



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

Lydia V. Luncz^{a, b, *}, Giulia Sirianni^b, Roger Mundry^b, Christophe Boesch^b

^a Institute of Cognitive and Evolutionary Anthropology, University of Oxford, Oxford, U.K.

^b Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

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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.

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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; Sahlin, 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

* Correspondence: L.V. Luncz, Institute of Cognitive and Evolutionary Anthropology, University of Oxford, 64 Banbury Road, Oxford, OX2 6PN, U.K.

E-mail address: Lydia.Luncz@anthro.ox.ac.uk (L. V. Luncz).

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; Frigaszy 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; Frigaszy et al., 2010; Massaro,

Liu, Visalberghi, & Frigaszy, 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.

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

Question 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.

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.

METHODS

Observational Data Collection

The study was carried out in the Taï National Park in Côte d'Ivoire, West Africa (5°50'N, 7°21'W). To compare nut-cracking efficiency between three neighbouring chimpanzee communities, we recorded tool material (stone versus wood) and tool size selection, the number of hits applied to open *C. edulis* nuts and the nut intake rate for all adult group members (aged 13 years or older) during January 2008 and February 2013. Observational data were collected during all day follows by L.V.L. and G.S. using the focal sampling method (Altmann, 1974). All individuals were fully habituated and reliably identified by the observer. During the observation period, we estimated hammer size using five size classes, and later, if possible, we took direct measurements of each tool's weight and length (14% of all estimated hammer sizes were confirmed by direct measurement to control for consistency between estimates and measurements, revealing 98% concordance). Ecological differences between the territories have previously been compared in detail (Luncz et al., 2012). Raw material availability and nut hardness were similar across study groups (Luncz et al., 2012).

Statistical Analyses

For statistical analyses, we used generalized linear mixed models (GLMM, Baayen, 2008) throughout fitted with negative binomial error structure and log link function (McCullagh & Nelder, 1989). All GLMMs were fitted in R (version 3.4.1; R Core Team, 2017) using the function `glmer` provided by the R package `lme4` (version 1.1–13; Bates et al., 2015). Throughout, we used the optimizer 'bobyqa' to avoid convergence issues. *P* values for the individual effects were based on likelihood ratio tests comparing the full model with the respective reduced models (Barr, 2013). To obtain confidence intervals of model coefficients, we bootstrapped the full model 1000 times (using the function `bootMer` of the package `lme4`). Prior to fitting the models, we z-transformed age, day in season and tool size (mean (SD) of the original variables were 29.189 (11.502), 54.510 (27.434) and 2.720 (1.281) for age (years), day in season (start marked at the first nut-cracking day of the season) and tool size (measured in accessible parameters for the respective material: length for wooden tools and weight for stone tools), respectively). In all models the sample size was a total of 357

nut-cracking sessions, observed for 47 individuals and on 95 days. A session was defined as the entire nut-cracking time a chimpanzee spent at an anvil using a given hammer. Once a chimpanzee moved to a different anvil that was more than 500 m away or once it dropped the hammer in use, a new session started.

During the study period the chimpanzees cracked *Coula* nuts exclusively on wooden anvils, most of which were *Coula* roots.

Overall comparison between groups (model 1)

We first tested for overall difference in nut-cracking efficiency between groups. If this model reveals no obvious effect of group, this means that the different groups cracked nuts with similar efficiencies, despite their differing tool preferences; if it reveals an effect of group, this means that certain tool choice preferences come at the cost of reduced foraging efficiency (see question 1 above). We included as the response variable the number of nuts consumed per session and included an offset term controlling for the duration of each session (log transformed; McCullagh & Nelder, 1989). As predictor variables with fixed effects we included the group, day in the season, age and sex of each individual. We further controlled for the day in the season the observation took place and individual identity by including them as random effects in the model. To keep type I error rate at the nominal level of 5% we included random slopes of age and day in the season within individual (Barr, 2013; Schielzeth & Forstmeier, 2009). We determined the statistical significance of the full model by comparing its fit with that of the null model (R function 'anova') lacking the predictor group but otherwise identical to the full model. For a summary of hypotheses, predictions and models see Table 2.

Influence of hammer properties on efficiency (model 2)

To test whether hammer properties (material and size) influenced the number of nuts consumed per unit time and whether this influence differed between groups, we used a GLMM which included the number of nuts consumed per session as the response variable. As predictors with fixed effects, we included the three-way interactions between tool size, tool material and social group (and the three two-way interactions as well as the three main effects comprised therein) as well as sex and age of the individual and the day in the nut season. The random-effects structure of this model was identical to that of model 1, with the exception that this time we also included a random slope of tool

