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Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups

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Cultural diversity among social groups has recently been documented in multiple animal species. Investigations of the origin and spread of diverse behaviour at group level in wild-ranging animals have added valuable information on social learning mechanisms under natural conditions. Behavioural diversity has been especially informative in the case of dispersal, where the transfer of individuals between groups leads to a sudden exposure to unfamiliar behaviour. Little is known, however, about the underlying costs and benefits of cultural transmission in animals and humans alike, as efficiency of cultural variants is often difficult to measure. The chimpanzees, *Pan troglodytes*, of the Taï National Park in Ivory Coast are known to exhibit a number of cultural differences between social groups, including hammer selection for nut cracking. This provides the unique opportunity to quantify the efficiency of cultural variants. We compared foraging speed and number of hits applied during nut-cracking events between three neighbouring chimpanzee groups. Our results showed significant differences in nut-cracking efficiency, caused by hammer material selection and differences in the applied power of impact per nut. Persistent behavioural coherence within the respective groups implies that immigrants adjust their behaviour to local nut-cracking techniques, even when individual foraging success might be compromised. This suggests that the benefit of belonging to a social group might outweigh the benefits of maximizing individual foraging efficiency. The differences in nut-cracking efficiency between chimpanzee groups add to the ever-growing body of cultural variants in wild chimpanzees and expand our knowledge of the importance of group belonging and conformity in wild chimpanzees.

Social learning can create behavioural diversity among populations and therefore has been suggested to act as the foundation of culture. An increasing body of empirical data demonstrates cultural behaviour in several animal species (van Schaik et al., 2003; Whitehead & Rendell, 2014; Whiten et al., 1999). Yet, culture has been suggested to differ fundamentally between humans and nonhuman animals, one aspect of it being that nonadaptive traits are unique to humans (Barnard, 2000; Kuper, 2000; Sahlins, 2013). By contrast, animal behaviour has been suggested to reflect mainly adaptations to specific environmental conditions that provide a direct benefit to individuals (Boyd & Richerson, 1988; Durham, 1991). Although some studies have presented evidence that the use of social information in animals can be costly (Beauchamp & Kacelnik, 1990; Day, MacDonald, Brown, Laland, & Reader, 2001; Laland, 1996; Laland & Williams, 1998), in most cases socially acquired information in the animal world is assumed to be beneficial (Alvard, 2003; Boyd & Richerson, 1988).

However, more precise information is needed to understand potential cost and benefits linked to cultural variation in animals. Are all cultural variants in animal behaviour equally efficient or are some more productive than others? Was one of the earliest examples of animal culture, wheat washing in Japanese macaques, *Macaca fuscata* (Kawai, 1965), more beneficial than simply eating unwashed wheat? Answering this question is complicated by the difficulties we encounter when trying to compare the benefits of different cultural variants.

The nut-cracking behaviour of chimpanzee, *Pan troglodytes*, communities in the Taï National Park, Côte d'Ivoire, presents a

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unique opportunity for quantifying individual performance (Boesch & Boesch, 1984; Boesch & Boesch-Achermann, 2000). Previous research with these communities showed that cultural diversity in nut-cracking behaviour exists among neighbouring groups (Luncz & Boesch, 2015; Luncz et al., 2012). Within-group diversity has been found to be comparatively low (Luncz & Boesch, 2014). The most striking difference was found in community-dependent hammer selection regarding tool size and selected material (wood and stone) when cracking *Coula edulis* nuts, despite similar raw materials and similarly hard nuts being available (for details on hammer selection pattern see Table 1). Diversity in tool selection among neighbours persisted over decade-long periods despite frequent female dispersal between communities (Luncz & Boesch, 2014; Luncz, Wittig, & Boesch, 2015).

In the present study we investigated whether group-specific hammer selection for *Coula* nut cracking influences the foraging efficiency of wild chimpanzees. Only through comparisons between several groups that display the same behaviour can the costs or benefits of cultural variants be determined. This comparison might provide insight into potential energetic advantages or disadvantages of behavioural variants.

In recent publications, the efficiency of percussive foraging activities has been measured in several different ways, including the number of hits per nut and the nut intake rate per unit time (Boesch & Boesch, 1984; Fragaszy et al., 2010; Neufuss, Humle, Cremaschi, & Kivell, 2016). For a competitive forager in a natural habitat, the intake rate of nutrients ([benefits − costs]/time) is important, and therefore the time needed to open and consume a nut is a key variable in foraging efficiency. Therefore, to compare the benefits of different cultural variants, the most efficient group was considered the one with the highest nut intake per unit time.

