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Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*)

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Recovering evidence of past human activities enables us to recreate behaviour where direct observations are missing. Here, we apply archaeological methods to further investigate cultural transmission processes in percussive tool use among neighbouring chimpanzee communities in the Taï National Park, Côte d'Ivoire, West Africa. Differences in the selection of nut-cracking tools between neighbouring groups are maintained over time, despite frequent female transfer, which leads to persistent cultural diversity between chimpanzee groups. Through the recovery of used tools in the suggested natal territory of immigrants, we have been able to reconstruct the tool material selection of females prior to migration. In combination with direct observations of tool selection of local residents and immigrants after migration, we uncovered temporal changes in tool selection for immigrating females. After controlling for ecological differences between territories of immigrants and residents our data suggest that immigrants abandoned their previous tool preference and adopted the pattern of their new community, despite previous personal proficiency of the same foraging task. Our study adds to the growing body of knowledge on the importance of conformist tendencies in animals.

1. Background

Human biological, cultural and cognitive evolution is tightly coupled with the emergence of percussive tool technology. Archaeological records of Palaeolithic technology demonstrate not only the evolution of material culture, but have also been used to draw conclusions on mental capacities and social systems of early humans. Depending on the quality and quantity of available artefacts, inferences on the behaviour patterns of extinct human populations can be quite detailed [1]. Lithic tools have been the main focus for archaeologists, as stone material is preserved for much longer than organic material. In addition, stones allow for use-wear analysis, providing precious indications about the potential artefact functions [2,3]. The earliest direct evidence of hominin stone tool production can be dated back to 3.3 Ma [4]. Indirect evidence, such as functional anatomy and molecular phylogenetic inference from great apes suggests that intentionally modified stone tools most probably evolved from precursor pounding tools, which were used to access encased food sources *ad hoc* when needed [5], moving tool use further back in time towards the phylogenetic split of humans and our closest living relatives, the chimpanzees. The percussive tools of humans and non-human primates are therefore of special interest for understanding the evolution and transmission of technology (for review, see [6]).

For many decades, anthropologists thought tool use was a defining characteristic that separated humans from other animal species. Only the discovery of tool use in wild chimpanzees forced them to revise the definition of tools [7]. With the emergence of multiple research sites across Africa, it became apparent that chimpanzees exhibit a diverse and regionally specific repertoire of extractive foraging tools, including specialized tool kits, tools used for termite and ant fishing, nut cracking, bone marrow probes, stick brushes for honey extraction and spears for hunting [8–11], reflecting the cultural variety of tool behaviour [9,12–14]. Most tools used by non-human primates are made of organic materials and therefore cannot be used for investigations of past behaviour as preservation is irrevocably compromised. However, several primate species are known to use stone pounding tools to access encased food sources [15–19].

The innovative field of primate archaeology developed to use similar basic archaeological premises to expand our knowledge on populations that cannot always be observed in greater detail [14,20–23]. Use-wear analysis might be able to shed light into the functional aspects of percussive tools of human and non-human species [24,25]. Primate archaeology has mainly been used to achieve three different goals: first to uncover the behaviour of unhabituated populations that leave artefacts in their home range from which behaviour pattern can be concluded [14,26,27]; second to uncover behaviour of past primate activity [21,28]; and third to detect geographical variations in behaviours that have been directly observed in one population [14,29–31]. Besides detecting spatial distribution of behaviour traits in certain populations, an archaeological approach can also be used to follow temporal variation in the presence of behavioural variants within populations, as has been shown in some instances for our ancestors [32].

In this study, we focus on the temporal variation of tool artefact accumulation which, combined with direct behavioural observations, can provide answers to critical questions concerning behavioural variations and cultural transmission of tool use in wild chimpanzees. Several studies have shown a diverse array of social and individual learning patterns in chimpanzees, especially when experimental approaches have been employed to understand underlying social learning mechanisms. A detailed review of mechanisms favouring cultural transmission can be found elsewhere in this issue [33]. Percussive tool-use observations in captive chimpanzees suggest that nut-cracking is socially learned [34,35]. However, identification of factors facilitating social learning under natural conditions in wild chimpanzee populations has remained challenging.

