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OBJECT MANIPULATION AND TOOL USE IN A COMMUNITY OF WILD CHIMPANZEES *(Pan troglodytes schweinfurthii)* OF THE BUDONGO FOREST, UGANDA

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GENERAL ABSTRACT

This thesis examines wild chimpanzee tool use, with a particular focus on the ontogeny of object manipulation, as well as transmission mechanisms and possibility of cultural evolution of tool use in this species.

Chimpanzees are known for their tool use proficiency and have been extensively studied regarding these skills. Previous studies on the ontogeny of tool use have focused on the development of one specific behaviour or on general object play in immatures without any link to tool use in adulthood. Furthermore, most studies on social transmission used experimental approaches with captive animals, mainly by seeding an artificial behaviour and studying its spread. Few studies were able to document the emergence and the spread of a naturally occurring innovation in the wild and even fewer looked at the establishment of the behaviour and not just the initial propagation. Finally, non-human cumulative culture is still a hot topic and few cases in the wild have been documented.

To provide further insights into these topics, I conducted research on the wild chimpanzees of the Sonso community, in the Budongo forest, Uganda.

In three studies, I first investigated the development of tool use by looking at object play in immatures, the proposed precursor of tool use, but also at adult object manipulations. I tested individual and social factors that could influence the type of object individuals played with. Second, I investigated the mechanism of persistence of a tool-related drinking behaviour, moss-sponging, which naturally emerged in the Sonso community three years prior to my research. Third, I evaluated whether moss-sponging constituted a case of cultural evolution and test whether this drinking variant meets the criteria for cumulative culture.

I found that, object manipulations generally decreased with age, while goal-directedness increased. I also found that adults manipulated preferentially leaves and woody vegetation, but never sticks, whereas non-adults had a preference for leaves, woody vegetation and sticks, with stick manipulation gradually decreasing to complete disengagement around the age of 15 years. Leaving stick manipulation aside, non-adults played and explored in higher proportions the materials manipulated most often by their mothers, providing good evidence for social learning from mothers. When investigating moss-sponging, I found that, over a period of three years, the behaviour spread from a small number of founder individuals (eight) to 17 additional group members. This spread was not random or influenced by spatiotemporal associations, but instead followed a matrilineal pattern, meaning that chimpanzees possessing a moss-sponging individual in their matriline were more likely to be themselves moss-spongers compared to individuals from matrilines that did not have a moss-sponger. Finally, I found that moss-sponging fulfils most of the criteria for cumulative culture

suggesting that it might have evolved from leaf-sponging and constitutes a basic case of cultural material evolution.

Overall, my research shows the importance of mothers and kin, with an influence already acting at an early stage of the tool use development. Furthermore, it shows that chimpanzees can display basic elements of cultural evolution, yet probably lacking high fidelity transmission mechanisms allowing them to reach a level of technological complexity found in humans.

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1. GENERAL INTRODUCTION

1.1 Animal tool use

1.1.1 Definitions and Distribution

Definitions

The study of animal tool use started decades ago with one of the earliest systematic surveys conducted by Hall (1963) on tool-using behaviours from different taxa such as insects, birds, and mammals. Research on tool use intensified after the first report by Goodall (1964) of wild chimpanzees fashioning tools to fish for termites. But from the burgeoning research on animal tool use arose a problem: the difficulty of defining 'tool', leading to an impressive number of different definitions. Early definitions have been criticised for their arbitrariness (Hansell, 1987), imprecision (Shumaker, Walkup, & Beck, 2011; St Amant & Horton, 2008) or anthropocentrism (Shettleworth, 1998), which has only increased the list of existing definitions but some authors do not even define explicitly tool use when reporting or discussing this topic. Early definitions tended to be brief, like Hall (1963), who defined tool use as "…the use by an animal of an object or of another living organism as a means of achieving an advantage" (p. 479), or Van Lawick-Goodall (1971), who defined tool use as "…the use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal" (p. 195), or Chevalier-Skolnikoff (1989), who described tool use as "…the use of one unattached object to effect a change in another" (p. 564). Yet, some authors proposed more comprehensive definitions, like Alcock (1972), who provided further details regarding the goal of tool use by defining it as "…the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object" (p. 464) or Beck (1980), who refined and broadened Alcock's and Goodall's definitions by defining tool use as "…the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool" (p. 10). Beck's definition became the reference in animal cognition literature and is usually utilized in tool use studies. Recently, St. Amant and Horton (2008) proposed a new definition articulated in two parts, the first related to tool use behaviour producing dynamic interaction with the environment and the second acting on the flow of information in the environment: "Tool use is the exertion of control over freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment" (p. 1203).

Despite a wide range of definitions and the desire to be as comprehensive as possible, there are always borderline cases where scientists disagree and which are usually related to amorphous objects, like water, or to a substrate, like hard surface, because there are usually not properly manipulable objects. Borderline cases, also labelled as proto-tool by some authors, are for example water droplets shot on terrestrial prey by archer fish to knock them off vegetation and then catch them at the water surface (Lüling, 1963) or the use of water by captive orang-utans to access a floating peanut in a tube (Mendes, Hanus, & Call, 2007) or, finally, birds (e.g. *Corvus sp* or *Larus sp*) dropping food items (e.g. mollusc, walnuts or eggs) onto the ground to crack-open them (Cristol & Switzer, 1999; Lefebvre, Nicolakakis, & Boire, 2002). Proto-tools are defined as the use of objects that are part of the substrate (Parker & Gibson, 1977) and are not considered as a true tools, yet they have been proposed to be the precursor of tool use (Panger, 1999, but see Shumaker, Walkup, & Beck, 2011) and cognitively less demanding than true tools (Marchant & McGrew, 2005; Parker & Gibson, 1977; but see Shumaker et al., 2011). This distinction between true tools and proto-tools (e.g. Beck, 1980; Parker & Gibson, 1977; Van Lawick-Goodall, 1971) was confirmed at least in birds (Lefebvre et al., 2002), with true tool users having a larger average brain size than proto-tool users, suggesting that these two categories required different degrees of cognitive ability. For my study on tool use, I adopted the definition proposed by Shumaker et al. (2011): "…the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible of the proper and effective orientation of the tool" (p.5). I also made the distinction between proto-tool and true tool (Parker & Gibson, 1977), when analysing interactions with substrates such as trunk or stout branches.

True tools can be classified into several categories (Shumaker et al., 2011): a) unique tools, b) tool sets, which consist of two or more tools used sequentially to achieve a single outcome (e.g. Boesch, Head, & Robbins, 2009; Sanz & Morgan, 2007), c) tool composites, where two or more tools are used simultaneously to achieve a single outcome (e.g. nut-cracking using hammer and anvil (Carvalho, Biro, McGrew, & Matsuzawa, 2009; Sugiyama, 1997)), d) compound tools (or meta-tool), where two or more components are combined as single working unit (e.g. leaf-sponges, propping anvil (Tetsuro Matsuzawa, 1994)) and, finally, e) tool-kits, which are sets of objects systematically employed as tools by a group or population (Fowler & Sommer, 2007; Mannu & Ottoni, 2009; Sanz & Morgan, 2007).

Another important distinction is between tool use and tool manufacture. Tool manufacture is relatively easier to define than tool use as an active act of creation (as opposed to mere acquisition of an object: Bentley-Condit & Smith, 2010). Shumaker et al. (2011) defined tool manufacture as "…simply any structural modification of an object or an existing tool so that the object serves, or serves more effectively, as a tool" (p. 11) and has been argued to be cognitively more demanding than mere tool-use.

Distribution

Reports of tool use and tool manufactures can be found across three phyla (Arthropods, Mollusca and Chordates) with birds and primates being clearly the most proficient and possessing the most diverse tool-kits (Bentley-Condit & Smith, 2010) compared to the big majority of animals using only one type of tool. Moreover, tool users are found across many animal taxa, such as hermit crabs using marine snail shells for protection against predators (Hazlett, 1981; Shumaker et al., 2011), whereas tool-makers are far less common, such as chimpanzees manufacturing sponges with leaves to drink water (Quiatt, 1999; Sousa, Biro, & Matsuzawa, 2009; Tonooka, 2001).

Within birds, Corvida and Passerida have been found to be the champions regarding tool use, demonstrating a wide range of true tool behaviours (Lefebvre et al., 2002). The most relevant example in terms of tool complexity and sophistication comes from New Caledonian crows (*Corvus moneduloides*). They manufacture sticks and hooked tools made from twigs and similar material (Hunt, 1996; Hunt & Gray, 2002, 2004) and long barbed edges of palm-like *Pandanus* leaves (Hunt, 1996). They all possess the same function: capturing invertebrates embedded in trees. But even though New Caledonian crows use a variety of tools to access out-of-reach food items possibly requiring high cognitive skills and are therefore specialized extractive foragers, their tool-using behaviours are restricted to the foraging context. This is also the case for many other species that are specialists at a single kind of tool, such as bottlenose dolphins (*Tursiops* sp.) that use sponges to probe the substrate for fish (Mann et al., 2008; Smolker, Richards, Connor, Mann, & Berggren, 1997), Galapagos woodpecker finches (*Cactospiza pallida)* that use twigs or cactus spines to get insects from crevices (Eibl-Eibesfeldt, 1961; Thomson, 1964) or sea otters who pound hard-shelled molluscs on rocks placed on their chests or abdomens (Fisher, 1939; Hall & Schaller, 1964). Yet, they are still far beyond the capacity of some primates, displaying extensive, and population-specific use of tools that varies in form, material, function and context (Gumert, Kluck, & Malaivijitnond, 2009; Ottoni & Izar, 2008; van Schaik, Ancrenaz, et al., 2003; Whiten et al., 1999).

1.1.2 Primate tool use

The famous declaration "Now we must redefine 'tool,' redefine 'man,' or accept chimpanzees as humans!" (Peterson, 2006, p. 212) from Louis Leaky, almost 50 years ago, when Jane Goodall, reported a chimpanzee using a blade of grass to fish for termites from a mound, set the stage for the flourishing study of primate's tool use. Only in the primate order one can find habitual or customary tool users, possessing multiple tool use skills, which are more broadly and flexibly applied across a variety of contexts than any other order in the animal kingdom. They have evolved hands and feet with prehensile fingers and toes that can accomplish impressive fine-tuned object manipulations (Christel, 1993; Shrewsbury & Sonek, 1986). Yet, most of the two hundred plus species of primates never or rarely use tools in nature or in captivity (Shumaker et al., 2011). If we take out humans and their unsurpassed complexity of tool use, chimpanzees (*Pan troglodytes*) are so far the most proficient tool

users (Fragaszy et al., 2013; Sanz & Morgan, 2007; Whiten et al., 1999). Within apes, only a second species similarly uses tools flexibly and regularly, orang-utans (*Pongo pygmaeus*) (Meulman, Seed, & Mann, 2013; van Schaik, Ancrenaz, et al., 2003). Surprisingly, the sister species of chimpanzees, bonobos, do not use tools regularly, despite living in similar habitats (Gruber, Clay, & Zuberbühler, 2010; Hohmann & Fruth, 2003). The only two other primates species considered as habitual or customary tool users are bearded capuchins (*Cebus libidinosus*) (Fragaszy et al., 2013; Mannu & Ottoni, 2009; Ottoni & Izar, 2008) and Burmese long-tailed macaque (*Macaca fascicularis aurea*) (Gumert et al., 2009; Gumert & Malaivijitnond, 2013). It is worth pointing out that all great ape taxa are proficient tool-users when experimentally tested in captivity (Gruber et al., 2010; Herrmann, Wobber, & Call, 2008; Manrique, Gross, & Call, 2010; Mulcahy & Call, 2006). This observation suggests that great ape species with an inexistent or minimal tool repertoire in the wild have lost their tool use. One can think of two hypotheses for this restricted use of tool by wild bonobos and gorillas (Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Gruber et al., 2010; Hohmann & Fruth, 2003; Wittiger & Sunderland-Groves, 2007). The first explanation would be that these species live currently in an environment proving them with all the relevant food sources, without requiring them to manipulate artefacts (Gruber et al., 2010; Hohmann & Fruth, 2003; McGrew, Ham, White, Tutin, & Fernandez, 1997). The second hypothesis it that long-term observations are absent and the number of study sites is restricted, leading to a possible underestimation of tool use for these species (Gruber et al., 2010; Hohmann & Fruth, 2003).

1.1.3 Approaches to study tool use

Physical cognition

Early studies on tool use were mainly interested in cataloguing tool repertoires of different species (e.g. Beck, 1980). More recently, interest has shifted to knowing how different species use tools and to which extend they understand the causal relations between tool and goal (Bluff, Weir, Rutz, Wimpenny, & Kacelnik, 2007; Helme, Call, Clayton, & Emery, 2006; Mulcahy & Call, 2006; Seed, Tebbich, Emery, & Clayton, 2006; Tebbich & Bshary, 2004; Visalberghi & Limongelli, 1994). This more cognition approach has shown that tool users either rely on low-level strategies, such as associative learning, or on more elaborated and cognitively demanding strategies, such as human-like causal understanding of tool functioning.

The first strategy consists of acquiring tool behaviours by learning to associate an action and its outcome by repeated use, without any comprehension of cause-effect relations. Wild Caledonian crows, for example, seem to rely on this strategy when using pandanus tools to dislodge insects from tree cavities. In an experiment, Holzaider and colleagues (2008) provided wild New Caledonian crows with functional (barbs facing backwards from the working tips) and non-functional (barbs

down/upside-down or barbless) pandanus tools to retrieve baits in holes drilled in a wooden log. They found that half of the subjects did not pay attention to the barbs' orientation or they chose randomly between barbed and barbless pandanus tools. The authors concluded that New Caledonian crows relied on a associative learning strategy when using pandanus tools, allowing them to know the sequence of operations required to make a successful pandanus tools, including flipping the tool when it was not working, yet lacking an understanding of the functional relevance of the barbs.

Some tool users, however, seem to possess more advanced physical cognition, which enables them to understand the relationship between means and ends, that is, between tool features and task demands. This causal understanding of tool physical affordance relies on the inference of the causal factors responsible for the observed effect (inferential causal reasoning). If the individuals then are able to transfer this knowledge to a new task using the same tool, this demonstrates that they possess a second cognitive mechanism, the analogical causal reasoning (Vaesen, 2012). These advanced cognitive strategies have been mainly tested in the laboratory, using the trap-tube task paradigm, in which subjects have to push a reward with a stick from the correct side of the tube, otherwise the reward falls in a trap (Figure 1.1, last drawing) (Limongelli, Boysen, & Visalberghi, 1995; Tebbich & Bshary, 2004; Visalberghi & Limongelli, 1994; Visalberghi & Trinca, 1989). A modified version of the apparatus have also been proposed, in which the subjects have the option to either push or rack the reward (Mulcahy & Call, 2006) (Figure 1.1).

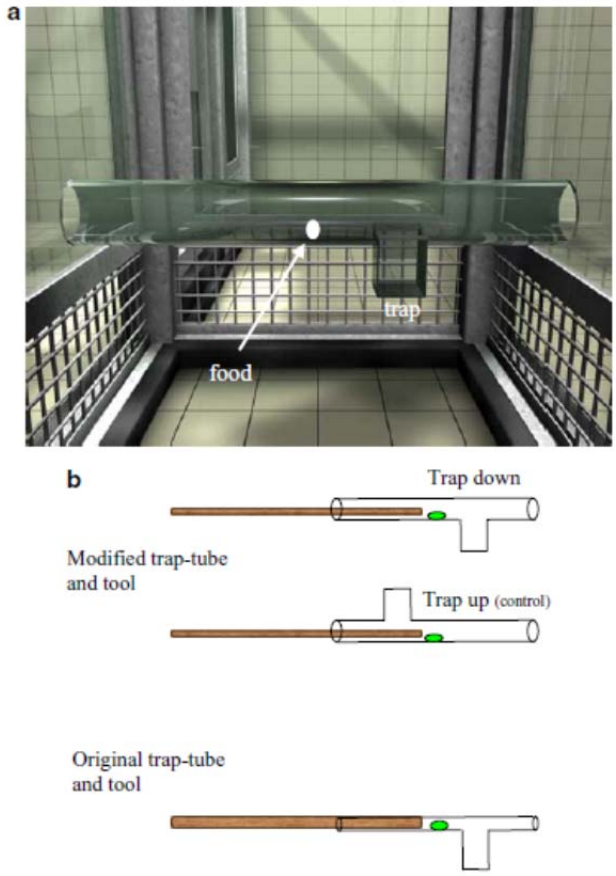

Figure 1.1. Trap-tube task developed to investigate understanding physical cognition in tool using animals. a) Experimental setup and **b)** experimental conditions**.** In the modified trap-tube, to succeed and avoid the food to fall in the trap, the subject can using a stick either to push the reward to the left from the right end of the tube or rack the reward to the left from the left end of the tube. Originally, the reward could only be pushed from either side of the tube. In the control condition, the trap is turned upside-down and becomes therefore irrelevant. After (Mulcahy & Call, 2006).Reproduced with permission from Springer.

Learning mechanisms

But how do animals learn to use a tool efficiently? Whether animals are able to understand the functional properties of a tool or just the interaction between an action with a tool and its effect, they need to learn it either by themselves (asocial learning) or from others (social learning). Learning mechanisms involved in the acquisition of tool-related behaviours are an important aspect of tool use, especially the role of social learning and the eventual social transmission across generations. This topic has received a lot of attention because of its relevance in understanding the evolutionary origins of human culture. The two mechanisms, social and asocial learning, are not mutually exclusive, and are, successively or simultaneously important during the acquisition of behaviour. For example, in apes and monkeys, it seems that some behaviours are acquired by stimulus enhancement or emulation, followed by trial-and-error learning (Fragaszy & Visalberghi, 1996; Lonsdorf, 2005; Tomasello,

1996). This theory of learning by social enhancement, followed by individual exploration and experimentation, has been called hybrid learning (Sterelny, 2006).

Ontogeny

What can generate opportunities to comprehend tool affordances and sequences of action necessary for tool use? These processes have been frequently suggested to be accomplished through a period of exploratory activity (Chevalier-Skolnikoff, 1989; Hayashi, Takeshita, & Matsuzawa, 2006; McGrew, 1977; Parker, 1974; Torigoe, 1985), which can be fairly long depending on the complexity of the tool use. In natural populations, the study of these developmental processes usually requires longitudinal or cross-sectional data to describe the changes in tool-related behaviour. Longitudinal studies (i.e. comparisons of several observations of the same subjects over a period of time) are usually based on long-term field surveys (e.g. *Enhydra lutris*: Payne and Jameson 1984; *Cebus apella*: De Resende et al. 2008; *Tursiops* sp.: Sargeant and Mann 2009; *Corvus moneduloides*: Holzhaider et al. 2010) and are therefore infrequent (Lonsdorf & Bonnie, 2010), especially if the subjects have an extended juvenile period like chimpanzees (e.g. Inoue-Nakamura and Matsuzawa 1997; Biro et al. 2006; Lonsdorf 2006; Humle et al. 2009; Sousa et al. 2009). Cross-sectional studies (i.e. comparisons of different subjects at a single point in time) are an alternative method used to deduce developmental patterns and are usually easier to conduct because they require less observational time (Koops, Furuichi, Hashimoto, & van Schaik, 2015; McGrew, 1977; Myowa-Yamakoshi & Yamakoshi, 2011). This is the method I adopted for my field research due to the restricted time available.

1.2 Animal culture

1.2.1 Definitions: Traditions versus Culture

The way modern humans behave is partly the result of millions of years of natural selection favouring behaviours that enhance individual fitness. But there is a second process that has shaped human behaviour: cultural evolution. Like natural selection, cultural evolution enables individuals to acquire, via social learning, new and adaptive behaviours that enhance their fitness (Mesoudi, Whiten, & Laland, 2006). Social learning, which refers to "learning that is influenced by observation of, or interaction with, a conspecific, or its products" (Heyes, 1994, p. 207) provides individuals with a "second inheritance system" (Whiten, 2005). This process offers much faster transmission of beneficial innovations than genetic evolution. But what is exactly a cultural behaviour and how can we measure it?

Humans are cultural beings, living in societies, possessing technical knowledge, language, art, beliefs, moral and customs (Hill, 2009). In the last decades, researchers have claimed that non-human animals

are also able to acquire cultural behaviours (de Waal, 1996; Hohmann & Fruth, 2003; McGrew, 1992; Rendell & Whitehead, 2001; van Schaik et al., 2003; Whiten et al., 1999). This statement triggered a lot of debate (Krützen, van Schaik, & Whiten, 2007; Laland & Galef, 2009; Laland & Janik, 2006), creating a gulf between those, who argued for the notion of animal 'culture' and others denying it (Galef, 1992; Hill, 2009), asserting that culture is uniquely human. There are also researchers thinking that culture is not restricted to humans but that there is only evidence in primates (Whiten & van Schaik, 2007). The main underlying cause of this debate has to do with the fact that culture is difficult to define. Some definitions are so restrictive and specific that they only can be applied to humans. This is true especially for early definitions from anthropologists like for example Tylor (1871) for whom : "Culture… is that complex whole which includes knowledge, beliefs, arts, morals, law, customs, and any other capabilities and habits acquired by man as a member of society." (p. 1) or Benedict (1934) for whom culture is "What really binds men together…, the ideas and the standards they have in common." (p. 28). Yet, some other definitions have been written in order to allow animal behaviour to qualify as cultural, such as the definition by Laland and Hoppitt (2003, p. 151) in which "…cultures are those group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information". Most restrictive definitions impose constrains regarding the social learning mechanisms, which should support the transmission of the cultural traits. For example, for Boyd and Richerson (1985), Galef (1992) or Tomasello (1994), the transmission mechanism of cultural behaviour should be limited to teaching or imitation. Furthermore, some authors make no distinction between the terms 'tradition' and 'culture' (Laland & Hoppitt, 2003; Laland & Janik, 2006) and use them interchangeably. To the contrary, other authors discriminate the two notions, with culture often being a set of traditions shared by members of a same group (Richerson & Boyd, 2005; Whiten, 2005; Whiten & van Schaik, 2007). Whiten and van Schaik (2007) illustrated the different notions in a pyramid (Figure 1.2).

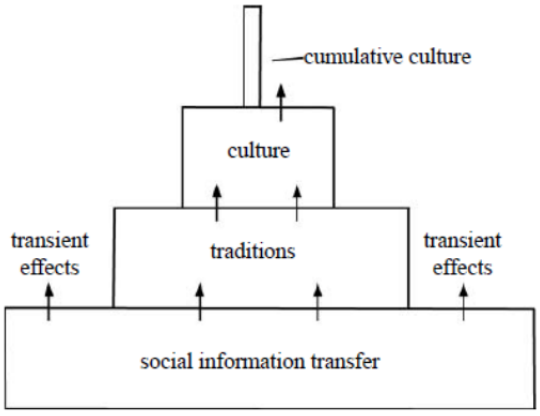

Figure 1.2. The culture pyramid. Social information transfer (foundation layer) is widespread in vertebrates and occurs also in invertebrates. However, only a subset of such transfer eventuates in sustained traditions (layer two), because effects of social learning are often transitory only (e.g. using public information to judge profitable foraging patches). The occurrence of traditions may also be more restricted taxonomically than use of social information per se. More rarely still, cultures exist

that are defined by the existence in the same species of multiple traditions forming unique local complexes (layer three). Cumulative culture (layer four) occurs when more complex traditions arise by elaboration on earlier ones, generating the richness of human cultures yet minimally evidenced in other species. Relative sizes of each layer are notional. Arrows indicate the reliance of each layer on pre-existing lower layers. After (Whiten & van Schaik, 2007). Reproduced with permission of The Royal Society.

