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Historical hypotheses of chimpanzee tool use behaviour in relation to natural and human-induced changes in an East African rain forest[1]

Hypothèses historiques à propos du comportement d'utilisation d'outils par les chimpanzés en relation avec les changements naturels et anthropiques d'une forêt tropicale d'Afrique de l'Est

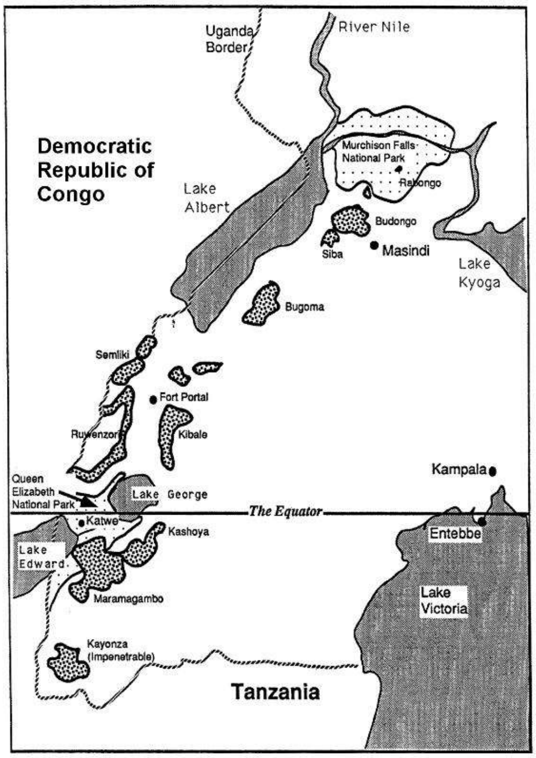
Thibaud Gruber

> "The Budongo Forest has existed for millennia as an isolated block detached from the central African forest. Until this century, it has had minimal contact with human populations. It was neither inhabited nor used extensively as a resource, though it was undoubtedly kept from spreading by human-instigated fires. The precolonial restraints on the forest's expansion were thus fire, human-controlled animal herds, and elephants. These conditions prevailed until the extension of the British protectorate to include Bunyoro in 1901." (Paterson, 1991, p. 186).

1 Introduction

1 Despite being highly adaptable and found in a wide range of habitats (Pruetz, 2006), chimpanzees remain forest dwelling-animals (Kortlandt, 1983). The forests they inhabit experience constant changes in surface, coverage and composition among other ecological characteristics. These changes occur either naturally or are induced by human activities, and it is important to analyze the dynamics of the interactions between the forests and the species they host to understand how the latter evolve. Changes in the forest can lead to changes in the behaviour of the animals, for instance if the forest becomes swarmed with human activities (Zommers *et al.*, 2013); conversely, the behaviour of some inhabitants can also lead to the phenomenon known as "niche construction" (Odling-Smee *et al.*, 2003), whereby a particular species can shape its own environment by its actions, which in return may lead to the emergence of novel selective pressures for the species itself but also for other species (the most famous example being the beaver dam). In this article, I will focus on a particular forest, the Budongo Forest in Western Uganda (fig. 1) and on the potential influence of forest changes on the appearance, maintenance and disappearance of cultural behaviours in wild chimpanzees (*Pan troglodytes schweinfurthii*). To illustrate the connection between ecological and cultural variation, I will focus on stick use, for which both observational and experimental data suggest a clear impact of the former on the latter.

Figure 1



Map of Western Uganda showing the location of the Budongo and Kibale forests (courtesy of James Paterson, with modification by the author).
Carte de l'Ouganda occidental montrant l'emplacement des forêts de Budongo et Kibale (avec l'aimable autorisation de James Paterson, modifiée par l'auteur).

2 Forests change throughout the ages: the long-term picture

2 A defining feature of the ongoing Quaternary geological period, which started about 2.6 MA ago with the transition from the Pliocene to the Pleistocene epoch, is the presence of several major glacial events (Gradstein *et al.*, 2004). The current epoch, the Holocene, considered an interglacial epoch in the ongoing ice age, followed the last glaciation at the end of the Pleistocene, 11,700 years ago. Temperature variation had an impact on forest coverage, and led to periods of expansion and contraction, notably in Sub-Saharan Africa (Kendall, 1969; van Zinderen Bakker and Coetzee, 1972; Moeyersons and Roche, 1982), where the maximum expansion occurred about 12,500 years ago (Hamilton, 1976; Haffer, 1982; Mayr and O'Hara, 1986; Hamilton, 1988). The Budongo Forest was then part of a larger forest originating from northeastern Democratic Republic of Congo and encompassing several Ugandan forests such as Kibale (Hamilton, 1976; Grubb, 1982; Howard, 1991), which subsequently became fragmented (Philipson, 1977; Hamilton, 1984; Hamilton *et al.*, 1986; Howard, 1991). The Budongo Forest became separated from other forest patches about 8,000 to 10,000 years ago (Reynolds, 2005).

