

# Behavioural Diversity among the Wild Chimpanzee Populations of Bossou and Neighbouring Areas, Guinea and Côte d'Ivoire, West Africa

## A Preliminary Report

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### Key Words

Chimpanzee · Material culture · Nut cracking · Cultural variants

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### Abstract

We present a preliminary report on the differences and similarities in material culture among four neighbouring chimpanzee (*Pan troglodytes verus*) communities. One of these communities includes Bossou, a long-term field site of wild chimpanzees, in Guinea, West Africa. We also conducted surveys of three new sites. Two of those surveyed areas, Seringbara in Guinea and Yealé in Côte d'Ivoire, are located less than 12 km away from Bossou in the Nimba Mountains region, which forms a natural boundary between Guinea and Côte d'Ivoire. The third, Diécké, is situated further south-west, closer to the border with Liberia. During the surveys, we gathered behavioural information about these neighbouring populations of chimpanzees. The differences, as well as similarities, in material culture were tabulated based on our findings. The three behavioural variants found so far involve differences in nut cracking behaviour with regard to the species of nut cracked. Some variation in materials used for nut cracking has also been recorded. However, we still need to establish whether these local variations can be explained by the demands of the physical and biotic environments in which the populations of chimpanzees live. If these alternative hypotheses can be excluded with continuing research at the study sites, these differences are likely to be cultural behaviours that are influenced by the social context and mode, i.e. horizontal, vertical or oblique, of transmission, by the social structure and organisation of each community and/or perhaps by some form of social norms prevalent within these communities.

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## Introduction

Four decades of field studies of chimpanzees (*Pan troglodytes*) in Africa have revealed distinctive differences in behavioural repertoire suggesting significant cultural variation across populations and communities [1, 2]. The list of these differences is extensive and includes a multitude of behaviours encompassing tool usage, feeding, social behaviour and communicatory behaviours [1, 3–9]. This integration of our knowledge of material culture in chimpanzees clearly reveals a great diversity of behaviours that are potentially culturally based and even beyond environmental determinism, as a few comprehensive studies have indicated [10, 11]. Boesch et al. [10] examined the distribution of nut cracking in Côte d'Ivoire. They showed that the eastern boundary of the pattern is the N'Zo-Sassandra River. Their detailed and extensive study revealed no obvious environmental variables that differed notably from one side of the river to the other. They therefore concluded that the environment could not explain the presence or absence of nut cracking at the local level [10]. By exclusion, they hypothesised that the best explanation was cultural, with the river acting as a zoogeographical barrier to diffusion of the pattern from west to east. Similarly, in their study at Lopé, Gabon, McGrew et al. [11] examined several hypotheses, mainly exploring environmental parameters, with regard to why chimpanzees at Lopé do not crack nuts. They concluded that the best current explanation for the absence of this tool use behaviour at the site was not environmental but cultural and that chimpanzees at Lopé never learned to utilise nuts, although they are a potentially valuable and plentiful resource in their habitat [11].

