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RESEARCH ARTICLE

Tradition Over Trend: Neighboring Chimpanzee Communities Maintain Differences in Cultural Behavior Despite Frequent Immigration of Adult Females

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The notion of animal culture has been well established mainly through research aiming at uncovering differences between populations. In chimpanzees (*Pan troglodytes verus*), cultural diversity has even been found in neighboring communities, where differences were observed despite frequent immigration of individuals. Female chimpanzees transfer at the onset of sexual maturity at an age, when the behavioral repertoire is fully formed. With immigrating females, behavioral variety enters the group. Little is known about the diversity and the longevity of cultural traits within a community. This study is building on previous findings of differences in hammer selection when nut cracking between neighboring communities despite similar ecological conditions. We now further investigated the diversity and maintenance of cultural traits within one chimpanzee community and were able to show high levels of uniformity in group-specific behavior. Fidelity to the behavior pattern did not vary between dispersing females and philopatric males. Furthermore, group-specific tool selection remained similar over a period of 25 years. Additionally, we present a study case on how one newly immigrant female progressively behaved more similar to her new group, suggesting that the high level of similarity in behavior is actively adopted by group members possibly even when originally expressing the behavior in another form. Taken together, our data support a cultural transmission process in adult chimpanzees, which leads to persisting cultural behavior of one community over time. Am. J. Primatol. 76:649–657, 2014.

Key words: chimpanzees; culture; tool use; group-specific traits; immigration

INTRODUCTION

Accumulation of empirical evidence has supported the existence of culture throughout the animal kingdom [Boesch, 1996; Krützen et al., 2005; Leca et al., 2007; Rendell & Whitehead, 2001; Sapolsky, 2006; Van Schaik, 2003; Warner, 1990; Whiten et al., 1999, 2001]. With growing recognition and acceptance of culture in free ranging animals, research, especially in primates, has progressively shifted from comparing behavior between populations towards investigating the driving forces that shape and nourish diversity among groups [Boesch, 2003; Gruber et al., 2009; Krützen et al., 2011; Lycett et al., 2007; Perry & Manson, 2003; Van de Waal et al., 2013]. One innovative approach deepening our understanding of the social impact on primate diversity is to focus on groups that live in close proximity to one another. This minimizes the impact of genetic and environmental influence. In chimpanzees (*Pan troglodytes*), previous studies have shown distinct cultural differences even among neighboring communities including tool use, social customs, and foraging styles [Boesch, 2003; Gruber et al., 2009; Luncz et al., 2012; McGrew et al., 2001; O'Malley et al., 2012]. This fundamental information provides new opportunities to further investigate the establishment, persistence, and maintenance of cultural traits within one population despite similar ecological conditions and frequent migration of individuals. With little knowledge about the longevity of cultural traits in chimpanzee communities over time we have often been left with a small window into the contemporary behavioral style of our study animals.

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In all chimpanzee populations studied to date, female group members leave their native community when they reach sexual maturity, an age when their behavioral repertoire is fully formed, while males (in Gombe, Mahale, and Taï) always remain in that natal group for their entire life [Boesch & Boesch-Achermann, 2000; Mitani et al., 2002]. Unhabituated chimpanzees are very scared of humans and might not chose communities, which are under observation by researchers to avoid additional stress. Therefore, observations of immigration are rare events and only a few revealing studies were able to document potential integration of socially acquired knowledge into a new community [Biro et al., 2003; Matsuzawa & Yamakoshi, 1996; McGrew et al., 2001; O'Malley et al., 2012]. Complementary insight can be gained from social learning experiments with captive primates where findings have suggested several possible mechanisms that lead to uniform behavior within one social group: (i) the majority effect, where an individual learned the behavior most frequently displayed in the community [Boesch & Tomasello, 1998; Haun et al., 2012, 2013]; (ii) the prestige effect, where a few prestigious group members were copied by others [Boesch & Tomasello, 1998; Horner et al., 2010]; and (iii) the conformity effect, where personal knowledge was dropped in order to adopt the behavior of the group [Bonnie & de Waal, 2007; Dindo et al., 2009; Hopper et al., 2011; Whiten et al., 2005]. In a natural setting, observations on underlying forces causing similar behavior remained rare, yet recent field studies investigating differences between social groups in capuchin and vervet monkeys were able to show that conformity might play a role in the maintenance of group dependent cultural traits [Perry, 2009; Van de Waal et al., 2013].

