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What Does a Notion of Weight Mean to Chimpanzees?

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Abstract – How to best understand how animals think about the world? Considering that cognition develops in interactions with the outside world, we need to compare the cognitive performance of individuals of the same species living under different ecological conditions. I propose here to compare the notion of weight studied in captive chimpanzees to the ones observed in a wild chimpanzee population that is using hammers of different weights to crack nuts during many months of the year. Detailing different situations where the chimpanzees have to select a hammer for cracking two species of nuts of different hardness, my colleagues and I could illustrate the flexibility of the causal reasoning performed by the chimpanzees, including stable anticipation of weight, combining weight with density and transport distance, and the gradual shift of selection criteria with increasing transport distance. Combined with results from captive studies on the notion of weight in chimpanzees, this suggests that when individuals face specific ecological challenges, they may acquire sophisticated causal reasoning generalized over different contexts. The evolution of cognition in chimpanzees suggests a complex interplay with ecology, memory demands, individual differences, and technical challenges important to the population.

Keywords – Chimpanzee, Cognition, Causal reasoning, Ecological validity, Notion of Weight

Cognition has been defined in different ways by different researchers within and across disciplines. Nevertheless, a consensual definition can be suggested that states cognition to refer to “adaptive information processing in the broadest sense, from gathering information through the senses to making decisions and performing functionally appropriate actions, regardless of the complexity of any internal representational processes that behavior might imply” (Shettleworth, 2000, p. 43). A “decision” implies the ability to consider alternative solutions to a given situation and make a choice between those alternatives. These are some of the essential elements of cognition (Shettleworth, 2000). Such a definition makes it clear that cognition develops in contact with the environment to permit the individuals to resolve some of the challenges encountered in their environment. Chiel and Beer (1997) discuss the need to ‘‘take into account the embeddedness of the brain in the body and world to understand cognition’’ (p. 556). According to this view, cognition develops in interactions with the outside world.

One of the most important aspects we learned about chimpanzees (*Pan troglodytes*) in the last decades is their behavioral and cultural diversity (e.g., Boesch et al., 2020; Whiten et al., 1999). Chimpanzees live in the tropical rainforest of the African continent as well as in more open habitats, including some dry areas, as long as gallery forests are present (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Pruetz & Bertolani, 2009; Wessling et al., 2018). This diversity of habitats experienced by chimpanzees, and the resulting behavioral and cultural diversity observed in chimpanzees raise, first, the question whether the same level of diversity is observed also in their cognition. Second, if cognitive differences were found in different habitats, what would be the factors that could explain their emergence?

To address these questions, we have at our disposal mostly data on cognitive studies done on chimpanzees living under captive conditions. Thus, new studies on cognitive abilities on chimpanzees living in different environmental conditions are needed. Moreover, to address the question of cognitive diversity, we need to compare what is comparable, and this means to compare wild chimpanzees facing similar challenges than those studied in captive conditions, as similar cognitive abilities underline them. To address this topic, I selected the notion of weight, as this has been extensively studied on captive chimpanzees (Hanus & Call, 2008; Povinelli, 2000, 2020; Povinelli & Eddy, 1996; Schrauf & Call, 2011). As those studies have been subject previously to discussions (Allen, 2002; Boesch, 2020, 2021; Buckner, 2012, 2013; Farrar et al., 2020, 2021; Schubiger et al., 2020; Whiten, 2001), I am provisionally considering them here as representative of the abilities in chimpanzees that experienced similar living conditions, i.e., captive environment.

From a cognitive point of view, a captive environment is mainly characterized by limited life-threatening challenges, very limited space, and regular and abundant access to rich food. On the other side, natural living conditions in the African forests require searching daily for food before competitors eat it, avoiding predator attacks, and navigating over long distances in an environment with limited visibility. For example, Taï chimpanzees range within a territory of 10 to 40 km^2, looking for food for about 40% of the daytime with day-journey distances of 5,000 to 10,000 meters (Boesch & Boesch-Achermann, 2000). In addition, for our study about weight, chimpanzees prefer to eat ripe fruits that are found high up in some of the tallest trees of the forest. This requires the chimpanzees to develop a precise understanding of the effect of their body weight on the branches of different sizes to prevent the risk of falling. Chimpanzees in the Taï forest extract the kernel of nuts from five different species of trees over many months of the year (Boesch & Boesch-Achermann, 2000). As those nuts are among the hardest found in Africa, they must use hammers of different weights to access them. How does the daily use and selection of hammers of different weights affect the understanding of weight in Taï chimpanzees, compared to captive chimpanzees that barely have the necessity to select objects of different weights to survive?

The Nut-Cracking Behavior of the Taï Chimpanzees

The nut-cracking behavior in Taï chimpanzees has been extensively studied. I am thus simply summarizing here the main points with regard to the topic of the notion of weight. In the Taï forest, all adolescent and adult individual chimpanzees have been observed to crack nuts during the abundant *Coula* season that lasts between December to March. During that period, they crack nuts on average, for about 90 minutes every day using different hammers, as they move in the dry parts of the forest between the many different *Coula* trees (Boesch & Boesch-Achermann, 2000). *Coula* nuts being relatively soft can be opened with wooden branches that have fallen from the trees, and so the nutcrackers will select one of them among the many littering the ground (Boesch & Boesch, 1983; Sirianni et al., 2015). However, the weight and hardness of the branches vary extensively, making the majority of them inappropriate as a hammer, being too soft. To crack the nuts, the chimpanzees need also to select an anvil on which they will place the nut. Again, the majority of the available surface roots are of a soft wood, and the nuts immediately sink into the wood when hit. Thus, chimpanzees must select a root that is sufficiently resistant to the many administered hits and not absorb all the kinetic energy through hammering. The selection of a granite hammer allows an energy gain per nut opened of 73% for *Panda* nuts, while the appropriate selection of a stone anvil permits to spare 78% of energy (for *Coula* nuts, the gain is of 42% per nut open for a stone hammer and of only 6% for a stone anvil: Boesch & Boesch, 1983, Table 2). Energy was calculated as the impulses ($I=Mass*gh^{-2}$) necessary to crack open the different nut species with a free falling wooden or stone hammer of 10 kg. Clearly, the optimal selection of tools contributes substantively to successful nut cracking. In general, stone material would be the best choice, but the availability of stones in the forest is much more limited than branches or surface roots.

