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The Extent of Cultural Variation Between Adjacent Chimpanzee (*Pan troglodytes verus*) Communities; A Microecological Approach

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ABSTRACT Chimpanzees show cultural differences among populations across Africa but also between neighboring communities. The extent of these differences among neighbors, however, remains largely unknown. Comparing three neighboring chimpanzee community in the Taï National Park, Côte d'Ivoire, we found 27 putative cultural traits, including tool use, foraging, social interaction, communication and hunting behavior, exceeding by far previously known diversity. As foraging behavior is predominantly influenced by the environment, we further compared in detail ecological circumstances underlying insectivore feeding behavior to analyze whether foraging differences on *Dorylus* ants and *Thoracotermes* termites seen between neighboring chimpanzee communities were caused by environmental factors. Differences in the prey characteristics of *Dorylus* ants (aggression level, running speed, and nest structure) that could influence the behavior of chimpanzees were excluded, suggesting that the observed group-specific variation is not ecologically driven. Only one community preyed on *Thoracotermes* termites despite a similar abundance of termite mounds in all three territories, supporting the idea that this difference is also not shaped by the environment. Therefore, our study suggests that transmission of cultural knowledge plays a role in determining insectivory prey behavior. This behavioral plasticity, independent of ecological conditions, can lead to large numbers of cultural diversification between neighboring chimpanzee communities. These findings not only deepen our understanding of the cultural abilities of chimpanzees in the wild but also open up possible future comparisons of the origin of cultural diversification among humans and chimpanzees. Am J Phys Anthropol 156:67–75, 2015. © 2014 Wiley Periodicals, Inc.

In humans, the ability to socially transmit knowledge influences the behavior of individuals and creates within group similarity, which over time can form established local cultures (Richardson and Boyd, 2005). This can create differences even between populations that live close to one another in similar ecological conditions. Very little is known about cultural diversity in animal populations that comprise multiple groups living in the same environment. Instead, recent research has focused on understanding the extent to which social learning and cultural transmission influences the behavior of animals within single groups. Culture, defined as socially learned behavior patterns that are not a result of biological inheritance (Hoebel and Frost, 1976), has been described in a variety of animal species (Rendell and Whitehead, 2001; Panger et al., 2002; Fragaszy and Perry, 2003; West et al., 2003; Laland, 2008). Due to their close relatedness to humans, primates, especially great apes, have received extensive research attention and our knowledge about their cultural abilities has expanded in recent years (Boesch, 1996; Whiten et al., 1999; Van Schaik et al., 2003). An important approach to explaining cultural variation has been to exclude ecological variation as its cause (Boesch, 1996; Panger et al., 2002). Because this method of exclusion has predominantly been used to find differences between populations that live far apart from one another, often under different ecological conditions, it has been criticized for not being able to fully exclude genetic and subtle ecological influences (Tomasello, 1994; Laland and Janik, 2006). In contrast to comparisons over large distances, fine spatial scale comparisons of communities living in close proximity with each other allow for better control of ecological differences (Möbius et al., 2008). Little is known about the spectrum of cultural differences between directly neighboring groups of chimpanzees that live under the same ecological conditions with no genetic diversity. We recently documented differences in tool use among three neighboring communities in the Taï NP, Cote d'Ivoire (Luncz et al., 2012), and less detailed evidence of between-community cultural differences exists for other sites (McGrew and Tutin, 1978; Uehara, 1982; Boesch, 2003). The availability of three adjacent habituated communities in Taï provides a unique opportunity to document cultural diversity in a single population thoroughly while controlling for ecological variation (Boesch et al., 2006, 2008).

The first aim of this study was to investigate the extent of cultural diversity among neighboring chimpanzee groups and to provide an updated list of Boesch's (2003) description of cultural variants among these three communities. Additionally, we present a detailed

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comparison of variation among communities in feeding on two species of insect prey, *Dorylus* ants and *Thoracotermes* termites, along with comparative data on variation in prey ecology and anti-predator behavior.