The base of the pyramid represents the general social information transfer, consisting mainly in temporally relevant public information like for example the location of a predator. When social information leads to consistent and transgenerational habits, they become sustained traditions, which is illustrated by the second layer. Only once a group of individuals display a multiple and diverse set of traditions, they then possess a culture, the third layer. However, the minimum number of traditions required to qualify as culture has not been specified. The fourth and most complex layer represents the process in which small changes from the traditional behaviours persist in the group and are socially transmitted over generations. This has led to the unsurpassed complexity of human technology (see below discussion on cumulative culture).

But to summarize, as mentioned by Sterelny (2009), the difference between definitions regarding cultural patterns seems to lie mainly in the research focus and in what and how it is investigated (for a list of definitions see Rendell & Whitehead, 2001). Based on that, there are therefore different ways of looking at cultural or traditional behaviours.

My PhD research on this topic focused on a specific behaviour and on the underlying learning mechanism but did not include any intergroup comparisons regarding tool repertoires or sets of specific behaviours. I therefore did not make any discrimination between culture and tradition and use traditional or cultural behaviour interchangeably.

1.2.2 Social learning: The underpinning mechanism of culture

Independently of which definition one decides to use, social learning remains the unique transmission mechanism underlying culture-like behaviour. Social learning was defined by Heyes (1994, p. 207) as "…learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products". Few years later, Hoppitt and Laland (2008) proposed a broader definition including social influences that might lead indirectly to social learning and defined it as " …any process through which one individual ("the demonstrator") influences the behaviour of another individual ("the observer") in a manner that increase the probability that observer learns" (p. 108). As highlighted by Hoppitt and Laland (2008), there are two general ways of learning from others: 1) by direct observations of the model's actions or the goal of its actions (the demonstrator presence is

therefore necessary), 2) by indirect social influence, where the learning process can be made by contact with artefacts left behind by other individuals (the demonstrator's presence is not necessary). Different social processes have been proposed and several updates and reviews can be found in the literature (Heyes, 1994; Heyes & Galef Jr., 1996; Hoppitt & Laland, 2008; Rendell et al., 2011; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004).

In Table 1.1, I only listed the main social learning mechanisms thought to be involved in culture-like behaviours. Later in my thesis, I will show that they are one of the main arguments used by some researchers to disclaim the existence of non-human animal culture and cumulative culture. More specifically, their differences in terms of degrees of copying fidelity are at the root of discussions regarding the requirements for a behaviour to be termed cultural or to be the result of cultural evolution processes. I therefore listed the social learning processes from the lowest degree of copying fidelity (stimulus/local enhancement) to the highest (imitation).

The study of animal culture is by definition closely tied to the study of social learning processes. Consequently, most of the approaches used to show the existence of cultural behaviours in animal involve the detection of the social learning mechanisms underlying the investigated behaviour.

Table 1.1 Main social learning processes involved in cultural behaviours.

Social learning processes	Subcategories	Definition	Social influence
Enhancement	Local	Local enhancement occurs when, after, or during a demonstrator's presence, or interaction with objects, at a particular location, an observer is more likely to visit or interact with objects at that location.	Indirect
	Stimulus	Stimulus enhancement occurs when observation of a demonstrator (or its products) exposes the observer to a single stimulus at time t1 and single stimulus exposure effects a change in the observer detected, in any behaviour, at t2.	Indirect or direct
Copying	Emulation	Emulation occurs when after observing a demonstrator interacting with objects in its environment, an observer becomes more likely to perform any actions that bring about a similar effect on those objects	Direct
	Imitation	Imitation occurs when directly through observing a demonstrator performing an action in a specific context, an observer becomes more likely to perform that action in the same context (contextual imitation) or when after observing a demonstrator performing a novel action, or novel sequence, or a combination of actions that is not in its own repertoire, an observer then becomes more likely to perform that same action or sequence of actions (production imitation).	Direct

Definitions were based on (Hoppitt & Laland, 2008). For the original sources of these definitions, see (Heyes, 1994; Hoppitt & Laland, 2008; Whiten et al., 2004).

1.2.3 Different approaches to study animal culture and the method associated

Observational data

The first reports claiming that nonhuman animal possess cultural behaviours have come from studies using observational data collected in the wild. The method of exclusion, also known as the ethnographic or geographic method, is one of the approaches using observational data to detect cultural behaviour in a population. This method consists in deducing culture from patterns of behavioural variation in time and space, which cannot be explained by environmental or genetic factors (Boesch, 1996; Perry et al., 2003; van Schaik, Ancrenaz, et al., 2003; Whiten et al., 1999). This method was used by Whiten and colleagues (1999) in a landmark collaborative research, where behavioural patterns of seven long-term chimpanzees studies were compared. They found that 39 different behavioural patterns, including tool uses, were habitual or customary amongst some communities, yet absent in others without any obvious ecological reasons. These behavioural patterns of variation were therefore considered as cultural. Although this research is regarded as a milestone in

the study of animal culture, it has also been vigorously criticised. The main critics came from the conceptual problem of this approach based on the absence of a cause. Indeed, it is conceptually impossible to demonstrate the absence of a phenomenon. Consequently it is impossible to rule out any unknown ecological factors that could have explained the behavioural variance (Laland & Janik, 2006). Furthermore, some researchers argued that genetic explanation was usually too swiftly excluded, without properly testing it (e.g. Laland & Janik, 2006; Tennie, Call, & Tomasello, 2009). Using genetic and behavioural data on nine groups of wild chimpanzees, researchers found that genetic and behavioural dissimilarities were strongly correlated and that only few behaviours varied between genetically similar groups (Langergraber et al., 2010). They thus concluded that genetic factors very likely play a role in structuring patterns of behavioural variation among chimpanzee groups. Finally, for a behaviour to be termed cultural it also has to be socially learned and this requirement cannot be tested using only the method of exclusion. Thus, social learning was often just inferred.

Experiments in captivity

Many researchers agree that behavioural differences between populations are unlikely to be determined by culture alone, but rather by an interaction between genetics, environmental conditions and opportunities for social learning (e.g. Humle, 2010; Krützen, van Schaik, & Whiten, 2007; Laland & Janik, 2006). Tomasello (1990) argued that the most productive approach to study cultural behaviour is to investigate the processes of social learning. Yet, the main contention remains that direct evidence for social learning, an essential component of cultural behaviour, has been lacking (Laland & Janik, 2006). Experimental work with captive animals aimed to address this concern by testing, under controlled settings, the transmission mechanism in play when a new behaviour is acquired. This experimental approach used mainly social diffusion experiments, with three main transmission designs: "open group diffusion" (e.g. Reader & Laland, 2000), "Linear chain" or also referred as "diffusion chain" (e.g. Curio, Ernst, & Vieth, 1978; Horner, Whiten, Flynn, & de Waal, 2006) and "Replacement" (e.g. Menzel, Davenport, & Rogers, 1972) (for a review see Whiten & Mesoudi, 2008). The general principal is to seed new behaviour in a group in order to study the transmission mechanism and subsequent spread. The different methods differ in terms of control over the social learning processes and ecological validity (Kendal, Galef, & van Schaik, 2010) (Figure 1.3).

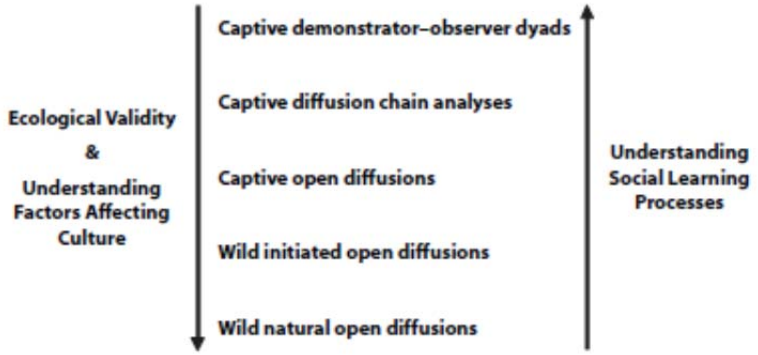

Figure 1.3 An illustration of how methods for identifying social learning lie on a continuum. At the top of the list, there is good control and understanding of social learning processes and relatively little ecological validity, whereas toward the bottom there is increased ecological validity but decreasing likelihood of even distinguishing social from asocial learning. The term 'initiated open diffusions' refers to cases, in which the experimenter provides a novel task, thus initiating the inception and spread of information. After (Kendal et al., 2010). Reproduced with permission from Springer.

Field experiments

Even though experimental approaches in captivity contributed greatly to our understanding of behaviour acquisition and transmission, some authors argued that they lacked ecological validity and proposed to work in the field to test transmission mechanisms by seeding either artificial behaviours (e.g. Müller & Cant, 2010; van de Waal, Claidière, & Whiten, 2015) or natural behaviours (e.g. Biro et al., 2003; Matsuzawa, 1994) in order to track any eventual spread (for a review of field experiments see Reader & Biro, 2010).

Mathematical and statistical models

One of the most applied mathematical methods to identify social learning processes involved in the transmission of a behavioural pattern is to plot the cumulative number of animals displaying the trait over time and then to fit mathematical curves to these data (e.g. Henrich, 2001; Lefebvre, 1995; Reader, 2004). If the data curves follow an accelerating diffusion curve (sigmoid-shaped curves, e.g. exponential or hyperbolic sine), the transmission mechanism is very likely social. In contrary, if the data fit a non-accelerating curve, the mechanism is very likely asocial (Reader, 2004). This method is called diffusion curve analysis (DCA), with network-based diffusion analysis (NBDA) as a more recent method to identify social learning (Franz & Nunn, 2009; Hoppitt & Laland, 2011). This technique tests if the spread of a behaviour follows a social network, containing potential social learning opportunities, created using an association matrix, which estimates the proportion of time individuals are associated (e.g. individuals in the same party, grooming, co-feeding, time spent in close proximity). The analysis incorporates either the time of acquisition of the behaviour (TADA) or

the order in which the individuals of a group acquire the behaviour (OADA). This method of analysis requires therefore a more detailed documentation of the spread than the DCA.

1.2.4 Human culture versus animal culture

In recent years, the notion of animal culture has become widely accepted, largely because of evidence for social transmission of novel behaviours in both captive and field studies, as mentioned above. Acknowledging culture in non-human species does not mean that this concept is similar in all respects to human culture. Indeed, there are still points of contention when it comes to compare human with non-human culture. One main difference could lie in the underlying transmission mechanisms, with human relying mainly on imitation and teaching to acquire behaviours (Boyd & Richerson, 1985; Galef, 1992; Morgan et al., 2015; Tomasello, 1994; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009), whereas lower fidelity mechanisms, such as stimulus/local enhancement or emulation, have been mostly demonstrated in non-human cultural behaviours acquisition (Horner & Whiten, 2005; Tennie, Call, & Tomasello, 2003). Additionally, the capacity to accumulate cultural variants towards enhanced complexity and efficiency, over generations, has been argued to be the major difference between human and non-human culture (Boyd & Richerson, 1996; Heyes, 1993; Tomasello, 1994; Tomasello, Kruger, & Ratner, 1993). Transmission mechanisms are also involved in this difference, in that only high fidelity copying processes allow cultural variants to ratchet up (Morgan et al., 2015). Observations of teaching and true imitations in non-human animals being rare, only human culture is cumulative if we agree with the high copying fidelity requirement (Boyd & Richerson, 1985; Tennie et al., 2009; Tomasello, 1994).

Human and animal cultures vary also regarding their respective contents (Whiten, Horner, & Marshall-Pescini, 2003). Animal cultures tend to be mainly restricted to foraging behaviour, whereas human cultures extend much further, with for examples, religions, arts or languages. This content variation leads to a last difference, more qualitative this time, namely, social norms. Indeed, some human cultural variations can become social norms, such as religious customs, clothing styles, sexual practices or social organisations. Not respecting these norms can trigger emotions and can subsequently lead to direct or third-party punishments. This notion of group identity, derived from social norms and expressed by means of culture-specific symbols, have been argued to be uniquely human (Perry, 2009).

To summarise, using varied techniques, researchers have been able to claim culture or traditions in various nonhuman species like, for example, dolphins and whales (Rendell & Whitehead, 2001), New Caledonian crows (Hunt & Gray, 2003), chimpanzees (Whiten et al., 1999), orang-utans (van Schaik, Ancrenaz, et al., 2003), Japanese macaques (Huffman, 1996) and Capuchin monkeys (Perry et al.,

2003). But even though animal culture is widely accepted, a gulf remains between nonhuman and human cultures. This difference has varied origins but mainly lies on the arguably unique human ability to accumulate cultural knowledge.

1.3 Cumulative culture

1.3.1 Definition and examples

Cumulative culture is defined as the accumulation of socially learned behaviour over many generations leading to the evolution of behaviours that no individual could invent on its own (Boyd & Richerson, 1996). This form of evolution has been argued to follow Darwinian's properties (Darwin, 1859), namely the principles of variation, competition due to differential fitness, and inheritance (Mesoudi et al., 2006; Richerson & Boyd, 2005). In this regard, Mesoudi et al. (2004, p. 2) defined cultural evolution as "… the idea that the information in [the] cultural domain frequently changes according to a similar process by which species change, that is, through the selective retention of favourable cultural variants, as well as other nonselective processes such as drift. ". With their paper, they offer a careful analysis of human culture by providing empirical data and testing them against the theory supported in *The Origin of Species*. Their analysis is conclusive, showing that human culture, through the accumulation of successive cultural modifications over time, exhibit variation, competition and inheritance.

Yet, they also bring to light characteristics which do not fit a Darwinian model. The first characteristic is the possible bias of cultural variation productions towards a certain solution to a problem, called "smart variants" by Laland et al. (2000) in opposition to "blind variants", which would correspond to the random mutation of genes in the biological evolution. Cultural variants are not created at random, as are biological variants, but are biased by past phylogenetic and developmental processes (Laland et al., 2000). Another difference between cultural and biological evolution is the medium for the transmission, with cultural variants passing from brain to brain, whereas biological changes are transmitted genetically through DNA. This difference in mediums might explain the difference in frequency of changes, with faster cultural changes compared to biological ones. This differences can be easily observed when we compare the evolutionary timeframe of speciation (using fossil records and dating methods) with for example the number of global patent applications rising to 2.9 million in 2015 (source: WIPO Statistics Database) or the numerous archaeological artefacts showing the evolution from the rudimentary Oldowan knapped stone industry, around 2.6 million years ago, to complex contemporary tools.

A final difference between biological and cultural evolution is the inheritance process, with biological characters being restricted to a transmission from parent to offspring, whereas cultural traits can, in

addition to vertical transmission from parent to offspring, also be transmitted horizontally, to nonrelated individuals.

The study of cultural evolution started decades ago and was mainly theoretical, using mathematical models (e.g. Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). This approach is still central in the study of cultural evolution but new approaches have emerged, including laboratory experiments (Caldwell & Millen, 2008; Caldwell & Millen, 2010; Kirby, Cornish, & Smith, 2008). These approaches have been first applied to humans but some researchers have started reporting possible cases of cumulative culture, the process in which culture can evolved, in non-human animals. Based on human cultural evolution studies, Dean and colleagues (2013) suggested three criteria to identify cumulative culture in non-human animals: "First, there should be evidence that the behavioural pattern or trait is **socially learned** and any variation in the character is not solely due to genetic or environmental factors (Laland & Janik, 2006). Second, there must be evidence that the character in question **changes over time** in a directional or progressive manner. This requires evidence that it has been transmitted between individuals through **social learning over repeated episodes**. It also requires evidence that the character has changed in the transmission process to achieve an **enhanced level of complexity**" (p. 5).

If we agree with these criteria, few authors have been able to demonstrate cumulative culture cases in non-human animals. For example, New Caledonian crows (*Corvus moneduloides*) manufacture sticks from the long barbed edges of palm-like *Pandanus* leaves to capture invertebrates in trees (Hunt, 2000; Hunt & Gray, 2003). Three distinct tool designs have been found with no ecological explanations for their differences, but a continuous and overlapping geographical distribution and similarities in the manufacture method. The authors suggested that at least two of the tool designs might have emerged through a process of cumulative change from earlier, more primitive versions. A second example is central African chimpanzees' (*P. t. troglodytes*) manufacturing brush-tipped probes from sticks when fishing for termites (Sanz, Call, & Morgan, 2009). Here, individuals have been seen to fray the end of herb stems before inserting them into the mounds to capture termites, a significantly more efficient way of collecting termites than by using unmodified fishing probes described in East and West African chimpanzees. This technique is thus a possible build up on a simpler ancestral technique consisting in using an unmodified stick (see also Boesch et al., 2009).

Even though these examples fulfil most of the criteria for cumulative culture behaviour, the limitations relative to observational studies in the wild prevents researchers to find any conclusive evidence for the required social learning. But a recent study on homing pigeons (*Columba livia*) provides interesting findings (Sasaki & Biro, 2017). The authors demonstrated the capacity of the pigeons to accumulate social information to improve a behaviour across generations. They used a "replacement"

diffusion chain experiment to test possible improvement of homing route over successive generations. To do so, they created artificial generations consisting in a pair with a knowledgeable individual (A) knowing the homing route and a naïve individual (B). After 12 releases, they replaced (A) with a naïve individual (C) and after another 12 releases replaced (B) by a naïve individual (D) and so forth, up to five artificial generations (Figure 1.4). They found that homing performance improved (i.e. decrease of the flying distance from the release point to the home loft) over consecutive "generations" of pairs. As mentioned by the authors, while satisfying the main criteria for cumulative culture, the problem stands in that the task had an end point represented by the maximal efficiency (i.e. the beeline path) and therefore does not prove that pigeons are, like humans, able to exponentially cumulate cultural knowledge.

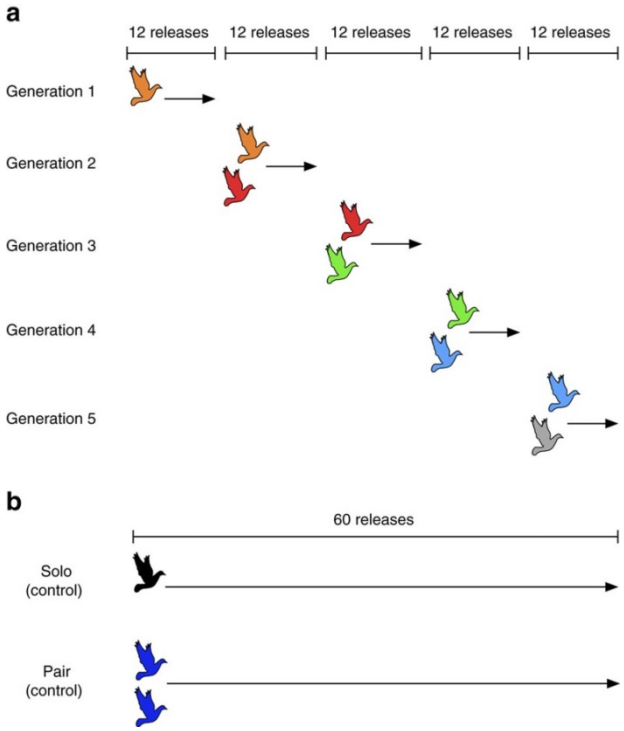

Figure 1.4. Homing flight release protocols. (a) Experimental group; **(b)** control groups. In each chain of the experimental group, a single pigeon (orange) was first released from the same site repeatedly 12 times, then partnered with a naive pigeon (red) and flown as a pair a further 12 times. The first bird was then replaced by a third bird (green) and this new pair (red +green) was also released 12 times. This procedure continued until the fifth-generation bird (grey) was added and flown a final 12 times. In the control groups (b), single pigeons and fixed pairs were released the same number of times as the total flown by the experimental group (60 flights). All three treatment groups contained 10 independent replicates (chains, solo birds or pairs). After (Sasaki & Biro, 2017). Reproduced with permission from Creative Commons CC-BY license.

Some experimental studies in captivity also brought insight into the possible capacity for non-human animals to ratchet up cultural behaviour (Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Yamamoto, Humle, & Tanaka, 2013). These findings remain ambiguous in the light of other studies failing to prove cumulative culture in chimpanzees (Dean, Kendal, Schapiro, Thierry, & Laland, 2012;

Marshall-Pescini & Whiten, 2008) and capuchin monkeys (Dean et al., 2012), two primate species considered as proficient tool users and possessing traditional behaviours. These results bring grist to the mill of researchers thinking that cumulative culture is restricted to humans (Boyd & Richerson, 1996; Heyes, 1993; Tomasello, 1994; Tomasello et al., 1993) and claiming that so far no conclusive study have demonstrated the existence of this ratcheting process in non-human animals.

1.3.2 Scepticism concerning nonhuman cumulative culture

Tennie and colleagues (2009) have been especially critical of all animal cumulative culture research, also in light of their model named "zone of latent solution" (ZLS), which refers to physical cognition skills enabling individuals to invent behaviour on their own. If a behavioural trait is within the ZLS of the individual, it cannot be seen as culturally cumulative, based on Dean et al.'s criteria (2013) stating that the trait has to be beyond a single individual's capabilities. Tennie and al. (2009) argue that none of the non-human cumulative culture cases reported so far involve behaviours stepping outside of the ZLS boundaries of the subjects. This difficulty to show cumulative culture in non-human animals have been proposed to come from important factors required for the ratchet effect, present in humans but absent in other animals and especially chimpanzees. One factor is a high-fidelity transmission mechanism (Lewis & Laland, 2012), like imitation (i.e. copying actions), present in humans but very rare in other species, like chimpanzees that seem to rely more on emulation (i.e. copying results) when acquiring behaviour (Tennie, Call, & Tomasello, 2012; Whiten et al., 2009). Teaching (through verbal instruction) and prosociality (altruism), two other socio-cognitive processes unique or extremely developed in humans, have been demonstrated to be responsible for the pattern of cumulative cultural learning (Dean et al., 2012). Yet, imitation or teaching have been shown not to be necessary for cumulative culture in humans (Caldwell & Millen, 2009; Zwirner & Thornton, 2015) or have been proposed to be the consequence rather than the cause of cumulative culture (Claidière, Smith, Kirby, & Fagot, 2014). So perhaps the difference between humans and other animals does not lie in what is unique to humans but rather in what mechanisms are predominant in other animals and minimal in humans. For example, conservatism and skills mastery have been argued to be the reason for the incapacity of chimpanzees to cumulate culture (Hrubesch, Preuschoft, & Van Schaik, 2009; Marshall-Pescini & Whiten, 2008; Whiten et al., 2009).

1.4 Study species and study site

1.4.1 Study species

Using some of the approaches mentioned earlier, my research aimed at investigating three main aspects of tool use in wild chimpanzees, namely the ontogeny of object manipulation and play, the

social learning mechanisms underlying acquisition, and the possibility of cultural accumulation. For several reasons, chimpanzees are relevant candidates to study these three topics.