The *Coula* nut season ends around March every year, when the *Panda* nut season starts, lasting until September, while the *Parinari* nut season starts around June and lasts until September as well. *Panda* nuts are especially hard and unlike for *Coula* nuts, heavier stone hammers are mandatory to crack them.

Stones being much rarer than wooden branches, transports of stones to crack nuts is frequent (Boesch & Boesch, 1983, 1984a). In addition, contrary to *Coula* trees, the *Panda* trees are much less abundant, and it is mainly the female chimpanzees feeding on *Panda*, as they are less concerned about isolating themselves from the other chimpanzees (see Boesch & Boesch, 1984b). The extraction of the edible kernels from a *Panda* nut is complicated by that fact that each nut entails 3 to 4 kernels embedded separately in the hard-shelled fruit and they need to be extracted one after the other, requiring precise and differentiated dosage of force to avoid smashing them all together.

Youngsters show very early on a strong interest in nuts, and mothers share nuts extensively with them. By the age of two, the youngsters are keen to try to crack the nuts by themselves, but initially ignore that they need both a hammer and an anvil to crack the nuts, and numerous trials and errors are seen during their attempts (Boesch & Boesch-Achermann, 2000). By the age of four, the youngsters systematically use a hammer to hit the nut placed on an anvil, and all of them succeed in opening their first nut by the age of five. Thereafter, the progress in nut cracking is regular and rapid as long as they have access to an optimal hammer, mostly obtained from their mothers (Boesch & Boesch-Achermann, 2000; Boesch et al., 2019).

Adult Taï chimpanzees are all adept nutcrackers, opening about two *Coula* nuts per minute, including the time to eat them, with an average of seven hits per nut for adults. Females are more efficient than males (Boesch & Boesch, 1984b). Chimpanzees in the Taï forest crack nuts daily for the four months of the *Coula* nut season every year, estimated to crack about 167 nuts for 1h30mn (this represents over 3,000 kcal per day). Over the course of four nut-cracking seasons, the chimpanzees were seen to transport a hammer for *Coula* nuts in 313 instances and 290 times for *Panda* nuts (Boesch & Boesch, 1984a). Of the 606 transports we could follow completely, the chimpanzees transported the hammers over 20 meters in 167 times; 121 of them being for the harder *Panda* nuts (Boesch & Boesch, 1984a). A detailed analysis of the 76 transports of stone tools for *Panda* nuts, with known transport distance and weight of all potential hammers around the tree where nuts were cracked, revealed that the chimpanzees selected 48 times the nearest stone to the anvil, 26 times the lightest one, and 40 times the one that represented the minimal energy expenditure (Boesch & Boesch, 1984a).

The nut-cracking behavior is a good example of a costly feeding behavior. When a chimpanzee uses a 7.14 kg wooden hammer, he will need an average of 3.5 strikes per *Coula* nut, requiring 600 strikes per day for the 167 nuts eaten on average. If he uses instead a stone hammer of the same weight, he will need only 400 strikes (Sirianni et al., 2019). With a 5 kg wooden hammer, he will spend 2.0 kJ of energy per second of nut cracking. Therefore, the benefit in choosing a good hammer can be consequent, as this can result in an improvement of 91%, which translates into an energy gain of 9.000 kJ (2.150 kcal) per day (Sirianni et al., 2019). Further illustrating the important investment in nut cracking over the years is the fact that Taï chimpanzees possess different metacarpal trabecular architecture in their hands, compared to non nut-cracking chimpanzee populations (Lazenby et al., 2011).

Weight as a Physical Notion

We expect that chimpanzees that are daily confronted with decisions where the notion of weight is a relevant parameter might develop it to a further extent than chimpanzees that live in an environment where weight has minimal relevance to decision-making. Captivity does not require a detailed notion of weight, and therefore, chimpanzees that have spent their whole life in captivity might have a notion of weight that remains limited (Buckner, 2012; Povinelli, 2012). Therefore, I want to address here what notion of weight wild chimpanzees develop in a population that is regularly confronted with a task where weight is a major component: The Taï chimpanzees have been shown to crack nuts for at least 4,300 years (Mercader et al., 2007). Do Taï chimpanzees understand more about weight than the chimpanzees studied in captivity? If yes, are the differences influenced by the extended practices of nut cracking in the forest?

The notion of weight is interesting as you cannot see the weight of an object, while you can see its color, size, and shape. Thus, the individual looking for an object of a given weight needs to find a way to ascertain the weight of the objects it is selecting. The foremost simple way is to manipulate the object and so feel its weight (Polanen & Davare 2019; Schneider et al., 2020; Wagman & Carello, 2001). However, for how long will this be remembered, in situations where some planning of future actions is needed or when having to decide between alternative potential tools? An alternative would be to establish a correlation between a directly perceivable attribute of the object, like its shape, volume, color, or material, and its weight. The most cognitively demanding alternative is to abstract a notion of weight as an unobservable property of the object from its perceivable attributes.