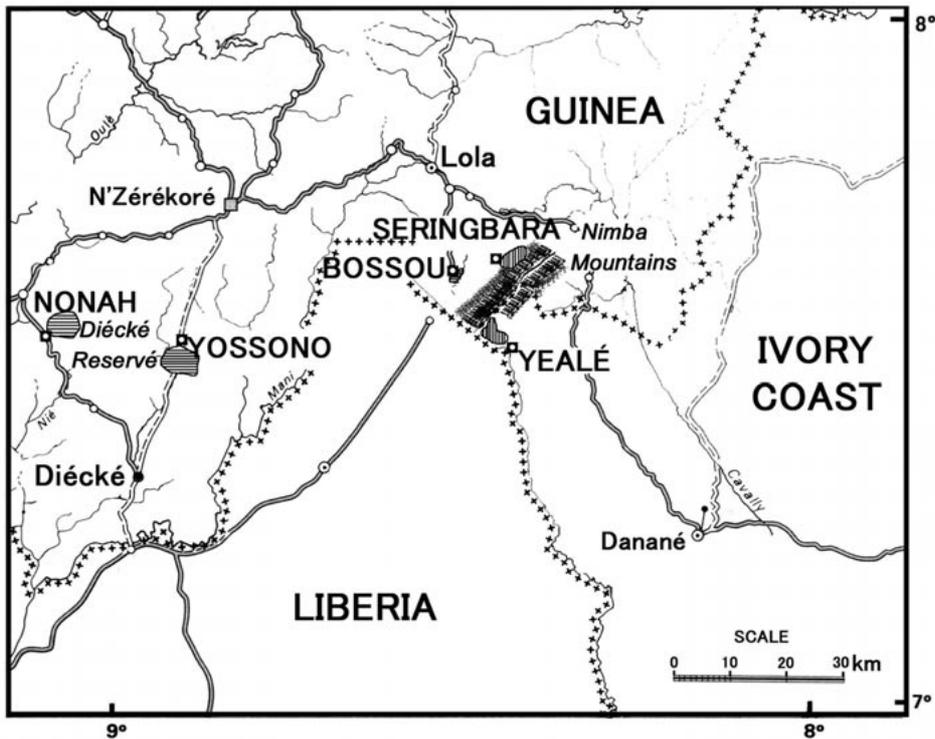
Cultures will be defined, herein, as 'representations of knowledge socially transmitted within and between generations in groups and populations within a species that may aid them in adapting to local conditions, i.e. ecological, demographic or social' [12, p. 432]. Clearly, unravelling this notion of culture in chimpanzees requires further inquiries into the processes and mechanisms of transmission taking place within communities, and possibly between communities, and into the shape and form of these cultural variants.

A long-term project of Kyoto University Primate Research Institute aims to address these issues. A region in the south-east of Guinea and in the north-west of Côte d'Ivoire is the focus of such an investigation. This region incorporates Bossou and the Nimba Mountains and surrounding forest areas, recently including the Diécké Reserve. We would like to summarise some of our preliminary findings and to present some of the similarities and differences in behaviour that have thus far emerged.

## Study Sites and Data Collection

### *Bossou, Guinea*

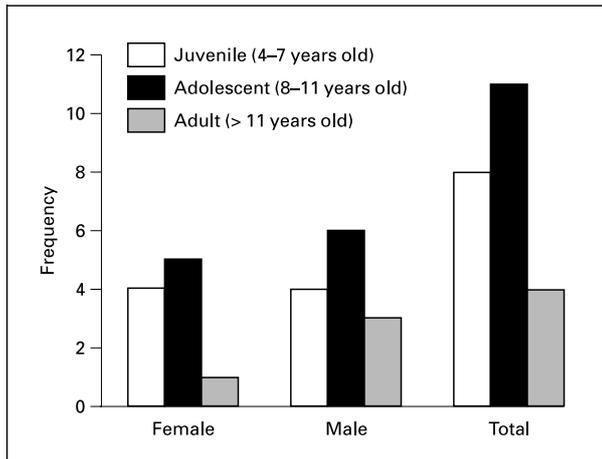
Bossou was discovered as an important chimpanzee field site by the French Zoologist M. Lamotte in 1942 [13]. During his first visit to Bossou in 1960, Kortlandt was the first primatologist to conduct research at this site [14]. However, Kortlandt did not continue to work at Bossou, and this study site was truly established in 1976 by Sugiyama from Kyoto University, Japan [15, 16]. Today, a small population of 20 chimpanzees (*Pan troglodytes verus*) can be found in the forest surrounding the village of Bossou (7°39' N and 8°30' W), and ever since 1976, group size has remained at about 20 (range: 16–23) [16–18].