Table 2
Summary of hypotheses, predictions and models

Question	Prediction hypothesis	Expected efficiency ^a	Full model	Null/reduced model	Tests
(1) Costly culture	Efficiency differs among groups	SG ≠ NG ≠ EG	Nuts per time~group+sex+day+age+offset+(random effects)	Nuts per time~sex+day+age+offset+(random effects)	Hypothesis 1
(2) Hammer properties and efficiency:					
(a) Tool properties influence efficiency	Stones increase efficiency Small tools increase efficiency	SG>NG, EG NG>SG, EG	Nuts per time ~ group*material* size+day+sex+age+offset+(random effects)	Null: Nuts per time~material*size+day+sex+age+offset+(random effects) Reduced: Nuts per time~group+material*size+day+sex+age+offset+(random effects)	Hypothesis 2
(b) Tool specialization equalizes efficiency	Most used group tool property increases efficiency	Stones higher efficiency in SG Small wood higher efficiency in NG Large wood higher efficiency in SG, EG			Hypothesis 2+ Hypothesis 3
(3) Different techniques (no. of hits per nut)	No. of hits differs among groups	na	No.hits~group*size*material+material+sex+age+day+offset+(random effects)	No.hits~size*material+sex+age+day+offset+(random effects)	Hypothesis 3

^a Efficiency: nut intake per unit of time; SG, EG and NG refer to South, East and North Group, respectively.

size within individual, and we also included the same offset term as described for model 1.

To test whether the effects of tool properties (material and size) differed between the three study communities, we first tested the significance of the interactions between tool material and size, on the one hand, and group, on the other, by comparing the full model with the respective reduced models lacking the three-way and the two-way interactions (but otherwise identical to the full model). If this test does not reveal significance it suggests that variation in hammer size and/or material did have similar effects in the three groups and that tools of the same properties were used with similar efficiencies in the three groups, indicative of culture being costly because of different tool preferences (i.e. members of different groups do use tools of the same properties with similar efficiencies but prefer different tool properties, see question 2a above). In this case, a model lacking the interactions should reveal a clear group effect despite controlling for tool properties and/or clear effects of tool material, size and/or their interaction. On the other hand, clear interaction effects would indicate that chimpanzees of different groups used tools of the same properties with differing efficiency. This would tell us whether chimpanzees specialize on a certain tool property (see question 2b above).

Number of hits per nut (model 3)

To investigate whether the strategy of nut cracking varied between the three groups, we analysed the number of hits to the target nut when individuals were using hammers of similar properties (see question 3 above).

We included the number of hits per nut-cracking session as the response variable and accounted for varying numbers of nuts cracked per session by including them as an offset term (log transformed). Since the key question was whether groups differed in their nut-cracking strategy (i.e. number of hits per nut) we included group and its three-way interaction with tool material and size (and all three two-way interactions and main effects it entails) as well as the sex and the age of the nut cracker and the day in the nut season. The random-effects structure was identical to that of model 2.

To test for differences between groups (either as a main effect or in the form of interactions of group with tool size and/or material), we compared the full model described above with a null model lacking group and its interactions with tool size and material but otherwise identical to the full model (Forstmeier & Schielzeth, 2011). This comparison was based on a likelihood ratio test.

General considerations

Collinearity, assessed by applying the function *vif* of the R package *car* (Fox & Weisberg, 2011) to a linear model lacking the random effects and interactions, appeared not to be an issue (Field, 2009; Fox & Monette, 1992). Neither was overdispersion (range of dispersion parameters 0.954–1.117). We assessed model stability by dropping levels of the random effects one at a time and comparing the estimates derived from models fitted to these subsets to those derived for the full data set. This revealed no influential levels of random effects (see Tables A1, A2, A5 in the Appendix).

Ethical Note

Data collection was noninvasive and in compliance with the requirements and guidelines of the 'Ministère de l'enseignement supérieure et de la recherche scientifique', which granted

permission for this research, and adhered to the legal requirements of the Côte d'Ivoire. We further strictly adhered to the regulations of the Deutsche Tierschutzgesetz and the American Society of Primatologists' principles for the ethical treatment of nonhuman primates.

RESULTS

Overall Comparison Between Groups (Model 1)

Overall, *C. edulis* nut-cracking efficiency differed between neighbouring chimpanzee groups (comparisons between the full and the null model, likelihood ratio test: $\chi^2_2 = 6.902$, $P = 0.032$; Fig. 1). There was no obvious difference between South and North groups, but both had a higher nut intake per unit time than their neighbouring East Group. In addition to group differences, the day in the season on which the nut was cracked also had a significant effect on the number of nuts cracked per unit time ($P = 0.025$). For a model summary and confidence intervals, see Appendix Table A1.

Influence of Hammer Properties on Efficiency (Model 2)

Overall, we found a clear effect of hammer properties on the nut-cracking efficiency in wild chimpanzees. The comparison between the full model and the model lacking the three-way interaction between group, tool material and tool size and the two two-way interactions between group and tool material and size, respectively, did not reveal significance ($\chi^2_6 = 3.919$, $P = 0.688$); neither did any of these three interactions (Appendix Tables A2 and A3). This shows that the effects of hammer properties on efficiency were roughly similar in the three groups. We therefore removed the interactions from the model (and the interaction between tool material and size, which did not reveal significance either; Appendix Table A3). The resulting model revealed that groups tended to differ ($P = 0.072$; Appendix Table A4). Additionally, stone hammers were found to be more efficient than wooden hammers ($P = 0.005$; Fig. 2). As our previous model showed as well, nut-cracking efficiency was higher at the end of the season when nuts were dry and easier to crack ($P = 0.012$). Finally, the model revealed a trend towards larger tools being more efficient than small tools ($P = 0.072$).