Five Notions of Weight in the Natural World

Before discussing in detail what an individual should consider before using a hammer to crack nuts, I feel it is important to clarify those notions. Let me proceed with the goal to clarify the notion of what aspects of weight are perceivable.

Mass of a Physical Object

In ordinary language, the terms "mass" and "weight" are often used interchangeably, and mostly, when comparing mass and weight of a same object on earth, without moving, the values of mass and weight are equivalent. However, physically the two are different, for mass is the amount of matter contained in a given object and it does not vary with changes in its geographical position in the earth's surface. Standard mass measures of an object are done using a lever balance and is measured in kilograms (kg). How much mass is in an object can be calculated as:

$$\text{Mass} = \text{volume} * \text{density} \tag{1}$$

This equation clarifies that weight includes a visually perceptible dimension "volume" that can be evaluated from the length, width and depth of the object, and an invisible dimension "density." Typically, a cube of 10 cm of side filled with water possesses a mass of 1 kg. However, if filled with steel nails, the cube mass will be much higher, although it possesses the same volume. In the case of nut cracking, in the Taï forest, stones used as hammer have an average density of 3.5 g cm^{-3}, while wooden clubs one of only 0.5 g cm^{-3} (Sirianni et al., 2019). Here, we already see that two types of perception are needed to estimate whether an object is heavy. That explains the challenge in estimating the mass of an object before touching it.

Weight of a Physical Object

A second, more complex notion is the weight of the object that is affected by the gravitational force. This means that the weight of an object will change according to its geographical locations, while the mass remains constant. The measure of weight is obtained as seen in equation 2:

$$\text{Weight (W)} = m * g \tag{2}$$

Where m is the mass of the hammer and g is the gravitational acceleration.

In humans, lifting an object requires precise scaling of forces based on a prediction of the object's weight. Classically, humans possess a size-weight illusion where different sized objects of identical mass feel being of different weights (Buckingham & Goodale, 2010; Polanen & Davare, 2019). At object contact, a series of tactile and visual events arise that are processed rapidly to fine-tuned motor commands for lifting the object (Polanen et al., 2019).

Weight as a Component of Kinetic Energy

The typical movement when opening a nut is the striking of the nut, in other terms the controlled percussion of the nut with a hammer held in position to hit the nut with the maximum of energy. This energy, called kinetic energy, is measured by the equation 3:

$$\text{Kinetic Energy } (E_t) = ½ m * v^2 \qquad (3)$$

where m is the mass of the hammer, and v is the speed of the center of mass of the hammer at the time of impact. In other words, the individual, by regulating the speed of the hammer when contacting the nut, will be able to crack it open, and when the mass of the hammer is too light to crack the nut, the individual will have to add muscular force to the hammer when hitting it. This force is not only added to increase the kinetic energy at impact but will also guide the downwards movement of the hammer to ensure the precision of the impact on the nut, as otherwise a lot of the kinetic energy will be lost.

In natural situations, objects will differ in mass and density, as shown in Figure 1. Therefore, once you have selected an object, you adapt the force to the specific mass of the hammer used. This requires combining flexibly weight with force, and for each different hammer, the force necessary needs to be reevaluated. This should be flexibly evaluated the harder the nut to crack. In addition, the size and sex of the individuals will also affect these evaluations (see also capuchin monkeys cracking nuts; Spagnoletti et al., 2011).

Force is a physical notion that is not directly perceivable, and since it has to be invested as the function of the mass of the hammer and the hardness of the nuts, it will require some conditional assessment for each nut-cracking session to evaluate adequately the force needed.

Figure 1

Natural Hammers Used by Chimpanzees in the Taï Forest to Crack Nuts

Note. Wooden hammers are dead branches found on the ground, and they are much more readily available than stones, and commonly used for pounding the abundant rather soft *Coula* nuts. The top right hammer is a branch of *Coula edulis* that is of very hard wood and can be used for many years. The one on the bottom left is a hammer of a softer wood with clear signs of wear. Stone hammers are necessary to crack the harder and much rarer nuts of *Panda oleosa*. The stone hammer in the center right consists of hard granite material, and it has been in use for decades, presenting deep traces of wear at its center of gravity.

Weight of an Object to Transport

There are many occasions in the forest where no good hammer is available at the anvil with nuts ready to be eaten. In such situations, transporting an optimal hammer is required and the individual needs now to consider the additional transport costs that will increase proportionally with the weight of the hammer and the distance of transport.

$$\text{Total Energy} = \text{Pounding Energy} + \text{Transport Energy} \tag{4}$$

When transport is necessary, the nutcracker needs to not only consider weight, force, and hardness of the hammer, but also distance to the anvil. This requires an integration of different phases of the nut cracking as the cost of transport will add itself to the cost of pounding the nuts, and the two are separated in time and space. The transport always happens before the start of pounding and often separately, as once at the nut-cracking site with the hammer, the individual will first collect some nuts before starting to open them. The nutcracker encounters here a conflicting condition, as heavier hammers allow cracking nuts with less hits, but they are more costly to transport. Therefore, if the individual is able to connect these two aspects, a compromise will occur to decrease weight as the length of the transport increases (thereby limiting total energy expenditure - Equation 4). This is particularly important when the transport distance exceeds the visibility range in the forest, i.e., when the endpoint of the transport cannot be seen from the starting point.

Integration of Weight when Cracking Nuts

The chimpanzees, when selecting a hammer in the forest, need to consider simultaneously distance to the anvil, composition and weight of the hammer. From my observations of nut-cracking behavior by the chimpanzees in the Taï forest, I suggest considering the different contexts under which the chimpanzees need to make a decision about selecting a hammer. To reflect this, I propose to discuss them following an order of growing complexity:

Context 1: A chimpanzee arrives under a tree producing ripe nuts with one anvil and with some hammers available.