**Fig. 1.** Map of Bossou field site and surveyed areas in Guinea and Côte d'Ivoire.

Bossou is situated about 6 km from the foot of the Nimba Mountains on the border with Côte d'Ivoire and Liberia (fig. 1). The village of Bossou is located at 550 m above sea level. It is surrounded by small hills 70–150 m high that are covered in primary and secondary forests [15]. At the foot of these hills, cultivated or abandoned fields and secondary, riverine and scrub forests form a patchy mosaic for about 6 km in all directions. This habitat constitutes the core area of the Bossou community. The home range of the Bossou chimpanzees is clearly dominated by secondary and scrub forest, with primary forest covering only about 1 km<sup>2</sup>. It is additionally surrounded by savanna vegetation interspersed with occasional gallery forests, which connect to small adjacent forests, beyond which lie, on the south-eastern side, the Nimba Mountains. The Bossou chimpanzees mostly confine their daily activity to a core area of about 6 km<sup>2</sup>, though they sometimes travel to adjacent forests using the few remaining gallery forest corridors that extend their home range to around 15 km<sup>2</sup>.

The last recorded immigration of a non-resident chimpanzee to the Bossou group was in 1982 [17]. No immigration of females has ever been recorded at Bossou; although there is suggestive evidence that one female of the community, Yo, was an immigrant to the Bossou community [19, 20]. In addition, 3 transient male immigrations into the community have been noted [16–18]. With regard to immigration of individuals, the Bossou community seems to have become recently isolated from adjacent communities of chimpanzees that are known to exist in the region of the Nimba Mountains.



**Fig. 2.** Histogram of the number of chimpanzees at Bossou that have disappeared since 1976, across different age-sex class categories. The group of male juveniles includes 1 reported death [44].

As far as emigration of individuals from Bossou is concerned, since 1976, 12 males and 10 females have disappeared as juveniles or during their adolescence or early adulthood (fig. 2) [18]. The greatest number of these disappearances has occurred among adolescent individuals of both sexes. Adolescence (8–11 years old) corresponds to the age at which chimpanzees, usually females, from other field sites have been reported to leave their natal group and migrate to another community [21, 22]. We have assumed that at least some of the individuals lost from the Bossou community have been able to emigrate successfully to neighbouring chimpanzee populations. Indeed, 6 Bossou females could have migrated away from Bossou, 5 as adolescents and 1 in early adulthood, as no traces of their remains were ever found. In addition, out of the 9 Bossou males that have disappeared as adolescents or older, all were healthy males and neither sickness nor weakness could easily account for their disappearance. Moreover, Bossou chimpanzees have been sighted as far as the village of Seringbara [Matsuzawa, pers. observation], which supports the possibility of successful migration.

The authors recorded behavioural data and observations of tool use during their visits to Bossou. Such data were collected while following the chimpanzees or while performing experiments in an outdoor laboratory set up within the home range of the chimpanzees [19, 23]. Ever since 1986, T.M. has been carrying out fieldwork at Bossou every year for a period extending between 1 and 3 months, during the dry season (November–February). T.H. has been carrying out fieldwork at Bossou now over three periods during the rainy season (period I: June–September 1995; period II: August–October 1997; period III: August–September 1999).

#### *The Nimba Mountains*

The Nimba Mountains are located directly to the south-east of Bossou forming a natural boundary between Guinea, Côte d'Ivoire and Liberia (fig. 1). Nimba is situated 230 km north-west of the Taï Forest, where a community of chimpanzees has been intensively studied since 1976 [24, 25]. The Nimba Mountains have attracted the inter-

est of scientists, including geographers, geologists, soil experts, botanists, zoologists and other specialists ever since the late 1930s [13]. In Guinea and Côte d'Ivoire, the Nimba Mountains are classified as a national reserve, the Réserve Naturelle Intégrale du Mont-Nimba, and as a 'Réserve de Biosphère et Site du Patrimoine Mondial' [26]. The reserve extends over 220 km<sup>2</sup>, and the highest peak is at 1,752 m. The Nimba Mountains are characterised by evergreen forest of medium altitude [27]. The region below 800 m is entirely covered by primary tropical forest and, above 800 m, where the mountain becomes steeper, the vegetation is interspersed with montane forest and patches of high terrestrial herbaceous vegetation and savanna. To date, however, little information is available about the population of chimpanzees in the region of the Nimba Mountains [10, 28, 29]. We have been conducting research at two sites in the Nimba Mountains: Seringbara, Guinea, and Yealé, Côte d'Ivoire.