3 According to the Pleistocene refugia theory (Haffer, 1969), repeated oscillations between dry and moist climatic periods led to the isolation of forest-associated taxa, which provoked genetic diversification. Modern populations descending from these isolated populations have a higher genetic diversity than the ones descending from sub-populations that colonized areas regained during forest expansion. The theory has been partly supported by data in birds (Roy, 1997; Smith *et al.*, 2000; Bowie *et al.*, 2006) and in primates (Jensen-Seaman and Kidd, 2001; Telfer *et al.*, 2003; Anthony *et al.*, 2007). With respect to the Ugandan case, the model is supported for red colobus monkeys (*Colobus badius tephrosceles*) (Struhsaker, 1975), but less for Eastern chimpanzees (Goldberg, 1996). During the last ice age, the Eastern chimpanzee population, which remained small, may have occupied woodland habitats during the more arid and colder episodes rather than retracting in forest refugia, before populating the regenerating forests during the subsequent interglacial expansion (Goldberg, 1996; Goldberg and Ruvolo, 1997b; Goldberg, 1998).

4 Forest types composing the forest also change with time. For instance, the Budongo Forest, described as a “lowland rain forest” by Eggeling (1947), was composed of four forest types in 1944: *Cynometra* forest, *mixed* forest, *colonising woodland* and *swamp* forest. The first three types followed an ecological succession, with the colonising woodland turning into the mixed forest that could potentially become the climax forest type dominated by *Cynometra alexandrii* (Eggeling, 1947). In 1944, the mixed forest was the most represented forest type (60%) with over fifty species of large trees, including the economically valuable mahogany trees *Khaya anthotheca*, *Entandrophragma cylindricum*, *E. utile* and *E.angolense* (Plumptre and Reynolds, 1994). As of 1944, the *Cynometra* forest type accounted for up to 35% of Budongo Forest and the colonising woodland, found at the edge of the forest, for 6%. Finally, the swamp forest, found along the streams and growing on soils that are flooded for part of the year, represented about 2% of the forest surface. By the 1970s, the *Cynometra* forest was reduced to only 15 to 20% of the forest, when it may have represented as much as 50% of the total area prior to 1890 (Paterson, 1991). In a different study, Plumptre found that between 1951 and 1990, the *Cynometra* forest, the

Cynometra-mixed forest, the colonising-mixed forest, the colonising woodland and the swamp forest lost respectively 41%, 62.2%, 26.6%, 33.2% and 0.7% of their surface. In contrast, the mixed forest gained 175.8% (Plumptre, 1996). In the following section, I will explore the factors that led to such a change.

3 The impact of wildlife, fire and humans on forest and the consequences on primate behaviour and diet

5 Two main phenomena shaped precolonial Ugandan forests: elephant migrations and fire. The main action of the elephants was to trample over the vegetation and to damage the trees by way of debarking (Buechner and Dawkins, 1961). Although it was not necessarily lethal to the tree, this peeling exposed fire-sensitive layers that could not resist bushfires. One consequence of debarking was therefore the easier propagation of fire that could carry on deeper in the forest. The combined effect of elephants and fire would thus be the loss of numerous trees as well as the transformation of zones of thick forest into grassland.

6 Forest fires can have a natural origin, but also result from human action, most particularly since the domestication of fire and its use for agriculture (Goldammer and de Ronde, 2004). In the Bunyoro area, where the Budongo Forest is located, this became especially true with the settlement of Bahima herders, more than 600 years before colonial rules were implemented (Paterson, 1991). The major aim of grassland burning was to provide fresh forage for the herds. However, it also had the benefit to repel tsetse flies by burning the savannah bushes where they rest and lay their eggs, thus favouring human settlement in the area. The combined action of fires and elephants maintained the Budongo Forest within its boundaries and prevented it from expanding for centuries.

