

Evidence for Cultural Differences between Neighboring Chimpanzee Communities

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Summary

The majority of evidence for cultural behavior in animals has come from comparisons between populations separated by large geographical distances that often inhabit different environments [1–6]. The difficulty of excluding ecological and genetic variation as potential explanations for observed behaviors has led some researchers to challenge the idea of animal culture [7–9]. Chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d'Ivoire, crack *Coula edulis* nuts using stone and wooden hammers and tree root anvils [10–12]. In this study, we compare for the first time hammer selection for nut cracking across three neighboring chimpanzee communities that live in the same forest habitat, which reduces the likelihood of ecological variation. Furthermore, the study communities experience frequent dispersal of females at maturity, which eliminates significant genetic variation [13, 14]. We compared key ecological factors, such as hammer availability and nut hardness, between the three neighboring communities and found striking differences in group-specific hammer selection among communities despite similar ecological conditions. Differences were found in the selection of hammer material and hammer size in response to changes in nut resistance over time. Our findings highlight the subtleties of cultural differences in wild chimpanzees and illustrate how cultural knowledge is able to shape behavior, creating differences among neighboring social groups.

Results

We studied naturally occurring nut cracking by 45 chimpanzees (*Pan troglodytes verus*) from three adjacent communities (Figure 1; [15]) for a total of nine months during three consecutive nut-cracking seasons between January 2008 and December 2010.

We compared hammer material selection for *Coula edulis* nut cracking and found that chimpanzees belonging to different communities showed marked differences in hammer material selection over the course of the *Coula* season (generalized linear mixed model [GLMM], interaction between group and season, likelihood ratio test: $\chi^2 = 10.76$, $df = 2$, $p = 0.005$; Figure 2; for detailed statistical results, see Table S1 available online). Nut hardness decreased over the course of the season in all three territories (see below). Whereas chimpanzees in the North and East groups selected stone hammers less frequently as the season advanced, the South group continued to use predominantly stone hammers throughout the season. A pairwise comparison of stone hammer selection between communities showed that the South group selected stone

hammers significantly more often at the end of the season than did the East group (interaction: $p = 0.001$). The North group also showed a decline across the season in the proportion of stone hammers used; this decline, however, was not as steep as in the East group and was not significantly different from the pattern seen in the South group ($p = 0.207$) or East group ($p = 0.176$), respectively. Neither sex ($p = 0.292$) nor age ($p = 0.342$) had an effect on hammer selection. The South group's persistent selection of stone hammers across the entire nut season contradicts an energetic explanation, because in a tropical rainforest stones are rarer than wooden clubs and finding them can be time consuming. The observed decline in stone hammer selection in the North and East groups, however, seems to fit an energetic explanation.

Chimpanzees from each of the three neighboring communities also differed from one another in the size of the wooden hammers that they selected over time (GLMM, interaction between group and season: $p_{\text{mcmc}} = 0.011$; Figure 3A; for detailed statistical results, see Table S2), concomitant with the decrease in *Coula* nut hardness. The North group used the smallest wooden hammers, whereas members of the East group selected larger hammers as the season advanced and the nuts dried. The South group used large wooden hammers throughout the season. It may seem counterintuitive that larger clubs should be selected when nuts get drier, as seen in the East group, but at the end of the nut season, hammers selected were of the same average size as wooden pieces that we randomly found on point transects in nut-cracking areas (Figure 3B). This suggests that at the end of the season, due to the decreasing nut hardness, chimpanzees used whichever hammer was close to them, without spending much time or effort to search for an appropriate piece of wood. At the beginning of the season, however, when nuts are still fresh and harder to crack, chimpanzees seemed to make an effort to find and use smaller wooden tools. In contrast, the size of stone hammers used did not differ between communities (GLMM comparison full null model: $\chi^2 = 3.75$, $df = 4$, $p = 0.441$) and stayed similar over the course of a season in all three communities (interaction between group and season: $p_{\text{mcmc}} = 0.754$).

Because males stay in their natal community and females immigrate at maturity with their full behavioral repertoire, we tested for within-group sexual variation. Hammer material selection (three-way interaction, group \times season \times sex: $p = 0.114$) as well as hammer size selection (three-way interaction, group \times season \times sex: $p = 0.606$) was not found to be more diversified between females than between males of a given community. However, due to small sample size, these results need to be treated with caution.