One of the main reasons apes have been studied for so long is their phylogenetic closeness with our own species. We shared a common ancestor with chimpanzees and bonobos approximately six millions year ago and they are our closest living relatives (Patterson, Richter, Gnerre, Lander, & Reich, 2006). Consequently, our common ancestor might have also possessed any similarities we can find between humans and chimpanzees or bonobos. Observing chimpanzees can provide a powerful tool in understanding human aspects and, in our case, human technology, culture and cultural evolution. Bonobos are in this respect less appropriate, as they have been so far rarely observed using tools in the wild (Hohmann & Fruth, 2003; Ingmanson, 1996). This difference between the sister species cannot be explained by differences in term of physical cognition because it seems that they have similar understanding of the functional properties of tools (Herrmann et al., 2008; Mulcahy & Call, 2006; Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995). Furthermore, the two species do not differ in significant ways regarding manipulation skills and motor sequences (Takeshita & Walraven, 1996). Ecological factors, like habitat composition and fluctuation of fruit production, or social factors, like social learning opportunities, seem neither an explanation for the striking difference in tool repertoire between chimpanzees and bonobos (Furuichi et al., 2015; Koops, Furuichi, & Hashimoto, 2015). It seems that the difference comes from intrinsic motivation to manipulate and play with objects (Koops, Furuichi, & Hashimoto, 2015). Chimpanzees engage more in object manipulation and object play than bonobos (Koops, Furuichi, & Hashimoto, 2015). So, looking into tool use, traditions and cultural evolution in chimpanzees can provide possible insights into the origins of early human elementary technology.

Another reason chimpanzees are an important study species regarding my PhD topics is that they are proficient and skilled tool users, surpassing other non-human species. Additionally, they display multiple traditions that have been shown to vary between geographic regions (Whiten et al., 1999, 2003; Whiten & van Schaik, 2007). Furthermore, like humans, chimpanzees rely on social learning to acquire traditional behaviours and share similar social learning processes, like emulation and imitation (Hopper et al., 2007; Horner & Whiten, 2005; Whiten et al., 2009 but see Call, Carpenter, & Tomasello, 2005; Tennie, Call, & Tomasello, 2003).

1.4.2 Study site

The Budongo Conservation Field Station (BCFS) was established in 1990 in the Budongo Forest Reserve, which is located close to the northern limit of the Western (Albertine) Rift in Uganda (between 1°37'N-2° 03'N and 31°22'– 31°46'E) at a mean altitude of 1,100 m. The Reserve includes 790 km^2 of forest and grassland of which 482 km^2 is continuous medium altitude semi-deciduous forest cover (Newton-Fisher, 2003; Plumptre, 1996). Rain distribution has a bimodal pattern with most

rain falling between March and May and again between September and November and a major dry season between mid-December and mid-February (Reynolds, 2005).

The Sonso community has been habituated to human presence since the mid-1990s. Data collected between 1994 and 1995 showed that their home range was about 7 km^2 at that time for a population of 46 individuals (Newton-Fisher, 2003). Their home range was relatively small compared to other chimpanzee communities. For example, the Kanyawara community, in the Kibale forest, which is at about 180 km south west from the Sonso community, had a home range of 15 km^2 for a population of 41 individuals between 1988 and 1991 (Chapman & Wrangham, 1993). At the beginning of my PhD research in January 2013, the community consisted of 63 individuals, distributed as followed: 20 adult females, 11 adult males, 7 subadult females, 3 subadult males, 15 juvenile females, 3 juvenile males, 2 infant females and 2 infant males. By the end of my research in February 2015, nine new infants had been born and one adult female had immigrated, resulting in a community size of 73 individuals. The Sonso community became larger since 1995 but the territory has not significantly increased from the 7 km^2 calculated at that time (Dr Hobaiter, personal communication; personal observation) increasing the chimpanzees density and therefore suggesting that the food resources are abundant in this part of the Budongo forest (Gruber et al., 2012; Newton-Fisher, 2003; Newton-Fisher, 1999). Subjects' age classes were assigned following Reynolds' (2005) classification: infant (birth to end of 4th year), juvenile (5th to end of 9th year), subadult male (10th to end of 15th year), subadult female (10th to end of 14th year) adult male (16 years +) and adult female (15 years + or age of first baby).

1.5 Thesis studies

In a first study, I investigated the ontogenetic aspect of tool use. We know that chimpanzees are proficient tool users and that from an early age they manipulate a variety of objects in playful manners (Kahlenberg & Wrangham, 2010; Koops, Furuichi, Hashimoto, et al., 2015; Van Lawick-Goodall, 1968). We also know that object play and exploration are likely to be an important precursor of tool use by providing individuals with the essential perceptual-motor experience when interacting with the material world (Hayashi et al., 2006; Kahrs & Lockman, 2014). So far, however, most studies on object manipulation in wild chimpanzees focused either on the ontogeny of a specific tool-related behaviour (e.g. Biro, Sousa, & Matsuzawa, 2006; Hayashi & Inoue-Nakamura, 2011; Humle et al., 2009; Lonsdorf, 2006; Nishie, 2011; Sousa et al., 2009) or on object play (Koops, Furuichi, Hashimoto, et al., 2015; Vauclair & Bard, 1983). The goal of this study was to integrate both approaches by looking at objects later be used as tools but also at objects that will not result in tool use later in development. In the Sonso community, individuals only manufacture and use two main types of tools in the feeding context, leaf-sponges and, since 2011, moss sponges (Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014). Remarkably, no Sonso chimpanzee has ever been observed

using a stick to extract food, although this is a widely used tool in almost all other East and West African communities studied to date (e.g. McGrew 1974; Teleki 1974; Boesch and Boesch 1990; Sanz and Morgan 2007; Watts 2008). There is no clear ecological or genetic explanation for this surprising lack of stick use in Sonso chimpanzees. However, the Sonso chimpanzees have developed a non-food related leaf technology, mainly used in body care but also in social interactions (Gruber, Muller, Strimling, Wrangham, & Zuberbühler, 2009; Reynolds, 2005). I therefore predicted that material that is never used as a tool by adults should be increasingly less manipulated by non-adults during play and exploration, whereas material used as tool should be increasingly more selected by non-adults. To test this prediction, I recorded all instances of object manipulations (i.e. object play and exploration and tool use) in 37 focal individuals from 5 months old to 52 years old and compared the rate and proportion of object manipulation across material.

A second relevant question in this ontogenetic study concerned individual and social factors that could influence the choice of material the immatures manipulate. Previous research has suggested that the social environment, and especially the behaviour of mothers, plays an important role in the acquisition of tool use (Hirata & Celli, 2003; Humle et al., 2009; Inoue-Nakamura & Matsuzawa, 1997; Lind & Lindenfors, 2010; Lonsdorf, 2006; van Schaik, Deaner, & Merrill, 1999). To find out if there is any factor influencing the choice of play material, we tested individual (age and sex) and social (maternal and spatially close individuals) parameters possibly responsible for the rate of object play in immatures across material.

In a second study, the focus was on one distinct tool-related behaviour: moss-sponging. The behaviour was first observed and its initial transmission investigated in 2011 (Hobaiter et al., 2014). The behaviour consists of harvesting clumps of moss in order to orally shape it into a sponge roughly the size of a golf ball, which is then used to dip into and absorb liquids. The tool use was first displayed by the alpha male in November 2011 upon which it rapidly spread through spatio-temporal association to seven other individuals. However, between 2011 and 2013 the behaviour was seldom observed by resident researchers and long-term field assistants, raising questions about its maintenance in this community. The aim of this study was first to see if the behaviour further propagated in the community three years after its emergence and rapid spread amongst a restricted number of individuals. Second, if the behaviour was indeed acquired by other community members, I wanted to investigate the mechanism involved in this second radiation and consolidation. The predictions were that individuals that acquired the behaviour socially in 2011 should continue to moss-sponge and that if moss-sponging had spread to other individuals in the three-year interval since the initial study, it should have spread preferentially to individuals that were socially close (either by family ties or by spatial proximity) to the original eight moss-spongers. To do so, I carried out a field experiment at the same clay pit at which the original innovation took place. I presented subjects with a choice of two

different materials by providing moss next to the naturally available leaves, which allowed me to systematically categorise group members as either moss- or leaf-spongers.

In a third study, I was interested in whether moss sponging emerged through cultural evolution. As indicated earlier, a key criterion for cultural evolution is that a cultural technique or behaviour must be significantly improved relative to the one it originates from. I tested this requirement with the following three sets of analyses. First, I compared the efficiency between the culturally novel moss-sponging (seen in some group members) and the traditional leaf-sponging (seen in all group members). Second, I then carried out a field experiment to test whether moss chimpanzees that had used moss-sponges at the clay pit, also preferred this technique in novel situations for which they had never used moss before. To do so, I presented single subjects with a standardized foraging problem, rainwater contained in an artificial cavity in a portable log. Subjects could choose between two provided materials, moss or leaves, to manufacture a drinking tool.

This third study concerned the puzzling fact that, since its emergence in 2011, moss-sponging was nearly exclusively observed at the site of its original invention, the clay-pit, despite uninterrupted daily focal follows by field assistants and researchers. Leaf-sponging, instead, continued to be observed in a range of contexts and throughout the forest, mainly at tree holes filled with rainwater, but also at rivers and water puddles. These observations are clearly conflicting with the cultural evolution hypothesis and suggest that moss-sponging could be limited to highly context-specific tool use behaviour and that chimpanzees do not perceive moss as general sponge material. To address this issue, I carried out a survey of leaf and moss distribution at different sponging locations, which included areas of mixed forest where most tree-holes filled with rainwater are located and swamps where clay-pits are located.

In summary, these three studies should help to better understand three key aspects of tool use in wild chimpanzees. The first study tests the importance of play and exploration in the acquisition of tool use. In parallel with the second study, they test the importance of the social environment during the early stage of the individual development but also later when acquiring a new behaviour. The third study addresses the highly debated question of the evolution aspect of some cultural behaviour.

2. STUDY 1: DEVELOPMENT OF OBJECT MANIPULATIONS IN WILD CHIMPANZEES

Manuscript submitted to Animal Behaviour

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2.1 Abstract

Chimpanzees' natural propensity to explore and play with objects is likely to be an important precursor of tool use. Manipulating objects provides individuals with pivotal perceptual-motor experience when interacting with the material world, which may then pave the way for subsequent tool use. In this study, we were interested in the influence of social models on the developmental patterns of object manipulation in young chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community of Budongo Forest, Uganda. This community is interesting because of its limited tool repertoire, with no observations of stick-based foraging in over 20 years of observations. We found evidence for social learning in that young individuals preferentially played with and explored materials manipulated by their mothers, except for sticks. We also found that object manipulation rates decreased with age, whereas the goal-directedness of these manipulations increased. Specifically, stick manipulations gradually decreased with age, which culminated in complete disregard of sticks around the age of 10 years, a pattern not found for the remaining tool materials, which were all used throughout adulthood. Overall, young chimpanzees developed their tool use by initially exploring and playing unselectively with any object found in the environment before becoming influenced by the mother's object manipulations. We discuss changes from individual to social learning in relation to the larger question about the evolution of animal culture.

2.2 Introduction

The study of animal tool use has a long history in science with evidence from a wide range of taxa, including insects, birds and mammals (Bentley-Condit & Smith, 2010). Humans are undoubtedly the most prolific and sophisticated tool users, followed by some non-human primates, especially chimpanzees (*Pan troglodytes*), who are known for their extensive and population-specific use of tools that varies in form, materials and function (Matsuzawa & Yamakoshi, 1996; McGrew, 1992; Whiten et al., 2001).

An important aspect of animal tool use concerns the learning mechanisms involved in the acquisition of tool-related behaviours, especially the role of social learning and eventual social transmission across generations. This topic has received a lot of attention because of its relevance in understanding the origins of human culture and has been investigated in both primate (Biro et al., 2003; Whiten, 2000; Whiten & Mesoudi, 2008) and non-primate species (Aplin et al., 2015; Brown & Laland, 2003; Galef et al., 1998; Galef & Laland, 2005; Reader & Laland, 2000; Whiten & Mesoudi, 2008). A relevant question within this topic is how subjects learn to manufacture and use tools adequately and what level of physical cognition underlies this process. Specifically, tool-use may be acquired by mere operant conditioning between actions and outcomes or by more profound comprehending of cause-effect relations (Bluff et al., 2007; Holzhaider et al., 2008; Tebbich & Bshary, 2004; Visalberghi & Limongelli, 1994) based on an understanding of the affordances of objects, surfaces, actions and spatial relations (Limongelli et al., 1995). Whatever the underlying mechanisms, acquisition of proficiency is based on a developmental period of exploratory activity (Chevalier-Skolnikoff, 1989; Hayashi et al., 2006; McGrew, 1977; Parker, 1974; Torigoe, 1985).

The current study was carried out with the Sonso chimpanzee (*P. t. schweinfurthii*) community of Budongo Forest, Uganda, who are known for their unusually small tool repertoire, especially in the foraging context (Gruber, Zuberbühler, & Neumann, 2016; Reynolds, 2005). Despite decades of observations, no Sonso chimpanzee has ever been observed using a stick to extract food, although this has been reported in almost all other chimpanzee communities studied to date (e.g., McGrew 1974; Teleki 1974; Boesch and Boesch 1990; Sanz and Morgan 2007; Watts 2008). There is no obvious ecological or genetic explanation for the surprising lack of stick use in the Sonso community, which is also notable because Sonso chimpanzees regularly use other objects in goal-directed ways for body care (e.g. leaf-squash, leaf-dab, leaf-napkin), as social signals (e.g. branch-shake, buttress-beat or leaf-clip), for construction (nest-building) or for liquid absorption (leaf-sponge or moss-sponge) (Table S2.1) (Gruber et al., 2009; Reynolds, 2005).

These intraspecies differences regarding tool use can also be found between species and have been shown to originate from difference already found in immatures. Koops et al. (2015), for instance,

argued that the main reason for the striking difference in tool use frequency between chimpanzees and their closest relative, bonobos (*P. paniscus*), is rooted in intrinsic differences in predispositions of immature individuals for object manipulation and play. Immature chimpanzees manipulated and played more with objects than bonobos, suggesting that the species differences in tool use already emerged early during development, a finding that may also explain within-species differences in chimpanzees. From an early age, chimpanzees spend considerable amounts of time manipulating tool-suitable objects, particularly leaves and sticks, but mostly in a playful manner (Kahlenberg & Wrangham, 2010; McGrew, 1977). This propensity is likely to be an important precursor of tool use by providing individuals with essential perceptual-motor experience when interacting with the material world (Hayashi et al., 2006; Kahrs & Lockman, 2014). Furthermore, previous research has suggested that the social environment, and especially the behaviour of mothers, plays an important role in the acquisition of tool use (Hirata & Celli, 2003; Inoue-Nakamura & Matsuzawa, 1997; Lind & Lindenfors, 2010; Lonsdorf, 2006; van Schaik et al., 1999). For example, Humle and colleagues (2009) investigated the social influences on the acquisition of ant-dipping by the chimpanzees of Bossou, Guinea. Ant-dipping consists of using a stick or stalk of vegetation to harvest army ants. The authors found that the behaviour was acquired at an age of around 2.5 years and that the mother was the prime model and target of observation. Infants with more opportunities for ant-dipping, assessed by the mothers' time spent ant-dipping, began observing the mother's behaviour earlier than infants with fewer opportunities, which led to faster acquisition and fewer errors.

Other studies in chimpanzees have shown sex differences in development (Lonsdorf, 2017). For example, at Kalinzu, Uganda, immature males showed higher rates of playful object manipulations than immature females (Koops, Furuichi, Hashimoto, et al., 2015). At Gombe, Tanzania, sex differences have been found regarding the development of termite-fishing, but here it was the immature females who acquired the behaviour earlier than immature males (Lonsdorf, 2005).

In this study, we were interested in age-related changes in patterns of object manipulation before tool use in young chimpanzees, specifically the choice and manipulation of tool materials and their goal-directed use. We defined tool use following Shumaker et al. (2011, p. 5) as: "…the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible of the proper and effective orientation of the tool". We defined a goal-directed object manipulation as an action on an object (tool) or substrate (proto-tool) to achieve a purpose, which is terminated when the action's outcome meets the purpose (see Table S2.1). We were interested in (a) how object manipulation rates, object choice and goal-directed use of materials were affected by age and sex and (b) what social factors influenced the choice and manipulation rates of materials.

2.3 Material and methods

2.3.1 Study site

The study was conducted with the Sonso chimpanzee community in the Budongo Forest Reserve in Western Uganda (1°37'-2°00'N, 31°22'-31°46'E). The reserve consists mainly of moist semi-deciduous tropical forest at a mean altitude of 1100m. The Sonso community uses a core home range of approximately 7 km^2 (Newton-Fisher, 2003) and community members have been habituated to the presence of human observers since the mid-1990s (Reynolds, 2005). At the beginning of the study, the community consisted of 20 adult females, 11 adult males, 7 subadult females, 3 subadult males, 15 juvenile females, 3 juvenile males, 2 infant females and 2 infant males (following Reynolds' classification (Reynolds, 2005)). By the end of the study, nine new infants had been born and one adult female had immigrated, resulting in a community size of 73 individuals.

2.3.2 Study subject and data collection

Behavioural data were collected between January 2013 and February 2015 (153 days) using continuous focal sampling on 37 individuals (6 infants (1F, 5M), 10 juveniles (7F, 3M), 4 subadults (3F, 1M) and 17 adults (11 F, 6 M). Object manipulation was defined as any interaction (i.e. holding, carrying, hitting or moving) of the focal animal with an object using the hands, feet or mouth (see Table S2.1 for a comprehensive definition). Data were recorded on an all occurrence basis and whenever possible documented on video (Panasonic HC-X909 camcorder). An object manipulation event started when the focal animal came into physical contact with an object for the first time, by abandoning another object or by resuming manipulation on the same object after at least 2 minutes of interruption. Relevant objects were classified as woody vegetation, leaves, sticks, trunks, or other materials (for description see Table S2.1). Manipulations were identified as either 'goal-directed' (manipulations of an object with a clear and unambiguous purpose, see Table S2.1) or 'non-goal directed', which consisted of solitary play or mere exploration.

2.3.3 Statistical analyses

Manipulation rates

We fitted a general linear model, with object manipulation rate (number of events divided by total observation time, log transformed) as the response variable and subject age (square root transformed) and sex as predictor variables. 37 individuals contributed data to the model (n = 22 females; n = 15 males; age range: 0.4 to 52 years).

Goal-directedness

We performed a generalized linear mixed model with binomial error structure and logit link function (GLMM) to predict the probability of a given object manipulation being goal-directed (yes/no) as a function of subject age and sex. We log transformed ages to obtain a symmetric age distribution. As subjects contributed with several data points (i.e. object manipulations) we fitted subject identity as random intercept (n = 880 object manipulations, n = 37 individuals).

Choice of material

First, we explored the rate of object manipulations across materials for adults and non-adults. We treated age as a categorical variable, i.e. as non-adults, comprising of infants, juveniles and subadults (i.e. <120 months) or adults (≥120 months). As sticks were only manipulated by non-adults but not by adults, we described the proportion of stick manipulation as a function of subject age and sex.

We then analysed the material categories manipulated both by adults (in goal-directed way) and non-adults (in exploration and play), namely leaf, woody vegetation and trunk. The goal was to investigate the potential social and individual learning mechanisms by which non-adults choose the materials they use to manipulate in non-goal-directed ways. To do so, we used multi-model inference to investigate the choice of materials by non-adult subjects (Anderson, 2008; Grueber, Nakagawa, Laws, & Jamieson, 2011). We built seven unique models (GLMMs with binomial error structure) with different sets of predictor variables, but with the same response variable. For each subject we determined the relative proportion of the three materials manipulated by the subject as the response variable. To control for repeated measures (each subject contributed with three proportions, corresponding to the three materials), we added subject ID as random intercept and we nested subject ID in mother ID because some subjects were maternal siblings (see Kulik et al., 2012) and Genty et al., 2015) for similar approaches). Two models addressed individual features: one model contained subject age and one model contained subject sex as predictor variable. Four more models addressed the potential influence of social (maternal and non-maternal) models. Regarding maternal models, one predictor variable was the mothers' manipulation rate per observation time for each material and the second predictor variable was the proportions of materials used by mothers relative to the total number of observed manipulation events. We calculated rates and proportions because it is not clear whether they affected subjects differently. For the two models looking at non-maternal influence, we calculated object manipulation rates and proportions for all other adults that were focal animals (n = 21). For each adult, we determined the association strength with each subject (i.e. with his or her mother), using half-weight indices (Bejder, Fletcher, & Bräger, 1998; Cairns & Schwager, 1987) from party composition data collected by experienced field assistants between November 2011 and December 2014. We had to exclude three individuals (FA, KX and OK3) because we were unable to collect systematic object manipulation data from their mothers. The last model represented a conceptual null model and consisted only of the material as the predictor variable. This null model reflects the

possibility that the proportion of materials chosen is independent of the six individual, maternal and social factors described above, and only allows for the possibility that individuals differ in their choices between materials. For example, one subject may predominantly choose leaves whereas another subject may predominantly choose woody vegetation to manipulate. The remaining six models each contain one of the six predictors in interaction with material category. These models reflect the possibility that the associations of the test predictors differ between materials. For example, there might be a positive association between subject choices and maternal usage rate for leaves but not for woody vegetation, or males, but not females, choose leaves over woody vegetation.

We then ranked the models, using an information-theoretic approach (Anderson & Burnham, 2002) with Aikaike's information criterion corrected for small samples. We interpreted model weights, which are standardized ratios of AICc differences between a given model and the best model (the one with the smallest AICc), such that a model weight is the probability of the target model being the best model among those tested (Anderson, 2008).

Model fitting and ranking were done in R (v.3.3.1, R Development Core Team, 2015: fitting: lme4, v. 1.1-12, Bates, Mächler, Bolker, & Walker, 2014; ranking: MuMIn, v.1.15.6, Bartòn, 2016).

2.4 Results

2.4.1 Object manipulation rate

The full model explaining manipulation rates as a function of age and sex and their interaction was significantly different from the null model ($F_{3,33}$=13.51, p<0.0001). There was no significant interaction between age and sex in object manipulations rates (LM: *n*=37, β= -0.031 ± 0.046, t= -0.68, p= 0.4993), so we removed the interaction.

We found that manipulation rates decreased with age (LM: *n*=37, β= -0.106 ± 0.022, t= -4.75, p< 0.0001, Figure 2.1) and that males manipulated objects significantly more than females, regardless of age (LM: *n*=37, β= 0.633 ± 0.284, t= 2.23, p=0.0326, Figure 2.1).

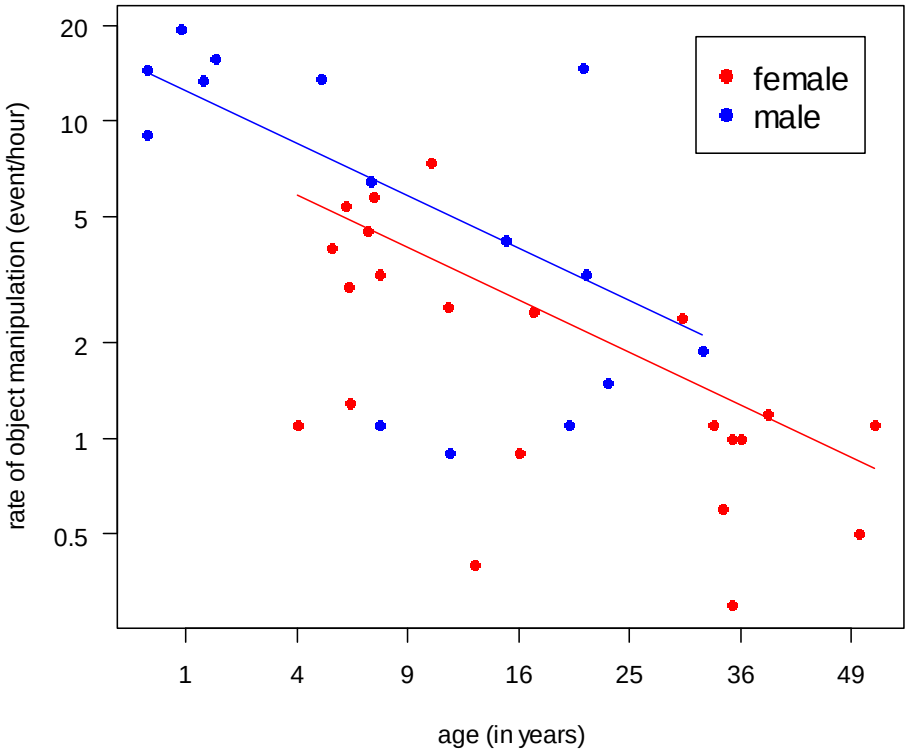

Figure 2.1. Rates of object manipulation across age and sex. Rates represent the number of object manipulations per time in sight (hour) for each subject (n = 37).