7 However, with the arrival of the British colonial power starting from the mid-nineteenth century, drastic measures were taken with respect to both fires and elephants and had numerous consequences on the forest (Paterson, 1991). The regulation of grassland burning in the 1920s led to the growth of bush savannah, the spread of the tsetse fly and the outburst of sleeping sickness (trypanosomiasis) in humans, cattle and wild species. The area became deserted and the forest started to expand over its previous boundaries. In the 1950s, to obliterate the tsetse fly, it was decided to shoot all its potential prey, notably big game such as buffalos and ungulates (including elephants). This led to the disappearance of these species south of the Nile. Elephants entirely disappeared in the 1960s, when the army shot them down during their annual migration (Reynolds, personal communication).

8 Other policies had a direct impact on the ecological composition of the forest as the Budongo Forest became of interest for forestry and logging activities. By 1926, a sawmill had been established at the heart of the forest, and by 1960, it was the largest timber producer in Uganda, with working plans established to support a sustainable extraction and favour the growth of usable trees (Plumptre, 1996). Because the *Cynometra* forest was not of economic value compared to the mixed forest, which contained valuable trees for production including the famous mahoganies, several poisoning campaigns in the 1950s and 60s aimed at reducing the amount of *Cynometra* trees in order to open the canopy and favour the development of the mixed forest tree species. These campaigns also aimed at removing “weed” species such as strangler figs (Plumptre, 1996). The areas treated with

arboricides saw an increase in mixed forest, but *Cynometra* remained an important part of the vegetation, albeit not dominant anymore. Interestingly, despite the initial goal of the poisoning, the campaigns unexpectedly favoured the growth of fig tree species (Plumptre *et al.*, 1997; Reynolds, 2005).

9 The increase in mixed forest in logged areas compared to non-logged areas led to the increase of the primate populations in the former for three species (*Colobus guereza*, *Cercopithecus mitis* and *Cercopithecus ascanius*, Plumptre and Reynolds, 1994) ; but not for chimpanzees or baboons (*Papio anubis*), possibly because of a greater sensitivity to human activities (Reynolds, 2005).

10 A more detailed analysis shows nonetheless some effects of logging. Chimpanzee faecal samples from the Sonso area (compartment N3, where the sawmill was located and thus a heavily logged area) had nearly eight times as many fig seeds as samples obtained from the unlogged Kaniyo Pabidi area (Plumptre *et al.*, 1997). Additionally, the Sonso chimpanzee started consuming the fruits and leaves of a species introduced at the sawmill for paper production, *Broussonetia papyrifera*, and absent in other parts of the forest. This species has an especially low concentrations of tannins, making it a chimpanzee favourite (Reynolds *et al.*, 1998). Human activities in the forest thus led to changes in the chimpanzee diet.

4 Digression: the impact of ecology on cultural behaviour and the unusual Budongo chimpanzees

11 While human activities have an impact on chimpanzee diet, they can also affect their behaviour. In the following paragraphs, I will only focus on the potential links between human activity and cultural behaviour in a long term perspective, but it must be noticed that chimpanzee behaviour may be affected more directly by human activities with sometimes a tense relationship between the two species (McLennan and Hill, 2010). Before developing hypotheses on chimpanzee cultural behaviour in Budongo Forest, I will first introduce some notions on chimpanzee culture.

12 Culture, as seen by zoologists, and most especially primatologists, consists of socially transmitted behaviours that vary between animal groups, for which the variation cannot be explained by obvious genetic or ecological factors (Whiten *et al.*, 1999). Following the chimpanzee findings, cultures (or traditions) have been inferred in other species such as orangutans, capuchins, whales and dolphins (Rendell and Whitehead, 2001; Perry and Manson, 2003; van Schaik *et al.*, 2003). However, some opposed this view, arguing that environment and genes cannot be excluded and always contribute to the shaping of behaviours (Laland and Janik, 2006). Since then, studies have aimed at quantifying what part of the behavioural variance could be attributed to the different factors (social, genetic and environmental). This approach still allows one to isolate a social component, for instance, in the case of ant-dipping, which justifies the use of the word ‘culture’ (Möbius *et al.*, 2008; Schöning *et al.*, 2008). Understanding what ecological factor drives the appearance, maintenance or disappearance of certain cultural behaviours, most notably tool use, has since been a hot topic in cultural primatology (Humle and Matsuzawa, 2002; Gruber *et al.*, 2012a; Koops *et al.*, 2013). Fox and colleagues (2004) proposed two major competing but non-mutually exclusive hypotheses to explain the influence of environment on orangutan tool use: the opportunity and the necessity hypotheses, a