As feeding behavior is most prone to ecological influence, comparative analysis of diet composition can provide good opportunities for testing hypotheses about sources of behavioral variation as variation in food availability and distribution can lead to differences in diet independently of any social influence on food choice (Perry and Manson, 2003). Chimpanzees mainly consume social insects where the clumped food source offers an effective nutritional pay-off (McGrew, 2001). Insects provide a valuable nutritional contribution to the diet, including protein, fat, vitamins, and essential minerals (McGrew, 2001; Finke, 2002). Both insect prey types that we compared in this study are abundant across the African continent and available at many chimpanzee research sites. Chimpanzees in many populations feed on *Dorylus spp*. ants. In some populations, the chimpanzees use tools to harvest adult workers from nest entrances or trails (McGrew, 1974; Boesch and Boesch, 1990; Sugiyama, 1995; Sanz et al., 2010). In other populations, the chimpanzees raid nests by directly extracting brood from underground cavities with their hands, (McGrew, 1974; Boesch and Boesch, 1990; Schöning et al., 2008) a behavior we compared here amongst neighboring groups. Those differences among populations were found to be cultural as well as influenced by the behavior of the ant prey species (Humle and Matsuzawa, 2002; Möbius et al., 2008; Schöning et al., 2008; Sanz et al., in press).

Termites are highly nutritious (Deblauwe and Janssens, 2007) and many species are consumed by chimpanzees at various field sites. At many sites chimpanzees were also observed using long grass stems which they insert into termite mounds (McGrew et al., 1979; Boesch and Boesch-Achermann, 2000; Bogart and Pruetz, 2008). However, precise descriptions of chimpanzee feeding techniques when preying on *Thoracotermes* termites are absent from the literature.

Background information on insect predation behaviors in Taï chimpanzees

***Dorylus* ant nest raiding.** When a chimpanzee finds a *Dorylus* ant nest, it approaches quickly, removes some soil from the entrance, crouches, inserts an arm deeply enough to take some of the larvae and eggs, then quickly removes its arm and moves away (Moebius et al., 2008). The largest ant workers have strong, falcate mandibles with which they cause painful bites when being attacked (Schöning et al., 2005). By comparing the techniques in the three chimpanzee groups, we noticed differences in the depth to which they introduced their arms ("arm depth" below). In North group, individuals inserted their entire arm into the nest, whereas in South group, individuals only inserted their arm up to the wrist into the ant nest.

***Thoracotermes* consumption and termite mound pounding.** All three study communities have been observed to feed on *Cubitermes*, *Procubitermes*, *Cephalotermes, Protermes*, and *Macrotermes* (Boesch, personal observation). However, only North group has been seen feeding on *Thoracotermes*, using a technique we will refer to as "termite pounding" (Boesch, 2003).

Thoracotermes mounds are vertical "pillar-box" shaped, roughly round in cross-section and can weigh up to 20 kg. The mounds are usually free-standing, but a few are built against the sides of trees. Foraging for *Thoracotermes* is a social event with usually more than five adult group members present. One individual pushes the mound over, they then pick up the mound and pound it on a hard surface or root to break open its cells and provide access to the termites. Group members often share one mound by distributing pieces amongst themselves. They pick up the termites with their lips from the ground, the open cells or from their hands. Chimpanzees in Taï mainly eat the winged form. Soldiers are also eaten but workers are mainly discarded. No tools were used in the context of *Thoracotermes* termite eating.

Observed behavioral diversity could be a response to different ecological conditions among territories. We therefore carefully evaluated ecological conditions (Table 1) and compared the behavior of the prey species in light of ecological conditions in their respective home range.

We then further discussed the emergence and possible reasons for diversity in neighboring chimpanzee communities with focus on theoretical models of cultural transmission.

METHODS

Study site

The study was carried out in the Taï National Park in Côte d'Ivoire (5°50'N, 7°21'W). The habitat consists of continuous primary rainforest (McGrew and Tutin, 1978; Boesch, 1996). All three study communities, North, South, and East group, have adjoining territories; together, the three territories cover approximately 92 km^2 (Fig. 1).