In the present study, we investigated within-group similarity in nut-cracking behavior of three neighboring chimpanzee communities (*P. troglodytes verus*). To broaden our understanding of the longevity of cultural traits, we analyzed tool selection over a course of 25 years. In the Taï National Park in Côte d'Ivoire, chimpanzees crack *Coula edulis* nuts with stone and wooden hammers, using a root as an anvil. Tool selection was found to be culturally learned, group specific and very diverse among neighboring communities. Differences between the three study communities were seen in hammer material choice and preferred hammer size, despite the same availability of tool material and average size in all three territories [Luncz et al., 2012]. In one community, South group, chimpanzees predominantly used stone tools throughout the *Coula* nut season, even though nuts became increasingly easier to crack at the end of the nut season when nuts had dried out on the ground and could be cracked with more abundant wooden tools. In two neighboring communities, North and East group, a decrease in stone hammer selection was observed throughout the season, following the decline in nut hardness. Those patterns persisted regardless of stone availability at a given nut-cracking site.

At the time of immigration, female chimpanzees are skilled nutcrackers and have learned their natal group-specific tool selection pattern. If immigrants retained familiar customs, variation in nut-cracking tools of post-immigration adult females would be expected to be higher compared to philopatric males in one community. Furthermore, we would expect a change of behavior in this community over time. We first determined if adult females that had presumably immigrated into our study communities showed higher diversity in tool selection than philopatric males.

As a possible example of the learning process leading to similar behavior we described one event of female immigration to document her hammer selection throughout the first two nut seasons in her new community. Additionally, long-term data collection has allowed us to analyze the persistence of a specific cultural trait by measuring the stability of within-group hammer selection over a period of 25 years in one of our long-term study communities. We lastly discussed in detail what could cause persistent within-group tool selection among Taï chimpanzees and the possible role ecology or social learning mechanisms might play in the continuity of cultural differences among wild-ranging chimpanzees' communities.

METHODS

Observational data collection in the field was solely non-invasive and in compliance with the requirements and guidelines of the "Ministère de l'enseignement supérieure et de la recherche scientifique" and adhered to the legal requirements of the Côte d'Ivoire. We further did not violate any regulations of the Deutsche Tierschutzgesetz or the ASP principles for the ethical treatment of non-human primates.

Study Site

The study was carried out in the Taï National Park in Côte d'Ivoire, West Africa (5°50′N, 7°21′W), where the habitat consists of continuous primary rainforest. The three study communities are directly neighboring and covered an area of approximately 92 km^2.

Observational Data Collection

To study sex differences in hammer use, we recorded tool selection by adult community members (age 13 years or more) of both sexes in three different communities, North, South, and East group, between January 2008 and December 2010 using 30 min focal

sampling and scan sampling [Altmann, 1974]. We collected data on selected tool material, that is, whether the chimpanzees cracked with stone or wooden tools. In order to compare the tool selection of one community (North group) of previous years (1983–1990), we used the Taï Chimpanzee Project long-term data bank of that community [C. Boesch, unpublished data] and extracted information about tool material (wood or stone) and wooden tool size for all observed nut-cracking events.

Statistics

General procedure

For statistical analysis, we used generalized linear-mixed models (GLMM) [Baayen, 2008] or generalized linear models (GLM) [McCullagh & Nelder, 2008]. 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 of the GLMM), using a likelihood ratio test [Dobson & Barnett, 2002] (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" [Fox & Weisberg, 2011]. Where required, we checked for absence of overdispersion and did not find any assumptions violated [Field, 2009]. All GLMMs were run in R [R Developing Core Team, 2010] using the function LMER provided by the R-package lme4 [Bates & Maechler, 2010] or the R function GLM.

Detailed Model Description

Within-group-specific tool fidelity among sexes

In order to analyze whether philopatric males or dispersing females, who have integrated into the group, showed more fidelity to the group-specific behavior, we compared the hammer material selection for *Coula* nut cracking of each individual. We used hammer material selection from South group members to address this question, because only South group members showed hammer material choice contrary to the ecological expectation, with group members preferring stone hammers throughout the season, even though nuts are easier to crack at the end of the nut season. The two neighboring communities showed an increase in wooden tool selection with decreasing nut hardness.