We further controlled for potential ecological influences on hammer selection. Availability of stones was compared by counting the number of stones found on line transects, which were distributed systematically across the total range of each community (Figure 1). Overlapping confidence intervals suggested no difference in overall stone availability between the territories (Figure 4B). However, we found that stones were not evenly spaced but rather occurred clumped in drier areas of all three territories. We did not find an increase in stone

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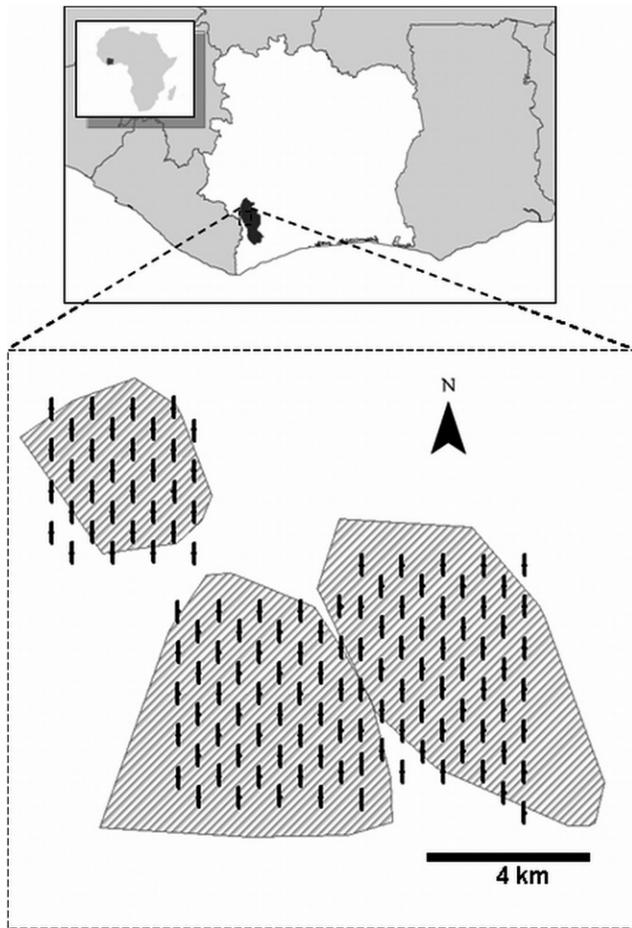


Figure 1. Territories of the Three Neighboring Study Communities in the Tai National Park, Côte d'Ivoire, West Africa

Left to right: territories of the North, South, and East groups. Polygons indicate home range areas; lines depict the location of line transects.

hammer selection when individuals foraged in areas of high stone availability compared with areas with low availability (test of main effect of availability: $p = 0.142$; Figure 4A; for detailed statistical results, see Table S3). We conclude that in the three study communities, chimpanzees did not select hammers according to availability of stones in their territories.

Wooden hammer availability, measured along point transects distributed through areas of high nut-cracking activity, appeared to be the same in all three territories, because overlapping confidence intervals suggest no difference in availability (see Figure S1).

Because *Coula* trees occurred at the same density in all territories and generally fruit at the same time, we tested *Coula* nut resistance across the season using a pounding machine (see Experimental Procedures). In all three territories, *Coula* nut resistance declined over time, and cracking nuts required significantly fewer hits at the end of the season than at the beginning ($p < 0.001$; see Table S5 for the number of hits needed to open nuts). In order to test for differences in changes of nut resistance among the three territories, we used a generalized linear model (GLM); we found that nut resistance decreased significantly more in the East than in the South and North territories (GLM: $\chi^2 = 15.45$, $df = 2$ $p < 0.001$; Table S4).