Observational data collection

Identifying behavioral differences. Habituation of the North group was completed in 1989, of South group in 2000 and of East group in 2007 (Table 2). Chimpanzees are observed every day for an average time of 10 h. Behavioral data are collected during this time by field assistants and researchers. A long-term data bank compiles these data. After we selected candidate behaviors which, from personal observation by the authors, appeared different, we searched for these behaviors in the long-term data bank and compared their existence among the three neighboring communities.

Insect foraging behavior. Consumption of *Thoracotermes* usually took place only in April and May, at the onset of the rainy season. Behavioral data collection spans 1989 through 2011 for North group, 1999 through 2011 for South group, and 2007 through 2011 for East group. This includes data collected by the senior author in 2007 to 2011. We collected data on ant nest raiding by North and South group members for 13 months during 2008 to 2010. We recorded whether the individuals inserted the hand or the entire arm into the nest. We collected ant samples from each nest and stored them in 70% ethanol for later identification by Caspar Schöning (at the Free University Berlin, Germany).

TABLE 1. Ecological factors potentially triggering between group behavioral differences in Tai chimpanzees: For each ecological factor and resulting behavior prediction of the target chimpanzee, we list the method we used to account for ecological variation among the territories

Foraging behavior	Ecological factor	Predicted behavioral response	Methods
	Potential environmental differences in prey features between the territories	Response of chimpanzees	Comparison between territories
Ant nest raiding (insertion of arm into the nest to harvest brood)	a. ant running speed: ants run faster up the stick in one territory → more rapid response of ants on predator → bite more rapidly	a. insertion of only the forearm into the nest	a. running speed: time measured ants need to run 10 cm on a standardized stick dipped into a nest.
	b. ant aggression: ants are more aggressive in one territory → rapid increase in number of ants on predator → increase of bites	b. insertion of only the forearm into the nest	b. aggression rate: counting number of ants on a standardized stick dipped into nest entrance after given time (2, 4, 6, 8 s)
	c. vegetation density: increased density around nest entrance in one territory → hindered access to nets entrance	c. insertion of only the forearm into the nest	c. measuring access and depth of nest structure through inserting standardized tools
	d. nest depth: smaller nest cavity depth in one territory	d. arm depth is correlated with nest depth →insertion of only the forearm into the nest	d. measuring possible insertion depth of standardized tool
	e. species of ants: different species composition in the three territories → a., b., c., d.	e. arm depth is a function of the ant species	e. sample collection of ants, identification of prey samples by ant experts
Termite mound pounding	a. termite mound availability: less in one territory → less foraging opportunity	a. no termite pounding	a + b. line transects (65.5 km) to evaluate abundance and mound activity in the three territories
	b. mound activity: smaller number of termite mounds inhabited → decreased foraging success	b. no termite pounding	

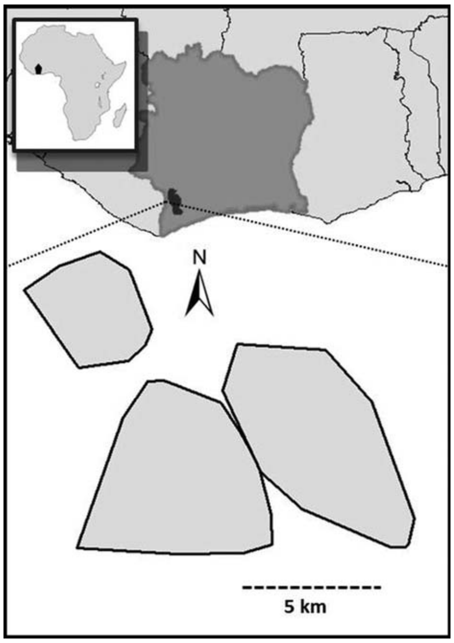

Fig. 1. Three neighboring chimpanzee communities in the Taï National Park in Côte d'Ivoire, West-Africa: The polygons represent the average home range areas of the communities (North, South, and East group).