distinction that has since be adapted to other species such as capuchins (Spagnoletti *et al.*, 2012) and chimpanzees (Koops *et al.*, 2013). Adapted to the chimpanzee species, the opportunity hypothesis states that “encounter rates with nuts, insects or tools explain tool use patterns” (patterns is here understood as the presence or absence of particular behaviours across Africa) while the necessity hypothesis states that “tool use is a response to scarcity of preferred foods (i.e. ripe fruit)” (Koops *et al.*, 2013, p. 175). Although the necessity hypothesis was favoured in the past (Yamakoshi, 1998; Lee, 2003), recent studies have argued in favour of the opportunity hypothesis, finding no support for the necessity hypothesis in current ecological settings (Spagnoletti *et al.*, 2012; Koops *et al.*, 2013).

13 Chimpanzees in Uganda are famous for having quite limited tool use behaviour (McGrew, 2010), notably when extracting food. In effect, the three most studied communities in Uganda, the Ngogo and Kanyawara communities (both found in Kibale Forest, see figure 1) and the Sonso community of Budongo Forest, display respectively 4, 2 and 1 food-related tool use behaviours (Gruber *et al.*, 2012a). The Sonso community has the smallest number of all, knowing only leaf-sponging (picking, folding and mashing leaves taken from the vegetation into a sponge to absorb water) but not using sticks in their daily life. The only observations of Sonso chimpanzees using sticks are when building a nest and when engaging in a tag-like game where one individual runs after another one carrying a stick. This is in contrast to other habituated Ugandan communities where the use of sticks as probes, levers and as tools to exploit food resources such as honey have been documented (Watts, 2008); and, more generally, to other long term study chimpanzee communities in Africa (Whiten *et al.*, 1999). This difference in tool use behaviour does not result from genetic factors, given low genetic variation among East African chimpanzee communities (Goldberg and Ruvolo, 1997a), nor from incomplete observations, the Sonso community having been under constant scientific scrutiny for more than twenty years (Reynolds, 2005). Additionally, recent experiments have confirmed the absence of the stick using behaviour in the community: the Sonso chimpanzees, when exposed to a hole filled with honey drilled in a natural log, manufactured leaf-sponges to extract the honey, in contrast to the Kanyawara chimpanzees who used sticks for the same task (Figure 2, Gruber *et al.*, 2009). The lack of knowledge of the Sonso community was later confirmed with more experimental work, showing that even when directly exposed to a stick plugged into the honey, the individuals who engaged with the task did not understand the affordances of the tool and did not develop stick use (Gruber *et al.*, 2011), suggesting that the development of a new tool behaviour may not be so straightforward in chimpanzees. How is it possible to explain such behaviour?

Figure 2

Kanyawara chimpanzee using a stick in the honey-trap experiment (courtesy of Andrew Bernard).
Chimpanzé Kanyawara utilisant un bâton dans l'expérience du piège à miel (avec l'aimable autorisation d'Andrew Bernard).

5 A potential scenario for changes in chimpanzee cultural behaviours in Budongo Forest

14 Analyzing the case of stick use in Budongo Forest through the opportunity and necessity hypotheses does not seem to yield convincing conclusions. Firstly, the opportunity hypothesis suggests that the encounter with bees' nests and sticks would favour the development of stick use. The experimental work conducted since 2009 argues against the fact that finding the food and the right tools nearby would lead necessarily to the development of the behaviour. Most compellingly, in one experimental setting, 20 chimpanzees (14 who had failed to reach the honey previously because they did not display any tool use and 6 who used leaf-sponges before to collect the honey) encountered a stick directly plugged into the honey but none of them, despite some of them engaging with the stick, started to use it as a tool (Gruber *et al.*, 2010; Gruber *et al.*, 2011). If taken in a larger perspective, the opportunity hypothesis may suggest that there is a difference in honey availability between Budongo and Kibale forests. It is hard to evaluate precisely how many bees' nests are present in the chimpanzee range. Bees' nests appear to be found and exploited opportunistically by chimpanzees although they remember where they extracted honey and come back even months afterwards to check whether honey is again available (Gruber, personal observations). However, the same genera of bees are present in the two forests (*Apis*, *Meliponula* and *Xylocopa*) and *Apis* or *Meliponula* bees appeared at all the testing sites to exploit the experimentally-provided honey, suggesting that their nest was in the vicinity. Similarly, the wide availability of

sticks anywhere in both forests makes unlikely that a difference in tool availability would cause a difference in stick use between the two communities.