Chimpanzees in the wild are known to use natural stone and wooden hammers to crack open various nut species [14,30,36–40]. Nut-cracking is a classic percussion behaviour whereby a nut is placed on a hard surface and a hammer is used to pound it until the nut breaks open. Stone hammers have been investigated to uncover the geographical extent of their use [14] as well as variations in the nut-cracking techniques [14,29]. Chimpanzees select pounding tools conditionally, taking multiple factors into account. When given the direct choice, stone tools are preferred over wooden material [41]. However, cultural differences between groups show that tool selection is flexible and influenced by group affiliation. We recently found variation in selected hammer materials between three neighbouring chimpanzee groups in the Taï National Park in Côte d'Ivoire despite similar ecological circumstances in their home range [42–44]. One community, the South Group, consistently used predominantly stone hammers to crack open *Coula edulis* nuts, while the two neighbouring communities, North and East Group, gradually increased the use of wooden hammers as the nut season advanced and nuts dried out and were easier to crack open.

Differences between communities remained stable over time despite frequent female migration between the groups, suggesting that the diversity observed in neighbouring communities could have its origin in conformist tendencies, where previous knowledge is discarded under the influence of the majority of group members demonstrating an alternative tool selection preference [44]. Conformist transmission mechanisms in chimpanzees are supported by an increasing body of research that shows how conformity plays an important role in social learning strategies in a variety of wild ranging animal species [45–47]. Some studies have begun to thoroughly investigate how cultural transmission in wild chimpanzees may occur [42,48,49], yet how and why chimpanzees adopt certain behavioural traits and abandon their previous behaviour remain largely unknown [50,51]. With this study, we are aiming to investigate further whether immigrating females actively change their nut-cracking behaviour to match the tool selection of their new groups despite previously having acquired different preferences.

In order to answer these questions, indications of behavioural pattern prior to immigration are important. These patterns remain difficult to discern as direct observations of immigrants prior to immigration are often not available, and the possibility of collecting behavioural data usually starts only with immigration. Female chimpanzees leave their native community with the onset of sexual maturity, at an age when they already display the cultural repertoire of their native community. At times of emigration, they are skillful nutcrackers and display the tool selection pattern of their natal community. Observing immigration is a rare occurrence, and only very few cases of female immigration have been described [44,49,52]. However, these cases do indicate that social learning follows migration events.

Recently, an unusually high number of females (seven) immigrated over the course of 23 months into one of the long-term study communities (South Group) of the Taï forest (table 1). They did not belong to one of the habituated communities and therefore no direct observation of their behaviour prior to their transfer was available. However, the following lines of argument provide supporting evidence that all these females originated from the chimpanzee community directly neighbouring the south of habituated South Group [42]. Long-term data of inter-group encounters of the Taï Chimpanzee Project reveal frequent encounters of the South Group with a large community in the south of their territory [51,53] (South of South, or SoS territory, figure 1). In early 2012, no more inter-group encounters were observed with the southern community of the South Group, while at the same time the males of South Group were observed exploring the SoS territory up to 5 km outside their own home range, without encountering any members of another chimpanzee community. Additionally, it was recorded that all seven new immigrants, during the first year after immigrating into the South Group, would never leave the SoS territory and it was the South Group males who would repeatedly visit them in the SoS home range. Only reluctantly after that time did the females start to follow the males into the original home range of the South Group. These combined observations suggest that these females originated from a community formerly located to the south of the South Group (SoS territory). Therefore, we proposed that by recovering hammer material at nut-cracking sites of the SoS territory, we could recreate the tool selection pattern of the females prior to immigration into South Group.