The results demonstrate the influence of the physical properties of hammers on nut-cracking efficiency. However, our test additionally revealed that, even when using the same tools (material and size), groups still tended to differ in their nut-cracking efficiency. East Group was generally less efficient than the North and South groups. This indicates that hammer properties alone do not explain the differences seen in nut-cracking efficiency in neighbouring chimpanzee groups.

Number of Hits per Nut (Model 3)

Overall, we found that, when the same hammer type (material and size) was used, the number of hits per nut (nut-cracking technique) differed between the three study communities (GLMM, full null model comparison: $\chi^2_8 = 54.047$, $P < 0.001$). In the full model, the three-way interaction between group, tool size and material appeared nonsignificant ($P = 0.213$; Appendix Table A5), and the two-way interactions between group and tool size or material, respectively, appeared nonsignificant ($P = 0.230$ and 0.743 , respectively; Appendix Table A6). After removal of all interactions involving group, we found that East Group clearly applied fewer hits per nut (Appendix Table A7, Fig. 3).

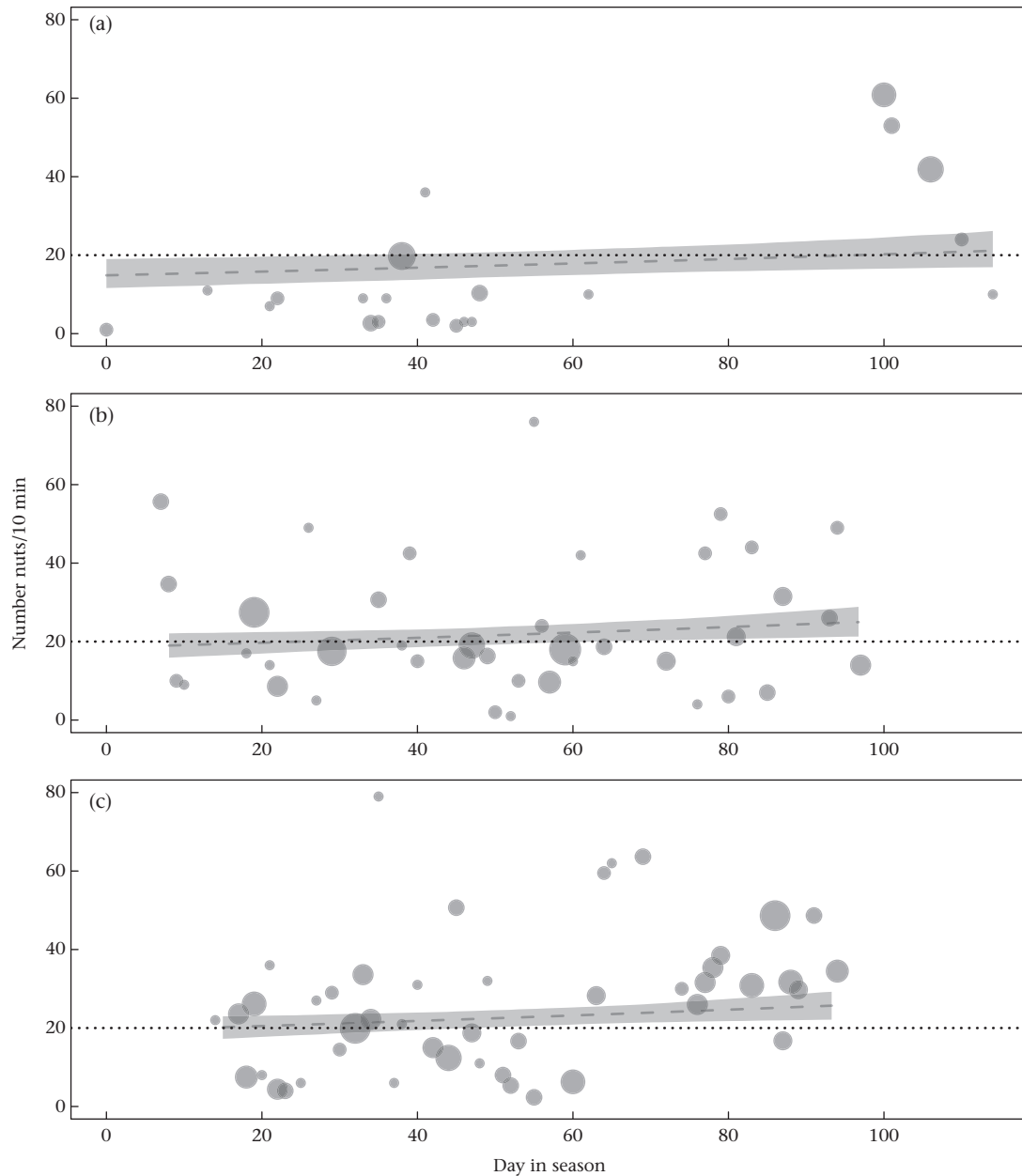


Figure 1. Comparison of Coula nut intake per 10 min in three neighbouring Tāi chimpanzee groups. (a) East Group, (b) North Group and (c) South Group. We included a horizontal dotted line at 20 nuts per 10 min for easier visual comparison. Each point represents the average number of nuts cracked per 10 min for 1 day. The size of the points represents the number of nut-cracking sessions observed per day (1–12). The fitted model and its confidence intervals are depicted by the dashed line and grey area, respectively.