*Seringbara, Guinea.* The village of Seringbara (7°38' N and 8°25' W) is located at the foot of the Nimba Mountains only 6 km to the south-east of Bossou (fig. 1). Sugiyama has visited Seringbara several times since 1976. He conducted interviews of the villagers, as well as two preliminary surveys of the forest surrounding the village, in order to determine the presence of chimpanzees at this site. He concluded that the chimpanzees in that area of the Nimba Mountains were only seasonally transient in the region [16].

However, in 2000, Shimada [30] has since provided confirmation of the occurrence of chimpanzees in the region: during two short surveys of the area in 1999, he found over 70 nests and the feeding remains of chimpanzees in the forest beside the village. In addition, vocalisations of chimpanzees were frequently heard. This strongly suggests the presence of a resident group at this site. This was further confirmed during T.M.'s and colleagues' visit to the Seringbara forest in January and February 2000 and T.H.'s week-long monthly visits to this site between June and September 2000, during which they recorded further evidence of chimpanzees in the area, including nests, feeding remains and indications of tool use. During the later visits, intensive searches for evidence of oil palm nut cracking were made by carrying out systematic examinations of the ground beneath any oil palm trees that were encountered.

*Yealé, Côte d'Ivoire.* The village of Yealé (7°32' N and 8°25' W) is located 12 km south-east of Bossou, on the other side of the Nimba Mountains in Côte d'Ivoire (fig. 1). T.M. established this study site in 1992 to habituate the chimpanzees in that area, in collaboration with a local project organised by the Centre des Eaux et Forêts of Danané. Preliminary surveys in the region and information from local people reveal that maybe three groups of chimpanzees reside in the area, each one adjacent to one of three major rivers found in the Reserve: the Nuon, the Yan and the Toua.

T.M. carried out several surveys in the area during the dry season [28]. Moreover, T.H. explored the forest of Yealé twice for a period of about 10 days each time, during the months of September 1997 and 1999, during the rainy season. Altogether, these surveys have yielded information about nests, diet and tool use behaviours, as well as ranging patterns of the chimpanzees inhabiting this region of the Nimba range. In particular, any indications of nut cracking were searched for. This type of tool use can readily be explored by inspecting the ground beneath nut-bearing trees and is easily identifiable. As was performed at Seringbara for oil palm trees, all nut-bearing tree species encountered during the surveys were systematically examined for signs of nut cracking. The presence of shell remains alongside or on the surface of stones, protruding roots or wooden clubs with indications of wear resulting from a pounding action was

used as the criterion for the presence of nut cracking. In order to exclude the possibility that nuts might have been cracked by humans rather than chimpanzees, at all sites nut cracking was ascribed to chimpanzees only if at least one of the following conditions was met: (1) if the chimpanzees were heard or seen cracking, (2) if fresh traces of chimpanzees, such as knuckle or foot prints, were found within 5 m of a recently used nut cracking site, (3) if the site of the nut cracking tools was practically inaccessible to humans, even children, e.g. under dense bush. The use of medicinal plants was established through the discovery of whole leaves in faecal samples that were collected at the various sites [31].

*Diécké, Guinea.* The Diécké forest is located about 50 km to the west of Bossou (fig. 1). It is a reserve extending over 700 km<sup>2</sup> in area, stretching about 35 km from north to south and 35 km from east to west. The forest is under the control of the Centre Forestier of N' Zérékoré. The two study sites, which were the target of this study, are located beside two villages, Yossono (west of the reserve: 7°38' N and 8°55' W) and Nonah (east of the reserve: 7°33' N and 9°05' W). The explored sites consist primarily of primary forest covering small hills, of which the highest peak is at 589 m above sea level [32]. It still remains undetermined as to how many chimpanzees inhabit this reserve and how many communities exist in the area.