15 Regarding the necessity hypothesis, the interpretation is at first sight also unlikely to yield significant results, given that even though no period of food scarcity has been documented in Sonso in the first twenty years of observations (Newton-Fisher, 1999; Reynolds, 2005), the Ngogo community (which has more tool use behaviours in their repertoire) appears to have the richest diet of the three studied communities (Gruber *et al.*, 2012a). However, the fact that the food supply was constant between 1990 and the early 2000s does not mean that it has always been the case in the past, and the diet of the Sonso or Ngogo chimpanzees may not have always been the same. One hypothesis proposed to explain the small genetic diversity in East African chimpanzees is that they survived in a mix of woodland and savannah-type areas rather than retreating into forest refugia during glacial events (Goldberg, 1998). The small size of the original gene pool suggests that the original population was kept low and survived in dry, marginal habitats where the food supply was probably reduced compared to the following interglacial period (Goldberg, 1996). This may have led to the development of stick use in East African chimpanzee populations as an adaptive behaviour, or at least, to the presence of a constant ecological pressure keeping the behaviour in the repertoire of the original population from which descended all modern East African communities (Gruber *et al.*, 2012a). This is supported by the fact that most studied East African chimpanzee communities have stick use in their current repertoire, a behaviour that is not so easy to develop and thus to re-invent in independent events (Gruber *et al.*, 2011). When the forest repopulated the areas where the chimpanzees were occupying woodland and savannahs, different ecotones came in place. For instance, in Budongo Forest, an important species is *Cynometra alexandrii*, which is also an important part of the community diet. This species is absent from the Kanyawara and Ngogo areas, probably because the Kibale Forest has a higher average elevation than the Budongo Forest (Chapman *et al.*, 1997; Gruber *et al.*, 2012a).

16 Could these subtle ecological differences in the re-established forests account for cultural differences between the communities? In a recent study, we showed that the Sonso area (and more generally, the Budongo Forest) appeared more diverse in terms of available edible tree species for chimpanzees, and that the Sonso chimpanzees consumed about twice as many items as the Kanyawara and Ngogo chimpanzees (Gruber *et al.*, 2012a). Our analyses led us to propose the diversity hypothesis with respect to food-related tool use behaviours, that is, the diversity of items consumed, by preventing periods of food scarcity (as opposed to food richness, which does not necessarily prevent food scarcity periods if ripe fruit availability is concentrated in given periods of the year), may influence tool use repertoire, notably by leading to the disappearance of food-related tool use behaviours. In other words, a mother chimpanzee having a constant range of food choices will not necessarily display tool-using behaviours, as opposed to a mother chimpanzee facing more limited food choices, and this may lead to the interruption of the transmission of one given behaviour within her matriline (and potentially to the extinction of the behaviour in the community if all chimpanzees cease to display the behaviour). As such, the Sonso community may have lost stick use because Sonso mothers stopped to display this behaviour in front of their infants. This event may have happened either in the past, at the time of forest recolonisation, or later on, or even during recent times following the effects of the logging activities in the forest (augmentation of fleshy

fruit tree availability in the area). Comparing the Sonso community with two other communities in the Budongo Forest (in Busingiro and Kaniyo Pabidi, respectively logged and unlogged areas of the forest), our preliminary results suggest that stick use may be absent in the entire Budongo Forest (Gruber *et al.*, 2012a). This may mean that logging was not directly responsible for the loss of the stick use behaviour, although it cannot be excluded that the Kaniyo Pabidi and Sonso communities experienced two independent losses. It could also be that neither community ever had stick use, in the hypothesis that the initial colonising population had already lost the behaviour. However, the finding of stick use for honey fishing in nearby Bulindi Forest (McLennan, 2011), as well as potentially in Kasokwa Forest (Wallis, personal communication), two satellite forests of the main Budongo block, makes this hypothesis unlikely. More data on other communities in Budongo Forest, as well as in other areas in Uganda will be necessary to understand the complete distribution of stick use in chimpanzee communities and decipher between the different hypotheses and potential scenarios.