In our study, we were able to observe directly the tool selection process after immigration of the new individuals, but had to infer the tool selection process before immigration by using archaeological methods to document the tool

Table 1. Immigration events in Taï chimpanzees: seven females immigrated into South Group.

immigrant	first sighting	observation of first nut-cracking	estimated year of birth	days after nut season started	observations of tool selection
PEM	Aug 2012	21 Dec 2013	2000 ± 1 year	previous nut season	20
UAP	Sep 2012	Nov 2012	2001 ± 1 year	previous nut season	
LUC	Jan 2013	17 Jan 2013	1999 ± 1 year	43	9
ASA	Mar 2013	17 Jan 2014	1998 ± 1 year	43	7
HAV	Apr 2013	24 Dec 2013	2002 ± 1 year	19	12
TOU	Jun 2014		1994		
XEL	Jun 2014		1994		

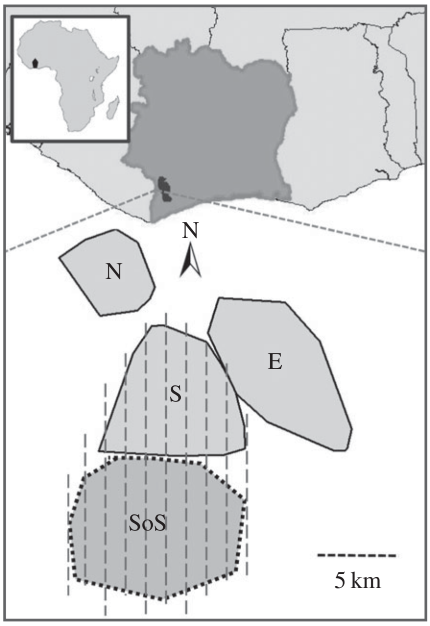

Figure 1. Home range area of the neighbouring study communities in the Taï National Park in Côte d'Ivoire. Polygons indicate the home range of the respective communities. The dotted home range polygon indicates the estimated home range of the SoS Group because direct observation of habitat use is absent. The lines show the locations of line transects.

selection process from tool remains at nut-cracking sites within the presumed natal territory of the individuals. We first controlled whether tool use remains at nut-cracking trees matched the observed tool selection pattern in the South Group, where individuals were habituated to human observers. We then used tool remains found in the SoS territory to reconstruct the tool selection pattern of SoS community members. After controlling for tool availability in the two territories, we compared the tool selection pattern of the newly immigrated females to the selection pattern seen in their new community (South Group) as well as to the tool artefact pattern from the females' former home range to detect potential changes in their tool selection pattern.

2. Material and methods

(a) Study communities

The study was conducted in the Taï National Park in Côte d'Ivoire, West Africa (5°50′ N, 7°21′ W) in a continuous stretch of primary rainforest. Long-term research of the Taï Chimpanzee Project has habituated three neighbouring study communities to the presence of humans (North, South and East Group). South Group, the community where the influx of immigration was observed, has been fully habituated since 2000 [42,50]. Based on the average home range size of our study communities according to group size, we estimated the potential home range of the SoS Group to have been approximately 36 km^2 [42,53].

Individuals in the SoS Group had not been habituated to human observers by the Taï Chimpanzee Project; however, being a neighbouring group to one of our research communities, we observed regular aggressive encounters with the South Group which gave insight into the demographics of this community [53]. Owing to civil unrest in 2012, the Taï National Park has been subject to heavy poaching pressure leading to a dramatic decrease in animal populations in large stretches of the park (www.wildchimps.org/reports/2012). Two unknown females (designated PEM and UAP) were first sighted by observers in the SoS territory in August and September 2012, as the males of South Group spent a few hours per day in the area of the SoS territory. In early 2013, females started migrating north into the South Group territory. Over the following 14 months, a total of seven adult females (table 1) immigrated into the South Group and progressively started to tolerate the presence of human observers. Only four of these females had accepted the presence of observers when the 2013 nut season started.