To compare group with individual behavior, we used a GLMM and set "hammer of selection" (stone or wood) as the response variable and as predictor variables with fixed effects we included "sex" and "season" (day of observation) to control for the seasonal changes in hammer preference. The latter was calculated as the number of days elapsed since the first nut-cracking event of the respective group. This allowed us to combine three consecutive seasons of nut cracking. In addition, we controlled for "date" and "individual" by including them as random effects in the model. We included all individuals that had five or more observations on more than a single observation day (which allowed for a curve to be established, showing their hammer choice over the course of the season). For the calculation of the individuals' tool selection, we either used a GLMM and included date as a random effect in cases when there was more than one observation per day or, when the individual was only observed at most once per each day, we used a GLM.

The models were fitted with a binomial error structure and logit link function. To achieve more easily interpretable estimates, the covariate "season" was z-transformed to a mean of 0 and a standard deviation of 1. We fitted the tool material model for the group, excluding each time one individual from the group, one after the other. We then compared the behavior of the group to the one of each individual and extracted the difference of the fitted individual and group values where they overlapped in time. To be able to predict a reliable model, we then excluded all individuals, which had fewer than 8 independent days of observation. A similarity index was then calculated as the mean absolute difference between fitted values of the group and fitted values of the individual with maximum conformity equal to 1. For easier interpretation of the results, we transformed this value to maximum similarity with the group when at 100% (equal) and a minimum at 0% (opposite). We then ran a t-test to analyze if sex had an impact on the similarity index of males and females.

Cultural transmission: a case study

We monitored the behavior of one newly immigrated female, Diva, into one of our study groups, South group, and compared her hammer selection to that of her new community, which preferentially used stone tools throughout the entire nut season.

To analyze whether the immigrant behaved differently than the group we used a GLMM. We set hammer selection (stone or wood) as the response variable and as the predictor variables with fixed effects we included age (all individuals older than 13 years at observation day), group affiliation (long-term group member vs. the immigrant Diva), the day of observation, and year (first and second nut season after immigration). We additionally controlled for date and individual by including them as random effects. The model fit was with binomial error structure and logit link function.

We tested a three-way interaction of group affiliation (immigrant Diva or South group), day of observation, and year. We also tested a two-way interaction between-group affiliation and day of observation for both nut cracking years independently.

TABLE I. Demographic Composition of Adult Group Members of the Three Neighboring Study Communities

	North group (1983–1990)	North group (2008–2010)	South group 2009	East group 2009
Females	27	6	12	14
Males	14	2	7	6

Cultural persistence over time

We compared hammer selection at two different time periods of the North group. We combined data from seven consecutive nut-cracking years from 1983 until 1990 and compared this time period to data that were collected from 2008 until 2010. Between the two periods North group decreased from 86 to 16 individuals and only 2 individuals present in the first period were still alive in the second period (Table I). In the years 2008 to 2010, North group chimpanzees selected significantly smaller wooden hammer than their neighboring communities [Luncz et al., 2012].

To analyze hammer material, we used a GLMM and set hammer of choice (stone or wood) as the response variable and as predictor variables with fixed effects, we included, "age" (all individuals older than 13 years at observation day), "season," and "time period." We additionally controlled for date and individual by including them as random effects. The model was fit was with binomial error structure and logit link function. To achieve easier interpretable estimates, the covariate season was z-transformed to a mean of 0 and a standard deviation of 1.

In order to investigate differences in hammer size over time, we fitted a GLMM with Gaussian error function and identity link. We checked for the assumptions of normally distributed and homogeneous residuals by visual inspection of residuals plotted against predicted values. After log-transforming hammer size we had no indications that these assumptions were violated. As predictor variables with fixed effects we included, "age" (all individuals older than 13 years at observation day), "sex," "season," and "time period" and the interaction between "time period" and "season." We additionally controlled for date and individual by including them as random effects. Into this model, we included an autocorrelation term into the model to account for potential temporal non-independence of residuals (for detail description of the autocorrelation term, see [Luncz et al., 2012]). In order to achieve more reliable P-values [Bolker et al., 2009], we used Markov chain Monte Carlo sampling to establish significance [Baayen, 2008]. For this, we used the function pvals.fnc of the R-package language R [Bates & Maechler, 2010] with 10,000 samples.