TABLE 2. Demographic composition of adult group members of the three neighboring study communities

	North group	South group	East group
Females	6	12	14
Males	2	7	6

Our collection contained five different *Dorylus* species which were classified into two main functional types, "epigaeic" (*D. nigricans, D. burmeisteri, D. mayri*) and "intermediate" (*D. emeryi, D. gribodoi*); (Schöning et al., 2005, 2008). These species are the same as those previously sampled at Tai (Möbius et al., 2008; Schöning et al., 2008). Voucher specimens have been deposited in the Hymenoptera collection of the Natural History Museum Berlin.

Experimental design to compare ant behavior between the three territories

Whenever we found a *Dorylus* nest, we noted whether the entrance was open or covered by vegetation by checking whether a standardized stick (width = 4cm) had free access to the entrance without removing vegetation. We further measured the depth of the nest by inserting that stick into the nest as deep as possible after all experiments were completed (see Methods Table 1).

To compare *Dorylus* behavior between the territories of South and North group, we simulated chimpanzee ant dipping behavior at nests of epigaeic and intermediate *Dorylus* species. We put two marks on the dipping stick, one 10 cm from one end inserted and the second 30 cm from this end. To compare how fast the ants run up a dipping tool, we inserted that end of the stick into the nest a 45° angle and measured how long it took the fastest ant to cover the 20 cm distance between the marks. We did this 20 times at each nest.

As a measure of ant aggressiveness we used the number of ants attacking the dipping tool. Because the ants become more alert after a nest has been attacked, and might also become more aggressive with increasing numbers of dips, we used dipping durations (2, 4, 6, or 8 s) in randomly chosen orders. Each duration time was repeated five times, which resulted in 20 dips per nest. To count the number of ants per dip we collected them in sealable plastic bags. Dips were separated by 20 s.

All experiments were recorded with a hand held video camera and coded with the Interact program Version 7.0 (Mangold International GmbH, Arnstorf, Germany).

Comparison of *Thoracotermes* termite mounds availability between the three territories

To control for the availability of termite mounds, we counted mounds along 131 line transects during the month of April, May, and June in 2009. Transects were 500 m long, and were distributed systematically throughout the territories at 500 m intervals. Total transect length was proportional to territory size (East territory = 28 km^2, 25.5 km line transect; North territory = 16 km^2, 18 km line transect; South territory = 25 km^2, 22 km line transect). All termite mounds within a maximum distance of 10 m left and right of each transect were counted and the distance to the transect was measured. We checked each mound for termite activity by removing the first layer of building material from a 2 cm^2 area. When any termites were present we marked the mound as active.

Statistical analyses

Ant nest raid foraging techniques. To investigate differences in ant nest raiding, we fitted a general linear mixed model (GLMM) (Baayen, 2008) with binominal error structure using the function lmer provided by the R-package lme4 (Bates and Maechler, 2010). We included the arm depth as a response variable and “sex,” “group,” and “species” as predictor variables and further controlled for the influence of “individual” and “date” by including them as random effects. We used a likelihood ratio test to calculate the impact of “group” where we compared the full model with a reduced version where we excluded “group” from the model.

Ant experiment: Comparing ant speed. To investigate differences in ant speed, we fitted a GLMM with Gaussian error structure using the function lmer, that included the interaction between “group” and “ant species” and the number of dips at each nest as predictor variables. We controlled for “date” and “nest identity” by including them as random effects into the model. We log transformed the response variable “ant speed” and verified that the assumptions of normally distributed and homogeneous residuals were fulfilled by visual inspection of residuals plotted against predicted values and a qq-plot. We used a likelihood ratio test (Dobson and Barnett, 2002) to compare the full model with a null model that contained only “ant species,” the “dip number” (1 through 20), and the random effects. The interaction was not significant (see Results) and we further tested the influence of the predictor variable “group” by comparing the model without the interaction with the null model. Model stability was tested by excluding the ant nests on which experiments were performed one by one from the data set and comparing the estimates and fitted values obtained with the original model when all data were included. Model diagnostics performed using the R package influence ME (Niewenhuis et al., 2013), which provides dfbetas and cooks distance for GLMM showed that no assumptions were violated (Field, 2009).