Although the individual PEM had already been sighted in August 2012, we have included her in our data analysis as a new immigrant as she was most probably not exposed to the tool selection pattern of South Group members. *Coula edulis* nut productivity was very low in the nut-cracking year of 2012. In all three study communities (South, East and North Groups), the chimpanzees did not spend time nut-cracking and foraging in groups; instead in that year nut-cracking was opportunistically carried out by individuals. Altogether, we observed only 65 tool selection incidents by adult South Group members in 2012 (compared to 438 in 2008 and 270 in 2009). Only in two nut-cracking occasions was an unknown female present. Tool selection by one adult South Group male was observed in the SoS territory, and we excluded that location from the tool assessment study.

At the time of the 2012 nut-cracking season, PEM had not yet been integrated into South Group but was only occasionally seen foraging in the SoS territory, where the South Group males explored more and more frequently. Only reluctantly and much later did she follow the males up into South Group's territory. The individuals LUC, ASA and HAV appeared after the nut-cracking season had ended in South Group territory in January 2013 (table 1). The female UAP was seen during the nut-cracking season of 2012 foraging with local South Group members in the South territory and therefore was excluded from the analysis as she might have been exposed to tool selection earlier than in 2013.

(b) Comparison of ecological conditions

We are building this study on previous detailed investigations of the nut-cracking behaviour of three neighbouring chimpanzee communities. Selection patterns and behavioural variation between these communities have been extensively studied in the Taï National Park, allowing us to adjust our investigation to the outcomes of that research [14,15,41–44,54,55]. By taking into account previous findings we are able to tailor our methods to new challenges without repeating investigations. Previous work has shown that stone size and mass correlate strongly with one another, and we found no difference in selected stone tool size between the three study communities [42]. Chimpanzees do not transport wooden tools over longer distances but select a new tool at a new nut-cracking location [15]. Since the SoS territory is neighbouring the South Group territory in a continuous stretch of forest, we assumed the ecological conditions to be similar. Wooden tools were found to be very abundant in this tropical rainforest (148 per 100 m^2) and are thus not considered as a limited resource. The limiting tool type in the Taï forest is stones (3 per 100 m^2); therefore we controlled for the availability of stone tools.

We systematically placed line transects throughout the home range area of South Group and the potential former home range of the immigrants, the SoS territory. Transects were of 500 m in a North to South direction, equally distributed and separated from one another by 500 m (figure 1). Total transect length in the South Group territory was 22 km, and in the potential former territory of the immigrants total transect length was 48 km. In the Taï forest, three different stone materials (laterite, granite and quartz) are used by the chimpanzees. Even though laterite is less sturdy than granite and quartz, chimpanzees still preferred it over wooden tools [15,41,42]. Stones found on the transects were only counted as potential tools when they ranged within the average selected hammer size (assessed from previous observations [42]); the minimum tool mass was determined to be 80 g, which translated on average into a minimum of 3 cm length on one side of the stone. The maximum tool mass was determined to be 10 000 g (which was only observed to be selected four times in three nut seasons). For our survey, stones with a minimum length of 3 cm were reliably visible and recorded as potential tools when found within a maximum distance of 1 m to the left and right of the transect. In order to compare the availability of potential stone hammers between the territories, we bootstrapped the number of stones found on each transect 1000 times using the statistical program R, and compared the confidence intervals at the level of 95%. The unit of bootstrapping was the individual transects.

To further analyse the significance of the differences of confidence intervals, the difference of the confidence intervals was calculated and a confidence interval was formed. If this confidence interval did not include the value zero, the results are significantly different. From this analysis, a one-way p-value can be formed; this is just an indication for a p-value, since the values are not independent from each other.

(c) Tool artefacts at nut-cracking sites

To assess tool selection pattern from artefacts at *Coula edulis* nut-cracking sites, we conducted recces [56] and deliberately searched for nut-cracking sites where we collected information on previously used hammers. In order to be classified as a hammer, the tool had to be within a radius of 1 m around a nut-cracking anvil (in the majority of cases a *Coula edulis* root) that had to show a visible dent from repeated placement of a nut. Wooden branches qualified as hammers when they showed wear marks of nut-cracking, including broken bark and dents in the centre of the wooden club [15]. Broken nut shells had to be visible surrounding the anvil within in a maximal distance of 1 m.