RESULTS

Immigration frequency: In the Taï National Park, research has been conducted for 33 years, starting in North group in 1980. Since then, 93% of all sub-adult females which grew up in our study communities emigrated at the onset of sexual maturity, only 2 out of 27 females remained in their native community.

Within-Group-Specific Tool Fidelity Among Sexes

Both sexes in South group showed a high preference for stone tools throughout the entire nut season from November to March. Despite the strong group-specific differences in hammer material selection to crack open *Coula* nuts existing between South group and its two neighbors, North group, and East group, no evidence for differences in hammer selection between males and females within groups were found (t-test: $t = -0.1153$, $\mathrm{df} = 12.771$, $P = 0.91$, Fig. 1).

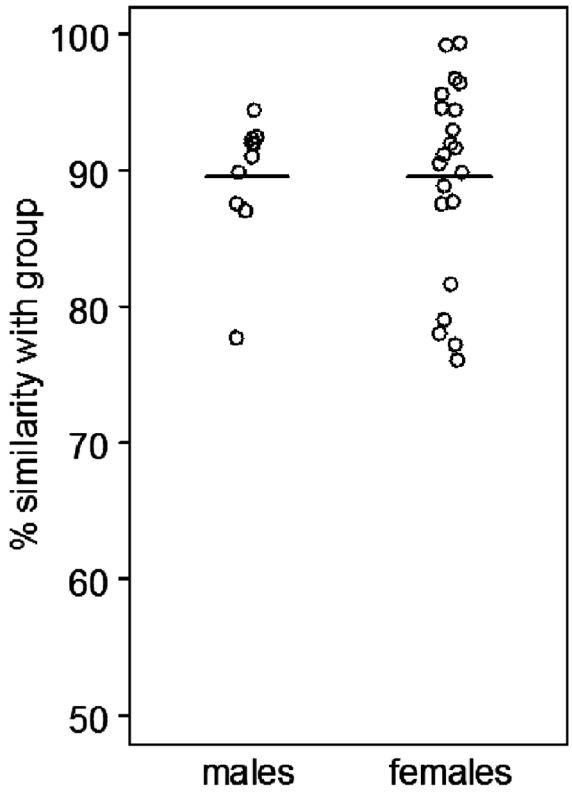

Fig. 1. Similarity of males and females measured from the proportion of stone hammers selected when cracking Coula nuts in the South group Taï chimpanzees, a cultural behavior. The y-axis shows the level of similarity (where 100% indicates maximum similarity = equality to group behavior). Each circle represents one individual with its average over 3 years.

TABLE II. Detailed Results of the GLMM: All Factors Affecting Hammer Material Used by Immigrant or local group

	Estimate	SE	*z*-value	*P*-value
(Intercept)	1.143	1.420	(1)	
age	0.004	0.013	0.355	0.722
Group_affiliation	7.740	5.095	(1)	
day of observation	−1.420	1.959	(1)	
year	2.738	3.062	(1)	
Group_affiliation:day of observation	13.916	6.848	2.032	**0.042***
Group_affiliation:year	0.422	10.116	0.042	0.966
day of observation:year	−0.502	2.734	−0.184	0.854
Group_affiliation:day of observation:year	−19.970	9.038	−2.209	**0.027***

Note GLMM: comparison of Full and Null model: $\chi^2 = 19.221$, df = 6, $P = 0.0038$.
(1) Significance test not indicated because it has no meaningful interpretation.

Immigration: A Case Study of Diva Immigrating into South Group

Divas precise age was unknown since she immigrated to our study community in April 2007 when she was already fully grown; her age can only be estimated. According to her permanent and small swelling which lasted for several months we estimated her age at immigration to be 13.

We tested the three-way interaction of year, day of observation, and identity of nutcracker (Diva vs. South group). The immigrants' behavior was significantly different between the two investigated years (GLMM, comparison full model with three-way-interaction with reduced model, including two-way-interaction, likelihood ratio test: $\chi^2 = 10.98$, df = 3, $P = 0.012$, Table II). The behavior of the immigrant was different from the rest of South group in her first year ($P = 0.027$), but became progressively more similar to the group's behavior as the first year advanced and remained so in the second nut cracking year one year later. The difference between South group and immigrant was not significant anymore in her second nut-cracking year ($P = 0.62$) (Fig. 2a and b).