DISCUSSION

Hammer preference during nut cracking of wild chimpanzees has previously been found to be culturally influenced, leading to differences in tool selection between three neighbouring groups in the Tāi National Park (Luncz et al., 2012). Our results show that these cultural variants lead to relevant differences in nut-cracking efficiency between groups. Hammer properties had a strong influence on the foraging efficiency of chimpanzees. As predicted, stones were generally more efficient to crack open nuts than wooden hammers, whereas hammer size, on the other hand, did not show such a large impact on nut-cracking efficiency, although larger hammers tended to be more efficient than small ones. Taking these results together with previous information on

different hammer preferences of the Tāi chimpanzee groups (Luncz et al., 2012), we conclude that South Group members, through their preferred use of stone tools, are inevitably more efficient than North and East Group members which both use mainly wooden tools. This shows that belonging (and conforming) to a cultural subgroup with distinct preferences for certain tool properties can indeed lead to foraging costs or benefits for individuals.

Unlike the results of studies of other tool-using mammals such as sea otters (Fujii, Ralls, & Tinker, 2017), our findings did not support the 'tool specialization hypothesis'. Although North and East Group members generally used more wooden hammers than the South Group, they did not show higher nut intake rates when using wooden tools. Likewise, members of South Group

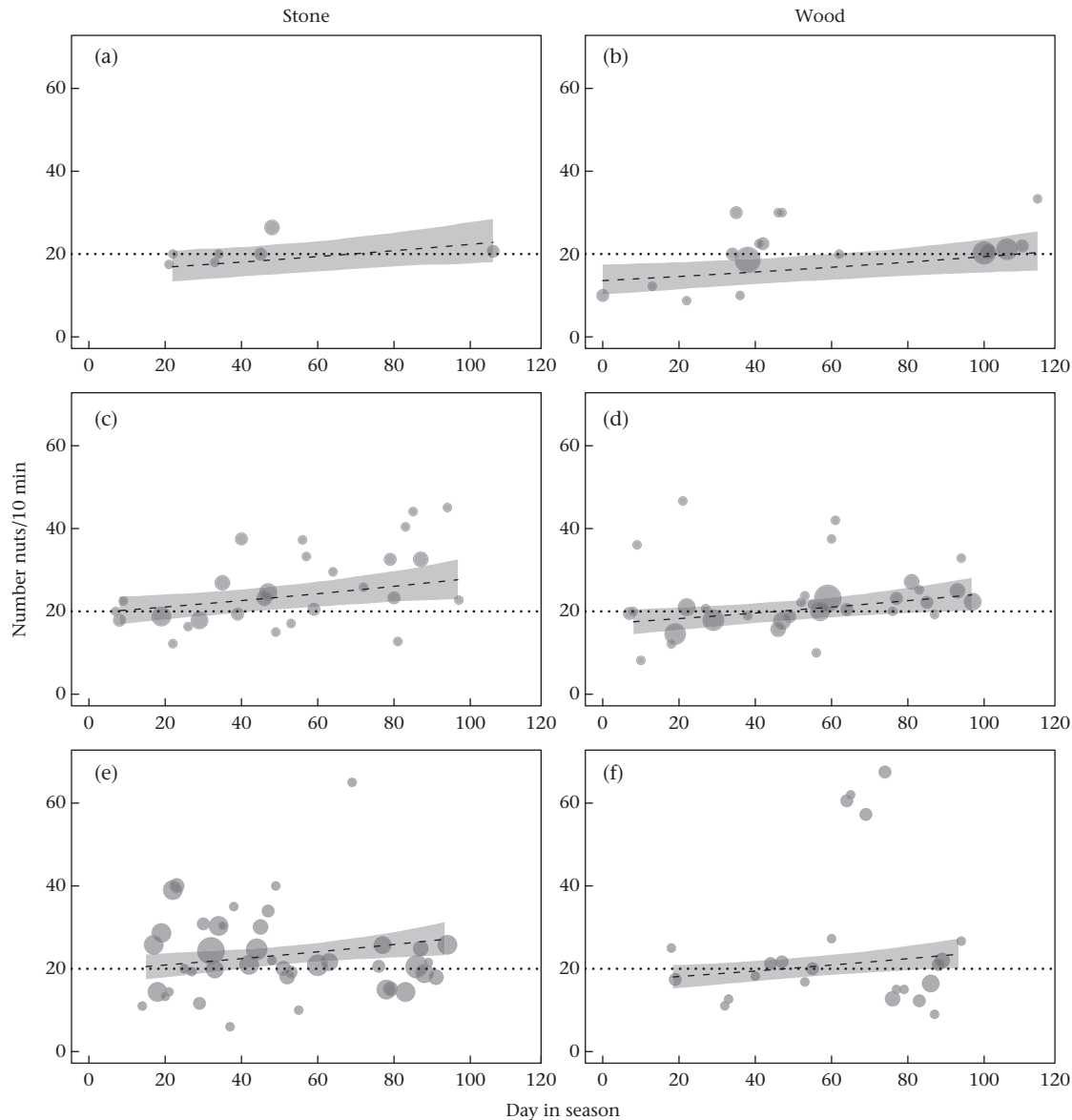


Figure 2. Comparison of *Coula* nut intake rate per 10 min in three neighbouring Tāi chimpanzee groups controlled for hammer material. (a, b) East Group, (c, d) North Group and (e, f) South Group; (a, c, e) stone hammers and (b, d, f) wood hammers. We included a horizontal dotted line at 20 nuts per 10 min for easier visual comparison. Each point represents the average number of nuts cracked per 10 min per day. The size of the points represents the number of nut-cracking sessions observed per day (1–10). The fitted model and its confidence intervals are depicted by the dashed line and grey area, respectively.

were not more efficient at using stone tools than their neighbours.

However, even when cracking nuts with hammers of similar properties, groups still differed in their nut-cracking efficiency. The South and North groups, which preferred different tool materials, still reached similar efficiencies. This indicates that tool properties alone did not predict foraging efficiency. In fact, the number of hits used to crack open *Coula* nuts differed between the three chimpanzee groups which eventually led to differences in foraging efficiency. Even though North and South groups preferred different hammer properties, the strategy these groups applied when cracking nuts was similar. Both groups used more hits per nut to crack open *Coula* nuts than the East Group. Hitting a nut multiple times with controlled energy is expected to increase the precision when a nut reaches its breaking point and is therefore a strategy expected to support the increased foraging speed. To