2.4.2 Goal-directedness

The full model explaining the probability of manipulating objects in goal-directed ways as a function of age and sex and their interaction was significantly different from the null model (LRT, χ^2=72.45, df=3, p<0.0001). There was no significant interaction between age and sex in goal-directedness of object manipulations (GLMM, β= 0.316 ± 0.044, z = 0.094, p= 0.925), so we removed the interaction.

We found that goal-directedness increased with age (β= 1.490 ± 0.122, z = 12.179, p < 0.0001, Figure 2.2) and that males had a higher likelihood of manipulating objects in goal-directed ways than females, regardless of age (β= 0.567 ± 0.230, z=2.463, p=0.0138, Figure 2.2).

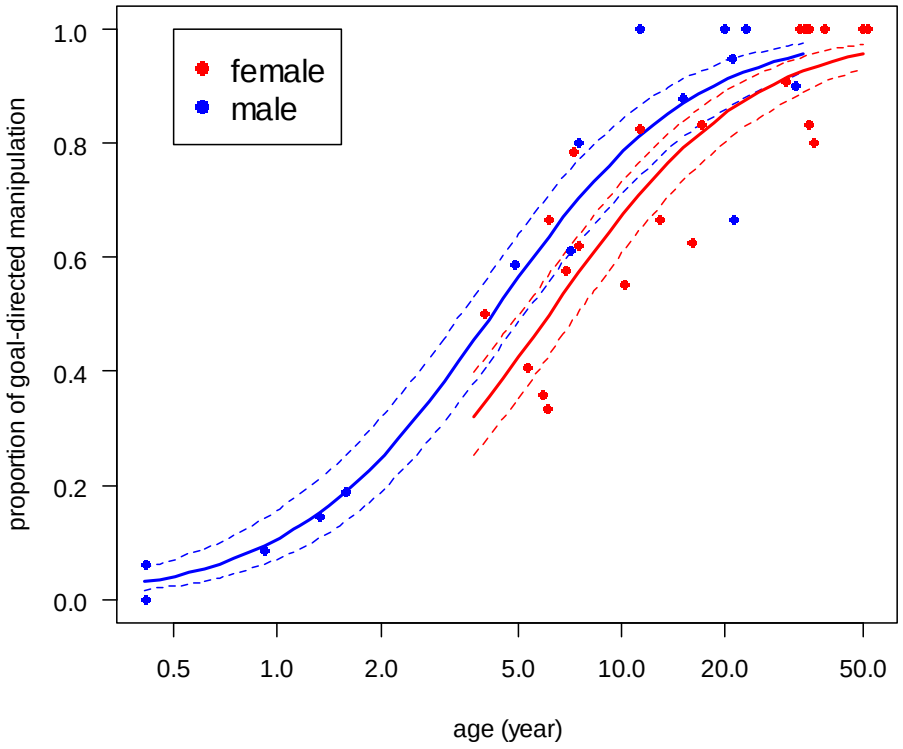

Figure 2.2. Proportions of goal-directed object manipulations as a function of subject age and sex. The blue (male) and red (female) solid lines represent the fitted model, with confidence intervals (dashed lines). The circles are the proportions of goal-directed manipulations, from the raw data, over all the manipulations for each of the 37 individuals and their age.

2.4.3 Choice of material

We found that for adults, leaves and woody vegetation are the most manipulated objects, while sticks are never manipulated. For non-adults leaves and woody vegetation were also the two most manipulated objects, but contrary to adults, sticks were also manipulated habitually (Figure 2.3). The transitional age from playing and exploring sticks to ignoring sticks was around 10 years old, which corresponded to the transition to adulthood (Figure 2.4).

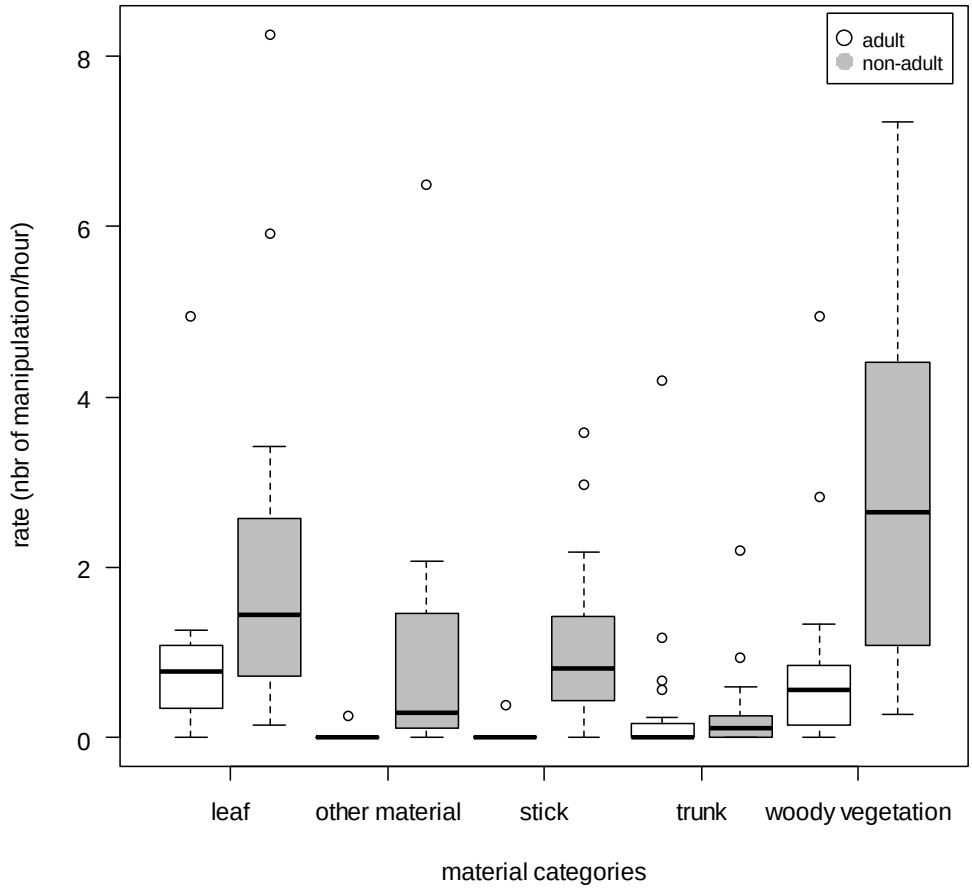

Figure 2.3. Rates of object manipulation across materials and age classes. Rates represent the number of object manipulations per time in sight (hour) for each material category and the two age-classes (105 object manipulations from 21 different adults, and 80 object manipulations from 16 different non-adults). Other material consisted of stone, flower, mud insect channel, moss, bark, soil, sawdust, thorn and termite mount.

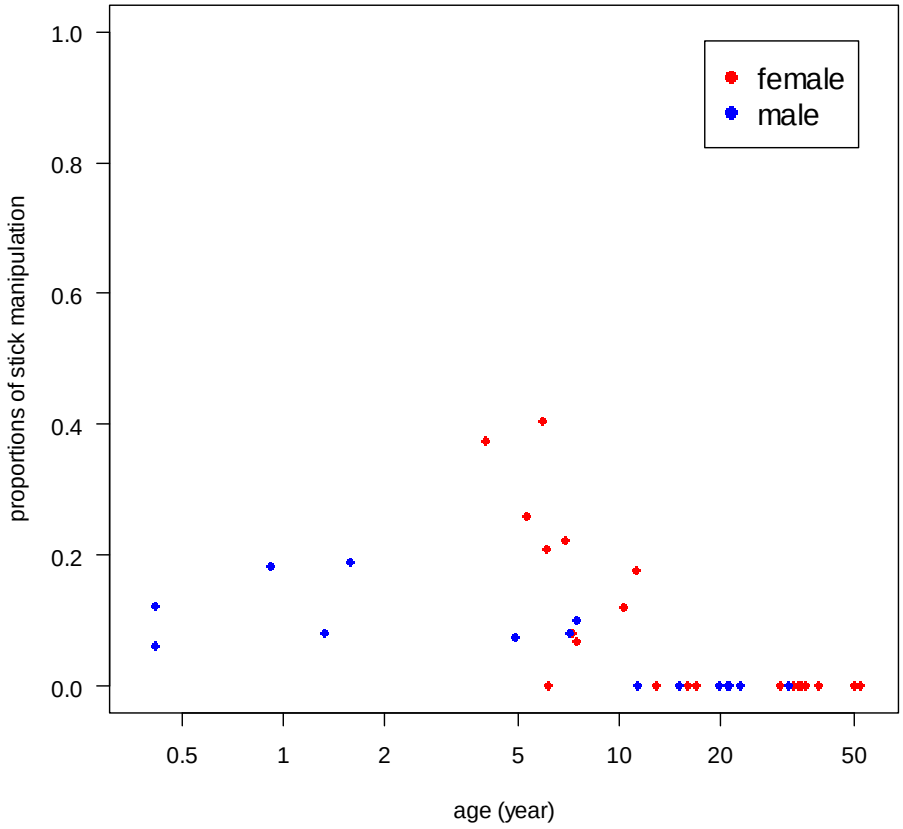

Figure 2.4. Proportions of stick manipulation in non-adult males and females. Females tend to be more active stick users than males, but in both sexes the behaviour disappears around the age of 10 (males: 7.5 years; females: 11 years), which corresponds to the transition to adulthood. Data are proportions of instances when sticks were manipulated relative to all instances when objects were manipulated.

We found that of the six non-null models, three were better than our conceptual null model, i.e., they had lower AICc scores than the null model (weight = 0.01, Table 2.1). Of these three, two suggest maternal influence of material choice of our subjects. The more likely of these two models (weight = 0.80) suggests that the rate with which mothers manipulate a given material is associated with their offspring's choices for that material. The model suggesting a link between proportional mother use and offspring choice had substantially less support in our data set (weight = 0.02). The final of these three models (weight = 0.17) suggests that offspring sex is linked to material choice. Finally, the models that addressed the social, but non-maternal, influence as well as the age model received essentially no support from our data set (weights < 0.01).

Table 2.1 List of the models ranked by their explanatory powers

Predictor variable	**df**	**AICc**	**ΔAICc**	**Weight**
Mother's **rates** of manipulations	8	263.7	--	0.803
Sex	8	266.9	3.2	0.165
Proportions of materials used by mothers out of their total observed number of object manipulation events	8	270.9	7.2	0.022
Conceptual null (material)	5	273.0	9.3	0.008
Age	8	275.3	11.6	0.002
Non-maternal adults mean proportions weighted by the mother's subjects association with all the non-maternal adults	8	278.5	14.8	0.000
Non-maternal adults mean rates weighted by the mother's subjects association with all the non-maternal adults	8	280.0	16.3	0.000

The response variable is the proportion of material the non-adult used in each of the three material categories (i.e. stick, leaf, woody vegetation).

2.5 Discussion

In this study, we were interested in age-related changes in patterns of goal-directed object manipulation in a chimpanzee community. This community is known for its striking absence of a key tool use behaviour seen in virtually all other studied chimpanzee communities, the use of sticks for extracting embedded or difficult-to-access food resources. We monitored 37 individuals ranging from 5 months to over 50 years of age and found, first, that object manipulation generally decreased with age and that males had on average higher manipulation rates than females, across all ages. Second, we also found that the goal-directedness increased with age, and that males generally manipulated in more goal-directed ways than females, across all ages. Third, we found that non-adults manipulated leaves, woody vegetation and sticks, with stick use gradually decreasing to complete disengagement around the age of 10 years. Finally, we found some evidence for social learning in that non-adults played and explored in higher proportions the materials manipulated most often by their mothers.

These results show that object manipulations in chimpanzees change gradually with age, initially mainly in the form of non-goal directed play and exploration behaviour, with goal directedness appearing around the age of 10. These findings suggest that once individuals have some causal understanding of tool use and become habitual tool users, they stop playing and exploring, supporting

the claim that object play and exploration are the precursors of tool use (Chevalier-Skolnikoff, 1989; Kahrs & Lockman, 2014; Parker, 1974; Torigoe, 1985).

Our analyses have also shown that the link between object play and tool use is not direct insofar as non-adults play with materials that they will not use as tools as adults. Specifically, non-adults regularly played with sticks, albeit this never developed into goal-directed tool use in this community. This finding suggests that although object play and exploration help the individual to develop the motor patterns required for tool use, it does not automatically lead to an understanding of object affordances. Social learning, it appears, is additionally required for this final step. Nonetheless, the two materials non-adults explored and played with most (leaves and woody vegetation) were also the ones that adults used for goal-directed object manipulations. Overall, these data strongly suggest that the material choices and manipulation rates by adults, especially the mothers, are the best predictors of non-adult play and exploration behaviour. Interest in material may initially be quite unspecific, but this increasingly changes and appears to get shaped by maternal manipulation, a lengthy process that may last about eight years in chimpanzees, which corresponds to the period offspring stay continually with the mother (Goodall, 1986; Pusey, 1983, 1990). The special role of maternal kin in the acquisition of tool use has also been demonstrated in a related study in which we found that the spread of a new drinking technique, moss-sponging, followed a matrilineal-based transmission pattern in this community (Lamon, Neumann, Gruber, & Zuberbühler, 2017). In sum, chimpanzee mothers play an important role in the acquisition and social spread of tool use (Hirata & Celli, 2003; Lind & Lindenfors, 2010; Lonsdorf, 2006), a process that appears to start already early with infant play and exploration behaviours.

Although we have not specifically addressed the social learning mechanisms underlying the acquisition of tool use, the social transmission observed in our study was most likely due to stimulus enhancement repeatedly identified as the main mechanism in the spread of tool use in primates (Call et al., 2005; Nagell, Olguin, & Tomasello, 1993; Whiten et al., 2004; Zuberbühler, Gygax, Harley, & Kummer, 1996). In our study, stimulus enhancement may have been responsible to focus subjects' choice of materials, while the perceptual-motor patterns required for proficient manipulation may have to be acquired by individual learning.

We also found males manipulating objects more than females across all ages, a pattern consistent with the results by Koops and colleagues (2015), who analysed immature chimpanzees. One hypothesis is that this difference is the result of sexual selection acting differently on males and females. Indeed, Lonsdorf (2017) argued that "…females are expected to show more behaviours related to offspring care and males are expected to show more behaviours related to competition for mating opportunities". In Sonso, there is no tool or proto-tool use primarily related to offspring care that we are aware of but

there are several tool use behaviours related to aggressive displays (i.e. aimed-throw, branch-shake, buttress-beat and drag-branch) and mating behaviour (i.e. leaf-clip, branch-shake and branch-slap), all of which mainly performed by males. If object play and exploration have evolved to facilitate the acquisition of tool use in adults, then sex difference may already be expected during development.

To conclude, our study suggests that immature chimpanzees develop proficiency in tool use by initially exploring and playing unselectively with any object they can find in their environment, but they become increasingly influenced by their mother's object manipulations. Our study also suggests that these changes are due to stimulus or possibly local enhancement combined with individual trial-and-error learning.

2.6 Acknowledgements

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2.7 Supplementary materials

Table S2.1. List of key concepts and definitions

Key concept	Definition
Object manipulation	Dynamic interaction (holding, carrying, moving, hitting) with a freely manipulable object or a substrate (i.e. stout branch, trunk, tree buttress) either in a goal-directed way (tool-use and proto-tool use) or in a non-goal-directed way (object play and exploration). We do not consider object manipulation when the individual ingest the object or part of it.
Tool use	the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible of the proper and effective orientation of the tool (Shumaker et al., 2011, p.5)
Proto-tool use	use of objects that are part of a substrate (T. S. Parker & Gibson, 1977) (e.g. scratching an arm against a stout branch)
Goal-directed behaviour	Actions deployed to achieve a clear purpose and which therefore stop when the action outcome matches the purpose. (i.e. all object manipulations except solitary plays and explorations) (e.g. nest building or leaf-sponging etc.)
Visibility	
In sight	Every body part of the animal is visible and video-recordable
Out of sight	At least one body part of the animal is not fully visible
Material category	
Leaf	Leaf detached or still attached to the branch
Stick	Broken piece of a branch, i.e. processed branch
Trunk	The stem of a tree that cannot be freely manipulable
Woody vegetation	Vine, sapling and branch
Other material	Stone, flower, mud insect channel, moss, bark, soil, sawdust, thorn and termite mount
Object manipulation	
Context	
Body-care	Use of an object to clean, scratch or inspect body parts or to help the destruction of ectoparasites found during a grooming session

Construction	Build a nest, improve a nest, or build a seat-vegetation
Drinking	Ingesting liquid using a leaf-sponge
Leaf-groom	Handling leaves using grooming movements with the thumbs
Social	Use of an object to interact or attract the attention of another individual
Solitary play/exploration	Solitary play: actions on an object, very often repetitive, consisting in manipulating, touching, biting, mouthing or shaking. Exploration: touching, scratching or rubbing fingers. Both don't have a clear goal or function. It is very hard to discriminate solitary play from exploration so most of the time we keep the two notions together.

Manipulation		**Goal-directed (yes/no)**	**Context**
Leaf-dab	Wound inspected by touching leaves to it, then examining leaves (leaves may be chewed)	Yes	Body-care
Aimed-throw	Throwing an object with clear tendency to aim	Yes	Social
Branch-din	Sapling, shrubs and similar vegetation pulled down then released to make considerable noise	Yes	Social
Branch-shake	A branch is shaken to attract another's attentions, as in courtship	Yes	Social
Branch-slap	Slapping a branch with an hand to attract another's attention	Yes	Social
Buttress-beat	Beating/drumming with hands or feet on the buttress or trunk of a tree	Yes	Social
Drag-branch	Dragging a large branch while running, as part of aggressive display	Yes	Social
Leaf-clip	Noisy ripping of leaf with teeth or lips or fingers, to gain attention for various social functions or as a solitary play	Yes or No (no, when solitary play)	Social or solitary play/exploration
Leaf-inspect	Ectoparasites placed on leaf on palm of hand, visually inspected, then eaten or discarded	Yes	Body-care
Leaf-napkin	Leaves use to clean body surfaces	Yes	Body-care
Leaf-squash	Squashing of ectoparasites on leaves after grooming	Yes	Body-care
Leaf-strip	Leaves torn off stem by fingers, generally by thumb and fingers encircled around stem and swept off end of stem in violent move that tears at several or many leaves simultaneously	Yes	Social
Play-start	Initiate play by incorporating an object	Yes	Social
Seat-vegetation	Bending leafy sapling or branches and placing the leaves on the ground for sitting or lying on	Yes	Construction
Leaf-groom	Manipulating leaves using grooming movements with the thumbs	Yes	Leaf-groom
Leaf-sponge	Wad of crumpled or folded leaves used to	Yes	Drinking

	collect water and then squeezed in mouth		
Nest building	Use of branches to build a structure to rest or sleep	Yes	Construction
Social play	Manipulation of an object during an interaction (play) with a group member	Yes	Social
Substrate interaction	Use of a substrate (stout branch, trunk, tree buttress) to alter the physical properties of the user (i.e. rub, scratch, clean body part against substrate)	Yes	Body-care
Substrate interaction	Trunk stomping, to display or attract the attention of a conspecific	Yes	Social
Substrate interaction	rub, scratch, touch or bite a substrate	No	Exploration
Try feeding	Mouth, bite or shew fruit	No	Solitary play/exploration
Active manipulation	Play with or manipulate an object, alone and with no evident purpose or detailed movements directed toward the unique characteristics of an object (ex. scratch bark, stick finger into tree hole)	No	Solitary play/exploration

Most definitions of manipulations are based on (Whiten et al., 2001)

3. STUDY 2: KIN-BASED CULTURAL TRANSMISSION OF TOOL USE IN WILD CHIMPANZEES

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3.1 Abstract

Current research on animal culture has focused strongly on cataloguing the diversity of socially transmitted behaviours and on the social learning mechanisms that sustain their spread. Comparably less is known about the persistence of cultural behaviour following innovation in groups of wild animals. We present observational data and a field experiment designed to address this question in a wild chimpanzee community, capitalising on a novel tool behaviour, moss-sponging, which appeared naturally in the community in 2011. We found that three years later, moss-sponging was still present in the individuals that acquired the behaviour shortly after its emergence, and that it had spread further to other community members. Our field experiment suggests that this secondary radiation and consolidation of moss-sponging is the result of transmission through matrilines, in contrast to the previously documented association-based spread amongst the initial cohort. We conclude that the spread of cultural behaviour in wild chimpanzees follows a sequential structure of initial proximity-based, horizontal transmission followed by kin-based, vertical transmission.

3.2 Introduction

In recent years, the notion of animal culture has become widely accepted, largely because of evidence for social transmission of novel behaviours in both captive and field studies (Allen, Weinrich, Hoppitt, & Rendell, 2013; Aplin et al., 2015; Hobaiter et al., 2014; Whiten et al., 2007; Whiten & Mesoudi, 2008). Several definitions have been proposed for cultural behaviours. These definitions differ mainly

in their descriptions of the underlying transmission mechanisms (Whiten et al., 2009). For instance, Fragaszy and Perry (2003) define tradition, the core component of every definition of animal culture, as "a distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning" (p.xiii). We use the same definition here but do not distinguish between traditions and cultural behaviours (for example, see Whiten, Horner, & Marshall-Pescini, 2003).

In the wild, animal cultural behaviour has been studied mainly through observational methods, particularly the method of exclusion (Perry et al., 2003; Rendell & Whitehead, 2001; Whiten et al., 1999 but see Biro et al., 2003), whereas captive studies typically use both observational and experimental approaches (Whiten, Horner, & de Waal, 2005). The method of exclusion is controversial because it is opaque with regard to the cognitive processes involved in learning and because it is difficult to rule out alternative explanations, such as the influence of genetic and environmental differences (Laland & Janik, 2006). In contrast, although experimental approaches can generate more powerful results, they usually lack ecological validity (Boesch, 2007).

In a recent study carried out in Budongo Forest, Uganda, Hobaiter and *et al.* (2014) reported that a newly-invented natural behaviour in wild chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community, moss-sponging, spread through the social network via social learning. Despite an intense and continuous behavioural research programme, which started in the mid-1990s (Reynolds, 2005), moss-sponging had never been observed until 2011. The behaviour was first displayed by the alpha male in November 2011 upon which it spread rapidly through spatio-temporal association to another seven individuals. However, between 2011 and 2013 the behaviour was seldom observed by researchers and long-term field assistants, raising questions about its maintenance in this community consisting of around 70 individuals.