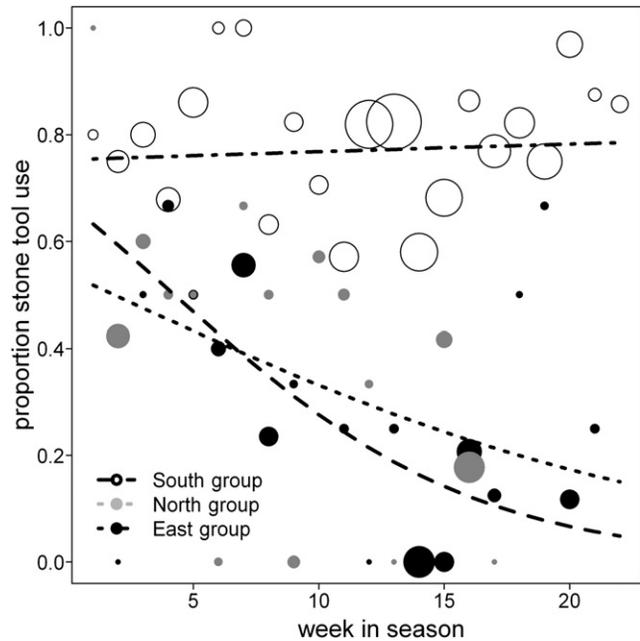


Figure 2. Variation in the Proportion of Stone Hammers Selected throughout the *Coula* Nut Season for Three Neighboring Chimpanzee Communities in the Tai Forest

Each circle represents one week of observation. The size of the circles indicates the number of observations per week (total $n = 2,576$). South group chimpanzees showed elevated stone tool use throughout the season, whereas selection of stone hammers declined in the North and East groups with the advance of the nut-cracking season.

Discussion

Hammer availability was similar in the three territories, and nuts became easier to crack as the season advanced in the territories of all three communities. Therefore, if hammer choice were made solely based on energy efficiency, we would expect that chimpanzees in all three communities would select more stone hammers at the beginning of the season, when nuts are harder. As the season advances, they should select more wooden hammers, because wooden hammers are more abundant. In clear contradiction to such expectations, the neighboring communities exhibited group-specific patterns of hammer selection. Thus, plastic response to subtly different ecological conditions alone is inadequate to explain the difference in hammer selection by Tai chimpanzees.

Cultural differences in chimpanzees have generally been studied using the ethnographic approach, comparing behavior among populations across Africa. This approach has been criticized due to the fact that the compared populations often live many hundreds or thousands of kilometers apart, and underlying ecological or genetic influences may be difficult or impossible to exclude [7–9, 13, 16–19]. In the present study, we have documented differences in hammer choice within a single forest block, with members of three different adjacent chimpanzee communities that are in regular contact with one another and thus are not genetically differentiated. Most ecological factors, such as rainfall, availability of raw material for tools, the general pattern of fruit production, and fruit availability, are known to be very similar across the area [20]. The main ecological factors directly affecting nut-cracking behavior, nut resistance and hammer availability, were an

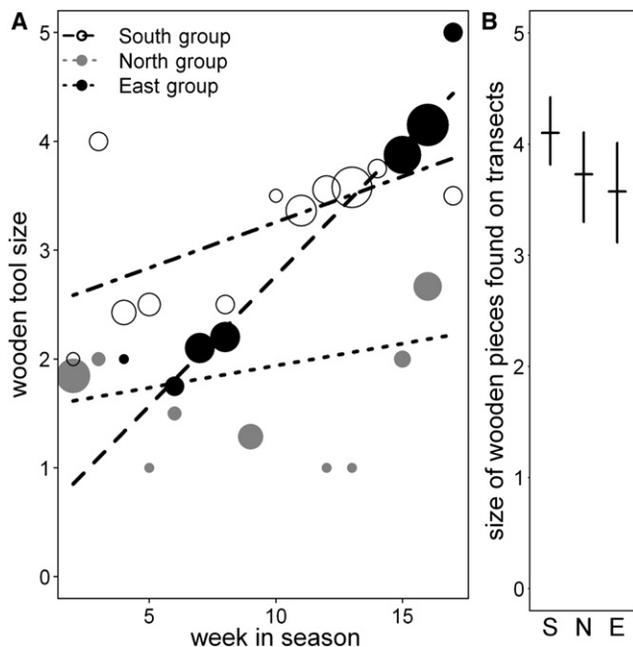


Figure 3. Variation of Wooden Hammer Size throughout the *Coula* Nut Season for Three Neighboring Chimpanzee Communities in the Tai Forest (A) The size of the circles indicates the number of observations per week (total $n = 125$). Early in the season, chimpanzees in all three communities chose relatively small tools. During the season, the size of wooden hammers in the East and South groups increased, with the East group showing the steepest increase in hammer size. (B) Average size of wooden hammers (with bootstrapped 95% confidence intervals) as found on point transects in the territories (S, South territory; N, North territory; E, East territory) of the three neighboring communities.