Coula nuts are hard shelled but rather softer than other nuts present in the Taï forest, and physical force is not the main limiting factor in accessing the inner kernel for adult chimpanzees (Boesch & Boesch, 1983). When cracking nuts, chimpanzees face a trade-off between power and control of the hammer. They need to deliver enough kinetic energy to fracture the shell (threshold energy). At the same time delivering very powerful strikes might smash the inner kernel, resulting in wasted time spent collecting nut fragments from and around the anvil (Sirianni, Luncz, & Gratton, 2017). Physical properties of the selected hammer are expected to influence power and control of the nut-cracking movements and thus the overall efficiency (Boesch & Boesch, 1983; Schrauf, Call, Fuwa, & Hirata, 2012; Sirianni, Mundry, & Boesch, 2015). The harder the hammer material, the smaller its deformations when it hits the nut and thus the smaller the dissipation of kinetic energy at impact (Pelcin, 1997). Stones are generally harder than wood, and cracking nuts with a stone hammer allows for 20% less energy expenditure than with a wooden hammer (Boesch & Boesch, 1983). The physical properties of the selected tools are expected to influence the energy (kinetic energy: $0.5 \times mv^2$) delivered onto the nut. On the one hand, heavier tools produce higher kinetic energy (therefore reducing the number of strikes; Boesch & Boesch, 1983; Bril, Dietrich, Foucart, Fuwa, & Hirata, 2009; Fragaszy et al., 2010; Massaro, Liu, Visalberghi, & Fragaszy, 2012; Schrauf et al., 2012). On the other hand, heavier tools may be less easy to manipulate and control (Sirianni et al., 2015, Sirianni et al., 2018). Therefore, denser materials (such as stones, as compared to wood) allow the animal to exploit the increased power associated with a heavier weight with a comparatively smaller decrease in control.

Table 1
Differences in tool selection for Coula edulis nut cracking in three neighbouring chimpanzee groups in the Taï National Park, Côte d'Ivoire

	East	North	South
Preferred hammer material	Stone->wood	Stone->wood	Stone
Preferred wooden hammer size	Small->large	Small	Small->large

The arrow indicates a gradual shift of preference over the season.

In particular, to shed light on potential costs and benefits of cultural traits in wild chimpanzees, we investigated the following three questions.

Qestion 1: Does nut-cracking efficiency differ between groups?

We first investigated whether there are overall differences in nut-cracking efficiency (nut intake per unit time) between neighbouring chimpanzee groups in the Taï forest. If tool use was an adaptive trait to ecological circumstances, we predicted that, despite differences in observed nut-cracking behaviour and tool preference, chimpanzees would develop multiple maximum foraging optima and therefore show similar foraging efficiencies between groups when cracking *Coula* nuts. Members of communities selecting less optimal hammers would be expected to compensate with muscular energy for the limitations of the selected hammer and therefore show equal efficiencies to those using more optimal hammers. If this analysis revealed differences between groups, we would further explore possible underlying reasons responsible for the differences seen.

Question 2: Do hammer properties influence foraging efficiency?

Question 2a: Do tool properties influence efficiency?

We hypothesized that hammer material and hammer size influence nut-cracking efficiency. We predicted that, being harder (less dissipation of energy at impact) and denser (weight being equal at a smaller size) than wood, stone hammers would be more efficient and allow for a higher nut intake per unit time. We further predicted that larger hammers would affect intake rate per unit time positively (supported by Sirianni et al., 2017). If our predictions held true, chimpanzee groups that displayed differences in the selection of hammer properties should consequently differ in their nut-cracking efficiency.

Question 2b: Does tool specialization lead to equal efficiency?

We took into account another hypothesis that, regardless of the physical properties of the hammer, chimpanzees become experts in handling their group-specific tool selection which ultimately leads to similar efficiency. This kind of tool specialization has been seen in other tool-using animals, for example sea otters, *Enhydra lutris nereis* (Fujii, Ralls, & Tinker, 2015, 2017; Tinker, Bentall, & Estes, 2008). Individuals that had more opportunity to use tools with certain properties (material and size) would be expected to be more efficient with these specific tool properties. We therefore predicted that, when using the same tool properties, groups would differ in their nut-cracking efficiency as their skill level with the respective material is expected to be different.

Question 3: Does number of hits per nut differ between groups?

Experimental tests measuring the hardness of *C. edulis* nuts revealed that they are of similar hardness in all three territories (Luncz et al., 2012) and therefore needed the same amount of kinetic energy to be cracked open. We predicted that chimpanzees across all study groups would deliver similar numbers of hits per nut when cracking with hammers of similar properties (size and material). This is expected to lead to similar foraging rates between groups when using hammers with similar properties.