Our study aimed to determine whether moss-sponging was still present and had further propagated throughout the community to become a component of its group-specific behavioural portfolio. We used this opportunity to address an important issue in the animal culture literature: the scarcity of documented evidence for maintenance of behavioural innovations before they can become cultural traits characteristic of a group (Laland & Galef, 2009; Laland & Hoppitt, 2003; Laland & Janik, 2006).

Although there is a considerable literature on behavioural innovations (Reader & Laland, 2003) and their spread, particularly in captivity (Whiten & Mesoudi, 2008), there are only few well-documented cases for the persistence of natural behavioural innovations in wild populations, especially in the tool use context, and even in those cases, the information is incomplete (Kummer & Goodall, 1985; Nishida, Matsusaka, & McGrew, 2009). The textbook case for innovation is the milk bottle foil-cap

piercing behaviour of parids in England in the 1950s, but little is known of the social dynamics underlying this behaviour (Fisher & Hinde, 1949). Another classic case is pine cone-eating in Israeli black rats (*Rattus rattus*) (Terkel, 1996), a behaviour shown to spread through stimulus enhancement, with pups learning by interacting with the partially eaten food left by their mothers (Terkel, 1996). However, in these cases, as well as in more recent studies in whales (Allen et al., 2013) and chimpanzees (O'Malley, Wallauer, Murray, & Goodall, 2012), the major problem is that the initial innovation was not observed, making the precise dynamics of propagation difficult to understand (Hobaiter et al., 2014). The best evidence for behavioural innovations and subsequent spread comes from long-term research on Japanese macaques (*Macaca fuscata*), where several feeding and play behaviour innovations by single individuals have spread to other group members (Huffman & Hirata, 2003). A well-known example is the transmission of sweet potato washing, invented by a juvenile female 'Imo' (Kawai, 1965). Here, the behaviour initially spread to individuals with close social ties to the initiator (that is, playmates and kin). Thus, the propagation of the behaviour occurred between individuals with a strong social affinity and with whom co-feeding was possible, namely to other females, which have a strong grouping tendency, and to kin (Hirata, Watanabe, & Kawai, 2001; Kawai, 1965). The spread within family units went upwards, from younger to older matriline members (Hirata et al., 2001; Kawai, 1965). Although the authors were able to meticulously describe the slow propagation process of the behaviour, it was not possible to discriminate between the two mechanisms responsible for the spread, spatial proximity and kinship, because mothers and children spend most of their time together and usually co-feed (Kawai, 1958). More relevant in this species is stone-handling, a solitary object play behaviour consisting of repetitively manipulating stones in various ways, which has been documented in various troops (Huffman, Leca, & Nahallage, 2010). In the best-documented case, the behaviour has been studied since 1979 (Arashiyama B troop, near Kyoto, Japan (Huffman, 1984)). The behaviour was socially transmitted (Leca, Gunst, & Huffman, 2010; Nahallage & Huffman, 2007), first horizontally from the innovator, a 3-year-old female, to other similarly aged individuals, and then vertically from the females to their offspring (Huffman et al., 2010). Although stone-handling could potentially lead to tool use behaviour (Huffman & Quiatt, 1986; Leca, Gunst, & Huffman, 2012), it is generally considered a non-adaptive, functionless play behaviour in Japanese macaques (Huffman, 1984; Huffman & Quiatt, 1986).

The goal of the current study was to investigate the mechanisms of maintenance of moss-sponging in a wild chimpanzee community in the years following its initial emergence and its rapid spread among a restricted number of individuals in 2011. At that time, moss-sponging was only seen in eight individuals, when it was used exclusively to absorb mineral-rich water from a single location, a natural clay pit (Figure S3.1 and Figure S3.2), despite the fact that the site was visited by most group members (Reynolds et al., 2015). Effectively, this led to the coexistence of two cultural subgroups: individuals that relied on the traditional drinking technique seen in all chimpanzee communities, that

is, manufacturing of a leaf-sponge to ingest liquids ('clay-pit leaf-spongers') and individuals that used moss to absorb clay water in addition to the traditional technique ('clay-pit moss-spongers'). Crucially, Hobaiter *et al*. estimated that 85%-99% of moss-sponging acquisitions were made through social transmission (Hobaiter et al., 2014). Some of this was due to individuals re-using moss-sponges discarded by others, a potential case of stimulus enhancement, which also qualifies as social learning (Spence, 1937). However, for moss-sponging to truly qualify as cultural behaviour, we predicted that individuals that socially acquired the behaviour in 2011 should continue to moss-sponge in the current study, that is, three years later. Furthermore, we predicted that if moss-sponging had spread to other individuals by social learning in the three-year interval since the initial study, it should have spread preferentially to individuals that were socially close (either by family ties or by spatial proximity) to the original eight moss-spongers.

To explore these questions, we carried out a field experiment at the same clay pit at which the original innovation took place. During two months in 2014, we presented subjects with a choice of two different materials by providing moss next to the naturally available leaves, which allowed us to systematically categorise group members as either moss- or leaf-spongers three years after the original innovation. From our long-term database, we could assign each individual to its matriline (i.e. mother-offspring units) and could document the association patterns of individuals since the time of innovation in 2011. We then combined long-term observational data from Budongo with our cross-sectional experimental results to describe the spread of moss-sponging over the three years following its innovation.

3.3 Material and Methods

3.3.1 Study site and subjects

The study was conducted in the Budongo Forest Reserve in Western Uganda. The Reserve consists mainly of moist, semi-deciduous tropical forest at a mean altitude of 1100m. The Sonso community uses a core home range of approximately 7km^2 (Newton-Fisher, 2003), and community members have been habituated to the presence of human observers since the mid-1990s (Reynolds, 2005). At the beginning of the study period in 2014, the community consisted of 68 individuals, 21 adult females, 12 adult males, nine subadult females, three subadult males, 13 juvenile females, three juvenile males, three infant females and four infant males, following Reynolds' classification (2005). By the end of the study, three new infant males had been born and one adult female had immigrated, resulting in a community size of 72 individuals.

3.3.2 Experimental design

The aim of the experiment was to investigate the choice of sponge material at a clay pit (N1 43.107; E31 32.473) three years after the emergence of the novel moss-sponging behaviour within the community. At the time of the study, the clay pit site, where the moss-sponging behaviour started in 2011 (Hobaiter et al., 2014), consisted of two ground waterholes at the bottom of two trees (Figure S3.1 and Figure S3.2). The cavities were filled with rainwater enriched with minerals dissolved from a high concentration of clay in the soil. Clumps of moss (*Orthostichella welwitschii* (*Duby*)), collected in swamp areas within the chimpanzees' natural home range and naturally hanging from tree branches, were hung in trees around the clay pit. No leaves were provided since the clay pit is located in a tree-dense area, with a large choice of leafy trees regularly used by the chimpanzees to manufacture leaf-sponges. We set up a "Bushnell HD Trophy Cam" motion-sensitive video camera during the first sampling period (11 September to 18 November 2014) and added two more cameras during the second sampling period (30 November to 8 December 2014) to monitor the area from three different angles. The cameras started recording videos as soon as a movement at the clay pit was detected and were set to 1min recording clips with a 1s interval between triggers. Although this set up was ideal with regard to the possible precluding disturbance of the presence of the researchers on less habituated individuals during the experiment and the systematic recording of any interaction with the clay pit at any time of the day, it did not allow data collection of the audience and possible direct observation of moss-sponging behaviour by other group members during the trials outside of the camera range.

3.3.3 Statistical analysis

Experimental data collected for the analyses were as follows: (i) the technique (leaf-sponging or moss-sponging) used by the subjects during tool-assisted drinking bouts, (ii) the age and sex of the subjects, (iii) whether subjects had at least one moss-sponger in their matriline, and (iv) subject-potential demonstrator dyad association index. "Leaf-sponging" was defined as using a wad of crumpled or folded leaves to absorb and consume liquid; "moss-sponging" was defined as using a clump of moss or mixture of moss and leaves for the same purpose. A tool-assisted drinking bout (that is a "trial") started when an individual was seen (i) manufacturing a sponge, (ii) re-using a discarded sponge, or (iii) adding material to an existing sponge. It ended when the individual (i) discarded the manufactured sponge without using it, (ii) stopped sponging to start with another activity, (iii) altered the structure of the sponge by adding material (leaf or moss), or (iv) went out of sight. A matriline consists of the mother and her offspring. We did not consider fathers because only 24 of the 40 participants had a known father: 14 of 24 died before the emergence of moss-sponging, and five did not participate in the experiment. As a consequence, the father's sponging technique was only documented for five participants but unknown for 19. Furthermore, several studies (Hirata & Celli, 2003; Lind & Lindenfors, 2010; Lonsdorf, 2006; Schneider, Call, & Liebal, 2012) have shown the crucial role of the

mother in the youngsters' acquisition of behaviours, mainly because of their constant association during the first years of life (Pusey, 1983), which is not found with the father (Lehmann, Fickenscher, & Boesch, 2006). Nulliparous immigrant females each got assigned their own matriline ID (Table S3.3). A potential demonstrator was an individual whose preferences for moss or leaves were known. A potential demonstrator was defined as (i) a moss-sponger if it had been observed moss-sponging at least once between 2011 and 2014 (that is, the individuals that moss-sponged during the experiment at the clay pit, the eight initiators, and one additional individual (NT) that was observed using a moss-sponge during an unrelated experiment that took place 10 months before our experiment at the clay pit) or (ii) a leaf-sponger, if it has been observed exclusively leaf-sponging. Note that NT's classification as potential moss- or leaf-sponger demonstrator had no effect on our conclusions (Table S3.1 and Table S3.2).

The association index between the subjects and the potential demonstrators was calculated using the half-weight index (Bejder et al., 1998; Cairns & Schwager, 1987) based on party compositions collected from November 2011 to December 2014 by experienced field assistants. We calculated the association index for all dyads that comprised individuals that were at least three years old during the study period (November 2011 to December 2014; $n = 67$), resulting in $n = 2211$ dyads (= 67 x 66 / 2). For 10 of 2211 dyads, association indices were not calculated because the two individuals were not co-resident in the community (that is, $n = 4$ dyads between a female that emigrated during the study period and an infant that turned three after the female emigrated, $n = 3$ dyads between a female that emigrated during the study period and a female that immigrated after the emigrant left the group, $n = 2$ dyads between an individual that died during the study period and a female that immigrated in the group after the death of the individual, and $n = 1$ dyad between an infant that turned three years old and a female that died before the infant turned three).

From a total of 12.4 hours of video recordings we identified $n = 157$ tool-assisted drinking bouts (that is, trials). We excluded $n = 13$ trials for which the choice of material could not be determined unambiguously from the recordings. Trials for which the subjects were among the original cohort that started using moss-sponges in 2011 ($n = 13$) were also excluded because we were interested in testing the transmission happening after the original spread in 2011. This resulted in a final dataset of $n = 131$ trials by 35 subjects.

For each trial, we assigned the subject to all potential demonstrators ($n = 43$). This resulted in 5633 combinations of subjects and potential demonstrators across the 131 trials (5633 = 131 x 43). However, for three trials, the subject, an adult female, immigrated in the group after one potential demonstrator (HL) had emigrated already; they were therefore never co-resident, and HL could not have been a possible demonstrator for this female. Thus, our overall data set comprised 3 trials with 41

potential demonstrators + 128 trials with 42 potential demonstrators = 5499 cases, that is, the combination of the subject in a given trial and one potential demonstrator. For each such case (represented as one line in our data table), we assigned the dyad's association index, the subject's choice in the trial, whether the potential demonstrator used moss, whether the subject had a moss-sponger in the matriline, and the subject's age and sex.

We had two major predictor variables in our model. First, for vertical transmission, we included whether subjects had at least one matriline member that had acquired the moss-sponging technique. Second, for horizontal transmission, we included the two-way interaction between the association index (between subject and potential demonstrator) and whether moss-sponging was observed in the potential demonstrator at any time between 2011 and 2014. We reasoned that, with potential demonstrators that were moss-spongers themselves, stronger associations should positively correlate with the probability of a subject moss-sponging in our experiment. In contrast, with potential demonstrators that were not moss-spongers, association strength should not affect the subjects' probability to use moss. In other words, if moss-sponging followed a horizontal transmission, then this should manifest itself as a significant interaction term in the model. We additionally included subject age and sex as control predictors. To account for nonindependence of repeated trials per subject and the way we set up our data set, we included random intercepts in our model for dyad identity, subject ID nested in dyad, and potential demonstrator ID nested in dyad. Both age and association indices were z-transformed (Schielzeth, 2010). Model fitting was conducted in R (v. 3.2.0) (R Development Core Team, 2015), using the lme4 package (v. 1.1-7) (Bates, Maechler, Bolker, & Walker, 2014).

Finally, we wanted to test whether the distribution of the two different techniques within the group was random and, therefore, whether moss-sponging was acquired by individual learning. To this end, we first assigned a technique to the 35 subjects that participated to the clay pit experiment by labelling individuals that had been observed moss-sponging at least once at the clay pit as "moss-spongers", and as "leaf-spongers" otherwise. Using the same technique as the association index in the previous model (see above), we calculated an average association with other moss-spongers in the community (individuals that had been seen moss-sponging at least once at the clay pit and the eight initiators in Hobaiter *et al.*'s study (2014). We then ran a generalized linear model on the 35 subjects and tested two main factors (having a moss-sponger in the matriline and the average association with other moss-spongers) along with two control factors (age and sex). To answer the question of whether moss-sponging was randomly distributed among the individuals with respect to the two main factors tested, we reran the model 10,000 times and extracted the parameter estimates. In each of the 10,000 models, the assignment of technique to a given individual was randomized. Our randomization kept the proportion of moss spongers in the group constant; that is, there always were 18 leaf-spongers and 17

moss-spongers. Finally, we compared the original estimates, that is, the effect we actually observed, to the distribution of parameter estimates from our 10,000 models.

3.4 Results

Data were collected in 2014, three years after the first appearance of the moss-sponging behaviour. At the time of this study, community members still visited the site of innovation, the clay pit filled with mineral-rich suspension.

In our experiment, five of the eight initiators in the study of Hobaiter *et al*. (2014) moss-sponged at least once at the clay pit, one was observed leaf-sponging only, one never visited the site, and for another one, the sponge material chosen could not be determined. In addition, a total of 48 individuals (~69% of the community) visited the experimental site and drank at the clay-pit using either moss- or leaf-sponges. We excluded eight individuals for whom we could not confirm that artificially provided moss was available during the experiment, leaving 40 participating individuals (median number of trials per individual, 3; range, 1 to 17: Table 3.1). Individual technique preference could not be tested because of the low numbers of data-points per individual. Of the 40 participants, 22 (55%) moss-sponged during at least one experimental trial (that is, 5 of the 8 initiators in Hobaiter *et al*.'s study and 17 new moss-spongers), and 18 exclusively leaf-sponged (45%; Table 3.1). In comparison, in Hobaiter *et al*.'s study (2014), 8 of 32 individuals (25%) moss-sponged to extract the clay pit mineral suspension, a notable increase. Nevertheless, leaf-sponging remained the predominant technique, with 33 of 40 individuals (83%) leaf-sponging at least once during the experiment, with 18 exclusive leaf-spongers, compared to 22 participants moss-sponging at least once, with seven exclusive moss-spongers.

Table 3.1 List of participants sorted by matrilines and their choices during the experiment (number of leaf-sponging event, number of moss-sponging event, total number of sponging event, proportion of leaf-sponging and proportion of moss-sponging).

ID (N=40)	age (year)	sex	matriline	nbr of leaf-sponging	nbr of moss-sponging	Total	Percentage of leaf-sponging [%]	Percentage of moss-sponging [%]
AN	24.3	f	AN[1]	4	0	**4**	100	0
CC	14.3	f	CC[1]	3	0	**3**	100	0
GL	38.3	f	G	4	0	**4**	100	0
GR	8.3	f	G	8	0	**8**	100	0
HR	5.0	f	H	3	4	**7**	43	57
HT	36.5	f	H	1	4	**5**	20	80
HW	21.3	m	H	0	1	**1**	0	100
HY	9.1	f	H	7	5	**12**	58	42
IN	15.3	f	IN[1]	2	1	**3**	67	33
JS*	8.4	m	J	0	1	**1**	0	100
KG	38.5	f	K1	2	0	**2**	100	0
KI	11.2	f	K1	0	3	**3**	0	100
KP	6.1	f	K1	2	0	**2**	100	0
KC	8.2	m	K2	2	0	**2**	100	0
KL	35.5	f	K2	3	0	**3**	100	0
KH	6.3	f	K3	3	2	**5**	60	40
KS	12.2	m	K3	1	1	**2**	50	50
KU	35.4	f	K3	0	1	**1**	0	100
KB*	7.8	f	K4	1	2	**3**	33	67
KR*	13.0	f	K4	0	4	**4**	0	100
KW*	33.4	f	K4	0	1	**1**	0	100
KZ	19.8	m	K4	1	0	**1**	100	0
KA	15.8	f	KA[1]	1	0	**1**	100	0
MB	5.9	m	M1	1	0	**1**	100	0
ML	39.5	f	M1	1	0	**1**	100	0
MI	7.0	f	M2	4	1	**5**	80	20
MK	34.4	f	M2	3	2	**5**	60	40
MS	23.3	m	N	3	0	**3**	100	0
NB*	52.3	f	N	3	1	**4**	75	25
NT	11.6	f	N	6	0	**6**	100	0

OK	18.5	f	OK[1]	2	0	**2**	100	0
PS	16.3	m	PS[1]	6	1	**7**	86	14
RF	7.3	f	R	1	1	**2**	50	50
RH	49.5	f	R	0	4	**4**	0	100
RM	12.1	f	R	2	0	**2**	100	0
RS	17.0	f	R	2	1	**3**	67	33
TM	10.5	f	TM[1]	1	1	**2**	50	50
UP	15.3	f	UP[1]	11	6	**17**	65	35
ZD	13.4	m	Z	1	0	**1**	100	0
ZG	17.4	m	ZG[1]	1	0	**1**	100	0
Median				2	1	**3**	**78**	**22.5**
Total				**96**	**48**	**144**		

Individuals marked with (*) are the initial moss-spongers in Hobaiter et al. (2014). Individuals without a known mother were assigned their own matriline and marked with ([1]). nbr means number.

Given that the number of moss-spongers had increased substantially over the three years following innovation, we were interested in the transmission patterns within the group. We tested two hypotheses, that is, that transmission occurred vertically (within matrilines) or horizontally (across the community, following association patterns). Using a generalized linear mixed model with binomial error structure, we estimated the probability of manufacturing a moss-sponge by individuals in a given experimental trial taking into account all potential demonstrators from which the subject may have learned the technique. Crucially, the full model included two terms corresponding to the two potential transmission modes. For the vertical transmission hypothesis, we tested whether having a moss-sponger in the matriline affected the probability of using moss in the experiment. For the horizontal transmission hypothesis, we tested the interaction term between the association strength between the subject and the potential demonstrator (as a proxy for the possibility to learn socially) and the sponging technique of the potential demonstrator. Specifically, if horizontal transmission was at work, we expected to see a positive relationship between the association index and the probability to moss sponge, but only with potential demonstrators that were themselves moss-spongers.

We found significant support for the vertical transmission hypothesis ($\beta = 1.35 +/- 0.11$, $z = 12.80$; likelihood ratio test (LRT): $\chi^2(1) = 184.22$, $P = 0.000$; Figure 3.1 and Table S3.1,) but no support for horizontal transmission ($\beta = -0.03 +/- 0.09$, $z =- 0.290$, LRT: $\chi^2(1) = 0.682$, $P = 0.877$; Figure 3.1 and Table S3.1). In particular, subjects with a moss-sponger in the matriline were more likely to use a moss-sponge during the experiment than subjects without a moss-sponger in the matriline (Figure 3.2),

whereas moss-spongers were not more strongly associated with other community members displaying moss-sponging from which they could have learnt the behaviour.

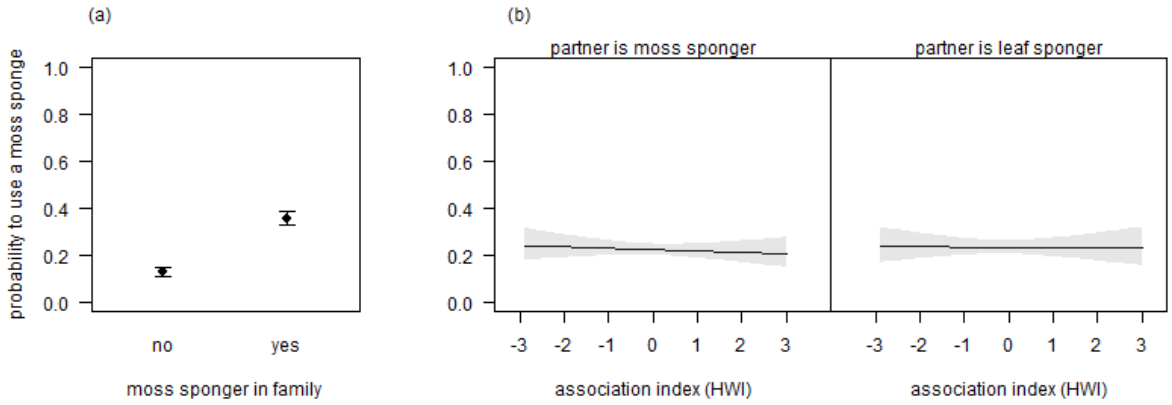

Figure 3.1 Social transmission of cultural behaviour in wild chimpanzees. (a) Probability of moss-sponging by subjects depending on whether they have at least one moss-sponger in the matriline: parameter estimates with standard errors. **(b)** Probability of moss-sponging by subjects depending on their association history with other moss- or leaf-spongers in the group: model estimates with standard errors (shaded areas). The numerical results are in Table S3.1.

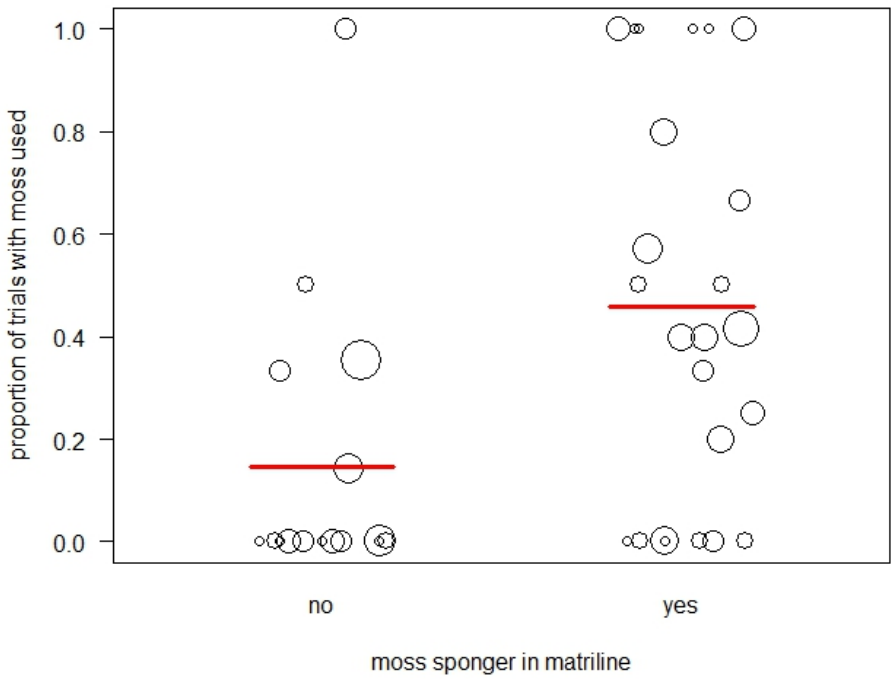

Figure 3.2 Proportion of trials with subjects using moss to manufacture a sponge. The size of the circles corresponds to the total number of trials observed (i.e. the larger the circle is, the more trials the subject had). The red lines represent the means. Note that the figure represents raw data. Results of the GLMM are in Table S3.1 and Table S3.2.