North Groups Tool Selection Over Time

In both time periods, chimpanzees of the North group selected tool material according to the decline of nut hardness; in the beginning of the season, when nuts are still hard chimpanzees used more stone tools than in the end of the season. There was no difference among the two time periods in the North group (GLMM, test of the two-way interaction between time period and season: $\chi^2 = 0.14$, df = 1, $P = 0.71$, Fig. 3a; Table III).

Especially relevant is the fact that the size of wooden hammers increased over the course of the season in a similar way in both time periods (GLMM, interaction between time period and season: $P_{mcmc} = 0.343$; Fig. 3; Table IV). North group old selected, on average, larger tools than what we

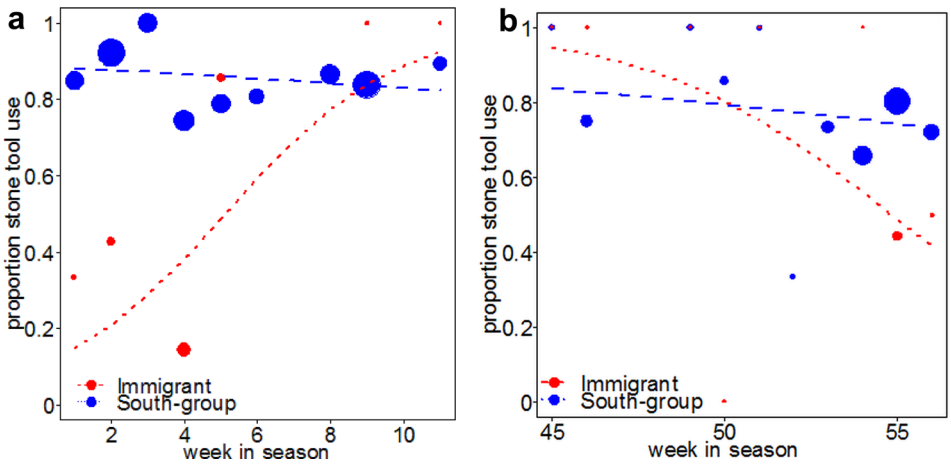

Fig. 2. (**a** and **b**) Hammer material selection of the South group compared with Diva, the new immigrated female in her first and second nut-cracking year. Each circle represents one week of observation and the size of the circles indicates the number of observations in the respective week. **a**: The first nut-cracking year showed a significant difference between community and immigrant (comparison South group with Diva; $P = 0.02$). **b**: One year later, this difference had disappeared and the immigrant showed the same tool selection than other members of her community ($P = 0.62$).