(d) Observational data collection

To investigate whether there was a difference in tool selection between the residents of South Group and the new immigrants, we observed all adult South Group community members (age 13 years or more) of both sexes in 2010 (six males and six females) and 2013 (four males and five females) and collected information on their hammer choice (wood or stone) using 30 min focal sampling and scan sampling [57]. Further, we were able to follow four of the newly immigrated females at a distance of sight to reliably identify the hammer material they used. During focal and group scan sampling, we recorded one hammer selection per nut-cracking site per individual. In order to minimize autocorrelation, we recorded a new observation only when a new nut-cracking site was at least 500 m away from the previous nut-cracking point.

(e) Comparison of tool selection: hammer accumulation and direct observation

To determine potential differences in tool selection between local residents of South Group and immigrants, we used a two-step approach. We fitted two generalized linear mixed models (GLMMs) [58] with binominal error structure for both datasets (accumulation of tools at nut-cracking sites and direct observation of tool selection). We set tool material (stone or wood) as the response variable for the first model, addressing the artefacts we found in the territory, and we included the location of the tool (anvil at which the tool was found) as a random effect into the model. To analyse the direct observations in the second model, we included group affiliation (immigrant or resident of South Group), the day in the nut season (z-transformed to a mean of zero and a standard deviation of unity) and as random effects date and individual. As the identity of the tool user was known through direct observation, we additionally included random slopes of date within individual into the model [59].

We then bootstrapped the estimates of the full model 1000 times and compared the confidence intervals at the level of 95%. We plotted the results to inspect visually the overlap the confidence intervals.

All GLMMs were run in R [60] using the function lmer provided by the R-package lme4 [61].

3. Results

(a) Comparison of stone tool availability

We found that ecological conditions which potentially could influence tool selection were similar between the two home ranges. We compared the amount of stones available in each home range and, controlling for territory size and number of transects, we did not find differences in stone availability between the home ranges of the South Group and the SoS Group ($p = 0.182$; figure 2).

(b) Comparison of tool selection pattern

To detect cultural transmission pattern in immigrating females, we first investigated whether the tool selection pattern of a known community (South Group) could be inferred from the hammers left behind at their nut-cracking sites. The tools found at nut-cracking sites in South Group's territory in 2010 (figure 3: South Group 2010, grey cross) corresponded with tools selected by the individuals we directly observed in 2010

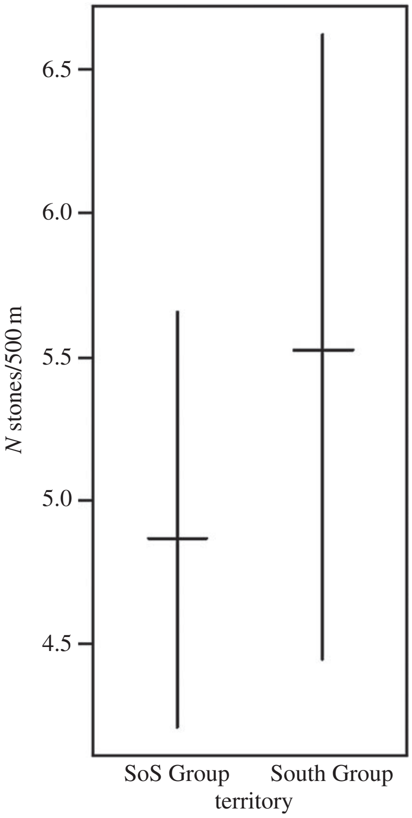

Figure 2. Stone availability on line transects in the territories of the South and SoS Groups.