In a complementary analysis we investigated the distribution of techniques across individuals (as opposed to the technique used in a given experimental trial). We devised a permutation procedure in which we randomly assigned techniques to subjects and estimated the effects of having a moss-sponger in the matriline and a subject's average association index with other moss-spongers on the probability that a subject was a moss-sponger. We then compared the observed effects of these two factors to the expected effects resulting from our permutation procedure. We found that the observed effect of having a moss-sponger in the matriline was significantly larger than we would expect (10,000 permutations, $P = 0.048$; Figure S3.3). This result suggests again that having a moss-sponger in the matriline increases the likelihood of belonging to the moss-sponging subgroup. We found no such effect with regard to the average association with other moss-spongers (10,000 permutations, $P = 0.4940$; Figure S 3.4).

3.5 Discussion

Here, we used natural and experimental observations to assess the propagation pattern and the maintenance of a novel tool technique, moss-sponging, first observed in 2011. Although we cannot exclude that some individuals developed the moss-sponging behaviour at the time of our experiment, our cross-sectional design aimed to uncover the present state of knowledge of the chimpanzees visiting the clay pit and to analyse whether the moss-sponging behaviour had spread in the community following its original innovation. Our results showed that, over a period of three years, the behaviour spread from a small number of founder individuals (eight) to 17 additional group members. Considering that moss-sponging is transmitted socially and that only a subset of the community members uses this technique (without any compelling genetic or environmental alternative explanations at hand), we consider this behaviour a subculture within the Sonso community. Nevertheless, most moss-spongers did not abandon their default drinking technique, leaf-sponging, and manufactured both leaf- and moss-sponges in parallel (Table 3.1).

Another major finding was that moss-sponging mainly increased in prevalence within matrilines (Figure 3.3) and not through either an association network, or by individual learning.

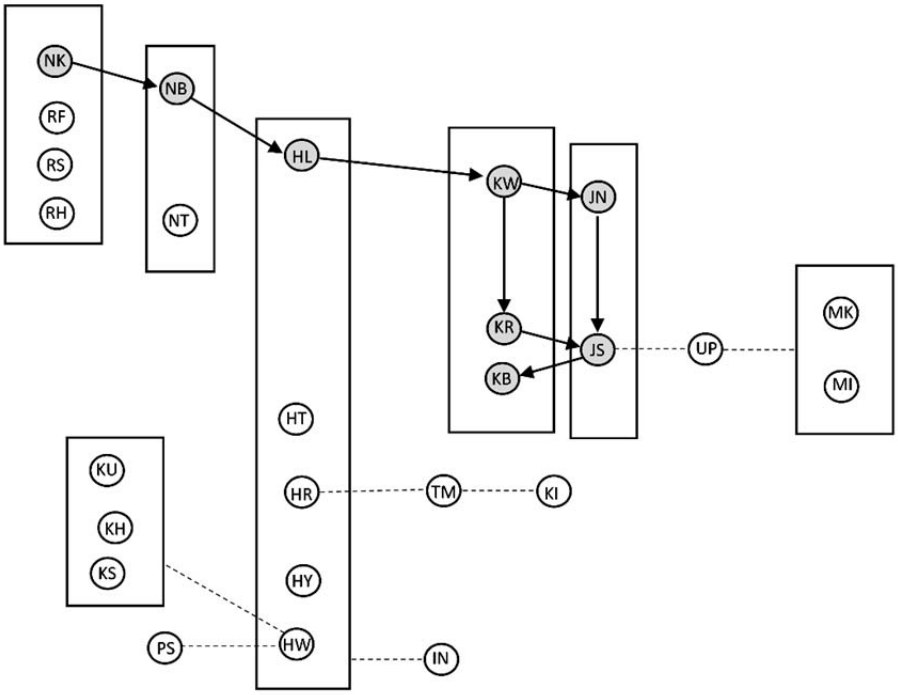

Figure 3.3 Model of the two-dimensional transmission pattern. Circles represent all individuals seen moss-sponging at least once between 2011 and 2014. The eight original moss-spongers from Hobaiter *et al.*'s study (2014) are represented in grey. The arrows represent the social transmission Hobaiter and colleagues found (Hobaiter et al., 2014). The squares represent matrilines in which vertical social learning took place, the main transmission mechanism involved in the spread. The dotted lines represent the possible learning path of the cases (n=7) in which individuals acquired the behaviour in the absence of vertical transmission because individuals did not have moss-sponging kin, suggesting learning from individuals they were highly associated with (linked with the individual with the highest association index).

Because kin usually associate together, kin-based transmission and association-based transmission are therefore often confounded and hard to discriminate (Mann, Stanton, Patterson, Bienenstock, & Singh, 2012; van Schaik, 2003). However, in our study, we were able to disentangle the two transmission mechanisms of close spatial association and close social links; and our results suggest that both are at work, albeit at different stages of the cultural transmission process. Specifically, we found that individuals from matrilines with moss-sponging individuals were more likely to be moss-spongers themselves compared to individuals from matrilines that did not have a moss-sponger. In contrast, moss-spongers did not associate more with each other *per se*, unlike other studies on cultural behaviour (for example, see Mann et al., 2012). Mere spatiotemporal associations with other moss-spongers alone could not explain the distribution, in contrast to the initial spread reported by Hobaiter *et al*. (2014). This suggests that, in chimpanzees, cultural behaviours become established by a

scaffolding of two distinct mechanisms. Whereas the initial spread of cultural behaviour appears to propagate through spatial associations, subsequent expansion proliferates mainly through matrilines (Figure 3.2). This pattern is reminiscent of findings in Japanese macaques, where various behaviours also spread throughout the group in possibly similar ways. Compared to the macaque cases, all possible acquisition pathways (adults to adults, youngsters to youngsters, and adults to youngsters or reverse) were observed (Hobaiter et al., 2014). Additionally, during this propagation phase, the transmission was not strictly vertical; otherwise, only the five matrilines of the eight initiators would have used this technique after three years, which was not the case. Rather, the behaviour propagated within a network of close associates, possibly kin-bonded and allied, leading to the co-existence of a subculture, the moss-spongers, within the community. Other factors, such as opportunities for social learning or the identity of the model, which we could not analyse at this stage of the spread of moss-sponging, may subsequently explain why a given behaviour becomes dominant during the consolidation phase.

We can think of several explanations for this observed change in the acquisition pattern, from horizontally to vertically governed. First, the change of transmission could be a by-product of special circumstances. The behaviour arose at a time when the clay pit contained a suspension with high levels of minerals (Reynolds et al., 2015), which appeared to be an exceptionally valuable resource (Reynolds et al., 2015; Reynolds, Lloyd, & English, 2012). Over time, the mineral content of the suspension may have decreased, because of intense exploitation by chimpanzees and guereza monkeys (*Colobus guereza*; NL, personal observation). Similarly, individuals may have started to exploit additional mineral sources (Reynolds et al., 2015), which could have led to a decrease in competition at the clay pit, with fewer opportunities for horizontal transfer. High levels of competition have been proposed as the main cause of innovation of moss-sponging behaviour in 2011 (Hobaiter et al., 2014). During this study, the average number of individuals simultaneously present at the pit was 2.2 (data extracted from camera trap clips), suggesting a possible decrease in competition between 2011 and 2014. Transmission dynamics of cultural behaviour may thus have been influenced by variation in both ecological factors and social competition.

Another hypothesis is that the acquisition of cultural behaviour generally follows a two-stage process in chimpanzees, in that innovations first spread via proximity-based social networks, whereas subsequent stabilisation within the larger group happens within relevant social units, which, for chimpanzees, are the matrilines (Nishida, 2011). However, this may also depend on the type of transmitted behaviour: different patterns of transmission may apply to different types of behaviours (for example, sexual behaviour may not be learnt by immature individuals; see the discussion by Huffman and Hirata, 2003). In the case of tool use behaviour, previous research has shown that

chimpanzee mothers play an important role (Hirata & Celli, 2003; Humle et al., 2009; Inoue-Nakamura & Matsuzawa, 1997; Lind & Lindenfors, 2010; Lonsdorf, 2006). Transmission through family members may be magnified by the chimpanzees' fission-fusion social system (Nishida, 2011), mainly because young individuals do not have regular contact with group members other than members of their matriline (Humle et al., 2009), although this does not appear to be a necessary precondition (for example, Japanese macaques (Nahallage & Huffman, 2007)). Moreover, chimpanzees are especially tolerant towards family members, which may preferentially facilitate transmission of novel behaviour, a model proposed by Matsuzawa and colleagues (Matsuzawa, Biro, Humle, Inoue, & Tonooka, 2001) as "education by master-apprenticeship". Possibly driven by a desire to act like others (that is, de Waal's Bonding- and Identification-based Observational Learning (BIOL) model) (de Waal, 2001), an individual may also have a strong tendency to copy matrilineal members. Our analyses show that within-matriline transmission is not solely restricted to unidirectional mother-offspring dyads but also probably includes cases of transmission from offspring to the mother (H matriline; see Figure 3.3) or between offspring (R or H matrilines; see Figure 3.3), as seen in Japanese macaque sweet potatoe washing (Kawai, 1965). According to this hypothesis, the fostering ground for cultural transmission in chimpanzees and macaques is the entire matriline (i.e. mother and offspring and the offspring of offspring), in line with what has been proposed for human cultural transmission (Magnus Enquist, Strimling, Eriksson, Laland, & Sjostrand, 2010).

Nevertheless we cannot completely rule out alternative explanations of our results. First, on the basis of Hobaiter and *et al.*'s findings (2014), we assumed that moss-sponging was generally socially learned between 2011 and the time of this study. It is possible, of course, that by artificially providing moss at the clay pit to sample group members, we increased the affordance of moss and thereby made individual learning possible. However, we do not find individual learning-based explanations very plausible, for the following reasons. On the one hand, during the initial propagation phase in 2011, social learning-based models were overwhelmingly more supported than individual learning-based models, and there is no obvious reason why chimpanzees would suddenly switch from social to individual learning in subsequent years. Of course, each moss-sponger has to learn individually the behaviour, but in all likelihood, this was facilitated by the social influence exerted by other group members that acted as models. On the other hand, the existence of a continuous social influence is supported by the fact that the distribution of moss-spongers in the group in our study was biased toward kin and not randomly, as we would expect if the transmission mechanism had been asocial. A random distribution would indeed be expected if individual learning was at work, as was found for the second behaviour studied by Hobaiter *et al.* (2014), leaf-sponge re-use, in the same context.

Second, it could be argued that moss-sponging matrilines were genetically more predisposed to this type of tool use than other matrilines. For example, moss-sponging family members may generally

show more traits essential for acquiring new behaviours, such as curiosity, inventiveness or boldness. According to this second explanation, the recent cohort of moss-spongers was more likely to acquire moss-sponging because of their genetic predisposition, albeit by individual learning. However, similarly, we do not find the family-specific genetic hypothesis very plausible. If we accept that genetic predispositions are the underlying process at play in the propagation phase investigated here, the same reasoning should apply to the initial spread of the behaviour described in Hobaiter *et al*.'s study. Following this reasoning, the behaviour should have appeared multiple times in response to the environmental stimulus, rather than follow a pattern based on observational learning only. Additionally, some kind of genetic relatedness between individuals should be observed in both the original and new cohorts of moss-spongers. Because of chimpanzees' philopatric system, females tend to have a more diverse genetic background compared to males (Gruber & Clay, 2016), but offspring will be sired by a limited number of resident males in the community. If moss-sponging innovation results from genetic predispositions, we should thus expect that offspring from the same father, which are genetically more related, display the same propensity to innovate the new technique. In the Sonso community, of seven fathers with at least two documented offspring, five had offspring using different sponging technique at the clay pit (Table S3.3), making it unlikely that a genetic predisposition triggered moss-sponging innovation.

In conclusion, our experiment allowed us to decipher how a new tool-assisted drinking behaviour persisted in a subgroup of the Sonso community and how it became part of their cultural repertoire. We also showed that although chimpanzees had the same opportunity to individually learn the moss-sponging behaviour by taking the provided moss or the discarded moss-sponges at the clay pit, only a subset of them incorporated this behaviour in their repertoire, by learning from members of their matriline. To our knowledge, this is the first study to disentangle the influence of proximity-based association networks and matrilines on the propagation and maintenance of a tool use invention, by showing how the two transmission patterns operate both during the emergence and during the consolidation of a novel behaviour within a group. Ultimately, because the propagation phase is not strictly vertical, it is likely that novel cultural behaviour will be able to reach the "habitual" or "customary" level in a population over time following this model (Whiten et al., 1999).

Our findings have some implications for understanding cultural transmission in modern humans, where cultural behaviour also tends to spread through close family units, although not exclusively so (Richerson & Boyd, 2005). Considering that early human groups lived in fission-fusion social systems, likely similar to chimpanzees, and had cultural repertoires similar to them (Wynn & McGrew, 1989), it is possible that early human cultural transmission followed the pattern found here, that is, an initial founding event (potentially triggered by ecological necessity and opportunity) followed by early spread to close associates and subsequent consolidation within the close family

units. However, human evolution is also characterised by increasingly more complex social cognition and a social life in large and highly cooperative groups with cooperative breeding and teaching, suggesting that the transmission of culture has become more efficient and widespread, extending beyond the original family core.

3.6 Acknowledgements

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3.7 Supplemental Materials

Table S3.1 Results of the generalized linear mixed model in the field experiment, with individual NT included as a potential demonstrator for moss-sponging.

Fixed effects (predictors)	β	Std. Error	z-value	p-value
Intercept	-2.214	0.120	-18.469	0.000
Potential demonstrator technique	-0.055	0.098	-	-
Association index	-0.008	0.012	-	-
Moss-sponger in family	1.346	0.105	12.793	0.000
Subject age*	0.196	0.045	4.340	0.000
Subject sex*	-0.875	0.138	-6.327	0.000
Interaction potential demonstrator technique x association index	-0.027	0.093	-0.290	0.772

*The null model against which the full model was tested included the random effects and the control predictors subject age and sex: likelihood ratio test, χ^2 (4) = 242.64; p = 0.000. Control predictors are marked with *. Z and p values for main effects comprised in interactions are omitted.*

Table S3.2 Results of the generalized linear mixed model in the field experiment, with individual NT included as a potential demonstrator for leaf-sponging (that is, if her moss-sponging event during an unrelated experiment is not taken into account).

Fixed effects (predictors)	β	Std. Error	z-value	p-value
Intercept	-2.210	0.118	-18.665	0.000
Potential demonstrator technique	-0.065	0.097	-	-
Association index	-0.008	0.070	-	-
Moss-sponger in family	1.346	0.105	12.795	0.000
Subject age*	0.196	0.045	4.340	0.000
Subject sex*	-0.875	0.138	-6.331	0.000
Interaction potential demonstrator technique x association index	-0.028	0.092	-0.302	0.763

*The null model against which the full model was tested included the random effects and the control predictors subject age and sex: likelihood ratio test, χ^2 (4) = 242.78; p = 0.000. Control predictors are marked with *. Z and p values for main effects comprised in interactions are omitted.*

Table S3.3 Individuals with a known sponging technique and their affiliation.

ID	Sex	Mother	Father	Sponging technique
KI	f	KG	BK	Moss
RM	f	RH	BK	Leaf
AN	f	NA	CH	Leaf
PS	m	PL	CH	Moss
MI	f	MK	DN	Moss
RS	f	RH	DN	Moss
HW	m	HT	JM	Moss
HL	f	HT	JM	Moss
MS	m	NB	MG	Leaf
NK	m	RH	MG	Moss
ZG	m	ZM	MG	Leaf
HR	f	HT	NK	Moss
HY	f	HT	NK	Moss
KH	f	KU	NK	Moss
KB	f	KW	NK	Moss
MB	m	ML	NK	Leaf
JS	m	JN	ZF	Moss
KC	m	KL	ZF	Leaf
KP	f	KG	ZF	Leaf
RF	f	RH	ZF	Moss
ZD	m	ZN	ZF	Leaf

NA means data not available

Figure S3.1 General view of the clay pit located between the exposed roots of two adjacent trees (*Cynometra alexandrii* and *Mimusops bagshawei*) consisting in two cavities. The red arrows show the two water-filled cavities in which the chimpanzees sponge to get the mineral-rich water.

Figure S3.2 Close-up view of the two cavities. I) shows the cavity on the left on Figure S3.1, including the obstructing roots, which prevent chimpanzees from drinking directly from the hole. **II)** shows the cavity on the right on Figure S3.1, with less obstructing roots allowing direct drinking. The grey colour of the soil results from the high concentration of clay it contains. The clay minerals are dissolved in the water, increasing considerably the mineral content of the water (Reynolds et al., 2015) consumed by the chimpanzees.

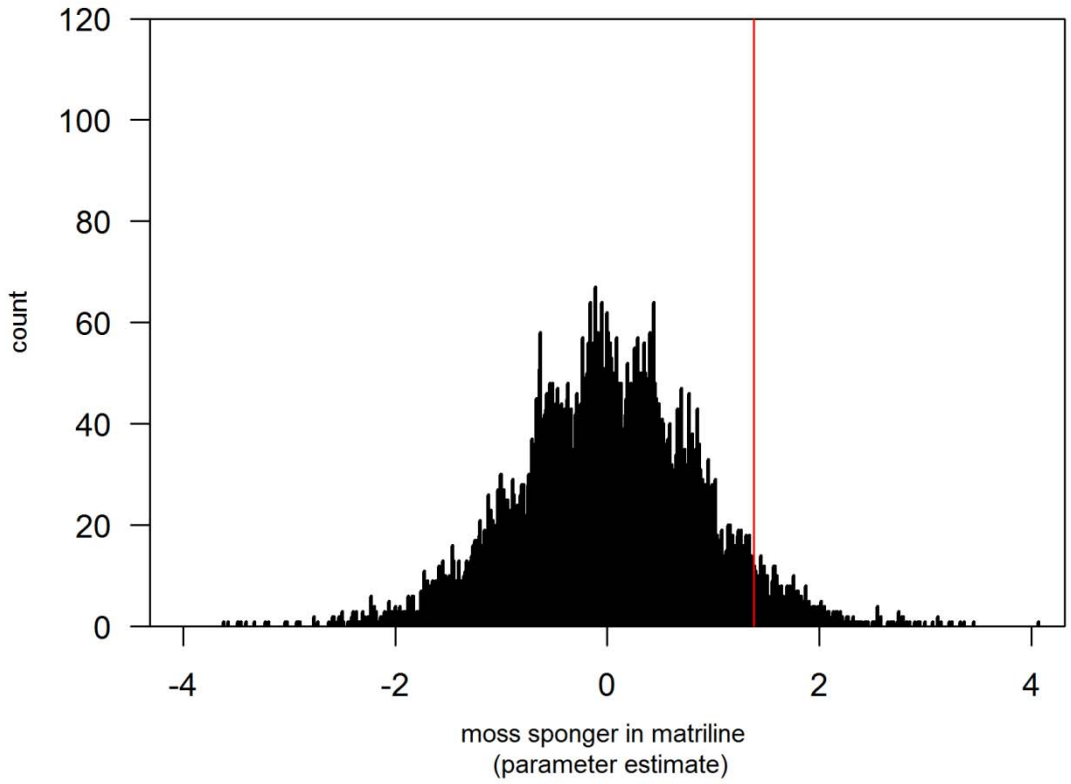

Figure S3.3 Histogram of parameter estimates for the factor moss-sponger in matriline. The histogram consists of 10,000 parameter estimates from models where the distribution of leaf-spongers and moss-spongers was randomized. The red line represents the observed estimate calculated from the observed distribution of leaf-spongers and moss-spongers in the group (1.38), which is larger than expected by chance (p= 0.048).

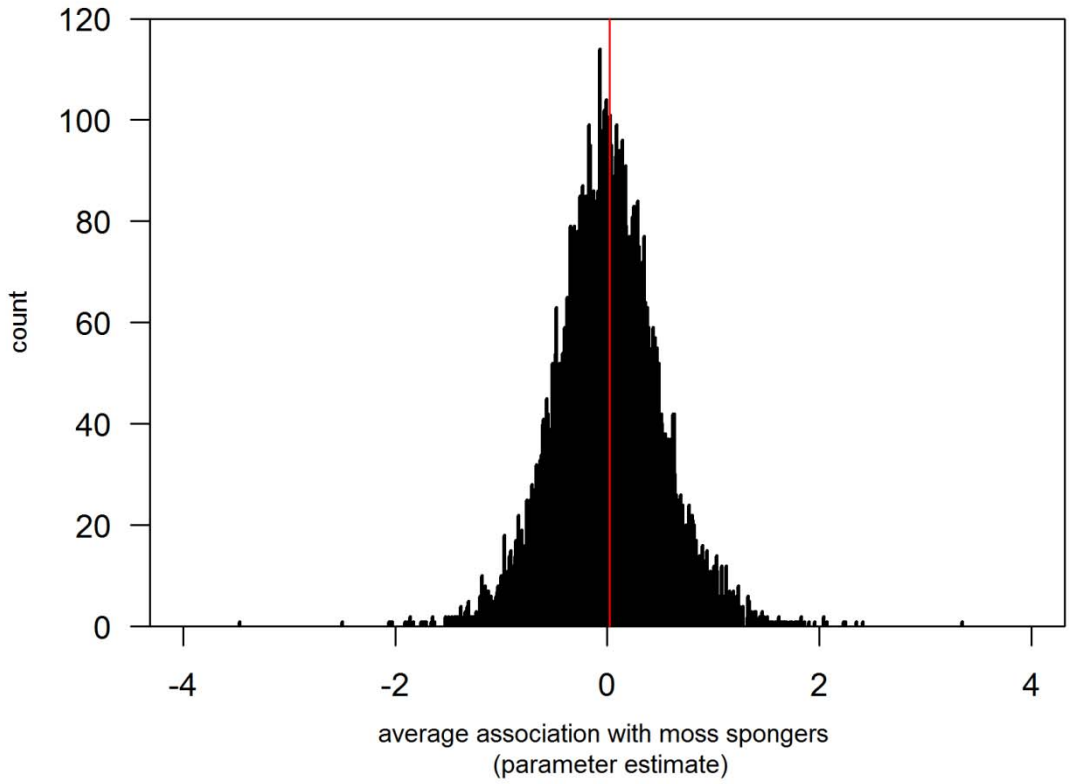

Figure S 3.4 Histogam of parameter estimates for the factor average association with moss-spongers. The histogram consists of 10,000 parameter estimates from models where the distribution of leaf-spongers and moss-spongers was randomized. The red line represents the observed estimate calculated from the observed distribution of leaf-spongers and moss-spongers in the group (0.022), which is not different from what would be expected by chance ($p = 0.4940$).