crack open *Coula* nuts of similar hardness, the fewer hits used by East Group members must have contained more energy per hit, potentially leading to decreased precision of force applied to each hit which in the end might be responsible for their loss in foraging speed. The three groups therefore used different nut-cracking strategies (number of strikes per nut) as a solution for the same task.

In summary, regarding the number of nuts consumed per min, East Group members were the least efficient nut crackers, whereas North and South Group members each displayed nut-cracking strategies that led to similar nut-cracking efficiency. All three chimpanzee communities had developed different nut-cracking cultures, causing them to differ in foraging efficiency. We therefore conclude that even within those cultural behaviours that are clearly advantageous to the individuals performing them, especially in the foraging context, following specific cultural traits

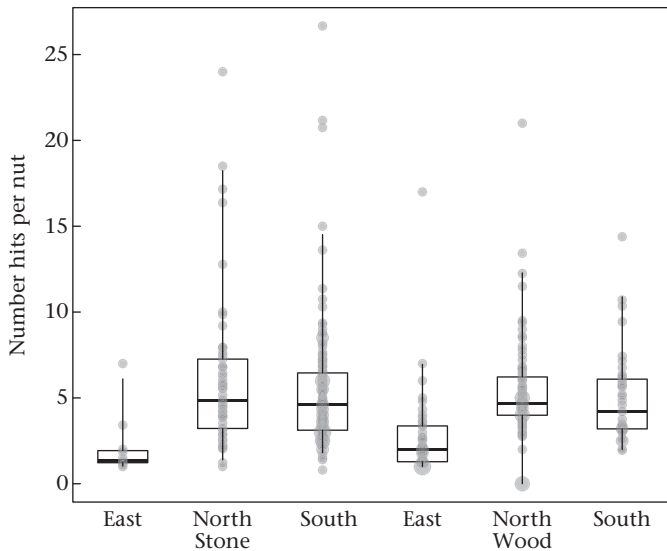


Figure 3. Number of hits per nut according to hammer material (wood and stone) in the three Taï chimpanzee groups. Horizontal lines and boxes depict medians and quartiles, respectively, and vertical lines depict quantiles (2.5 and 97.5%); the circles show the individual observations. The size of the points is proportionate to the number of observations per group, number of hits per nut and session (1–4).

within a group (e.g. tool selection or tool use strategies) can entail costs or benefits for individual foragers.

Overall, however, nut cracking is an energetically beneficial cultural behaviour, compared to populations that do not crack nuts, despite the presence of consumable nuts (Boesch, 1991; Guenther & Boesch, 1993). Therefore, it is possible that the costs of selecting suboptimal hammers might be small compared to the overall benefits of cracking nuts. The costs of a particular variant of a behaviour of a group's repertoire may be offset in other domains by group-specific variants that could either increase energy intake or reduce expenditure. Nevertheless, intergroup competition between chimpanzees is high and long-term effects of suboptimal foraging tools and techniques might have a negative impact on overall fitness. Overall, a forager from South Group for example ingests on average 5400 more nuts per season (30 nuts/h times 1.5 h of daily nut ingestion (Guenther & Boesch, 1993) times 4 months) than an East Group chimpanzee (that equals an energetic advantage of roughly 309 616 kJ per year). Only long-term observations of the groups displaying cultural variants will provide definite answers. However, all chimpanzee groups under study in the Taï forest successfully occupy a large territory and exhibit normal interbirth intervals, which suggest that while there may be differences in foraging efficiency for *Coula* nut cracking, these do not necessarily have a direct negative effect.