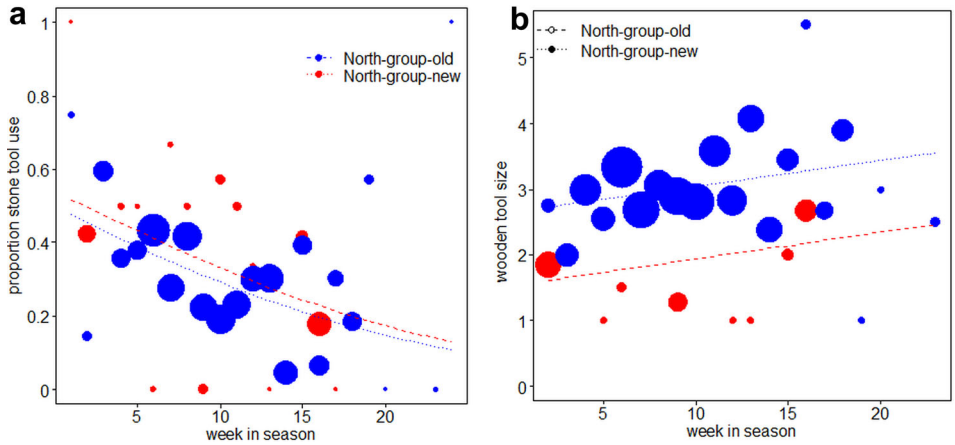

Fig. 3. (**a** and **b**) Hammer selection by North group members in the two time periods compared (North group old = 1983–1990, North-group new = 2008–2010). Each circle represents one week of observation and the size of the circles indicates the number of observations in the respective week. **a**: Hammer material use in North group between two time periods (North group old = 1983–1990, North group new = 2008–2010): In the beginning of the season, the chimpanzees showed an elevated use of stone hammers which, as the seasons advanced, changed to predominant wood hammer use. The size of the circle indicates the number of observations in 1 week of observation (total observations on material selection: North group old = 762, North group new = 235). **b**: Wooden hammer size in North group between the two time periods (North group old = 1983–1990, North group new = 2008–2010): Community members of North group old used larger wooden tools than North group new when group members were reduced to only 16 members. The size of the circle indicates the number of observations in one week of observation (total number of observations in wooden tool size: North group old = 265, North group new = 139).

observed in North group new (GLMM: $P_{mcmc} = 0.037$). However, North group in both time periods still selects smaller wooden tools than both of their neighboring communities [Luncz et al., 2012].

DISCUSSION

To gain insight into the maintenance of cultural traits, we analyzed the fidelity to group-specific behavior among males and females to see if dispersing females showed a higher variety in tool selection than patrilocal males. Additionally, to examine if wild-ranging chimpanzee have long-lived traditions that are preserved over time we further examined hammer selection for *Coula edulis* nut cracking in one community over a period of 25 years. The results of our study showed that despite high levels of female intergroup migrations, diversity between neighboring groups persisted over time, with no significant difference in group-specific tool selection between males and females.

TABLE III. Results of a GLMM on the Effects of Various Predictors on Hammer Material Selection Between the Two Time Periods

	Estimate	Std. Error	*z* value	*P* value
(Intercept)	−0.502	0.582	(1)	
age	−0.010	0.017	−0.601	0.548
time period	−0.312	0.399	(1)	
season	−0.350	0.195	(1)	
time period:season	−0.088	0.227	−0.389	0.697

GLMM: Comparison of null and full model: $\chi 2 = 17$, df = 3, $p < 0.001$
(1) Significance test not indicated because it has no meaningful interpretation

Supporting our main results, the case study of one immigrant illustrated how such a process can develop over time. At time of immigration, the females' behavior differed from her group, however, after several weeks, this difference disappeared and the female Diva showed the same tool choice as her new community. Thereby, Diva adopted the behavioral patterns of her new group and the local tradition was retained. We presented three complementary lines of evidence that suggest maintenance of group-specific local behavior traits in chimpanzees that leads to long-term cultural differences among neighboring communities.

How could group-specific tool choice have persisted over time despite frequent immigration?

Ecology and Hammer Availability

Even though ecological pressure can be difficult to completely exclude in a natural setting, the likelihood of ecological reasons shaping tool selection

TABLE IV. Detailed Results of the GLMM: Influence of Various Predictors on Hammer Size Selection Between the Two Time Periods in the North Group

	Estimate	SE	P_{mcmc}
(Intercept)	0.509	0.124	0.0002
Sex	−0.028	0.062	0.632
age_years	0.001	0.003	0.879
Decade	0.477	0.097	**>0.001**
z.day_in_season	0.055	0.028	**0.045**

Note GLMM: comparison full and null model, without interaction: $\chi^2 = 27.393$, df = 4, $P > 0.001$.

our study communities was low since hammer availability was similar among the three territories [Luncz et al., 2012]. The range when foraging for *Coula* nuts included a large area of many square kilometers and was not centrally located at a few nut-cracking sites and tools were too dispersed to accumulate at nut-cracking sites. If behavioral unity was caused by individuals reusing hammers lying at nut-cracking sites, then we would not have seen the significant difference for Diva at the very beginning of her stay, when she was already exposed to such hammers as she entered her new group. Additionally, in a tropical rain forest, wooden tools are much more abundant than stone tools; therefore, availability is unlikely to have shaped tool choice. If social learning would not play a role in tool choice, we would expect all individuals to follow a seasonal decline in stone tools over the course of the nut season, since this is the ecological most efficient tool selection solution. Since we observed the opposite, ecological explanations were excluded.