Context 2: A chimpanzee arrives under a tree producing ripe nuts with some hammers and some anvils available.

Context 3: A chimpanzee arrives under a tree producing ripe nuts with some hammers available, but all of them some meters away at visible distance to the anvil where they are going to crack the nuts,

Context 4: A chimpanzee wants to crack nuts under a tree producing ripe nuts where no hammer is available within visibility to the anvil.

These four contexts represent the spectrum of contexts that chimpanzees will encounter whatever the species of nuts they want to crack, and they present, therefore, different challenges they need to solve. The first context is the one closest to most of the common situations that have been presented in experiments about weight in experimental studies (e.g., Bril et al., 2009; Povinelli, 2012).

Context 1: A chimpanzee arrives under a tree producing ripe nuts with one anvil and with some hammers available. Since *Coula* trees tend to grow in the driest part of the forest, chimpanzees will crack nuts in one session under more than one tree. This explains that only in 20% of the observations did the chimpanzee select a hammer that was already present at the anvil where they cracked the nuts (Sirianni et al., 2015). In such a situation, the chimpanzee can select the best hammer in two alternative ways: The first would be to select the hammer based on a proxy for weight, most likely the volume of the hammer. Alternatively, he can first manipulate the hammer and then from the tactile information collected, he selects the hammer.

Weight when Selecting the Hammer. With some experience, an individual can note that, under some conditions, a larger hammer increases the success to open a nut (see equation 1). However, more experiences with cracking nuts with wooden hammers of different sizes, colors, and shapes, will be necessary to realize that size alone is not enough to predict the success. In the natural forest conditions, the association between volume and mass will be weak, as wooden hammers decay continuously in the forest as a function of the time the branch broke off the tree, and the level of seasonal humidity. In other words, the density of the hammer decreases with time (see equation 1), and does not correlate to its color, shape, or size.

Alternatively, visual and sensorimotor information can be gained once the individual touches the tool and this can allow him to quickly predict the mass of the hammer (Buckingham & Goodale, 2010; Flanagan & Beltzner, 2000; Johansson & Westling, 1988). What we observe in Taï chimpanzees is that they lift the hammer the first time with a force that seems well adapted to the weight of the hammer (Sirianni et al., 2018). When fooled with hammers of which we artificially had decreased the mass (by removing part of the wooden mass without destroying the outer shape), the acceleration when lifting the hammer was significantly higher for the first lift with the hollow hammer compared to the natural hammer. This 'overshot effect' likely results from an anticipation of weight based on the size of the hammer. However, this error is corrected rapidly, as we did not measure any differences compared to natural hammers for the second lift measured 0.5 seconds later. Humans can recall from memory an anticipatory representation of the weight of an object they have never interacted with before (Buckingham et al., 2009; Gallivan et al., 2014; Gordon et al., 1993; Polanen & Davare, 2015). This representation (described as a 'long-term force profile' by Povinelli, 2012 and as an 'internal model' by Krakauer & Shadmehr, 2006) is formed through a generalization of repeated previous experiences with similar objects and is rapidly updated using kinesthetic information acquired during the movement itself, if the predicted weight does not match the subsequent perception (Polanen & Davare, 2015). Taï chimpanzees had year-long opportunities to form 'long-term force profiles' via generalization of past experiences when interacting with objects used in daily life that belong to a well-defined functional category, including thousands of individual objects that are, or could be, used in a goal-oriented and ecologically relevant routine (Sirianni et al., 2018). Like in humans, Taï chimpanzees quickly react to a mismatch between expected and perceived weight by integrating kinesthetic information acquired during the initial phase of lifting into an updated motor plan.

In Taï forest, the chimpanzees crack five species of nuts, each with a different size and hardness. This requires some flexibility, as regularly up to three of the species are edible during one or two consecutive months. In other words, a hammer optimal for the soft nut species (e.g., *Coula edulis*) will be suboptimal for the very hard nut species (e.g., *Panda oleosa*). Chimpanzees have been seen to select the weight and density of the hammer used for each nut species quite distinctively and precisely (Boesch & Boesch, 1983). Recent data show that they are very aware of the hardness of the *Coula* nut, as it decreases as the season advances, and chimpanzees within days will select lighter and less dense hammers to open them (Luncz et al., 2012). Hence, the long-term force profiles based on experience formed by the chimpanzees are specific enough to produce different anticipations of optimal weight of a hammer for each of the nut species cracked in the forest.

Weight as a Component of Kinetic Energy. To crack a nut, the decisive factor is the amount of kinetic energy that is going to impact the nut (Bril et al., 2009, 2012). The kinetic energy at the time of impact should not be too high, as it risks smashing the kernel and making it inedible; at the same time, it must be high enough to start the breaking process of the shell. The result is that chimpanzees tend to use more than one strike before breaking the shell and good nutcrackers can then extract the intact round kernel (see Figure 2 top left). Chimpanzees strike *Coula* nuts with consecutive hits with similar amplitude until the first crack of the nut, and then they add a few strikes with much less amplitude to free the kernel from the husk. This dynamic solution allows controlling the deformation process of the nut so that breakage of the shell arrives without damaging the kernel.

Figure 2

Taï Chimpanzees Cracking Nuts with Natural Hammers

Note. Top left: Fitz holds an intact extracted *Coula* nut between his lips, as he had opened the shell with a perfect dosage of force. Top right: Darwin holds a middle-sized wooden hammer in his right hand. Center left: Kiri using an 8 kg heavy granite stone hammer with both hands. Center right: Perla holds a long hammer with two hands to ensure stability of the hits. Below left: Ulysse carries the hammer in his mouth while collecting *Coula* nuts to bring to the anvil. Below right: Goma carries the hammer in her left arm elbow while collecting nuts in both her hands.