Costs, however, might arise when dispersing individuals take up a less efficient cultural variant of their new group. At the onset of sexual maturity female chimpanzees leave their natal group and integrate into a new one (Boesch & Boesch-Achermann, 2000). As it is rare that females remain in their natal group, most adult females in the Taï research groups had immigrated at one point in their life. Despite personal knowledge of proficient nut cracking, immigrating female chimpanzees have been reported to take up the nut-cracking strategy of their new community within weeks (Luncz & Boesch, 2014; Luncz et al., 2015), leading to stable cultural differences between groups over a period of decades (Luncz & Boesch, 2014). Here chimpanzee females are confronted with the decision to follow the group's

behaviour even though it might imply a personal disadvantage. Females moving into the East Group therefore potentially conform to less efficient nut-cracking solutions than those of its neighbouring groups. Accepting local customs nevertheless may indicate that the benefit of belonging to a group outweighs the benefits of maximizing individual foraging strategies. The mechanisms and driving factors underlying conformity have been well studied in humans (Asch, 1956; Haun & Tomasello, 2011; Morgan & Laland, 2012) and several recent studies have provided valuable information for better understanding similar social learning mechanisms in nonhuman animals (Aplin et al., 2015; Claidière & Whiten, 2012; Kendal, Coolen, & Laland, 2004; Lamon, Neumann, Gruber, & Zuberbühler, 2017; van Leeuwen, Kendal, Tennie, & Haun, 2015; van de Waal, Borgeaud, & Whiten, 2013). Only observations of females before and after immigration would give definite answers to the costs entailed in cultural transmission. Observing immigration is rare in the wild, and the habituation and long-term observation of multiple chimpanzee groups needs to be guaranteed. Up to now, our conclusions are inferred from persistent behavioural differences observed between neighbouring groups.

The different nut-cracking strategies described in our study add to the known cultural diversity among the three communities in the Taï National Park and support previous findings of group-specific cultural solutions, including nut cracking (Luncz & Boesch, 2014; Luncz et al., 2012, 2015). Our results additionally show that suboptimal cultural behaviours exist in wild chimpanzees, and that such traits are therefore not unique to the hominin lineage. While there are no precise cost–benefit analyses of the different alternatives for the majority of human cultural traits, a number of these traits have been shown to impose either direct or long-term fitness disadvantages to their holders (Durham, 1976; Hewlett & Cavalli-Sforza, 1986).

Differences between human groups (societies, countries, villages) are sometimes actively implemented to reinforce loyalty to the group (Baumeister & Leary, 1995; Fiske, 2010). Group members do not select the best solution available to them but copy those in their social group. Some authors have proposed that conforming to social norms can override the biological costs for individually detrimental cultural traits (Boyd & Richerson, 1988; Henrich & McElreath, 2003) and these social norms are sometimes implemented through communal force by institutionalized authorities. Our observations of wild chimpanzees have never detected any punishment for instances where the group-specific behaviour was not performed, suggesting that the adoption of a certain solution is based on individual observations and decisions rather than imposed by local group members.

By finding consistent differences in nut-cracking solutions between neighbouring groups, our study highlights the fact that we cannot assume that individuals in certain groups within a species have adopted the optimal solution based on individual learning, as is often suggested (Laland & Hoppitt, 2003; Laland & Janik, 2006). It remains to be investigated whether cultural variants documented in various other chimpanzee populations with multiple habituated groups (Koops, Schöning, Isaji, & Hashimoto, 2015; Luncz et al., 2012; Whiten et al., 1999) could present similar costly differences. The existence of multiple, potentially equally optimal solutions to the same problem sets the stage for cultural elaboration to develop, with individuals able to switch between different strategies based on the social context.

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Appendix

Table A1

Results of the GLMM (model 1) investigating overall group differences in nut intake rates per unit time

Term	Estimate	SE	Lower CL	Upper CL	χ^2	df	P	Min ^a	Max ^a
Intercept ^b	3.969	0.093	3.762	4.141			NI ^c	3.899	4.010
Groupnorth ^d	0.220	0.104	0.031	0.429	6.902	2	0.032	0.174	0.287
Groupsouth ^d	0.260	0.098	0.062	0.467				0.208	0.326
Sex ^e	−0.013	0.062	−0.129	0.098	0.045	1	0.833	−0.063	0.022
Age ^f	0.029	0.027	−0.023	0.082	1.082	1	0.298	0.004	0.041
Day in season ^f	0.085	0.038	0.008	0.159	5.026	1	0.025	0.066	0.093

^a Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time.

^b The model was fitted with an offset term: the logarithm of the duration of the session divided by 30 min.

^c Not indicated because it has a limited interpretation.

^d Group was dummy coded with East Group being the reference category; the indicated likelihood ratio test refers to the overall effect of group tested by comparing the full model with a reduced model lacking group.

^e Sex was dummy coded with female being the reference category.

^f Z-transformed to a mean of 0 and SD of 1.