Ant experiment: Comparing ant aggression. To account for potential differences in ant aggression, we fitted a GLMM with negative binominal error structure and log link function using the function glmmadmb of the R package glmmADMB (Fournier et al., 2012) after a Poisson model revealed overdispersed residuals. We first included interactions between “group,” “ant species,” and “dip number” (range = 1–30) as predictor variables with fixed effects into the model. We included “nest identity” and “date” as random effects. To control for variation in dip duration, we included the “duration of the dip” (log-transformed) as an offset term. Comparison of the null model, which comprised only “ant species,” “dip number,” the offset term, and the random effects, with the full model revealed no significance and we removed the interaction from the model. The final model comprised the predictor variables “group,” “ant species,” and “dip number” without the interaction. We compared this model with the null model using a likelihood ratio test. To test for model stability we removed “nest identity” and “date” one by one and compared the results of those models with those revealed when analyzing all data. Removing “nest identity” or “date” did not have any impact on the main results.

All Generalized Linear Mixed Models were run in R (R Developing Core Team, 2010).

Termite mounds availability. We included all *Thoracotermes* termite mounds found on transects through the territories and distinguished between active and inactive mounds. We used a Pearson χ^2 test to check for significant differences between the number of active and inactive termite mounds between the territories. To compare the overall availably of termite mounds, we used a Pearson χ^2 test and combined the number of active and inactive mounds per territory. We corrected for the length of transects walked per territory.

RESULTS

Overview on subculture dimensions among the Taï chimpanzee communities

Table 3 lists 27 behavioral elements for which we found between-group differences that were unlikely to result from ecological differences. This only includes differences that we are confident did not result simply from differences in observation time.

Differences in *Dorylus* ant nest raiding

Group difference in ant nest raiding behavior. We observed 77 successful ant nest raids (North = 43, South = 34) during which the depth of hand insertion was clearly visible. Only six (North = 5, South = 1) nests were of the intermediate species. Arm depth differed significantly between North and South group ($\chi^2 = 40.588$,

TABLE 3. List of behavioral elements that we were able to distinguish between the three neighboring Tai chimpanzee communities and for which there is no known ecological explanation

Community	North	South	East
A: Tool use			
All tool use occurrence frequency	+++	+	++
Rubbing one's back on vegetation after rain	+	+	−
Leaf sponging to drink	Leaf	Leaf/bark	Leaf
Container use for drinking[a]	−	+	−
Nut cracking:			
Hammer material (over the course of one nut season)	stone→wood	Stone	Stone→wood
Average wooden hammer size	Small	Large	Small→large
Wood hammer transport in mouth	+	−	+
Nut cracking in trees	s/w (♀♂)	s (♀)	s/w (♀)
B: Foraging			
Thoracotermes mound pounding	+	−	−
Diospyros mannii fruit consumption	Seed swallow	Seed spit	Seed swallow
Dorylus spp. ant nest raid, hand depth	arm	wrist	?
Frequency of insect consumption	+++	+	
Treculia Africana hard-shelled fruits			
State of fruit when eaten	Decomposed/fresh	Fresh in trees	
Location of fruit pounding			
Parts of *Haloplegia azurea* eaten			?
Part of *Strychnos aculeata* fruit eaten	Seeds in decomposed fruit	Flesh in fresh fruit	
C: Social interaction and communication			
Day nest constructed for play start	−	+	+
Leaf held in mouth for play start	+	−	?
Day nest constructed for courtship	+	−	?
Knuckle knock courtship	+	−	−
Leaf clipping before drumming[b]	Rip leaf to pieces	Rip leaf to pieces	Rip leaf off pieces
Buttress drumming	♀♂	♀♂	♂
Rain dance	Slow/calm		?
D: Hunting behavior			
Vocalization during hunt	−	−	−
Prey captured most often	B	B	B/P
Monkey skull pound open	+	+	−
Presence of ♀-hunters	+	+	−
Meat-sharing (individuals receiving the most)	Hunters	Hierarchy	Hunters

+ = present; (frequency of observed behavior: += once a week, ++= at least twice a week, +++= daily). − = absent.? = lack of observation time. B = *Piliocolobus badius*. P =*Colobus polycomos*.