Similarity of Behavior Prior to Immigration

Despite the similarity in ecological conditions, between-group tool selection is highly diverse among the three neighboring communities, supporting the hypothesis that behavioral diversity might be high among more communities. At a fourth site, Djouroutou in the Taï National Park, only 40 km south of our original study communities, chimpanzees crack *Coula* nuts exclusively with stone tools (Soiret and Boesch, personal communication) further strengthening this hypothesis. Therefore it is likely that the immigrating females initially had a different tool selection pattern than their new community. However, it could be argued that females chose their new group on the basis of similar hammer selection and therefore would not need to adapt to a new behavior. This scenario seems unlikely since most female transfer happens outside of the nut-cracking season [Boesch & Boesch-Achermann, 2000, chapter 3], at a time when the hammer selection criteria of their new groups could not be evaluated. Additionally, the high level of intergroup aggression seen between all neighboring groups would preclude detailed knowledge of the behavior in each neighboring group before immigration. Although females with full swellings were excluded from such aggression, and often paid short visits to neighboring communities, these sexual visits were not concentrated during the nut season [Boesch et al., 2008], again preventing a better knowledge of group-specific hammer selection.

Cultural Transmission

Adopting the nut-cracking styles of a new community would not necessarily include learning new skills. Nut cracking with stone or wooden tools was observed to exist in all three study communities and therefore was likely to be part of the behavior repertoire of each female immigrant. Thus, slight adjustments in hammer selection could quickly produce similarity to the new community. This would suggest conformist tendencies in immigrating females, where they partly abandoned familiar behavior to perform the behavior shown by the majority of her new community.

What could drive immigrant females in chimpanzee communities to drop their original behavior and conform to their new group? Territories were unknown to newly immigrated females and they relied on their new group members for any information about the territory. Information such as where to find fruiting trees, water resources, where the territory borders end, and which individual is high ranking were crucial for survival. High uncertainty about new circumstances could pressure females to adapt quickly to the group behavior of her new community ("informational conformity" [Claidière & Whiten, 2012]). In the Taï chimpanzee example, tool selection would be a part of the panel of new behavioral patterns an immigrant female acquired from her new group. Additionally, intrasexual aggression against immigrating females by resident females, sometimes resulting in serious wounds and even death, may have created additional social pressure [Boesch & Boesch-Achermann, 2000; Kahlenberg et al., 2008]. Knowing and adopting the behavior pattern of the new community might have helped to reduce xenophobic behavior and aggression towards the immigrant females which can have immense physical and social benefits and permitted more rapid integration in their new groups ("normative conformity" [Claidière & Whiten, 2012]).

In humans conformity is thought to have a leading role in the evolution of culture and several studies show the importance of this transmission process that leads to stable in-group uniformity and between-group diversity [Asch, 1956; Baumeister & Leary, 1995; Fiske, 2010; Henrich & Boyd, 1998]. Models of cultural transmission have suggested that conformist tendencies would facilitate acceptance into the group and would likely lead to increased fitness, since, in an unfamiliar environment, copying what the majority does is an economical way of acquiring an adaptive behavior [Coultas, 2004; Henrich & Boyd, 1998]. Differences among human populations remain over long periods of time despite the exchange of individuals between neighboring groups through marriage and migration, mainly driven by conformity to the behaviors of the new group [Barth, 1969]. Normative conformity, group belonging and the desire to fit in has been suggested to be stronger in humans than in apes [Boesch & Tomasello, 1998; Over & Carpenter, 2012] but might also be of importance in wild-ranging chimpanzees. A cultural transmission process is likely but we can

only speculate about the underlying mechanism that lead to uniform behavior in one social group despite immigration. Support for conformist tendencies can be found in captive studies [Hopper et al., 2011; Whiten et al., 2005] and other primate species, for instance, a study where it was shown that wild vervet monkeys conform to group-specific behavior after immigration, despite different personal knowledge [Van de Waal et al., 2013].

However, the lack of conformity found in some captive chimpanzee studies [Van Leeuwen et al., 2013] might arise from the absence of essential survival pressure which might be responsible for triggering conformity in wild-ranging primates but which are impossible to evoke in captive settings.

Our findings suggest that chimpanzee communities have long-lived cultures that are passed on conservatively throughout time [see also Mercader et al., 2007]. Since cultural transmission can lead to increased adaptive fitness of an individual, especially in a new unfamiliar environment, possible mechanisms involved in maintaining cultural traits are of conformist nature. However, more information, especially on immigration events, is needed to fully understand the cultural transmission mechanisms that result in this high within-group similarity over time.

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