Table A2

Results of the full model (GLMM; model 2) investigating potential predictors influencing nut intake rate per unit time

Term	Estimate	SE	Lower CL	Upper CL	χ^2	df	P	Min ^a	Max ^a
Intercept ^b	2.900	0.182	2.479	3.250			NI ^c	2.640	3.063
Sex ^d	−0.015	0.060	−0.138	0.090	0.063	1	0.803	−0.061	0.024
Age ^e	0.030	0.026	−0.025	0.080	1.264	1	0.261	0.006	0.042
Day in season ^e	0.095	0.039	0.023	0.173	5.977	1	0.014	0.078	0.111
Tool size ^e	−0.004	0.192	−0.457	0.378			NI ^c	−0.146	0.163
Tool material ^f	−0.077	0.186	−0.428	0.344			NI ^c	−0.291	0.105
Groupnorth ^g	0.323	0.195	−0.056	0.765			NI ^c	0.157	0.580
Groupsouth ^g	0.254	0.186	−0.088	0.686			NI ^c	0.087	0.513
Tool_material*tool size	0.054	0.203	−0.347	0.502			NI ^c	−0.066	0.206
Tool material*Groupnorth	−0.147	0.200	−0.579	0.245			NI ^c	−0.329	0.066
Tool material*Groupsouth	−0.035	0.199	−0.467	0.341			NI ^c	−0.220	0.179
Tool size*Groupnorth	0.067	0.198	−0.331	0.525			NI ^c	−0.100	0.211
Tool size*Groupsouth	0.043	0.197	−0.348	0.491			NI ^c	−0.124	0.190
Tool material*tool size*Groupnorth	−0.154	0.217	−0.610	0.291	2.204	2	0.332 ⁱ	−0.304	−0.036
Tool material*tool size*Groupsouth	−0.003	0.217	−0.498	0.430				−0.158	0.116

^a Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time.

^b The model was fitted with an offset term: the logarithm of the duration of the session divided by 10 min.

^c Not indicated because it has a limited interpretation.

^d Sex was dummy coded with female being the reference category.

^e Z-transformed to a mean of 0 and SD of 1.

^f Tool material was dummy coded with stone being the reference category.

^g Group was dummy coded with East Group being the reference category.

ⁱ The indicated likelihood ratio test refers to the overall effect of the respective interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Table A3

Results of the reduced model (GLMM; model 2a; lacking the nonsignificant three-way interaction) investigating potential predictors influencing nut intake rate per unit time

Term	Estimate	SE	χ^2	df	P
Intercept ^a	2.870	0.162			NI ^b
Sex ^c	−0.015	0.060	0.060	1	0.806
Age ^d	0.031	0.026	1.342	1	0.247
Day in season ^d	0.096	0.038	6.120	1	0.013
Tool size ^d	0.060	0.074			NI ^b
Tool material ^e	−0.050	0.168			NI ^b
Groupnorth ^f	0.341	0.177			NI ^b
Groupsouth ^f	0.287	0.166			NI ^b
Tool material*tool size	−0.017	0.050	0.114	1	0.736
Tool materialwood*Groupnorth	−0.156	0.184	1.320	2	0.517 ^g
Tool materialwood*Groupsouth	−0.051	0.180			
Tool size*Groupnorth	−0.026	0.075	0.255	2	0.880 ^g
Tool size*Groupsouth	−0.002	0.073			

^a The model was fitted with an offset term: the logarithm of the duration of the session divided by 10 min.^b Not indicated because it has a limited interpretation.^c Sex was dummy coded with female being the reference category.^d Z-transformed to a mean of 0 and SD of 1.^e Tool material was dummy coded with stone being the reference category.^f Group was dummy coded with East Group being the reference category.^g The indicated likelihood ratio test refers to the overall effect of the respective interaction with group (tested by comparing the full model with a corresponding reduced model lacking the interaction).**Table A4**

Results of the reduced model (GLMM; model 2b; lacking all interactions) investigating predictors potentially influencing nut intake rates per unit time

Term	Estimate	SE	Lower CL	Upper CL	χ^2	df	P
Intercept ^a	2.948	0.099	2.741	3.125			NI ^b
Sex ^c	−0.010	0.059	−0.122	0.096	0.027	1	0.871
Age ^d	0.031	0.026	−0.026	0.080	1.325	1	0.250
Day in season ^d	0.097	0.038	0.023	0.172	6.244	1	0.012
Tool size ^d	0.043	0.023	0.004	0.091	3.226	1	0.072
Tool material ^e	−0.142	0.048	−0.238	−0.051	8.063	1	0.005
Groupnorth ^f	0.225	0.103	0.022	0.444	5.262	2	0.072 ^f
Groupsouth ^f	0.217	0.100	0.027	0.423			

^a The model was fitted with an offset term: the logarithm of the duration of the session divided by 10 min.^b Not indicated because it has a limited interpretation.^c Sex was dummy coded with female being the reference category.^d Z-transformed to a mean of 0 and SD of 1.^e Tool material was dummy coded with stone being the reference category.^f Group was dummy coded with East Group being the reference category; the indicated likelihood ratio test refers to the overall effect of group (tested by comparing the full model with a corresponding reduced model lacking group).**Table A5**

Results of the full model (GLMM; model 3) investigating predictors potentially influencing the number of hits used to crack nuts