[a] Container use for drinking: In South-group females ($N = 4$) have been observed to drink out broken shells of the *Strychnos* fruits that filled up with rain water. Once the water was drunk they did not refill the container.

[b] Leaf clipping: Before buttress drumming and display, male chimpanzees break a leafy stem from surrounding vegetation and, without ingesting the leaves, rip bites off the leaves which make loud ripping sounds. In South and North-group, chimps rip multiple pieces off one leaf, whereas in East-group the leaf is ripped off the stem once, then they go onto ripping off the next leaf.

d$f = 1$, $P < 0.001$): members of North group inserted their entire arms into nests in 70% of observations, and only their hands in 30%, whereas South group members inserted only their hands in 100% of cases.

Potential ecological explanation: Ant nest structure. Comparison of ant nest structure showed no significant difference between the territories of South and North groups. Only 35% of nests in the South territory ($n = 15$) were directly accessible, and none of the seven nests in North territory were directly accessible; this difference was not significant ($\chi^2 = 1.1126$, d$f = 1$, $P = 0.2915$).

Likewise, nest depth did not differ significantly ($\chi^2 = 0.156$, d$f = 1$, $P = 0.692$). Average depth was 38 cm in the South territory and 41 cm in the North territory. Nest depth did not differ significantly between epigaic ($N_{\mathrm{North}} = 5$, $N_{\mathrm{South}} = 6$) and intermediate ($N_{\mathrm{North}} = 2$, $N_{\mathrm{South}} = 6$) ant species ($\chi^2 = 1.405$, d$f = 1$, $P = 0.235$).

Potential ecological explanation: Ant speed. The speed of the ants running up the digging tool was the same for both territories (comparison of reduced model without interaction to null model: $\chi^2 = 1.263$, d$f = 1$, $P = 0.260$). In the North territory ants needed on average 3.4 s (number of nest tested = 7) and in the South territory 4.5 s (number of nest tested = 13) to walk 10 cm. Both ant species groups, epigaeic (number of nest $\mathrm{tested}_{\mathrm{North}} = 5$, number of nest $\mathrm{tested}_{\mathrm{South}} = 6$) and intermediate (number of nest $\mathrm{tested}_{\mathrm{North}} = 2$, number of nest $\mathrm{tested}_{\mathrm{South}} = 6$), showed the same speed in the two territories, and the interaction revealed no significance and was removed from the model. ($\chi^2 = 1.484$, d$f = 2$, $P = 0.476$).

Potential ecological explanation: Ant aggression. Aggression rates did not differ significantly between the two territories (likelihood ratio test comparing the null model with a reduced model without the interaction: $\chi^2 = 2.08$, d$f = 1$, $P = 0.149$). In the North territory, on average 27 ants attacked the dipping stick, and in South territory on average 20 ants attacked the dipping stick. The ants at nest entrances were equally aggressive in both territories ($\chi^2 = 2.6$, d$f = 2$, $P = 0.272$) (epigaic: number of nest $\mathrm{tested}_{\mathrm{North}} = 5$, number of nest $\mathrm{tested}_{\mathrm{South}} = 6$;

intermediate: number of nest tested$_{\text{North}} = 2$, number of nest tested$_{\text{South}} = 6$).

Differences in *Thoracotermes* foraging

Thoracotermes foraging behavior in Tai, North group. We empirically analyzed termite pounding of the year 2010. All North group members (adult/subadult/juvenile males = 2/4/4, adult/subadult/juvenile females = 5/2/2) except infants were observed to pound and eat *Thoracotermes* termites. On average, group members spent 17 min eating the termites per pounding session ($n = 116$ individual pounding session observations were made on 16 independent days between February 27th and April 12th 2010. Termite pounding was not observed outside this time period in North group. Termite pounding has never been observed in South (13 years of observation) or East groups (6 years of observation).