A research team led by T.M. conducted the initial reconnaissance trip to the forest of Diécké in January-February 2000. In addition, T.H. visited the two sites initially surveyed, Yossono and Nonah, for 10 days in August 1999. We succeeded in observing the chimpanzees directly at this site. Any evidence of chimpanzees was recorded in the same way as for the Yealé and Seringbara sites.

## Results

Table 1, which is based on our findings and other published information, consists of a preliminary summary of the comparison of chimpanzee material culture between Bossou, Seringbara, Yealé and Diécké. This table does not include social behaviours, since direct observation of chimpanzees at the Nimba sites and the Diécké reserve is still infrequent due to lack of habituation of the chimpanzees. Since quantitative data on density and distribution of nut-bearing tree species are not yet available for all the sites, qualitative terms, such as abundant, common, patchy or peripheral, were used in the following sections. The use of these terms results from a consensus among the researchers involved in the surveys and are employed to provide some appreciation for differences across the sites in terms of density and distribution of these tree species.

### *Behaviours Unique to the Bossou Community*

Some behaviours, listed in table 1, are unique to the Bossou community and have not yet been reported at the other three sites or anywhere else in Africa [2]. These include the use of an anvil prop, or a wedge beneath an anvil stone for stability during nut cracking bouts [19, 33], pestle pounding, using a removed leaf for pounding and softening the apical meristem or palm heart before eating it [34, 35] and, finally, algae scooping, using sticks to fish for algae at the surface of a pond [36]. Moreover, evidence for the use of a leaf cushion [37], termite fishing for *Macrotermes* sp. [20], the use of leaves for drinking [15, 38, 39] and the use of the leaves of *Ficus mucoso* for medicinal purposes [28] have not yet been found at any of the other three surveyed sites.

**Table 1.** Table comparing chimpanzee material culture in Bossou, Seringbara, Yealé and Diécké [8, 20, 23, 28–32, 34–37, 39, 45]

Behaviours	Bossou	Seringbara	Yealé	Diécké
Nut cracking	+	?	+	+
<i>Elaeis guineensis</i> <sup>1</sup>	+	○	+	○
<i>Coula edulis</i>	–	?	+	+
<i>Panda oleosa</i>	–	?	○	+
<i>Carapa procera</i>	○	?	+	?
Use of a wooden anvil	+	?	?	+
Anvil prop	+	?	?	?
Food pounding	+	?	+	?
<i>Strychnos</i> sp.	○	?	+	?
Ant dipping <sup>2</sup>	+	+	+	?
Use of digging sticks for ant feeding	+	?	?	?
Building ground nests <sup>2</sup>	+	+	+	?
Termite fishing for <i>Macrotermes</i>	+	?	?	?
Use of leaves for drinking	+	?	?	?
Pestle pounding	+	?	?	?
Algae scooping ( <i>Spirogyra</i> sp.)	+	–	–	?
Leaf cushion (seat vegetation)	+	?	?	?
Medicinal use of leaves	+	?	+	?
<i>Polycephalum capitatum</i>	+	?	+	?
<i>Ficus mucosa</i>	+	?	?	?

+ = Present; – = absent, since not available in the habitat; ○ = absent, although available; ? = presence or absence not yet confirmed, target food or prey available in habitat. Note: For Bossou, three of the behaviours listed – termite fishing with sticks [20], the use of digging sticks during ant dipping [8] and the use of a wooden anvil [39] – have only been observed once, although studies at this site have been carried out since 1976. All other behaviours listed as present in the above table are based on several reported independent observations, except *Carapa procera* nut cracking at Yealé for which only one single occurrence was ever recorded [28].

<sup>1</sup> Yealé: T.H., pers. observation.

<sup>2</sup> Seringbara: T.M., Hirata and T.H., pers. observation.

#### *Nut Cracking: Differences and Similarities*

We were able to confirm the occurrence of nut cracking behaviour at all sites, except Seringbara in the Nimba Mountains. All four of the nut-bearing species mentioned in table 1 were present in Seringbara. They were observed, though, to occur at low densities or peripherally to the presumed home range of the chimpanzees. Nevertheless, as noted in table 1, we have been able to establish variations in the species of nut cracked, as well as overlaps.