Term	Estimate	SE	Lower CL	Upper CL	χ^2	df	P	Min ^a	Max ^a
Intercept ^b	0.834	0.195	0.416	1.135			NI ^c	0.497	1.041
Sex ^d	−0.093	0.069	−0.227	0.057	1.760	1	0.185	−0.126	−0.056
Age ^e	−0.054	0.029	−0.109	0.003	3.342	1	0.068	−0.068	−0.036
Day in season ^e	−0.037	0.033	−0.101	0.028	1.229	1	0.268	−0.050	−0.022
Tool size ^e	−0.362	0.209	−0.779	0.041			NI ^c	−0.537	−0.155
Groupnorth ^f	0.791	0.206	0.437	1.220			NI ^c	0.583	1.126
Groupsouth ^f	0.724	0.198	0.392	1.136			NI ^c	0.521	1.056
Tool material ^g	0.093	0.206	−0.265	0.560			NI ^c	−0.034	0.432
Groupnorth*tool size	0.005	0.220	−0.428	0.449			NI ^c	−0.199	0.179
Groupsouth*tool size	0.004	0.215	−0.407	0.443			NI ^c	−0.206	0.180
Groupnorth*tool material	−0.039	0.221	−0.532	0.341			NI ^c	−0.380	0.087
Groupsouth*tool material	0.028	0.221	−0.437	0.406			NI ^c	−0.307	0.156
Tool size*tool material	0.283	0.222	−0.149	0.714			NI ^c	0.055	0.401
Groupnorth*tool size*tool Material	−0.076	0.236	−0.534	0.385	3.092	2	0.213 ⁱ	−0.192	0.153
Groupsouth*tool size*tool material	−0.263	0.237	−0.748	0.202				−0.382	−0.031

^a Minimum and maximum of model estimates obtained when dropping levels of random effects one at a time.^b The model was fitted with an offset term: the logarithm of the number of nuts cracked per session.^c Not indicated because it has a limited interpretation.^d Sex was dummy coded with female being the reference category.^e Z-transformed to a mean of 0 and SD of 1.^f Group was dummy coded with East Group being the reference category.^g Tool material was dummy coded with stone being the reference category.ⁱ The indicated likelihood ratio test refers to the overall effect of the interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Table A6

Results of the reduced model (GLMM; model 3a; nonsignificant three-way interaction removed) investigating predictors potentially influencing the number of hits used to crack nuts

Term	Estimate	SE	χ^2	df	P
Intercept ^a	0.766	0.170			NI ^b
Sex ^c	−0.083	0.070	1.388	1	0.239
Age ^d	−0.053	0.030	3.194	1	0.074
Day in season ^d	−0.035	0.033	1.108	1	0.292
Tool size ^d	−0.227	0.091			NI ^b
Groupnorth ^e	0.871	0.184			NI ^b
Groupsouth	0.781	0.175			NI ^b
Tool material ^f	0.158	0.182			NI ^b
Groupnorth*tool size	−0.096	0.102	2.937	2	0.230 ^g
Groupsouth*tool size	−0.161	0.095			
Groupnorth*tool material	−0.121	0.201	0.594	2	0.743 ^g
Groupsouth*tool material	−0.048	0.198			
Tool size*tool material	0.130	0.056	5.321	1	0.021

^a The model was fitted with an offset term: the logarithm of the number of nuts cracked per session.

^b Not indicated because it has a limited interpretation.

^c Sex was dummy coded with female being the reference category.

^d Z-transformed to a mean of 0 and SD of 1.

^e Group was dummy coded with East Group being the reference category.

^f Tool material was dummy coded with stone being the reference category.

^g The indicated likelihood ratio test refers to the overall effect of the interaction (tested by comparing the full model with a corresponding reduced model lacking the interaction).

Table A7

Results of the final model (GLMM; model 3a; nonsignificant three-way and two-way interactions removed) investigating predictors potentially influencing the number of hits used to crack open Coula nuts

Term	Estimate	SE	Lower CL	Upper CL	χ^2	df	P
Intercept ^a	0.869	0.098	0.686	1.042			NI ^b
Sex ^c	−0.081	0.069	−0.216	0.055	1.365	1	0.243
Age ^d	−0.053	0.029	−0.107	0.010	3.185	1	0.074
Day in season ^d	−0.034	0.033	−0.102	0.028	1.056	1	0.304
Tool size ^d	−0.356	0.039	−0.437	−0.276			NI ^b
Groupnorth ^e	0.742	0.097	0.554	0.924	47.636	2	<0.001 ^f
Groupsouth	0.686	0.095	0.509	0.862			NI ^b
Tool material ^g	0.076	0.054	−0.029	0.182			NI ^b
Tool size*tool material	0.168	0.052	0.054	0.267	10.321	1	0.001

^a The model was fitted with an offset term: the logarithm of the number of nuts cracked per session.

^b Not indicated because it has a limited interpretation.

^c Sex was dummy coded with female being the reference category.

^d Z-transformed to a mean of 0 and SD of 1.

^e Group was dummy coded with East Group being the reference category.

^f The indicated likelihood ratio test refers to the overall effect of group (tested by comparing the full model with a corresponding reduced model lacking group).

^g Tool material was dummy coded with stone being the reference category.