6 Temporal dynamic characteristics as added values to ecological factors leading to cultural differences: A dynamic model of the influence of ecology on food-related tool use behaviour

17 The analysis of the situation, past and present, at Budongo Forest, despite needing more data points to evaluate the different hypotheses, allows me to underline that the opportunity and necessity hypotheses must include a temporal dimension in all cases:

18 The opportunity hypothesis is modulated by the diversity hypothesis in its cognitive dimension: while chimpanzees may encounter the suitable food and the right affordances to develop tool use at a given time, the development of tool use may not happen if the current diet already provides a buffer against food scarcity. Additionally, the development of new techniques may be prevented if the current tool use behaviour (e.g. leaf-sponging to extract honey) is efficient enough to extract the calories or nutrients necessary. Nevertheless, innovation may be still possible in the case of independent explorations, irrelevant of ecological conditions, for instance by young individuals while their mother is foraging). Why think of developing novel behaviours when there is a next-to-preferred available resource nearby? In other times, when the diet is not so optimal, development of tool use may happen.

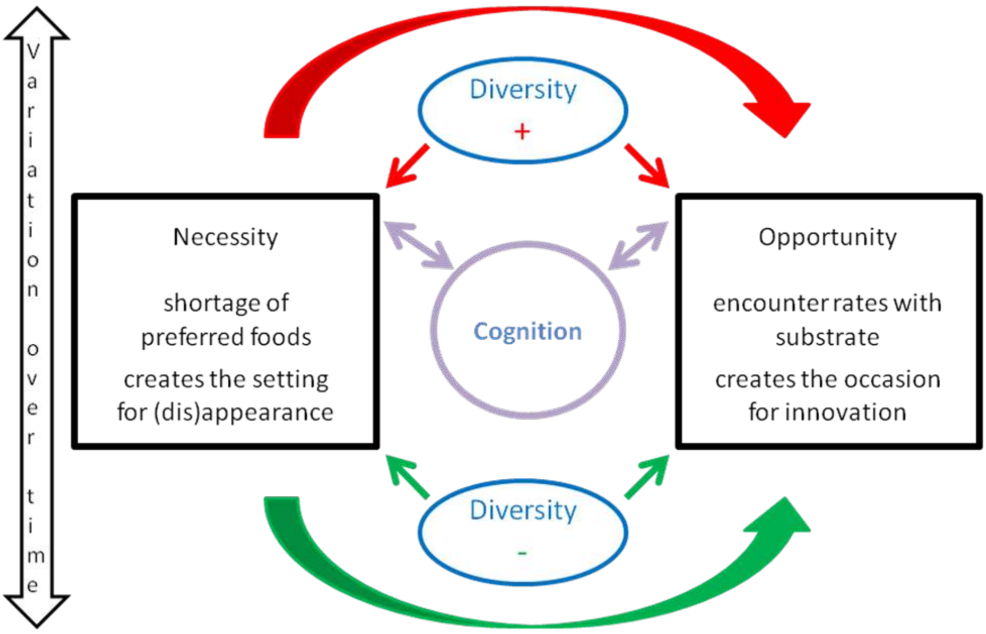
19 The necessity hypothesis is modulated by the diversity hypothesis in its ecological dimension: a community will adapt to its environment depending on whether the environmental pressure changes over time. A given behaviour may develop because of ecological constraints, but if the pressure disappears, the need to use this behaviour may also disappear, leading to the potential disappearance of the behaviour in the end.

20 In both cases, the factor to take into account is that ecological conditions change over time, and this has an impact on both the necessity and opportunity to develop a novel tool-using behaviour. For instance, the ecological pressures faced by the ancestors of Budongo Forest communities were different from the ones faced by modern Sonso chimpanzees. In the case of Ugandan forests, the environmental variation is best represented by the variation in diversity of food available rather than its quality, thus our decision to call it the 'diversity hypothesis' (Gruber *et al.*, 2012a). However this does not

preclude other environmental characteristics (e.g. quality of the diet) from influencing the opportunity and necessity factors in other sites or situations (i.e. in another community, it may not be the diversity of food available that will influence the development or the disappearance of a food-related tool use behaviour as in Sonso, but potentially a change in food quality or another relevant ecological factor in this period of time).