4. STUDY 3: CULTURAL EVOLUTION OF TOOL EFFICIENCY IN WILD CHIMPANZEES

Manuscript under revision

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4.1 Abstract

Some animals have basic culture but, in contrast to humans, little evidence suggests that animal cultures evolve. To qualify as cultural evolution, a behaviour must have derived from a less complex and less efficient form, and subsequently spread through social learning. We investigated a recent tool innovation in chimpanzees, moss-sponging, which had spread socially through several matrilines as an alternative to traditional leaf-sponging. To evaluate whether moss-sponging constituted a case of cultural evolution, we quantified its efficiency and found that moss-sponges absorbed more water, were faster and structurally less complex to manufacture than leaf-sponges. Despite this, moss-sponging was mostly observed at one clay-pit, suggesting that chimpanzees may not consider moss suitable general sponge material. To test this, we offered rainwater in a portable log with a choice of moss and leaves to assess tool material preference. We found that established moss-spongers, who possessed the two drinking techniques in their tool repertoire, preferred moss, whereas non-moss-spongers, who did not know the novel technique, preferred leaves. Additionally, moss was absent in most forest areas, explaining its limited use to the clay-pit context where moss was abundant, underlying the continuous influence of ecology on cultural behaviour. Together, these results provide evidence for cultural evolution of tool use in wild chimpanzees.

4.2 Introduction

In modern humans, cultural traits, such as technology, language or social organization, are caused by a capacity to accumulate cultural information over generations. The basic model is that complex cultural traits are the result of cross-generational improvements via a "ratchet-effect" (Tennie et al., 2009; Tomasello et al., 1993). During this process, improved behaviours replace their predecessors and persist until a further modification is invented. Yet, the origins of the capacity for cumulative culture continue to remain elusive (Tomasello et al., 1993). In hominins, the earliest documented evidence of cultural evolution is in the form of increased complexity in stone flaking from the arguably primitive Lomekwian and Oldowan phases to more sophisticated stone knapping during the Acheulian phase (Caruana, D'Errico, & Backwell, 2013; Harmand et al., 2015). Following these early slow beginnings, the evolution of human tool technology has developed exponentially in terms of efficiency, volume and complexity, with unprecedented changes to the entire planet (Enquist, Ghirlanda, Jarrick, & Wachtmeister, 2008).

Most evidence for animal culture in the wild is in the form of stagnant, population-level behaviour differences, with hardly any compelling evidence of cultural evolution within groups or populations (Boyd & Richerson, 1996; Dean et al., 2013; Mesoudi et al., 2006; Tennie et al., 2009) This is also true for chimpanzees (*Pan troglodytes*), the most prolific species regarding culturally acquired tool use (Whiten et al., 1999). Chimpanzees are sophisticated social learners, especially well documented in captivity, with good evidence for some social learning mechanisms, such as stimulus or local enhancement and emulation (e.g. Call, Carpenter, & Tomasello, 2005; Nagell, Olguin, & Tomasello, 1993). On the other hand, evidence for imitation and teaching, often pictured as hallmark of human social learning and the mechanisms necessary for cumulative culture (Tennie et al., 2009; Tomasello, 1999; Tomasello et al., 1993 but see Caldwell & Millen, 2009; Zwirner & Thornton, 2015) is rare, minimal or absent in chimpanzees (teaching: Boesch, 1991; Hoppitt et al., 2008; imitation: Horner & Whiten, 2005; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). This has led to the hypothesis that animals in general may simply not have the ability to improve previously acquired cultural behaviours over time (Tennie et al., 2009), suggesting that cultural evolution is a uniquely human capacity. The notion of cumulative culture in wild animals is equally disputed because of lack of evidence for two basic requirements (Dean et al., 2013), which are that any modification of a behavioural pattern must be characterised by increased complexity or efficiency and that such modifications must subsequently be transmitted through social learning.

Nevertheless, a number of case studies have suggested that some form of ratcheting may be present in the animal kingdom, although for most studies there are alternative explanations. For example, central African chimpanzees (*P. t. troglodytes*) manufacture brush-tipped probes from sticks to fish for termites (Sanz et al., 2009). Here, individuals fray the end of herb stems before inserting them into

termite mounds, a more efficient technique compared to unmodified fishing probes as described in East and West African chimpanzees (see also Boesch, Head, & Robbins, 2009). However, while termite-fishing with unmodified probes is likely to be socially learned (Lonsdorf, 2005, 2006), there is no such evidence regarding the modified version, and nothing is known about the transition from simple to more complex tools.

In West African chimpanzees (*P. t. verus*), some individuals have been seen to place stones beneath anvils during nut cracking to keep the surface flat and stable. Although the behaviour qualifies as a functional improvement it may also be the result of individual trial-and-error learning, with no evidence for social learning (Matsuzawa, 1994; Sugiyama, 1997).

Other examples come from New Caledonian crows (*Corvus moneduloides*) that manufacture sticks from the long barbed edges of palm-like *Pandanus* leaves to capture invertebrates in trees (Hunt, 2000; Hunt & Gray, 2003). Here, three distinct tool designs have been found with no ecological explanations for these differences, apart from continuous and overlapping geographical distribution of manufacturing methods. The authors suggested that at least two of the specific tool designs might have emerged through a process of cumulative change from earlier, more primitive versions. But here again, there is no evidence for socially learned transmission and no information on the transition from one variant to the other. Yet, New Caledonian crows have been shown to be able to learn socially an experimental foraging task through emulation but not imitation (Logan, Breen, Taylor, Gray, & Hoppitt, 2016).

The currently best evidence for material cultural evolution come from experiments carried out with captive chimpanzees. In a first example, individuals were provided with a straw-tube to obtain juice from a 1cm diameter hole in an out-of-reach container (Yamamoto et al., 2013). Initially, subjects spontaneously solved the problem with either a dipping (<2ml/min) or a more efficient sucking technique (>100ml/min). However, after observing a demonstrator performing the more efficient sucking technique, all dipping individuals switched to sucking. In another experiment, chimpanzees were trained a multi-step, repetitive, inefficient method to access a puzzle box, and later switched to a second more efficient method (Davis et al., 2016). While these studies suggest that cultural changes may occur rapidly in animals, it remains unclear whether these capacities are present and applied to problems encountered in natural environments (Nishida et al., 2009).

In this study, we address this question by capitalizing on recent observations from the Sonso chimpanzee community (*P. t. schweinfurthii*) of Budongo Forest, Uganda (Hobaiter et al., 2014). In 2011, a behavioural innovation, moss-sponging, naturally spread within a subset of the community via social learning (Hobaiter et al., 2014). Moss-sponging is an alternative to commonly found leaf-

sponging, a behaviour present in virtually all wild chimpanzee communities that have been studied for sufficient amounts of time (Whiten et al., 2001). Both leaf- and moss-sponging consist of harvesting a handful of leafy vegetation or clumps of moss, respectively, in order to orally shape it into a sponge roughly the size of a golf ball, which is then used to dip into and absorb liquids. Moss-sponging was first seen at one specific location in the community's home range, a clay-pit which consisted of two cavities in clay ground, filled with a mineral-rich suspension (Reynolds et al., 2015). Immediately after its appearance, the new behaviour spread rapidly across seven individuals via proximity-based social learning (Hobaiter et al., 2014). In the subsequent three years, moss-sponging then propagated through the community, albeit now mainly independent of social proximity but within the matrilines of cohort members that initially learned the technique(Lamon et al., 2017). The fact that moss-sponging continued to spread through the community, despite the presence of an already existing technique for absorbing liquids (i.e. leaf sponging), led us to hypothesize that the spread may have been caused by enhanced efficiency of moss-sponging, and therefore may qualify as a case of cultural evolution.

However, the puzzling fact remained that, since its emergence in 2011, moss-sponging was nearly exclusively observed at the site of its original invention, the clay-pit, with only n=5 observations elsewhere, despite uninterrupted daily focal follows by field assistants and researchers. Leaf-sponging, instead, continued to be observed in a range of contexts and throughout the forest, mainly at tree holes filled with rainwater, but also at rivers and water puddles. These observations are clearly at odds with the cultural evolution hypothesis and suggest that moss-sponging could be little more than a highly context-specific tool use behaviour and that chimpanzees do not perceive moss as universal sponge material. Moss-sponging chimpanzees, in other words, may simply use moss at the clay-pit because of the highly specific ecological or social factors encountered at that location, but the behaviour may not have become incorporated to their cultural repertoire.

Here, we address this question with three sets of data. First, we tested whether moss-sponging was indeed more efficient than leaf sponging, a basic prerequisite for cultural evolution. We predicted that moss should be more efficient in absorbing liquids and manufacturing time compared to leaves. We also investigated the complexity of the two types of tools.

Second, despite years of observations, moss sponging was only ever observed at one particular location, the clay pit, in swamp forest. To investigate whether this was simply a by-product of uneven distribution of moss or due to a more general inability to appreciate moss as universal sponge material we conducted a survey of leaf and moss distribution at different sponging locations throughout the forest, which included areas of mixed forest where rainwater filled tree-holes are located and swamps where the clay-pit is located. If cultural evolution drove the spread of moss sponging, we predicted

that the geographically limited use of moss sponging was simply due to limited availability of the material throughout most parts of the forest.

Third, to test whether moss-sponging would be favoured over leaf-sponging by knowledgeable individuals outside the context of the clay-pit, we tested a large number of subjects with a standardised field experiment. The experiment consisted of giving subjects a choice between the two raw materials suitable for manufacturing a sponge, leaves and moss, which we presented on a portable log with an artificial cavity filled with natural rainwater. We chose rainwater rather than mineral suspensions to remove any potential inherent advantage that moss might have over leaves in absorbing minerals (Reynolds et al., 2015). Another important criterion was to test subjects in isolation to rule out social influence or competitive pressure. To this end, we positioned the portable log ahead of a solitary subject's travel path, outside its visible range, so that the subject was likely to encounter the apparatus alone. Subjects were individuals that had previously been observed manufacturing moss-sponges at the clay-pit ('moss-spongers'), and individuals never observed manufacturing moss-sponges ('leaf-spongers'). If moss-sponging had become part of the behavioural repertoire of some group members, we predicted that the proportion of individuals who selected moss during the experiment would be higher among the moss- than leaf-spongers, mainly because leaf-spongers would not consider moss as a relevant material for fabricating a sponge.

4.3 Material and methods

4.3.1 Ethics Statement

Permission to conduct this research was given by the Uganda Wildlife Authority (UWA), the Ugandan National Council for Science and Technology (UNCST), and the National Forestry Authority (NFA).

4.3.2 Study site and subjects

The study was conducted in the Budongo Forest Reserve in Western Uganda (1°37'-2°00'N, 31°22'-31°46'E) with the Sonso community, a group of wild chimpanzees (*Pan troglodytes schweinfurthii*). The reserve consists mainly of moist semi deciduous tropical forest, at a mean altitude of 1100m. The Sonso community utilizes a home range covering an area of approximately 7 km^2 (Newton-Fisher, 2003) and members have been habituated to human presence since the mid-1990s (Reynolds, 2005). At the time of the study, the community consisted of 68 individuals (21 adult females, 12 adult males, 9 subadult females, 3 subadult males, 13 juvenile females, 3 juvenile males, 7 infants).

4.3.3 Tool features

To compare leaf-sponges and moss-sponges in terms of *complexity*, we assessed the folding behaviour necessary to manufacture the tool, which occurred in the mouth of the chimpanzees. To do so, we unfolded leaf-sponges collected during daily focal follows (n=46) and after the experiment (n=10). Then we counted the number of folding lines on each leaf of the sponge, which corresponds to the number of times a subject folded the leaf in his or her mouth. We could then obtain the average folding lines per leaf-sponge by calculating the mean of the folding lines of all the leaves constituting the sponge. No folding lines were found on moss-sponges.

Tool efficiency was assessed in terms of *absorbency* and was defined as the amount of liquid that a leaf-sponge or a moss-sponge could carry, the assumption being that the more water it could absorb, the more efficient it was. '*Leaf-sponging*' was defined as using a wad of crumpled or folded leaves to absorb and consume liquid; '*moss-sponging*' was defined as using a clump of moss or mixture of moss and leaves for the same purpose (Figure 4.1). Sponges manufactured by chimpanzees during daily follows and during the experiment were collected whenever possible and their absorbency was measured and analysed. Over 153 days of focal follows and experiments between January 2013 and February 2015, we collected 96 sponges on 48 separate days from 28 identified and 3 unidentified individuals. We measured the absorbency for 67 of them (51 leaf-sponges and 16 moss-sponges) as follows: 20 sponges were collected at the clay-pit, 23 after drinking in a natural tree hole and 6 at a river or a water puddle and 18 during the experiment. Absorbency was determined by dipping the sponge in water and then squeezing it, comparing the weight before and after squeezing using a scale (Factory weigh^{TM}PRO-VA 1234, precision: 0.01g). This procedure was repeated 10 times for each sponge and then averaged.

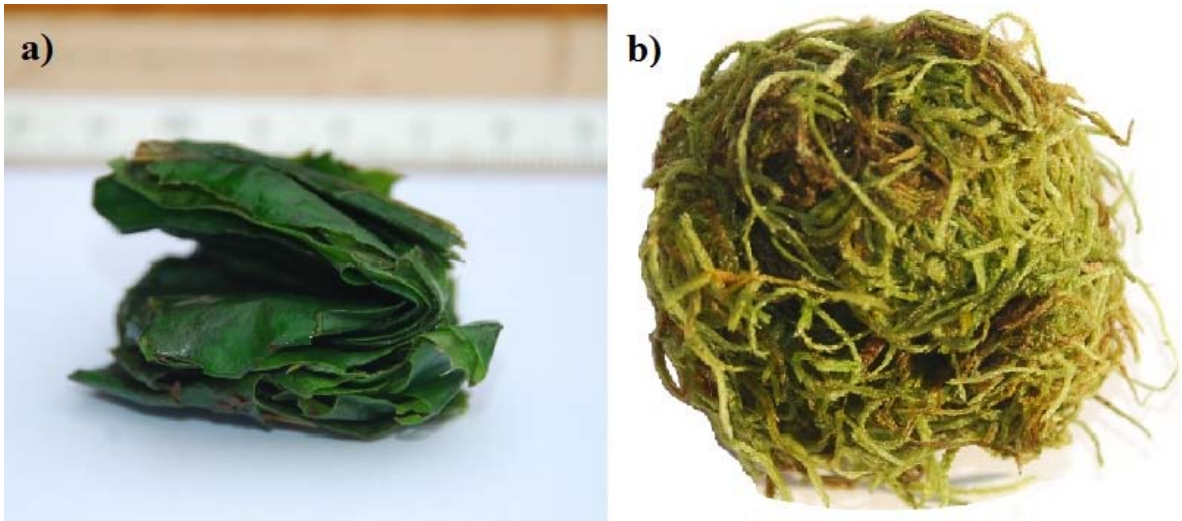

Figure 4.1. Two examples of drinking tools manufactured during a log experiment. a) Leaf-sponge made of *Alchornea floribunda*, **b)** moss-sponge made of *Orthostichella welwitschii*.

4.3.4 Availability

The cultural evolution hypothesis predicted that the reason moss sponging was never seen outside the clay pit, was because of lack of availability of moss. To address this, we carried out a survey to assess the availability of sponging material (i.e. leaves and moss) around locations where the chimpanzees had been observed sponging. The prediction was that swamp areas where clay-pits are located contained more moss than mixed forest areas where natural tree holes tend to be located. To this end, in December 2016, we surveyed all locations where chimpanzees had previously been observed sponging from tree holes or clay-pits. We could do this for 28 locations, n=8 in swamp areas and n=20 in mixed forest areas. We chose a 5m radius around the source and surveyed a cylinder of 3m high (i.e. about 230 m^3). To assess leaf availability, we counted all stems of *Acalypha spp*. and *Lasiodiscus mildraedii,* the species most frequently picked by the chimpanzees to manufacture leaf-sponges. To assess moss availability, we counted several species of moss and liverworts, *Orthostichella welwitschii* (*Duby*) (mostly hanging from tree branches) and *Porotrichum elongatum (Welw & Duby) Gepp., Plagiochila sp,* and some undetermined species (growing on the tree bark), using 20cm x 20cm assessment units.

4.3.5 Experiment

To investigate what tool 'clay-pit leaf-spongers' and 'clay-pit moss-spongers' would select if given the choice of the two materials in a controlled context, we manufactured a portable log (length: 33.5 cm; diameter: 14 cm) (Figure 4.2a) with an artificial cavity drilled in the centre (opening: 8.0x8.5 cm; depth: 8.0 cm), similar to natural tree-holes accessed by chimpanzees throughout the forest. For the experiments, we filled the cavity with 20 ml of rainwater. The apparatus was a modified version of the honey-trap apparatus used in previous experiments (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011). To minimize the risk of disease transmission from humans to chimpanzees, we boiled rainwater collected from tin roofs prior to each experiment. We positioned the apparatus in the absence of any individuals and supplied tool material at equal distance from the hole (Figure 4.2a) in the form of two clumps of moss (*Orthostichella welwitschii* (*Duby*)) and two leafy branches of *Acalypha spp*., a plant species most commonly selected by chimpanzees to manufacture leaf-sponges.

Figure 4.2. Log experiment. a) Experimental apparatus. Tool manufacturing was studied in a controlled way by providing 20 ml of drinking water in a natural portable log (size 33.5 cm x 14 cm), with an artificial cavity (size: 8.0 cm x 8.5 cm x 8.0 cm). The log was placed throughout the chimpanzees' home range on the predicted pathway of a possible subject prior to its arrival. In each trial, tool material naturally used by the study group to absorb mineral suspensions at clay pit was provided in the form of two bunches of moss (*Orthostichella welwitschii* (*Duby*)) (yellow arrows) and two branches of leaves (*Acalypha spp)*(red arrows) scattered around the log. **b)** A male chimpanzee of the Sonso community (KZ) uses a leaf-sponge to retrieve water from the experimental log.

By anticipating the subjects' travel direction, we were able to target specific individuals for this experiment. We only presented the apparatus to individuals that were alone (except for mothers with dependent offspring) (Figure 4.2b). The choice of subjects was therefore opportunistic and not blinded. Trials had to be repeated occasionally, with at least 24-hours intermissions, when the subject interacted with the log but did not manufacture a sponge (see Table 4.1). The log was removed once the subject stopped interacting with it and was out of sight. All trials were video recorded by two experimenters (NL and her field assistant) with Panasonic HC-X909 video cameras in order to get two different angles of the scene. Since individuals were unconstrained in their daily movement patterns, it was unavoidable that in some trials (8 of 20) another group member joined the subject, while in n=1 trial two additional group members joined the subject during the experiment and also participated. If both materials were still available to such later joining individuals, we included their choices in the analysis. If an individual participated several times, we only took the choice of the first trial into account. Experimental data included a) the identity of the subject and eventual bystanders, b) whether or not the subject had been seen moss sponging before and c) the technique used to retrieve the water from the hole. Based on their presumed knowledge (Lamon et al., 2017), subjects were categorized as either "moss-sponger" or "leaf-sponger". Moss-spongers were individuals who had been seen at least once moss-sponging before the experiment; otherwise they were categorized as "leaf-spongers" by default.

There were two experimental periods (January 2014 and January 2015) chosen as they corresponded to the annual dry season, which is when chimpanzees are most likely to search for water in tree holes. 20 individuals participated in the experiment: six adult females, five adult males, two subadult females, one subadult male, four juvenile females and two juvenile males. Nine participating individuals were classified as "moss-spongers" (Table 4.2), while the remaining 11 were classified as "leaf-spongers".

The absorbency of the sponges (9 moss-sponges and 9 leaf-sponges) manufactured during the experiment was also measured and analysed as described above. Additionally, we evaluated efficiency in terms of manufacturing time, which was defined as the time an individual needed to make a sponge, soak it and move it into its mouth. The assumption was that the faster a tool could be manufactured and used, the more efficient it was. Data were extracted from videos recorded during the experiment, starting when the subject touched the material and ending when the sponge was put in the mouth after the first dip in the water hole. We were able to analyse 17 leaf-sponges and 8 moss-sponges during the experiment.

4.3.6 Statistical analyses

To test any differences regarding the proportion of moss choice during the experiment between leaf-spongers and moss-spongers, we used a one-tailed proportion test testing the hypothesis that there were significantly more moss-users in the moss-sponger group than in the leaf-sponger group. To assess differences in sponge absorbency we made a linear mixed model with the lme4 package in R 3.2.0 (Bates, Maechler, et al., 2014; R Development Core Team, 2015) with identity of the manufacturer as random effect and type of material (moss, leaves) and sponge weight as fixed effects. We log-transformed the absorbency values and square root transformed and standardized the sponges' weight to obtain homogenous and normally distributed residuals. In order to assess whether absorbency differed according to the material used, we compared the full model (with material and weight as fixed effects) against a null model (omitting the material effect), using a likelihood ratio test (LRT, Dobson, 2002). To assess differences in the manufacturing time during the experiment, we built a linear mixed model with the material (i.e. moss or leaves) as fixed effect and sponge manufacturers as random effect. We square root transformed the manufacturing time to fulfil the assumptions of normality and homoscedasticity of the residuals.

4.4 Results

4.4.1 Tool features

To manufacture a leaf-sponge, chimpanzees collect a bundle of leaves either with their fingers or directly with the mouths in order to fold them in their mouths. We found that leaf-sponges (*n*=45) consisted on average of 16 (range: 2-45) leaves and fragments of leaves. The average number of folding lines per leaf-sponge was of 1.6 folding lines (range: 0-4.3). In contrast, chimpanzees manufactured moss-sponges by picking a clump of moss with their hands and rolling it into a ball-shape sponge in their mouths. There was thus no folding involved in the manufacture of moss-sponges, resulting in less complex structure (*n* =7). While almost all moss sponges were made of only moss, we found one sponge that was made of both leaves and moss (see also Hobaiter et al., 2014).

Moss-sponges collected at the clay-pit absorbed significantly more liquid than leaf-sponges collected at the clay-pit, around tree holes or along a river (Linear mixed model, LMM: n = 49 sponges by 27 individuals, $\beta = 0.50 \pm 0.12$, $t = 4.16$, likelihood ratio test, LRT: df=1, $\chi^2 = 13.30$, p=0.0003, Table 4.1, Figure 4.4, controlling for sponge weight and manufacturer ID).

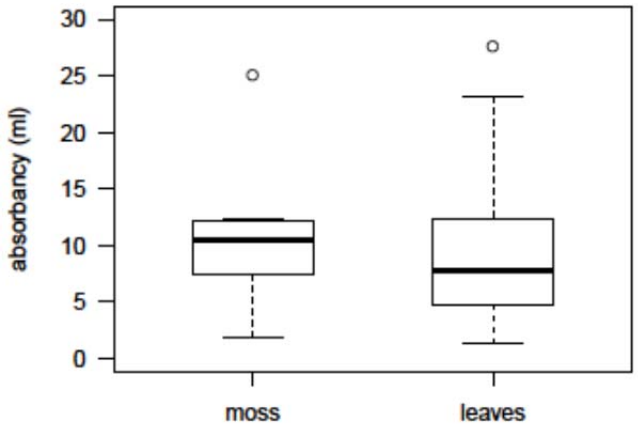

Figure 4.3. Moss-sponges (*n* =7) absorbed more liquid than leaf-sponges (*n* =42). The leaf-sponges were collected after the chimpanzees used them to get water from tree holes, at the clay pit, at a river and at water puddles. Moss-sponges were collected mainly at the clay pit and for 3 cases at a water puddle and for 2 cases in a deep hole in a fallen tree. We calculated the median per individual and per method.