The pounding movements are also adjusted to the shape and size of the hammers, as either long or curved ones require special attention and stabilization effort during hitting to ensure the impact happens at the hammer's center of gravity to prevent diffusing the kinetic energy. As observed on captive chimpanzees (Bril et al., 2009), chimpanzees using lighter hammers produce a much larger amplitude to hit the nut, clearly from above the shoulder, while when using a heavier hammer that amplitude can barely reach the chest (Boesch & Boesch, 1984a). For *Coula* nuts, chimpanzees prefer hammers of a medium size that they can handle with one hand producing large amplitude (see Figure 2 top right). Longer or curvy hammers need to be held with both hands to ensure the stability during the hits and will therefore be used with less amplitude and more muscular force (see Figure 2 middle right). Hammers that are over one meter long are generally supported in addition by one foot diminishing proportionally the amplitude and requiring more added force. Therefore, chimpanzees adopt dynamic solutions, integrating the effects of the hammer weight, hammer density, hammer shape, amplitude of the strike, and the hardness of the nut.

Dynamic solutions are even more important for the *Panda* nuts, as each one possesses three to four different kernels that need to be extracted one after the other. Initially to open the *Panda* nuts, a nutcracker not only needs to position the nut very carefully to hit the nut between the dehiscent lines of two kernels, so as not to smash them, but the force required to open the first kernel is much higher than the one needed to access the other ones. Even with heavy stones of 3 to 5 kilograms, chimpanzees will lift the hammer above their head (see Figure 2 middle left) to crack open the shell and access the first kernel. Thereafter, they use much more gentle small hits to access the other kernels, after having replaced the nuts carefully to hit another dehiscent line.

Chimpanzees' dosage of the force of the hits is very impressive and they react to an unexpected weight extremely quickly (Sirianni et al., 2018). Nut cracking per se is not the problem, but the precise dosage of the force to add is (see also Bril et al., 2009). The female Taï chimpanzees are outstanding in extracting nut kernels during hours with high precision to avoid smashing them (Figure 2). This shows impressive sensorimotor skills based on years of practicing the task. As has been shown in human experts in different specialized skills, like professional musicians, or athletes (see review Boesch, 2020, 2021), Taï chimpanzees have most likely developed some specialized areas in their brain for nut cracking that made them highly skilled at manipulating and predicting force when using a pounding tool. Nut cracking seems also to have selected for a population-specific morphology of the bones of the hands (Lazenby et al., 2011).

Context 2: A chimpanzee arrives under a tree producing ripe nuts with some hammers and some anvils available. The Taï forest has a continuous canopy with a high tree density, so that around a nut-producing tree more than one root is normally available that could be used as an anvil. Nearly all anvils selected by the chimpanzees are surfacing roots that are abundant in the forest, but not mobile nor modifiable and differ in hardness. We saw many instances of chimpanzees trying to crack a nut near a tree with no previously used anvil, testing several roots until finding one that is hard enough to resist the hits. However, in most situations, chimpanzees have the choice to select one of the previously used anvils, clearly visible with its wear traces from pounding and the numerous nutshells littering the ground around the roots. This copying mechanism makes the selection of an anvil quite easy. In addition, as chimpanzees spend sometimes up to 2 hours during a session in a region with abundant *Coula* trees, they walk on while collecting about 12-15 nuts at a time and change anvils found along their strides. On the contrary, good hammers can and will be carried along as they collect nuts, except for mothers with 3-5 years old infants who tend to leave their hammers behind on the anvil for the youngsters, thereby motivating them to start first trials (Boesch & Boesch-Achermann, 2000). The impression is, therefore, that selection of anvils follows either a copying mechanism or a trial-and-error process, both of which are cognitively less demanding than selecting a hammer.

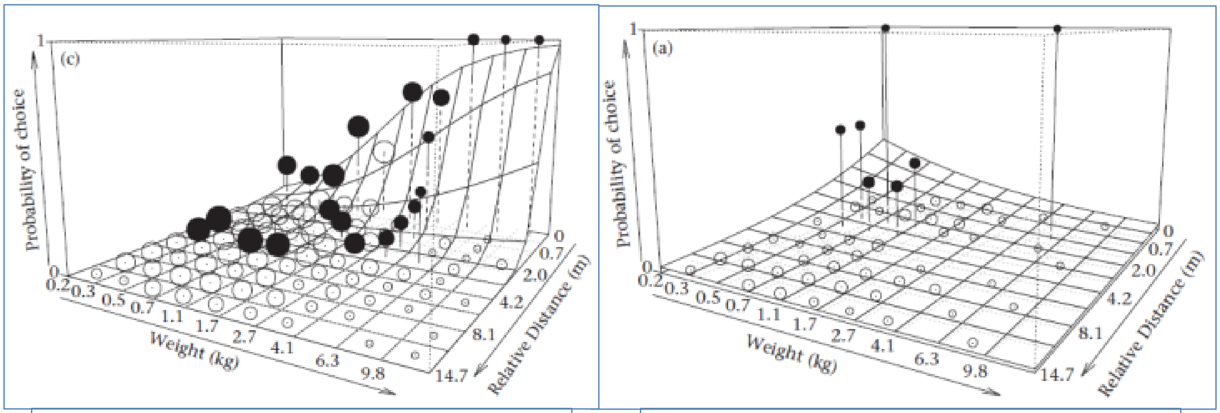
Context 3: A chimpanzee arrives under a tree producing ripe nuts with some hammers available, but all of them some meters away at visible distance to the anvil where they are going to crack the nuts. In almost all situations of cracking *Coula* nuts, the chimpanzees are confronted with many different branches littering the forest floor that can be potential hammers (average number of potential hammers to select from was of 16.38 in 113 hammer selection episodes we followed precisely; Sirianni et al., 2015). Further, adult female chimpanzees reuse a hammer already present at an anvil in only 20% of the nut-cracking sessions (Sirianni et al., 2015). Thus, typically during the last meters before arriving at the anvil, the chimpanzees will look at the branches available around, select one and take it along to the anvil. This selection process is purely visual, and we never saw a chimpanzee manipulating or testing some of them before selection. Therefore, it looks as if the chimpanzees were able to estimate weight and hardness of a potential hammer precisely enough by sight only, and to classify them so as to be able to select one hard and heavy enough to be used for cracking *Coula* nuts (Sirianni et al., 2015). As to confirm this, once selected, chimpanzees always did then use this specifically selected hammer. Over the 113 selection episodes, we saw them touching a hammer before selection in 11 cases, and lifting one twice (Sirianni et al., 2015).