Potential ecological explanation: Thoracotermes mounds availability and mound activity. The overall availability of termite mounds, corrected for territory size, did not vary significantly ($\chi^2 = 6$, d$f = 4$, $P = 0.199$) among the three territories, North ($N_{\text{total}} = 48$), East ($N_{\text{total}} = 107$), and South ($N_{\text{total}} = 114$). The ratio of active compared with inactive termite mounds differed between territories (North$_{\text{active/inactive}} = 1.8$; East$_{\text{active/inactive}} = 3.8$; South$_{\text{active/inactive}} = 4.4$). In North territory more termite mounds were inactive than in the two neighboring territories ($\chi^2 = 5.941$, d$f = 2$, $P = 0.051$).

DISCUSSION

Although cultural diversity among chimpanzee populations has previously been described, the extent of the difference between neighboring groups has not yet been measured. Previously estimated numbers of behavioral differences among chimpanzee populations have been inferred from comparisons of populations located thousands of kilometers apart from one another (Whiten et al., 1999). This made it difficult to exclude subtle ecological variation or genetic predisposition as a source for observed behavioral differences. Here we compared the degree of variation with respect to a suite of behaviors between directly neighboring communities that live in a continuous stretch of forest with bordering home ranges and frequent female exchange, thereby reducing possible ecological and genetic causes.

We set out to collect a list of all behaviors in which diversity was seen between the three study communities in the Taï National Park in Côte d'Ivoire and for which ecological explanations could be excluded. Our final list of 27 cultural variants among those groups far exceeds previous estimates of diversity (Boesch, 2003; Luncz et al., 2012). Differences occurred in numerous behaviors such as tool use, foraging, social interactions, and hunting behavior. As foraging behavior is the most likely to be influenced by ecological conditions we investigated in more detail possible underlying causes for observed diversity in insect foraging.

Two groups displayed different strategies in ant nest raiding. To investigate whether this was due to ant ecology or chimp behavior, we performed experiments at *Dorylus* ant nests and compared aggression and yield of the prey species as well as nest structure. We did not find differences in the prey behavior among the respective home range areas of the chimpanzees. Diversity in ant nest raiding behavior is therefore not caused by the prey species.

We next looked at the distribution of *Thoracotermes* termite mounds across the three home ranges. Despite the similar availability of termite mounds in all three territories, only members of North group consumed them, suggesting termite availability is not a contributing factor to this behavior. The density of active termite mounds was actually lowest in the North group territory, providing further evidence against an ecological explanation. Additionally, during periods of frequent termite consumption, we found that other food sources were sufficiently available, including the most favored fruits, in all territories, and thus termites were unlikely to be a fallback food.

These observed differences in ant and termite foraging could therefore not be explained by differences in prey ecology or behavior. Due to the long dispersal distances (Kronauer et al., 2010) genetic variation in prey subpopulations was also ruled out as a cause for the observed differences in raiding techniques.

With similar ecology and genetic conditions we conclude that the observed diversity is a matter of existing subcultures within one cultural repertoire of a population. Recognition of such subcultures within one chimpanzee population raises the question of the origin for localized diversification. Theoretical models of cultural transmission include three main types of dissemination: vertical, oblique, and horizontal (Cavalli-Sforza and Feldmann, 1981; Boyd and Richerson, 1985). Vertical and oblique transmission occurs from parents or other adults to offspring (or to immature individuals generally) and is usually highly conservative. Innovations are rare and very slow to spread. Horizontal transmission, on the other hand, occurs between individuals of the same generation. It can happen rather quickly and is favored when environmental change occurs faster than generation time (Laland et al., 2003). Consequently, horizontal transmission may allow the rapid spread of innovations. This model of transmission tends to generate the highest uniformity within the group (Cavalli-Sforza and Feldman, 1981), which leads to conservative maintenance of local traits especially in spatially and temporally varying environments (Henrich and Boyd, 1998). Previously, we have suggested that rapid environmental change that induces high uncertainty about new circumstances should favor adaptive horizontal transmission. For example, when females leave their natal groups and immigrate into new, unknown groups with unfamiliar territories, they could face pressure to seek social cues and to adapt quickly to the group behavior of their new communities (Luncz and Boesch, in press). Social cues are important in group living animals. Individuals adjust their behavior in response to the behavior of others in their group, which can lead to the development of local cultures (Henrich and Boyd, 1998). Horizontal transmission of cultural traits therefore best explains our observations of behavioral differences between the three neighboring chimpanzee communities in Taï, given that adult chimpanzees are conservative about adopting new behaviors, presumably due to the cost of investing time in learning to perform them and the uncertainty of success (Biro et al., 2003). As a result, although innovation is common, many innovations never spread (Boesch and Boesch-Achermann, 2000). Modifications to behaviors occur more frequently than invention, but are also rarely adopted by all community members (Boesch, 1995). Similarly, although O'Mally et al. (2012) reported the possible spread induced by an immigrant female, new behaviors brought by immigrants do not typically seem to spread among resident adult community members (Biro et al., 2003). Furthermore, female immigrants take up the behavior of their new communities; such conformist tendencies lead to persistent group behavior (Luncz and Boesch, in press).