*Oil Palm Nuts* (*Elaeis guineensis*). Bossou chimpanzees crack open only one species of nuts, oil palm nuts, to gain access to the kernel using a hammer and anvil stone [15]. Oil palm trees are very common in the habitat of the Bossou chimpanzees. Evidence for nut cracking of oil palm nuts has been obtained for chimpanzees in Yealé, where oil palm trees are patchily distributed. However, neither at Seringbara, the other site in the Nimba Mountains, nor at Diécké did we find any indication of cracking of oil palm nuts

by the chimpanzees, although oil palms are present at both these sites. Nevertheless, these are only available at low densities and tend to be mostly present at the periphery of the chimpanzees' home range.

*Panda oleosa Nuts.* Even after careful examination of the ground beneath *Panda oleosa* trees for signs of nut cracking, no evidence of nut cracking in this species was found in the Yealé region, although it is common in certain parts of the home range of these chimpanzees. This observation, therefore, reinforces Joulian's [29] finding, during his brief survey of nut cracking in the area, that, although *Panda* nuts were available in the habitat of the chimpanzees, these appeared not to be cracked by the chimpanzees. The absence of cracking of *P. oleosa* nuts at Bossou can be explained simply by the fact that this species is absent from the home range of this community. Chimpanzees at Diécké, though, readily cracked *Panda* nuts and almost always used embedded stone anvils for cracking this species of nut. Indeed, out of 13 anvils discovered at this site, 10 were large embedded rock anvils, while the other 3 were emergent roots.

*Coula edulis Nuts.* At Diécké, we also found indications of cracking of *Coula edulis* nuts. Evidence for cracking of *C. edulis* nuts was also found at the Yealé site. This species of nut-bearing tree does not, however, occur at Bossou.

*Variation in Materials Used for Nut Cracking and Carapa procera Nuts.* At all three study sites where nut cracking was confirmed, all hammers found were made of stone. However, chimpanzees at Diécké used emergent roots or embedded stones as anvils for cracking open nuts more frequently than the chimpanzees at Bossou and Yealé. At Bossou and at Yealé, on the other hand, chimpanzees have generally been observed using only loose stone anvils for cracking nuts. One exception, reported for Bossou, involved the use of a stone hammer and a wooden anvil, the trunk of a fallen tree, to crack open oil palm nuts in an outdoor laboratory [40]. Another exception is the nut cracking technique used at Yealé to open *Carapa procera* nuts.

Nut cracking of *C. procera* at Yealé involved the use of a vertical tree trunk as an anvil and a stone as a hammer. Matsuzawa and Yamakoshi [28] recorded evidence of this behaviour, while carrying out a survey of the chimpanzees in this region of the Nimba Mountains. The smashing of a food item by pounding it, without the use of a hammer tool, against a hard woody surface, like the base of a tree, is customary for Bossou chimpanzees and chimpanzees at Mount Assirik, Senegal, and Gombe and Mahale, Tanzania. It has also occasionally been observed at Budongo, Uganda [2]. Finally, cracking of *Carapa* nuts has never been observed at Bossou, although there is no clear explanation for its absence in this community since this tree species is readily available in the habitat of the chimpanzees, although at low densities.

#### *Absence of Other Behaviours*

Chimpanzees at Bossou do not pound the hard-shelled fruits of *Strychnos* sp. against a hard surface, although this species occurs in the periphery of their home range. One instance of this behaviour was reported at the Yealé site [28]. Moreover, Nimba chimpanzees are unlikely to perform algae scooping, a customary behaviour observed at Bossou, since sources of stagnant water containing surface algae of the *Spirogyra* sp. type are non-existent in their habitat.