To the human observer, visual perception alone makes it hard to classify the weight between the different branches laying on the ground. Since the chimpanzees do not touch them before selection, they have to use the anticipation of weight that we already identified in the previous contexts. Sorting the weight of two objects requires only determining the heavier one, while sorting the weights of 16 hammers requires some form of transitivity helping the chimpanzees to know, for example, that, among objects of the same length, thinner ones are lighter than thicker ones, while this would not apply to a similar thin one that is longer. This broad transitivity rules should be flexible enough to repeat the sorting for each selection that will include a different combination of weight, hardness, and size of hammers (this was the case in 70% of the selection episodes; Sirianni et al., 2015). In other words, the chimpanzees were able to associate a precise relative weight to hammers they have possibly not touched for days or weeks. This means they seem able to generalize the associative rules they formed with certain hammers from previous precise proprioceptive experiences later to other hammers in the absence of current direct proprioceptive feedback. These weight anticipations are therefore stable over extended periods of time, abstract enough to "transfer their knowledge from one task to others that are perceptually dissimilar but share the same underlying structure" (Buckner 2013, p. 148), and precise enough to order up to 16 of them so as to select an adequate one. "Adequate" for nut-cracking means to have a hammer of a mass that produces enough potential energy when used to hit, so that the required kinetic energy can be achieved with relatively less muscular force than with another of the available hammers (Boesch et al., 2019; Bril et al., 2009; Koya, 2006).

When transporting the hammer, the chimpanzees gradually alter the selection criteria used in the first two conditions to integrate the additional cost of transport (equation 4). They seem very sensitive to these costs, as they shift weight preference already for small transport distances, so that the original preference for heavier hammers decreases gradually with increasing transport distance, ending with a clear preference for lighter hammers for long distances (Sirianni et al., 2015, see Figure 3).

Figure 3

Hammer Weight Selection in Taï Chimpanzees for Coula Nuts According to the Transport Distance



Hammer selection, when the closest hammer is 0 to 4.5 meters from the anvil

Hammer selection, when the closest hammer is 29 to 164 meters from the anvil

Note. As can be seen when the potential hammers are close to the anvil (on the left), chimpanzees select significantly heavier hammers to crack the *Coula* nuts. This preference disappears with increasing distance, so that when the potential hammers are farther away from the anvil, they start to select increasingly smaller hammers (on the right) (adapted from Sirianni et al., 2015, Figure 5, p. 160).

This inversion in the selection criteria from "prefer heavier" to "prefer lighter" as a function of a small distance increment requires a dynamic reset of the mental evaluation that suggests some abstract mathematical-like reasoning. The data presented in Figure 3 (left) suggests that chimpanzees start this for small increments of transport distances for heavy hammers, as a strong shift is seen when the distance increases by 2 meters for hammers of 1.7 kg, while they still prefer heavier hammers at the same distance for weights of less than 1.0 kg. As was noted when sorting potential hammers of different weights, the estimation of distance seems rather precise. Furthermore, this conditional integration of weight in the evaluation process reveals some hierarchical structuring, as weight is valued differently when "close" or "far" from the anvil.

It is important here to remember that, for the human child, comparing the length of two objects placed parallel to one another is first possible when the ends of the two objects are placed at the same level (Piaget et al., 1948). Then about a year later, the child starts to be able to compare the lengths of two objects in parallel but with the ends spatially mismatched. This requires some mental manipulations allowing shifting one object so that one of its ends is levelled with one end of the second object; while comparing the length of two objects oriented differently in space requires first to mentally rotate them and then shift them at the same level. For some children, the last ability is regularly achieved around the age of 9 years (Piaget et al., 1948). Thus, even when all potential hammers are visible to the chimpanzee, the sorting and selection of an adequate hammer is cognitively challenging.

Context 4: A chimpanzee wants to crack nuts under a tree producing ripe nuts where no hammer is available within visibility to the anvil. Chimpanzees transport hammers over distances exceeding visibility (30 m) in the forest in 11.7% of the transport of hammers for the soft *Coula* nuts, while this proportion increases to 29.3% for the harder *Panda* nuts (Boesch & Boesch, 1984a; Sirianni et al., 2015). Furthermore, except in the rare case where a better hammer was already present at the goal anvil, the transported hammer was the one used to crack the nuts. How do chimpanzees know where hammers are in a forest, as visibility on the ground is limited to 20 or 30 meters at most? How do they remember the weight and locations of the different potential hammers?