Relations between chimpanzee communities are invariably hostile; peaceful intercommunity interactions do not occur and between-group alliances do not exist (Wilson et al., 2004; Watts et al., 2006; Boesch et al., 2008). Opportunities for between-community social transmission are almost entirely limited to female transfer. Therefore, innovations that do spread within the groups of their inventors remain restricted to those groups. This suggests that cultural divergence between chimpanzees communities evolve in partial isolation which increases within-group homogeneity and between-group diversification. With constant ecological conditions, cultural changes arise only slowly within a group through individual errors and modification of existing traits. This would result in communities adapting to the given circumstances in the environment, with diversification leading to plateaus at possible multiple optimal solutions, reinforcing differences between communities (Henrich and Boyd, 1998).

In regard to our findings of diversity in insect foraging, social learning is very likely to play an important role. Trial and error learning in foraging contexts can impose danger and might even lead to life threatening conditions for naive individuals (Boesch, 2012). Chimpanzees presumably learn how to identify food sources mostly by observing group members, especially their mothers (Nishida et al., 1996). At Gombe, for example, foraging behavior of juveniles correlates closely with their mother's behavior (Londsdorf, 2005). Therefore, cultural conservatism and persistent group similarity in foraging behavior would be expected.

Observational evidence for cultural transmission in wild chimpanzee communities (Lonsdorf, 2005; Luncz et al., 2012) is complemented with multiple experimental studies in which captive chimpanzees have demonstrated the ability to transmit socially learned behavior between peers through several social learning mechanisms, such as conformity and the influence of prestige and of majority bias (Whiten et al., 2005; Horner et al., 2006; Whiten et al., 2007; Hopper et al., 2007). Although not all studies have provided evidence for such learning mechanisms (Van Leeuwen et al., 2013, Tennie, 2012), they could still be sources of group-specific behavior in wild chimpanzee communities. We have previously suggested that life challenging events like intergroup encounters, group transfer, and even just foraging might evoke pressure to adapt behavior seen in other group members (Luncz and Boesch, in press), but such challenges cannot be recreated in a captive setting. Recent innovative research that combines both approaches to controlled field experiments provides detailed insight into the abilities of primates in their natural environments (Gruber et al., 2009, Van de Waal, 2013). More of these studies are needed to truly understand the mechanisms of cultural transmission.

Our work has shown that fine-scale cultural variation exists among neighboring chimpanzee communities. These differences we found in neighboring groups give insight into the cultural abilities of chimpanzees in the wild. We have documented more extensive cultural variation among neighboring communities than previously estimated.

The situation in Taï chimpanzees is most likely not unique. For some time the Mahale Chimpanzee Project in Tanzania followed two neighboring groups and found evidence for culturally based differences between the groups (Whiten et al., 1999; Itoh and Nishida, 2007). Similarly, cultural differences in termite fishing have been found among four neighboring communities at Goualougo (Sanz and Morgan, 2007). We expect that these are not the only populations in which such variation occurs and therefore urge researchers working elsewhere to do similar studies to broaden our understanding of underlying transmission mechanisms and of cultural variation in wild primates.

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