integral part of the study. Nut hardness varied throughout the season, and chimpanzees responded to such changes in a group-specific manner. Thus, for nut cracking, as has already been demonstrated for ant dipping [21, 22], group-specific solutions mix with ecological constraints, producing cultural solutions. A field experiment carried out in East Africa also found that communities living in the same vicinity exhibit and rely on different cultural knowledge [23]. These fine-scale approaches complement and concur with continent-wide comparisons of chimpanzee behavior.

Some authors have proposed that behavioral differences in chimpanzees may have a genetic basis [9, 13]. The present study provides a clear refutation of the genetic explanation of behavioral variation in chimpanzees, because the three communities studied are neighbors with regular intergroup encounters and regular female transfers [11, 24, 25]. Furthermore, it indicates a strong resilience of community-specific solutions despite regular gene flow between communities. The lack of a genetic explanation for behavioral differences has also been shown in other great ape species [26].

Young adult females, when transferring between communities, have already acquired their group-specific behavioral repertoire and are skilled nut crackers. A field experiment performed in Bossou, Guinea, showed that adult group members do not seem to pay attention to the nut-cracking behavior of others [27]. However, controlled experiments in captivity have shown that individual chimpanzees are more likely to acquire the dominant technical solution prevailing in their group even if they find an alternative equally effective [28].

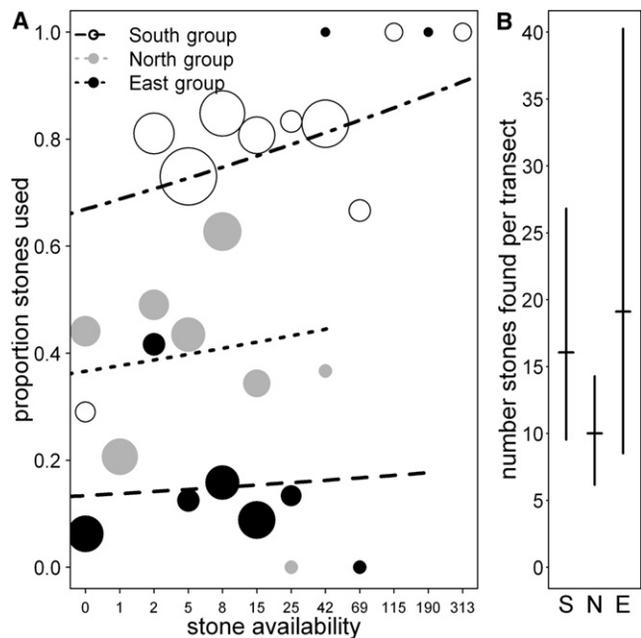


Figure 4. Hammer Material Selection in Relation to Stone Availability during the *Coula* Nut Season for Three Neighboring Chimpanzee Communities in the Tai Forest (A) Proportion of stone hammers used by the chimpanzees of three neighboring communities at different availabilities of stones, as measured in the grid cell of the hammer use. The size of the circles represents the number of observations per bin of availability (total $n = 1,691$). (B) Average number of stone hammers (with bootstrapped 95% confidence intervals) found per line transect in the territories (S, South territory; N, North territory; E, East territory) of the three study communities.

Our observations in Tai chimpanzees suggest that a similar mechanism might occur, although immigrants do not need to learn a new nut-cracking technique altogether but need only make subtle adjustments in hammer selections. Community-dependent behavioral uniformity of tool selection in neighboring communities suggests a cultural transmission process occurring in adult female group members.

Our study shows that cultural differences in chimpanzees can be found over a very small spatial scale and between neighboring communities. In this regard, chimpanzees show a strong similarity to humans, for whom ecology, genes, and cultural inheritance interact to produce a variety of different cultural solutions. It has generally been assumed that in humans, culture overwrites ecological and genetic influences on behavior, and that once it has evolved, it allows for more independence from ecological constraints [29–32]. The results of the present study suggest that in wild chimpanzees, cultural practices can also to some extent overwrite ecological pressures, and that their cultural systems can be resilient.