As we saw, length is a notion that develops slowly in humans, especially when comparing lengths oriented differently in space (Piaget et al., 1948). This becomes even more complicated when evaluating distance out of sight from one and the other, which is regularly the situation faced by the chimpanzees for *Panda* nuts, as heavier stone hammers are rare in the forest and are found in all cardinal directions from the future anvil, often more than 100 meters away (Boesch & Boesch, 1984a). Besides proceeding to mental evaluations based on memory, one can suggest that chimpanzees instead could visit all potential hammers within a distance from the goal tree before selecting one. We know from previous studies that Taï chimpanzees have a very good memory of tree locations (Janmaat et al., 2014), and therefore, it would not be unlikely that they could remember stone hammer locations. Alternatively, they may simply carry the first hammer they find with a minimal weight, without taking into account if others may be present or not.

Panda nuts are among the hardest species of nuts growing in Africa, and to open them, the chimpanzees need to find a stone as hammer that possesses some high density (too heterogeneous stone material would fragment with the powerful hits administered) and weighing of 2 kg or more (Boesch & Boesch, 1983, 1984a). Those stones are rare in the forest and most of those that have the convenient weight have already been transported to a *Panda* anvil, where they were left after use. Thus, when a chimpanzee wants to crack *Panda* nuts under a tree where no hammer is available, a stone hammer may lie not far under another *Panda* tree. "Not far" means at distances ranging between 50 to 200 meters from the goal tree (Boesch & Boesch, 1984a). Within a circle of 300 meters around a Panda tree, we found 2 to 8 stones belonging to this weight category. If chimpanzees had adopted a random search strategy, they would have selected the lighter or closer stone with a probability of 0.262. In reality, they selected the lighter stone more frequently with a probability of 0.342. The random search strategy was further rejected by the fact that they selected the minimal transport distance with a probability of 0.631. In addition, they selected minimized energy expenditure by selecting among the lighter ones the one located at a relatively smaller distance with a probability of 0.526 (all significantly different from the random search prediction) (Boesch & Boesch, 1984a).

Hence, for *Panda* nuts, chimpanzees combine in their reasoning the weight and density of the hammer with the distance of transport, making a selection of the hammer mostly without seeing it. Selecting a hammer out-of-sight following either the minimal distance or minimal energy expenditure requirements necessitates remembering precisely the distances of transport of the different potential hammers, while comparing the distances only for the hammer possessing a minimal weight. This memory was flexible enough to reset the distances attributed to one hammer for each different possible goal tree, but stable enough to compare mentally distances oriented in different directions in space (Boesch & Boesch, 1984a). Therefore, the selection strategy used previously for the context 1 to 3 is now altered in that heavy hammers are selected only when the distance does not exceed certain values. However, since the gain from using a heavy hammer is so much larger for the *Panda* compared to the *Coula* nuts, we saw that the shift in preference from "heavy" to "light" occurs only when the transport distance exceeds 20 meters (Boesch & Boesch, 1984a). This stresses how precise and flexible chimpanzees are in the graded response to the interaction between weight and distance between different nut species.

In my understanding, this suggests that chimpanzees are making inferences about the consequences of their hammer selection (*sensu* Buckner, 2011). Without seeing the whole transport distance and possibly not seeing more than one hammer, the chimpanzee needs to evaluate the different hammers' weight and position and infer from these their respective contribution to minimal transport distance or minimal energy expenditure. This is done flexibly anew for each transport, as the hammer selected and the goal tree for pounding the nuts will differ each time (Boesch & Boesch, 1984a). Thus, the criteria for inference are met, whereby conclusions are reached based on evidence and reasoning, the ability is demonstrated in a diverse range of tasks and domains, the behavior deviates from simple conditioning or S-R predictions, and the behavior manifests in novel perceptual circumstances on tasks never before attempted (Buckner, 2011).

The precision of the shift of preference from "heavy" to "light" for one nut species or across different species strongly suggests that chimpanzees possess mathematical-like reasoning to optimize the total energy of the entire nut-cracking session (equation 4). These levels of complexity in the cognitive evaluation of weight have not yet been tested with captive chimpanzees, which makes direct comparisons of potential differences in the cognition of weight difficult between the two environments.

Discussion

In a sense, we have arrived at a point where we must ask whether chimpanzees "can solve weight-related problems in a flexible, transferrable way that is not tied to idiosyncratic perceptual similarities or contingencies" (Buckner, 2013, p. 148), with the background expectation that only humans "solve tasks in a domain-general fashion, transferring their knowledge from one task to others that are perceptually dissimilar but share the same underlying structure" (Buckner, 2013, p. 148; Povinelli, 2012). In this discussion, I would propose that we must allow for a graded level of sophistication between a purely associative response and a strictly abstract, non-perceptual domain general one. After all, it is through experience with the outside world that animals will progressively learn regularities in the environment that can be used to predict and conceptualize about them. This gradual acquisition of competence is also seen in the ontogeny, as subadults interacting with the outside world (Boesch et al., 2019). We have seen that depending upon the context, Taï chimpanzees combine psychophysics, memory, learning and inference about weight. It should be expected that those combinations will vary as needs and experiences vary in different environments (Boesch, 2021).