#### *Overlap in Material Culture between Bossou and Nimba*

Some overlap in material culture between the Bossou and the Nimba sites can be noted. The two behaviours they have shown in common, so far, are ant dipping using

wands and ground nest building. These behaviours have not yet been observed at Diécké. It still has to be confirmed whether the target prey species for ant dipping are the same or not and whether the processing technique employed is similar. At Bossou, chimpanzees use a stick to collect the swarming ants and then most frequently pick the ants off directly using their lips to eat them [41]. Manual wiping of the stick before consuming the ants, which is the most common technique used by chimpanzees at Gombe and Mount Assirik [2], is not a technique often observed in the Bossou chimpanzees [T.H., pers. observation].

The use of ground nests has been detected, although infrequently, at Gombe and Budongo [2]. Nests on the ground have also more commonly been observed at Taï [2, 41] and at Bossou [2]. At Yealé, Matsuzawa and Yamakoshi [28] reported that 35.4% of the 464 nests found during their survey in the area were ground nests. They also suggested that some of the ground nests found in the Nimba region of Yealé may have occasionally served as night nests, as at Gombe and Budongo, where such night nests have been observed in the making, although rarely [2]. Ground nests were also found at the Seringbara site, while none has yet been discovered at Diécké. Finally, only direct observation of the chimpanzees of the Nimba Mountains while in nests or during nest building will help establish what proportion of ground nests is used as night or day nests.

## Discussion

We have presented a preliminary report on the differences and similarities in material culture between neighbouring chimpanzee communities in a small region of Guinea and Côte d'Ivoire, West Africa. Many behaviours included in the repertoire of the Bossou chimpanzees have still not been observed at any of the other three sites, but could be present. Only further studies of the chimpanzee populations in the Nimba area and in the Diécké reserve will confirm their absence or presence. However, due to poor habituation of the chimpanzees at Nimba and Diécké, no evidence only tentatively suggests absence. Only long-term field work will confirm any trends in differences. The only exception is nut cracking behaviour for which evidence can easily be sought. Indeed, the cultural variants emerging from our present findings all involve nut cracking. These include, with most certitude, the absence of cracking of oil palm nuts at Seringbara, of *Panda* nuts at Yealé and of *Carapa* nuts at Bossou. In all three cases, the specified nut-bearing species is common in the habitat of the chimpanzees. Variations in tool choice for nut cracking were also noted in relation to materials used as anvils. A fuller picture of the similarities and differences between these four study sites will continue to emerge as fieldwork proceeds in those areas.

Several authors have proposed that some behaviours or traditions are transferred by individuals migrating from one community to another, so that a 'cultural region' larger than the original community is formed [1, 28, 42, 43]. Based on the history of individual interchange and the seemingly current one-way migration of individuals between Bossou and Nimba, we therefore predict that behaviours, especially tool use, performed by the Bossou community will also be performed by the chimpanzees in the Nimba region. This prediction, however, does not perhaps hold for the Diécké site, which is further away. Clear ecological differences, such as absence, presence or even divergences in the distribution and abundance of target species, though, may be the simple explanation of the absence of some behaviours.

What other explanations could there be for any differences that we may find? Subtle ecological differences should be explored. Matsuzawa and Yamakoshi have suggested that 'behavioural differences between communities are formed and maintained by balancing adjustments to local environments with dynamic cultural interchange' [28, p. 229]. Indeed, target species phenology, tool availability as well as presence and accessibility of alternative food resources may subtly affect the adoption of a behaviour within a community or the frequency of its occurrence.

Propagation of a behaviour within these neighbouring communities may also be restricted by the mode of transmission of the behaviour. It could also possibly be limited by the social context in which its transmission takes place or even by some form of social convention prevalent in the community and maintained by its members.

Finally, this ongoing comparative study is the first of its kind exploring, in particular, aspects of culture among three geographically adjacent chimpanzee populations – Bossou, Seringbara and Yealé – which have recently undergone or are still experiencing individual interchange. Quantitative data are being collected at present to explore whether environmental parameters could explain these emerging variations in behaviour. Moreover, a fuller picture of the behavioural repertoire displayed by these communities will help us further explore the above hypotheses. Ultimately, we believe that by continuing research at Bossou [45] and surrounding areas, we will be able to clarify many of those questions surrounding the issues of culture and cultural transmission in wild chimpanzees.

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