledge – e.g., as here with regards to know-how development. For example, a local lack of know-what can in this way suppress certain types of know-how, even if the latter are latent solutions. Applied to the study of Koops et al., one cannot expect these chimpanzees to start developing the know-how of using tools to crack nuts open as they clearly lack the local know-what of eating these nuts.

Chimpanzee Nut-cracking Develops in a Sensitive Age Range that is Largely Outside that Accessed by Koops et al. (2022)

Negative data purporting to show the absence of innovation in foraging tasks require that the individuals are sufficiently motivated to obtain the food. Yet, even if that had been the case here, the task would have had to be administered to a large enough number of motivated individuals. Note that, to be categorized as a latent solution, it is not necessary that all tested subjects innovate the underlying know-how, as long as *some* individuals do so. Using this logic, the minimum sufficient sample size of motivated subjects *for studies that fail to find complex tool reinnovation* at all – in any subject – has been calculated to be 16 (Bandini & Tennie, 2018), a requirement not met by Koops et al. (2022). First, juveniles are the most likely innovators (Kummer & Goodall, 1985[1]). Second, data from wild chimpanzees suggests that juveniles who are exposed to the materials of the behavior within a sensitive learning window (between the ages of 3 and 5 years) are by far the most likely to *start to develop* nut-cracking know-how (Biro et al., 2003). Notably, even the very rare cases of beginning to nut-crack outside this age range are still close to these ages (see Jeje, 7 years old at the time, in Matsuzawa, 2011). It therefore seems well justified to call this range (3 to 5 years; perhaps 3 to 7 years) the chimpanzee sensitive age range (or "learning window") for the initialisation of the development of nut-cracking behavior. Thus, while other age ranges may be adequate in other chimpanzee innovation studies, studies specifically targeting nut-cracking should focus on subjects within this age range (Neadle et al., 2020). Translating Koops et al.'s age classes into age brackets (Koops, pers. comm.), and matching these to this relevant age bracket, we can see that only their infant (0 to 4 years) or juvenile class (4 to 7 years) could have contained subjects with a meaningful likelihood of innovating the behavior. However, in Koops et al.'s study only one chimpanzee that belonged to these relevant age classes ever even explored the materials, and did so only briefly (Experiment 2). True, this subject did not begin to show any stage of nut-cracking behaviour. Yet, given a single relevant test subject, combined with the tested population's lack of motivation to eat even pre-opened nuts, it is not surprising that nut-cracking was not re-invented in Koops et al.'s study.

Concluding Remarks and Outlook

In summary, Koops et al.'s (2022) study fails to meet two key requirements for the generation of interpretable data when the outcome is a lack of target know-how: test motivation and an adequate sample size of relevant subjects (i.e., here, those within their sensitive age range). Although we admire Koops et al.'s efforts to test wild chimpanzees, their study clearly represents an invalid sample of the latent solution hypothesis for chimpanzee nut-cracking behavior. Therefore, we argue that their interpretation – that nut cracking know-how is unlikely to be a latent solution in chimpanzees – is unwarranted. We still do not know whether nut cracking is more likely inside or outside of the chimpanzee ZLS (compare Neadle et al., 2020). Thus, this question awaits further empirical testing on motivated chimpanzees who fall within the sensitive age range reported for this behavior in the wild. Future field experiments on nut-cracking innovation should follow Koops et al.'s lead but provide conditions that are more likely to foster the necessary interest in the provisioned materials. For instance, one could first provide naïve subjects with

[1] In a more recent review that pooled several age classes together, "non-adult chimpanzees" showed slightly higher counts of innovation than adult chimpanzees – though the relationship was not significant (Reader & Laland, 2001). Moreover, innovation was defined broadly, encompassing multiple areas and tasks, and was not specifically focused on nut-cracking know-how.

open nuts mixed with food that is known to be valued locally, and perhaps even with shelled nuts injected with such food (e.g., honey). Once a sufficient and reliable motivation for consuming nut kernels is established, subjects will be more likely to interact with the materials and nuts – including those whose age make them more likely to develop the target behavior of nut-cracking. Only tests on motivated subjects, of the right age, will generate interpretable data that can answer the question of whether chimpanzee nut-cracking is a latent solution or not.

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