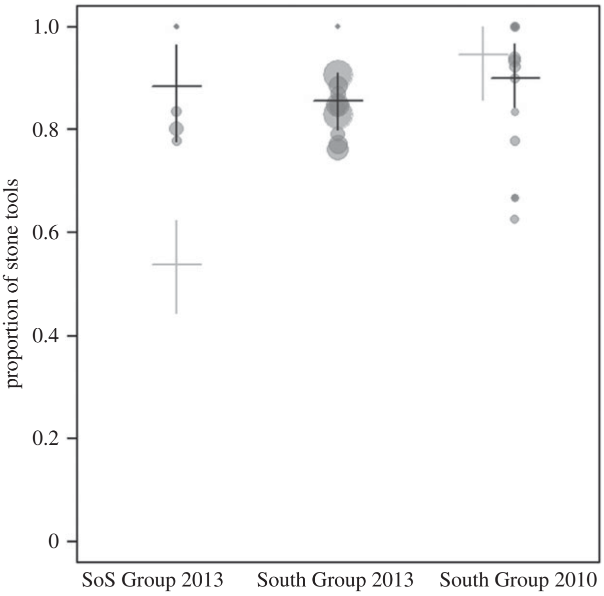

Figure 3. Proportion of stone hammers used for *Coula edulis* nut-cracking in two Taï chimpanzee communities: the grey cross represents the mean amount of stone hammers found left behind at nut-cracking sites (the lengths of the vertical lines in the crosses are the confidence intervals). The black cross represents the mean amount of stone hammers observed to be selected by individual focals. For the SoS females, the hammer selection information is missing prior to immigration. The black cross for SoS Group 2013 represents the immigrants' tool selection after immigrating into South Group. South Group 2013 therefore shows the tool selection of South Group members, excluding the immigrants. The grey circles represent the tool selections directly observed on focal follows. Each circle represents one individual; the size of the circle represents the number of the observations for one individual.

(figure 3: South Group 2010, black cross). This is indicated by the widely overlapping confidence intervals with the mean observed tool selection being within the confidence interval of the tools found in the South Group's territory. Our comparison showed that the physical evidence left behind at nut-cracking sites reliably corresponds to the observed tool selection of individuals. This result gives us confidence in our claim that we can draw behavioural conclusions from tool artefacts.

We extrapolated this result to the SoS territory, where direct observations were missing and artefacts recovered at nut-cracking sites were the only available evidence for tool selection patterns. We compared the tools found in the SoS territory with the artefacts found in the South Group territory. The lack of overlapping confidence intervals (at 95%) showed that the tools we found in the SoS territory of the immigrants (figure 3: SoS Group 2013, grey cross) were significantly different from the hammers we found in the territory of South Group (figure 3: South Group 2010, grey cross). This suggests that the former inhabitants of the SoS territory used a significantly lower proportion of stone tools (*ca* 50%) than the residents of South Group in 2010 (*ca* 90%).

The comparison of observational tool selection between South Group resident members and immigrants in 2013 showed that immigrants as well as South Group members displayed the same tool selection pattern (approx. 90% stone tool use; figure 3: South Group 2010, black cross; SoS Group 2013, black cross). The first observation of hammer selection for each immigrant was observed on day 19 and 43, respectively, after the start of the nut-cracking season (determined by the first nut-cracking observation of a member of South Group; table 1). Our findings imply that immigrants prior to immigration displayed a different tool selection pattern than after immigration into South Group.

4. Discussion

To understand cultural transmission in tool use following migration events in wild chimpanzees, we investigated the temporal variation in hammer selection by combining archaeological methods with direct behavioural observations. Hammers recovered at abandoned *Coula edulis* nut-cracking sites in the habituated South Group accurately represented the tool selection pattern known from direct behavioural observation of individuals. South Group chimpanzees persistently selected over 85% stone hammers throughout all investigated nut seasons, which equalled the percentage of stone tools recovered at nut-cracking sites. As direct observations were missing for the SoS community, we used site information to investigate the tool selection pattern of four female immigrants prior to immigration in their presumed former home range (SoS territory). Stone and wooden hammers found at the nut-cracking sites in the SoS territory revealed that members of the SoS Group used more wooden tools than members of South Group. The proportion found in the SoS territory could reflect the tool selection patterns described for North and East Group, where community members adapt their tool selection pattern according to the variations in nut hardness [42]. However, after immigration into South Group, the new females showed no difference in their hammer selection compared to resident South Group members.