21 Taking time into consideration, an opportunity ignored at a given moment may become of crucial value for survival in a different setting. In fact, far from being opposed to each other, the necessity and opportunity hypotheses may go hand in hand: while the opportunity to create a novel behaviour (innovation) may either depend on the ecological pressure faced by the individuals at a given moment or not (giving the possibility to innovate both in periods of critical necessity or not), the spread of the behaviour within the community may also depend on whether there is an immediate necessity (for survival) for the group to adopt this behaviour. Thus, raising the necessity parameter will favour both the opportunity to develop a new behaviour (if there is no second choice, there is a bigger need to explore one's surroundings) and its spread in the community (if my neighbour is feeding and I am not, I should take some interest in how he got the food). Similarly, even if a behaviour exists in the community, it may be lost if the environment changes (for instance in proposing more easily accessible food, easing the necessity aspect that drove the appearance of the behaviour in the first place) and limits the opportunities for one generation to display the behaviour to the next generation (the youngsters are less exposed to the substrate and technique because the adults fail to exploit the resource). In effect, the necessity factor determines the general setting to develop a novel behaviour (if there is an ecological 'need' to develop or maintain a behaviour) while the opportunity factor will determine the occasions to develop such behaviours (if there is something new to notice and explore to answer to this need). This reasoning is summarised in Figure 3.

Figure 3



A dynamic model of the acquisition of food-related tool use in wild chimpanzees. Green: favours development of tool use; red: impedes development of tool use. Arrows: effect of factors on each other. The ovoid circles show the impact of environmental variation (food diversity in the case of Budongo Forest) on the opportunity and necessity to develop a particular tool using behaviour.

Un modèle dynamique de l'acquisition de l'utilisation des outils liés à l'alimentation chez les chimpanzés sauvages. Flèches:effets des facteurs les uns sur les autres. Flèche verte: favorise le développement de l'utilisation de l'outil; flèche rouge: contrecarie le développement de l'utilisation de l'outil. Les cercles ovoïdes montrent l'impact des variations de l'environnement (diversité alimentaire dans le cas de la forêt de Budongo) sur l'opportunité et la nécessité de développer un comportement d'utilisation d'un outil spécifique.

22 A second important point is that ecological factors alone will not necessarily lead to the appearance or disappearance of a given behaviour. The difficulty of the Sonso chimpanzees to develop stick use in the honey-trap experiments (Gruber *et al.*, 2011) illustrates that developing a novel behaviour, even as simple as stick use, may not be straightforward. Thus, both the opportunity and necessity hypotheses must be modulated by specific cognitive characteristics of the community considered (general intelligence, presence of innovators, opportunities for social learning, see van Schaik and Pradhan, 2003). This, in turn, may depend on genetic predisposition, for one thing, but most probably on the already present cultural niche in which the individual was born (Gruber *et al.*, 2012b). That Sonso chimpanzees adapted a leaf-based behaviour that is normally used to fetch water to solve the honey-trap experiment is not random and suggests that chimpanzees will explore new solutions in their environment close to their already existing state of knowledge. This may support the idea that chimpanzees have a zone of latent solutions (ZLS, Tennie *et al.*, 2009) that defines what solutions they can find. However rather than being defined at the species level as presented by Tennie *et al.*, the data presented here suggest that the ZLS is different for each chimpanzee, or at least, for each community, and is deeply influenced by their cultural knowledge. For instance, a chimpanzee who was born in a 'leaf-oriented' community such as Budongo will have a very different ZLS from a chimpanzee who was born in a 'stone-oriented' community such as Bossou. As such, cognition may also play a role in how chimpanzees may realize that there is an opportunity to develop a novel behaviour or not. If an object of their

environment has never been considered *as* a tool, which necessitates quite developed representational abilities (Gruber, submitted), it may be harder for chimpanzees to consider this object as a potential solution to their problem. But the other way is also possible: being exposed to the properties of a given object several times – and as such, being given the 'opportunity' to understand how it can be used – may be necessary to start using it. Similarly, the links between cognition and necessity have to be explored. Necessity may be the mother of invention (Lee, 2003) but a lack of necessity, by bringing all required and potentially even improved sources of nutrients, may also favour brain activity, innovation and the development of novel techniques (Wrangham, 2009). The links between cognition and the different sides of the model will have to be explored to understand fully how food-related tool use behaviours develop in wild chimpanzees.

7 Conclusion: chimpanzee cultural behaviour changes over time and humans are bound to play a role

23 In this article I attempted to put the study of chimpanzee culture into perspective, adopting an historical framework going back to the last ice age and the Pleistocene to underline how cultural evolution and ecological changes are linked, similar to what is claimed in humans (Richerson *et al.*, 2001). I also argued in favour of including a temporal dimension in the current debate on the influence of ecology on cultural behaviour. In the last paragraphs, I showed that many factors intervene and interplay in the development of chimpanzee cultures. Past human activities around and inside Budongo Forest have had a huge impact on the composition of the forest and had direct and indirect consequences on chimpanzee diet and behaviour. The proposed model is adapted to the case of the Budongo Forest and its chimpanzees, but I believe the general framework that mixes the opportunity and necessity factors leading to the development of novel tool use behaviour may be adapted to other chimpanzee communities or primate species, as far as the specific ecological pressures that they face in each case are considered.