How flexibly can chimpanzees in the Taï forest transfer their notion of weight from one perceptual condition to another one? And how different should these conditions be to be granted "domain-general thinking"? We can assume such a question will be answered differently depending on the background or inclination of the researcher. In his book, Povinelli (2012) distinguishes four different contexts from weight <u>lifting</u>, to weight <u>sorting,</u> weight as <u>impediment</u>, and then the <u>impact</u> of weight. He then proceeds to argue that because the chimpanzees he studied could not generalize from the first context to the second, or the third and fourth, that they would be trapped in idiosyncratic perceptual judgments. We saw that the Taï chimpanzees <u>sort</u> the weight of different hammers when selecting one out of an average of 16 to crack nuts and adapt their lifting movements to the weight of the hammer. They predict dynamically the impact of the weight on the different nut species and during the extraction steps for *Panda* nuts. Finally, they integrate the weight into their energy expenditure evaluations, even in contexts where they cannot perceive all physical features. This pattern of behavior hints at a notion of weight in Taï chimpanzees is more elaborate than a simple associative evaluation and including some precise abstract elements allowing them to generalize about weight flexibly depending on the numerous different contexts they encounter in the forest. Chimpanzees do this, although different individuals may possess different levels of precision when judging about weight, as generally illustrated by the fact that adult females manipulate the weight of the hammers more efficiently than adult males (Boesch & Boesch, 1984b).

I proposed this discussion on the Taï chimpanzees' nut-cracking behavior considering all studies done over the past four decades to stimulate a discussion of the value of observational study to understand chimpanzee's folk physics and to understand the contribution of daily life experience to cognition. In a previous study of weight with one population of captive chimpanzees, a full-blown notion of weight has been denied to them, although some elements of understanding the notion of weight were present (Povinelli, 2012; but see discussion in Buckner, 2012). The daily situations requiring a precise notion of weight differ dramatically between these two populations, the captive and the Taï one, and it is tempting to consider the daily experience of weight in the context of nut cracking as one driver for this difference. There is presently an important move towards considering more seriously ecological validity in cognitive science (Boesch, 2020, 2021; Bräuer et al., 2020; Buchanan et al., 2013; Cesario, 2021; LaDouce et al., 2017; Levitt & List, 2008; Mettke-Hofmann, 2014; Morand-Ferron et al., 2015; Pravosudov & Smulders, 2010; Rosati et al., 2014; Rosati, 2017; Smulders et al., 2010; Webster & Rutz, 2020).

The complexity of natural situations is a key driver of cognitive development, and studies in captivity face the strong risk of presenting over-simplified situations to the animals that would not elicit the level of cognitive performance seen in the wild (Boesch, 2021; Webster & Rutz, 2020). If, in theory, captive experiments can isolate a specific cognitive mechanism and study it without any interference from other factors, the reality in nature is that animals are confronted constantly with high levels of "confounding" factors that they must consider in their response. As we saw in the nut-cracking behavior, chimpanzee possibly never reason about weight alone, as the weight of a hammer never acts in isolation from density. Hence, for a wild chimpanzee, weight alone does not exist. Instead, it is always integrated into a compound "weight-hardness": they may perceive the shape, size, and color of the hammer but, to them, the determinant for success in opening the nuts lays in the composite factor "weight-hardness."

Reasoning about this composite factor "weight-hardness" is not hard-wired in chimpanzees, but strongly influenced by culture. A comparison of hammer selection across three neighboring groups of chimpanzees in the Taï forest revealed some striking differences; members of the South Group systematically preferred stone hammers (the material with the highest density) over wooden hammers that members of the North and East Group would favor only once *Coula* nuts had softened as the season progressed (Luncz et al., 2012). This result was obtained after we had controlled for the different availability of the potential hammer materials. Furthermore, members of the East Group systematically selected heavier wooden hammers compared to the members of the North Group (Luncz et al., 2012). Such cultural influences on the preference for different densities and weights of hammers stress the socially learned dimension of these notions in the context of nut cracking, despite the energetic consequence they have (Luncz et al., 2018).

A further factor to consider is that chimpanzees enjoy the taste of the nuts and will readily spend some time eating them, looking at the nut as they bite bits away to chew. To better enjoy the nuts, the chimpanzees were seen to prefer to use more hits to open the nuts at the cost of eating speed and, thus, they tend to prefer mid-weight wooden hammers, to ensure not smashing the nut (Sirianni et al., 2019).

When the selection pressure in a given environment is strong enough, chimpanzees, like other species, will develop the cognitive skills needed to survive. This is a basic tenet of evolutionary biology. The kind of abstract reasoning about weight we are suggesting that Taï chimpanzees exhibit should not be found only in the nut-cracking context. A similar level of abstract reasoning has been shown in this population when foraging for ripe fruits (Boesch, 2021; Janmaat et al., 2013, 2014, 2016; Normand et al., 2009): Finding ripe fruits is one of the major challenges in the tropical rainforest, and chimpanzees demonstrated not only an ability to memorize the location of hundreds of trees, but also to associate to each tree specific information about their size, their past productivity, and about their level of synchronicity of fruit production.

Other populations of chimpanzees are known to live in an environment where the same nuts as in Taï forest are available, but the chimpanzees ignore this rich food source, possibly because abundant alternative food sources were present, as is seen in the chimpanzee populations east of the Sassandra River in Côte d'Ivoire (Boesch et al., 1994). In Gabon, the Loango chimpanzees have access to much larger honey production from different species of bees than in Taï forest, possibly a reason why the Loango chimpanzees do not or did not learn to use tools to pound the nuts present in the park (Boesch at al., 2009). In Taï, nut cracking represents a very rich part of their diet for many months every year, and the benefit of optimal tool selection is high. If the mothers abundantly provision youngsters for 3 to 4 years, young chimpanzees are expected to have become proficient tool users when their mothers give birth to the next offspring. Thus, in the Taï forest, the time to learn to become a proficient nutcracker is limited to a few years, resulting in high pressure to acquire the necessary skills. The array of cognitive reasoning demonstrated when selecting and using a hammer in the Taï forest reveals the power of experience in shaping cognitive development.

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