Our findings support previous suggestions that immigrating females in Taï chimpanzee communities adopt the cultural behavioural repertoire of their new group [44]. The original behaviour of immigrants (prior to immigration) has remained difficult to ascertain due to the time consuming challenge of habituating several wild chimpanzee communities. Only a few immigration events have been observed in the past, which have added valuable information to understanding the transmission of social knowledge between chimpanzee communities [44,48,49,52]. Previous studies conducted in three neighbouring chimpanzee communities in the Taï National Park demonstrated that cultural traits were maintained in neighbouring groups despite regular individual transfer [42]. All chimpanzees in the Taï forest research groups know how to use wooden and stone hammers to crack open nuts, and adjustment to the new group's behaviour therefore lies in the frequency of hammer material selection. Despite potential different personal tool preference, the selection pattern of the new community was adopted rapidly by immigrants. Behavioural stability within communities therefore does not persist due to similarities between the immigrants' new and former community but is most probably due to adjustments in hammer selection through social learning after immigration. Previous work in the Taï National Park showed that not only tool selection patterns are influenced by conformist social learning, as we found 27 behaviours to be both different and stable between three neighbouring communities [43].

Conformity has been presented as an essential feature of human culture [62]. However, it becomes increasingly difficult to exclude this mechanism for other social animals [63]. Novel findings in wild animals have also been supported by an array of empirical studies in a captive or semi-captive setting where conformity plays a role in social learning mechanisms of non-human primates [64–66]. So far only chimpanzees and humans have been found to converge on the behaviour variant that is most common in the group, even if they have alternative behaviours in their individual repertoires that accomplish the same goal just as efficiently [67]. Conformist transmission has been proposed to restrict the accumulation of traditions in non-human [27,37,49] and human [62,68] populations. Therefore, local differences between populations remain despite individual exchange through marriage and migration [69], preventing cross cultural homogenization but protecting cultural diversity among neighbouring communities. Moreover, cultural transmission models have proposed that conformist tendencies would facilitate acceptance into a group and would likely lead to increased fitness, as copying others is an economical way of adopting an adaptive behaviour in an unfamiliar environment [70].

Coula nut-cracking in wild chimpanzees is a social event whereby a large proportion of group members are foraging together within (at least) audio distance of each other, providing a fruitful ground for social learning. However, exact underlying mechanisms driving immigrants to conform to a group's tool selection pattern are difficult to detect in the wild where observations are opportunistic. Several mechanisms have been found in captive chimpanzee populations that lead to behavioural similarity within one social group, and we will therefore discuss their relevance with regard to our observations in wild communities.

In captivity, the number of demonstrators performing a task was found to play an influential role in an individual's decision to abandon their personal strategies and to match the majority of the group [71,72]. This mechanism might also play a role in wild chimpanzee communities. Despite being several (five in total), the immigrant females in our study were still the minority compared with local group members. Even though the immigrants appeared at different times during the year, the nut-cracking season started for all individuals at the same time with the ripening of *Coula* nuts. At the time of the immigration period, there were nine adult individuals in South Group (five females and four males). This suggests that the majority of adult group members may have had an influence on decision-making of whom to copy.

Additionally, immigrants did not seem to copy the behaviour of juvenile and infant group members which generally does not yet represent the tool selection pattern of their community. It takes young group members many years to become a proficient nutcracker [73]. With first nut-cracking attempts, they use inappropriate tools like their fist, only mimicking the correct action. The ontogeny of tool selection shows that with increase of age their tools selection pattern reflects the unique selection pattern of their group (L. Luncz 2010, unpublished data). Only adult group members permanently display the typical behaviour of a community. Chimpanzees in captivity were found to seek social cues preferentially from higher ranking, prestigious and older individuals, which leads to uniform group behaviour [72,74,75]. These findings might explain the fact that immigrants did not copy all group members present at a similar rate but favoured social information from resident group members over their personal knowledge only if they were considered higher ranking.