24 Additionally, although I anchored the scenario in the forest's past, the interaction between ecological conditions and cultural knowledge is an ongoing process that is not static and that must be understood as a continuous dynamic system where human activity, with their constant uses of the forest, has an important role. This is not limited to chimpanzees, as a recent study showed that the famous stone tool-using Burmese long-tailed macaques (*Macaca fascicularis*) are now under threat of losing their cultural knowledge because of human activities (Gumert *et al.*, 2013). The presence of a research camp for the last twenty-three years has prevented illegal logging or hunting to spread into Sonso territory, turning this area into a haven for several species including monkeys or duikers, but the current trend in the forest is toward a decrease in food availability (Babweteera *et al.*, 2012). Whether this is directly linked to current human activity in the forest (most notably illegal logging and poaching) or to global climate change is to be determined. Nonetheless, the impact of these human-induced changes on chimpanzee behaviour and culture will have to be monitored in the future.

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NOTES

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ABSTRACTS

Chimpanzees and humans have co-existed in Africa for millennia. The forests inhabited by chimpanzees have experienced numerous changes in recent time, most notably during the last 12,000 years, as the current interglacial age started. In this article, I will study the case of

Western Ugandan forests to describe the different factors, natural and human-induced, which affect a tropical forest, and draw hypotheses on the influence of these changes on chimpanzee cultural behaviour. Before colonial times, the Budongo Forest was shaped by elephant migrations and fires lit by the pastoralists who settled in the area. Later on, the British colonial power organized the exploitation of the forest through work plans aimed at insuring sustainable extraction of valuable timber. The human activity resulted in unexpected consequences in the forest. Interestingly, the resident chimpanzees are nowadays remarkable in the small size of their tool use repertoire. Ecological analysis and tool use observations in Uganda only support partly the opportunity and necessity hypotheses that are currently proposed to explain the influence of ecological factors on tool-using behaviour. Rather, the data I present here suggest that the temporal dimension of ecological changes in the forest must be taken into account to explain tool use behaviour variation in Ugandan forests. I propose a dynamic model connecting the necessity and opportunity factors influenced by ecological changes over time, most salient in Ugandan forests through the variability in food diversity. Finally, I conclude on the ever-changing ecological situation in Budongo Forest.

Les chimpanzés et les humains ont coexisté en Afrique depuis des millénaires. Les forêts habitées par les chimpanzés ont changé de manière importante dans le passé récent, tout particulièrement depuis 12 000 ans et le début d'un âge interglaciaire. Dans cet article, j'étudierai le cas particulier des forêts de l'ouest de l'Ouganda pour décrire les différents facteurs, naturels et induits par l'homme, qui influent sur la forêt tropicale, et j'esquisserai des hypothèses à propos des effets des changements qui en résultent sur le comportement culturel des chimpanzés. Avant l'ère coloniale, la forêt de Budongo subissait les migrations des éléphants et les feux de brousse allumés par les populations pastorales des environs. Plus tard, les autorités coloniales britanniques ont organisé l'exploitation de la forêt en engageant des plans durables d'extraction du bois précieux. L'activité humaine eut des conséquences imprévues pour la forêt. De manière intéressante, les chimpanzés de Budongo ont un répertoire culturel limité comparé aux autres communautés. L'analyse écologique et les observations d'utilisation d'outils en Ouganda ne supportent que partiellement les hypothèses dites de 'nécessité' et d''opportunité' proposées pour expliquer le développement d'outils chez les primates non-humains. Au contraire, les données que je présente suggèrent que la dimension temporelle des changements écologiques de la forêt doit être prise en compte pour expliquer la variation des répertoires d'utilisation d'outils en Ouganda. Je propose un modèle dynamique qui connecte les facteurs de nécessité et d'opportunité via l'influence des variations écologiques au travers du temps, qui transparaît notamment en Ouganda à travers la variation en diversité de nourriture accessible à un moment donné. Je conclus sur l'évolution permanente de la forêt de Budongo.

INDEX

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