Experimental Procedures

Observational Data Collection and Transect Design Comparison of Individual Hammer Choice

In order to compare the selection of hammers between the three communities, we recorded tool selection of adult community members (age 13 years or more) of both sexes (for precise numbers, see Table S6) between January 2008 and December 2010 using 30 min focal sampling and scan sampling [33]. For further information on observational data collection, see Supplemental Experimental Procedures.

Availability of Stone and Wooden Hammers

To control for the availability of stone hammers, we used a systematic design of 131 line transects throughout the territories (Figure 1). Transects were of 500 m lengths in a north-to-south direction, distributed equally throughout the territories, and separated from one another by 500 m (total transect lengths: East territory, 25.5 km; North territory, 18 km; South territory, 22 km). All stones within a maximum travel distance of 1 m to the left and right of the transect were counted and weighted. Stones were classified into ten categories according to their weight: 0–250 g, >250–500 g, >500–750 g, >750–1,000 g, >1,000–2,000 g, >2,000–4,000 g, >4,000–6,000 g, >6,000–8,000 g, >8,000–10,000 g, >10,000 g.

In order to compare the availability of wooden tools across the three territories, we used a systematic design of point transects in selected sampling areas with elevated nut-cracking activity, because chimpanzees do not tend to carry wooden hammers over long travel distances [10, 12]. Per community, two such nonoverlapping sampling areas of 500 × 500 m each were selected at a maximum distance of 200 m from previously visited nut-cracking sites from 2008, 2009, and 2010. Each sampling area contained 25 point transects, separated from one another by 125 m (total $n = 150$). A radius of 5 m was measured at each point transect, which produced a sample area of 3,927 m² per territory, within which we counted and measured all potential wooden hammers. Pieces of wood were counted as potential hammers when their length fell within the range of measured wooden hammers that chimpanzees had used in previous observations (10 to >250 cm). Additionally, each potential hammer had to withstand two of the researcher's strikes against a tree trunk without breaking. Potential wooden hammer tools were divided into ten categories according to their lengths: 10–25 cm, >25–50 cm, >50–75 cm, >75–100 cm, >100–125 cm, >125–150 cm, >150–175 cm, >175–200 cm, >200–250 cm, >250 cm.

Nut Resistance

At the onset of each nut-cracking season, *Coula edulis* nuts are more difficult to crack because they are still protected by a thick outer layer of fresh skin [12]. Several weeks after the onset of the *Coula* season (which coincides with the dry season), nuts begin to dry and the fleshy outer protective layer decomposes, leaving the kernel inside exposed to further desiccation. To compare nut hardness in the territories, we performed controlled nut-cracking experiments during the months of the nut season (December 2010 and January 2011). We tested cracking difficulty one time at the beginning of the season and one time six weeks later, when the nuts had already begun to dry. In order to achieve an efficient sample size, we collected 100 nuts in each territory and performed the experiments on the same day. We used a tube of 50 cm length and 5 cm width; the hammer piece (weighing 500 g) was dropped through the tube from a height of 50 cm on the nut to avoid variance of hitting angle. All nuts were cracked using a concrete floor as an anvil. The number of hits needed to crack open the hard internal core was counted.

Statistical Analyses

For statistical analysis, we used generalized linear mixed models (GLMMs, [34]) or generalized linear models (GLMs, [35]). For each model, we first determined the statistical significance of the full model by comparing its fit with that of the null model (comprising only the random effects in case of a GLMM, and potentially an autocorrelation and/or an offset term) using a likelihood ratio test [36] (R function “anova”). Only if this revealed significance, we investigated the influence of individual predictor variables by excluding them from the model, one at a time. For all models, we tested various model diagnostics when required and available using the R functions “vif” [37], “dffits,” “dfbeta,” and “cooks.distance”; we checked for overdispersion and did not find any assumptions violated [38]. All GLMMs and GLMs [34, 35] were run in R [39] using the function “lmer” provided by the R package lme4 [40] or the R function “glm.” For detailed description of the models, see Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes one figure, six tables, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2012.03.031.

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