Previous research in wild chimpanzees showed that lower ranking individuals are especially receptive to social transmission [48,49,76]. Higher innovation rates in juveniles and lower ranking group members does not lead to an increase of cultural features in a group, as older group members do not seek social information from the young or lower ranking ones [77]. This could be a reason why innovations and also behaviour of immigrants does not seem to spread throughout the group. Only if innovators persist can they add to the behavioural pool by disseminating their innovations once they are older [48,76]. However, the ontogeny of cultural traits within a community remains a topic of investigation as only a few studies have reported the spread of new behaviours within a chimpanzee community [13,49]. In those cases, the spread of the innovations were reported for non-arbitrary behaviours and implied increased fitness through additional foraging sources.

Seeking information from knowledgeable individuals can provide opportunities to acquire and shape preferences in situations in which it may be difficult or costly to gather the requisite personal information [62,78]. Immigrants are not familiar with their new environment; thus conforming to the knowledgeable majority would allow them quickly to take up potential locally adaptive strategies [62,79]. The strategy local chimpanzees use in their territory has worked best for this particular community. An immigrant's lack of information about their new circumstances creates an environment of uncertainty, and it is crucial for their survival to seek social information from knowledgeable group members, regarding the location of food and water, territory boarders or hierarchies. The especially rapid cultural transmission therefore could result from immigrants immediately seeking social cues about their new environment from the resident inhabitants of this territory.

Immigration is risky and very stressful as local females direct high rates of contact aggression towards the newcomer. Animals in captivity are under no external stress, they are familiar with their group members, are physically well cared for and their life is under no threat. In such a setting, social information has been shown to be applied only when higher payoffs were achieved with an alternative strategy [80]. When comparing work carried out in captivity and the wild it is important to take into account the conditions under which the study was carried out. In a recent study on translocation events of zoo chimpanzees (which mimics the immigration events in the wild), it was found that the immigrating individuals conform to vocalization pattern of their new group [81]. Studies in captivity have shown that adjustments based on the desire to create or maintain a positive group sense might exist in chimpanzees [64,65,82,83]. Adjusting behaviour potentially could reduce differences between the local group member and the immigrant and favour acceptance into the group.

The underlying reason for the observed adjustment of immigrating females is probably influenced by a combination of the above factors, and we do not wish to overly stress one or another of these at this early stage. Clearly, more information on immigrating females is needed to disentangle social learning mechanisms responsible for conformist tendencies in wild animal populations.

5. Conclusion

By combining information on tool artefacts with behavioural observations, we were able to improve our understanding of the past and present behaviour of immigrating chimpanzee females. Applying archaeological methods to complement the limitations of behavioural observations proved a very fruitful approach to uncover temporal changes in behaviour patterns, when the geographical origin of the individuals could be predicted. This approach might be of general interest to archaeologists and primatologists. With our study, we further add to the growing evidence that conformist mechanisms play an important role in social learning of wild animals. The insight that percussive tool selection is influenced by social learning in chimpanzees might suggest that precursor tools to the Oldawan may have already been influenced by social information.

Ethics. All our work was conducted in compliance with appropriate animal care regulations and national laws. Behavioural data collection was 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 strictly adhered to the regulations of the Deutsche Tierschutzgesetz or the ASP principles for the ethical treatment of non-human primates.

Authors' contributions. L.V.L. conceived and designed the study, supervised the collection of field data, carried out the statistical analyses and wrote the manuscript; R.M.W. designed the study and wrote the manuscript; C.B. conceived and designed the study and wrote the manuscript; all authors gave final approval for publication.

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