Table 4.1 Results of the models testing differences in absorbency and manufacturing time.

Fixed effect (predictor)	beta	Standard error	*t*	*p* (LRT)
Non-experimental sponges (N=49): Absorbency ~ weight + material (moss or leaves) + (1 | manufacturer ID)				
Intercept	1.97	0.06	34.28	
Material	0.50	0.12	4.16	0.0003
Weight	0.57	0.05	12.40	
Experimental sponges (N=18): Absorbency ~ weight + material + (1 | manufacturer ID)				
Intercept	1.92	0.13	14.68	
Material	1.18	0.20	5.91	<0.0001
Weight	0.30	0.10	2.95	
Manufacturing time ~ material + (1 | ID)				
Intercept	13.01	1.55	8.38	
Material	-4.92	1.82	-2.70	0.0117

Chimpanzees use most often the leaves of Acalypha spp. and Lasiodiscus mildraedii to manufacture leaf sponges. We found that both species were more readily available around tree hole sponging locations in mixed forest areas (n=20 locations) than in swamp areas (n=8 locations), but not significantly so (Mann-Whitney U test: n_1=20, n_2=8, W=105.5, exact p=0.2034, Figure 4.4). However, there was significantly less moss at sponging locations in mixed forest than in the swamp areas, where the clay-pit is located (Mann-Whitney U test: n_1=20, n_2=8, W=5, p<0.0001, Figure 4.4).

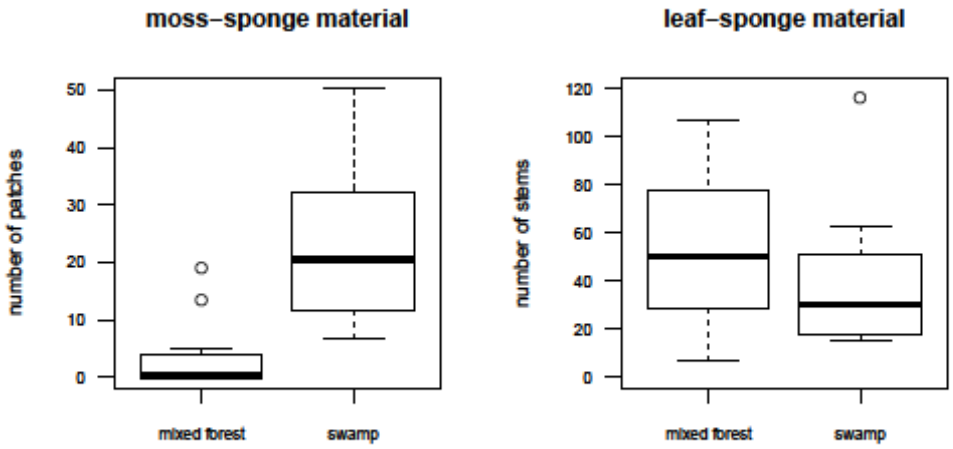

Figure 4.4. Moss was more abundant in swamp areas than in mixed forest areas, while plants used to manufacture leaf-sponges was more abundant in mixed forest areas than in swamp areas. For the moss-sponge material availability, the unit is a 20cm x 20cm square patch, whereas for the leaf-sponge material (i.e *Acalypha spp*. and *Lasiodiscus mildraedii*), the unit is the number of stems. *n*=20 locations in mixed forest and *n*=8 in swamp areas.

4.4.2 Experiment

We tested 20 individuals with the apparatus (Figure 4.2a). In line with our prediction, the proportion of individuals who used moss was higher among the moss-spongers than the leaf-spongers (proportion test: χ^2 =3.23, one-tailed p = 0.0361, moss-spongers: 7/9, leaf-spongers: 3/11, Table 4.2). When testing the absorbency with the sponges collected during the experiment, the difference in efficiency remained, with moss-sponges absorbing more water than leaf-sponges (Table 4.1). Leaf-sponges manufactured during the experiment consisted on average of 9.4 (range: 1-22) leaves and fragments of leaves. The average number of folding lines per leaf-sponge was of 2.2 folding lines (range: 0-4). Because of the controlled setting of the experiment, we could also compare manufacturing time between sponges and we found that moss-sponges were manufactured significantly faster than leaf-sponges (LMM: n=25 sponges by 15 individuals, β = -4.92 ±1.82, t = -2.70, LRT: χ^2_1 = 6.35, p=0.0117, Table 4.1 and Figure 4.5).

Table 4.2 List of participants, their presumed knowledge based on documented moss-sponging events before the test and their choice during the experiment.

ID (N=20)	age class	sex	moss sponging observations before test	Moss-sponger	material choice during experiment	number of trials until sponging
HW	adult	m	clay-pit (2014)	Yes	Moss	0
JN*	adult	f	clay-pit (2011)	Yes	Leaves	1
JS*	juvenile	m	clay-pit (2011)	Yes	Moss	0
KB*	juvenile	f	clay-pit (2011)	Yes	Moss	1
KH	juvenile	f	no moss-sponging before test	No	Moss	0
KR*	subadult	f	clay-pit (2011)	Yes	Moss	0
KS	subadult	m	no moss-sponging before test	No	Leaves	0
KW*	adult	f	clay-pit (2011)	Yes	Moss	1
KZ	adult	m	no moss-sponging before test	No	Leaves	1
MB	juvenile	m	no moss-sponging before test	No	Leaves	0
ML	adult	f	no moss-sponging before test	No	Leaves	1
NB*	adult	f	clay-pit (2011)	Yes	Moss	3
NT	subadult	f	clay-pit (2013)	Yes	Moss	0
RF	juvenile	f	no moss-sponging before test	No	Leaves	0
RS	adult	f	no moss-sponging before test	No	Leaves	0
SM	adult	m	no moss-sponging before test	No	Leaves	3
ST	juvenile	f	no moss-sponging before test	No	Moss	0
UP	adult	f	clay-pit (2013)	Yes	Leaves	0
ZG	adult	m	no moss-sponging before test	No	Leaves	2
ZL	adult	m	no moss-sponging before test	No	Moss	0

Group members are presented in alphabetic order. Individuals marked with (*) are the initial moss-spongers in Hobaiter et al.(2014). Age classes are assigned following Reynolds'(Reynolds, 2005) classification. Moss-spongers were determined based on data collected prior to the experiment, i.e., from camera traps set at the clay pit in 2014 ("clay-pit 2014"), during focal follows ("clay pit data 2013") or published data from Hobaiter et al.(2014) ("clay pit data 2011"). Individuals who had been observed moss-sponging before the experiment were considered moss-spongers (Yes), otherwise (i.e. "no moss-sponging before test") they were considered by default leaf-spongers (No).

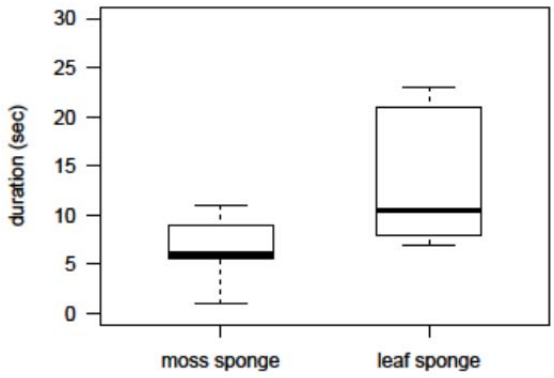

Figure 4.5. Chimpanzees were faster manufacturing moss-sponges (*n*=8 from 8 different individuals) compared to leaf-sponges (*n*=17 from 10 different individuals). Manufacturing time was defined as the time an individual needed to make a sponge, soak it in the water contained in the experimental log and move it into its mouth (see Material & Methods). These values were extracted from the video recordings of the experiment and we calculated the median per individual and per method.

4.5 Discussion

In this study, we tested experimentally whether moss-sponging, a relatively novel behaviour first observed in the Sonso chimpanzee community of Budongo Forest in 2011, could constitute a case of cultural evolution. Several lines of evidence suggest that this was the case. First, chimpanzees who had been observed moss-sponging at the clay-pit continued to manufacture moss sponges in our experiment, showing that moss was considered a suitable sponge material regardless of whether it was used for mineral-rich clay suspensions or natural rain water. This was in contrast to other individuals who had never been observed moss-sponging before and who were significantly less likely to choose moss in the same task. These results demonstrate that moss-sponging is not tied to a particular ecological condition but generally available to individuals who have learned the novel technique from others before.

We also analysed the physical properties of the novel tool compared to its ancestral version to analyse possible improvements in terms of complexity or efficiency, a requirement for cultural evolution (Dean et al., 2013). Moss-sponges were more efficient, fabricated more quickly and structurally less

complex than leaf-sponges, insofar as they had a better liquid absorbency, were manufactured faster and were generally less complex than leaf-sponges.

Our results also indicate that the reason natural moss-sponging was not seen outside its original context (clay-water sponging) was most likely a consequence of an uneven availability of moss throughout the forest. Our survey data showed that moss was rare in most parts of the forest, except in swamp areas where clay-pits were located, which effectively prevented moss-spongers from executing their behaviour because of a lack of opportunities (Gruber et al., 2016; Sanz & Morgan, 2013). The two most common plant species to manufacture leaf-sponges (*Acalypha spp*., *Lasiodiscus mildbraedii*), however, were abundant throughout the forest and also present at the 28 locations where chimpanzees had been observed leaf-sponging. Nevertheless, if artificially made available, as in our experiment, moss represents a viable material to solve any tool-based liquid extraction task, if provided subjects are familiar with the material.

Does moss-sponging qualify as cumulative cultural evolution?

Evidence for cumulative culture, according to Dean and colleagues (2013), requires that the behavioural trait must be learned socially and change over time in a directional or progressive manner towards enhanced complexity or efficiency. We interpret our findings as consistent with this definition, suggesting that chimpanzee moss sponging qualifies as a case of cultural evolution towards a simpler, more efficient tool for a general function, fetching liquids that are not directly accessible by mouth. The existence of composite tools made of both leaves and moss, evidenced in our study and in Hobaiter et al.(2014), further suggests that moss-sponges are a modification of the existing drinking tool (leaf-sponge) and makes it less likely that moss-sponges are a simple case of accumulation, that is the addition of a behavioural trait in the repertoire, rather than the modification of an existing one (Dean et al., 2013).

In this study, we do not provide any direct evidence for social learning, but in previous, related work we have already demonstrated that moss sponging spreads by social learning (Hobaiter et al., 2014; Lamon et al., 2017). Moreover, material choice in our experiment was not the result of ad hoc individual decisions, but better explained by moss spongers' prior experience acquired by social learning. In contrast, leaf spongers consistently selected leaves to manufacture a sponge, suggesting they did not to represent moss as sponge material (Gruber, Zuberbühler, Clément, & van Schaik, 2015). Nevertheless, three individuals classified as leaf-spongers (KH, ST, ZL, see Table 4.2) manufactured a moss-sponge during the experiment. We can think of two possible reasons for this finding. The most likely one is that, unbeknownst to us, they had acquired the behaviour prior to the experiment, either via individual or social learning, but never shown it in our presence. A second

possibility is that they individually invented the behaviour at the time of the experiment. Generally, however, we find explanations based on individual learning less plausible because all previous studies have all shown that social learning appears to be the main mechanism of moss-sponging acquisition (Hobaiter et al., 2014; Lamon et al., 2017). Moreover, Sonso chimpanzees appear particularly resistant to the use of novel tools in experimental contexts (Gruber, 2016).

The second criterion, put forward by Dean et al (2013), requires evidence for directed change towards enhanced complexity or efficiency. Here, our data show that moss-sponges are more efficient than leave-sponges in retrieving water. They are also faster to manufacture and structurally less complex, suggesting that they qualify as an improvement in terms of resource exploitation efficiency. Whether or not the moss-spongers chose moss because they understood and compared the physical properties of the two materials cannot be decided by our data. However, other related studies have concluded that animals are able to understand the physical properties of their tools (wild: Western African chimpanzees (Sakura & Matsuzawa, 1991), capuchin monkeys (*Cebus libidinosus*) (Visalberghi et al., 2009); captivity: all great apes (*Pan troglodytes, Pan paniscus, Pongo pygmaeus* and *Gorilla gorilla*) (Lehner, Burkart, & van Schaik, 2011; Manrique et al., 2010), New Caledonian crows (*Corvus moneduloides*) (Chappell & Kacelnik, 2002), funnel ants (*Aphaenogaster sp*.) (Maák et al., 2017)).

Two of nine known moss-spongers opted for the traditional technique, leaf-sponging, which might have been the result of differences in individuals' conservatism, manufacturing skills, or taste aversion. For example, some individuals may prefer the technique they are more used to, even if they understand the differences in efficiency (Gruber et al., 2011). Leaves are the more habitual material to manufacture a sponge, which may have hindered some individuals from seeing the more efficient moss solution (Gruber et al., 2015). Other individual differences may be in how proficient some individuals are in manufacturing leaf-sponges or simple aversion for the taste of moss, which may have biased their choice towards leaves. Overall, our results suggest that context and personality differences may interact with each other and determine an individual's choice of tool material, even in controlled situations (Gruber, 2016, for a review).

Conclusions

Our experiment showed that moss-sponging was not intrinsically restricted to clay-pits but readily executed in another context, as long as the material was available, suggesting that chimpanzees who already had experience with both materials were able to choose tool materials according to its efficiency. Our data also showed that moss-sponges were more efficient in terms of manufacturing time and capacity to absorb water. We interpret these results as consistent with the hypothesis that moss-spongers have gone through a process of cultural evolution, in this instance not because of increased complexity but increased efficiency (Dean et al., 2013).

We acknowledge that the notion of cumulative culture has been defined in different ways. For example, human culture can be cumulative in terms of the sheer number of cultural items, but also in terms of efficiency and complexity over generations (Enquist et al., 2008). In our case, the criteria regarding social learning and the increase in efficiency are fulfilled. A final criterion for cumulative culture is that a behaviour should increase in complexity and be beyond what a single individual could have invented alone (Tennie et al., 2009). While moss-sponging is certainly within chimpanzees' physical cognitive skills, requiring less complexity than leaf-sponges overall, some external (ecological) or internal (physiological or motivational) conditions had to be met for the behaviour to emerge. It is also unclear what constitutes a behaviour complex enough not to be innovated within a lifetime in chimpanzees and other animals, and such judgment may not be made by human observers. The Sonso chimpanzees had been observed for over 20 years before the behaviour appeared, with dozens of chimpanzees visiting the swamp forest but never innovating the behaviour before its social spread in 2011. Our findings show that moss-sponges build on leaf-sponges, and spread socially in the current generation of chimpanzees, who adopted the more efficient form compared to the ancestral trait. In any case, it will be interesting to see how new generations of Sonso chimpanzees, regularly exposed to moss-sponging, magistrate between the old tradition, leaf-sponging, and the more recent tradition, moss-sponging, in tool-assisted drinking contexts.

4.6 Acknowledgements

We thank Samuel Adue for his invaluable help in the field and to all the field assistants for contributing to the long-term data collection, Dr Michelle Price for moss species identification and Dr Caroline Asiimwe for her expertise and advice regarding chimpanzee health and experimental design. We thank the Uganda National Council for Science and Technology (UNCST), the Uganda Wildlife Authority (UWA) and the President's office for permission to conduct our research in the Budongo Forest Reserve and The Royal Zoological Society of Scotland (RZSS) for supporting The Budongo Conservation Field Station (BCFS). This work was funded by the European Research Council under the European Union's Seventh Framework Program (FP7/2007-2013) / ERC grant agreement n° 283871 and the Swiss National Science Foundation (SNSF, Project 310030_143359 to KZ). TG was supported by an Interdisciplinary Project CR13I1_162720 / 1 grant and an Advanced Postdoc.Mobility fellowship P300PA_164678 / 1 from the SNSF.

4.7 Supplementary materials

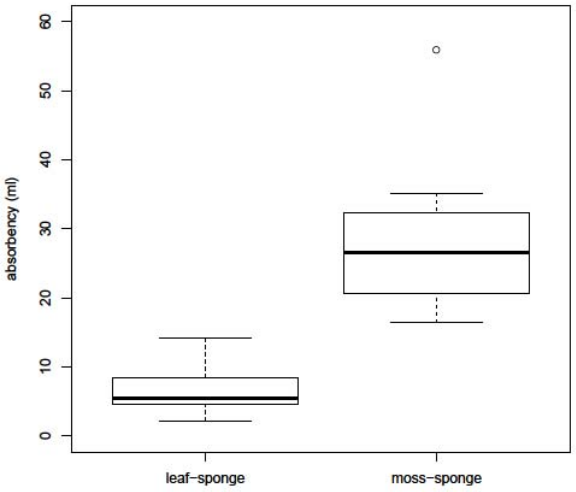

Figure S4.1 Moss-sponges (*n*=8) absorbed more liquid than leaf-sponges (*n*=9). Leaf-sponges and moss-sponges were manufactured by the chimpanzees during the experiment. We calculated the median per individual and per method.

5. GENERAL DISCUSSION

5.1 Summary of the studies

The main goal of this thesis was to examine different aspects of tool use in a wild chimpanzee community of Budongo Forest, Uganda, the Sonso group, with three distinct empirical contributions. The first aspect was a study on the developmental processes of tool manufacture and use across different age groups. The second aspect was a study addressing the mechanisms underlying the acquisition, spread and persistence of a new tool-related technique unique to the Sonso community, moss-sponging. Finally, the third aspect was a field experiment combined with survey data to suggest a basic form of cultural evolution in this species. To address these questions related to these three aspects of tool use, I carried out field research, presented in three studies, designed to (a) investigate the importance of object play and its social influences on the ontogeny of tool use, to (b) investigate the social learning mechanisms sustaining a secondary radiation and maintenance of a new drinking tool, moss-sponging and to (c) carry out work to test the hypothesis that moss-sponging meets the basic criteria put forward for cumulative culture.

In the first study, I investigated the developmental patterns of tool and proto-tool use in the Sonso chimpanzee community of Budongo Forest, Uganda. This community is known for its striking absence of a key tool-related behaviour seen in virtually all other studied chimpanzee communities, the use of sticks for extracting embedded or difficult-to-access food resources (Gruber et al., 2009; Reynolds, 2005; Whiten et al., 1999). This pattern suggests that stick use is somehow natural to wild chimpanzees, but that in the Sonso community the behaviour has been lost for unknown reasons. If this is correct, then one predicts that sticks are as eagerly manipulated by young individuals as other objects, albeit never towards tool related activities. To address this hypothesis, I was interested in the link between object play, exploration and tool use, with special attention to stick manipulations, in the different age groups. I was also interested in the possible factors influencing the choice of play material.

I monitored 37 individuals ranging from 5 months to over 50 years of age and found, first, that object manipulations generally decreased with age (Figure 2.1), while goal-directedness increased (Figure 2.2). Second, I found that adults preferentially manipulated leaves and woody vegetation, but never sticks, whereas non-adults had a preference for leaves, woody vegetation and sticks (Figure 2.3), with stick manipulation gradually decreasing to complete disengagement around the age of 15 years (Figure 2.4).

Another interesting finding was that young individuals were strongly affected by a simple form of social learning, stimulus enhancement, from observing their mothers. In particular, the rate with which mothers manipulated a given material as tool was associated with their offspring's choices for that

material during play and exploration, providing good evidence for maternal influences on object play (Table 2.1). Finally, I found that males had consistently higher manipulation rates and manipulated in more goal-directed ways than females, across all ages, a finding somewhat at odds with previous chimpanzee tool use studies, notably from Tai Forest, Ivory Coast (Boesch & Boesch, 1984) and Gombe National Park, Tanzania (Lonsdorf, 2005; Lonsdorf, Eberly, & Pusey, 2004; McGrew, 1979).

In the second study, using natural and experimental observations, I assessed the propagation patterns and maintenance of a novel tool technique, moss-sponging, documented for the first time about three years before my own data collection started (Hobaiter et al., 2014). I found that over a period of three years, the behaviour spread from a small number of founder individuals (eight) to 17 additional group members (Table 3.1). The major finding here was that chimpanzees from matrilines with moss-sponging individuals were more likely to become moss-spongers themselves compared to individuals from matrilines that did not have a moss-sponger amongst themselves (Figure 3.1 and Figure 3.2.) Moss-sponging, thus, mainly spread within matrilines and not through close spatial association, nor by individual learning (Figure 3.1).

These findings thus provide evidence that moss-sponging has been transmitted socially. Yet, only a subset of the community members used the technique, without any compelling genetic or environmental alternative explanations, suggesting that moss sponging behaviour qualifies as a subculture within the Sonso community.

For the last study, I tested experimentally whether moss-sponging could constitute a case of cultural evolution. To do so, I presented the chimpanzees with a simple experimental apparatus, which consisted of a portable wooden log, with a hole in the middle filled with rainwater (Figure 4.2). The subjects were given the choice between two tool raw materials, moss and leaves, to manufacture a sponge. My findings suggest that, indeed, moss-sponging constitutes a case of cultural evolution. This was because, first, chimpanzees that had been observed moss-sponging at the clay-pit also preferred to manufacture moss sponges in my experiment, showing that they generalised the tool to new foraging problems, here to extract rainwater from a small cavity (Table 4.2). On the other hand, individuals who had never been observed moss-sponging naturally were significantly less likely to choose moss in the same task. These results demonstrate that moss-sponging is not tied to a particular ecological condition but generally available to individuals who have learned the novel technique from others before. I also provide survey data showing that the near absence of moss-sponging outside of its original context, absorbing mineral solutions from clay pits, was most likely a consequence of the fact that moss is unavailable in most parts of the forest, except swamps (Figure 4.4).

Finally, by analysing the physical properties of the novel tool compared to its ancestral version, I found that moss-sponges were more efficient (Figure 4.3 and Table 4.1), fabricated more quickly (Figure 4.5 and Table 4.1) and structurally less complex than leaf-sponges. These results suggest that

moss-sponging fulfils most of the criteria put forward for the definition of cultural evolution, a cultural improvement from chimpanzee-traditional leaf-sponging.

These three studies provide insights into the devolvement of tool use, through object play and exploration, the social influences involved in play and tool use acquisition and especially the crucial role of the mothers and finally the basis for material cultural evolution.

5.2 Mothers as the primary model

Both the study on immature chimpanzees' object play and the study on the propagation mechanism of a new behaviour highlight the influence of mothers in object play and tool use acquisition. In object play, I found that non-adults' choices of material they played with and explored were associated with their mother's rates of tool use (Table 2.1). Concerning the propagation of moss sponging, I found that the behaviour spread mainly through matrilines (Figure 3.1 and Figure 3.2), further highlighting the central role of mothers in chimpanzee culture. Overall, both findings indicate that mothers play a fundamental role in their offspring's object manipulations.

Nevertheless, while I showed the importance of mothers in the choice of play material selected by the offspring, the influence was only present for material later used to manufacture a tool. Indeed, I showed that young Sonso chimpanzees also played with sticks, a material absent in the tool repertoire of the community, and can therefore not be influenced by any stick-tool observation. A similar finding was reported by Koops and colleagues (2015) with the chimpanzees of Kalinzu, Uganda, but interpreted differently. They found that immatures played with leaves, a material not used by adults in the foraging context. Based on this observation, they suggested that "…object manipulation by immatures was almost certainly not socially induced, and thus not simply a result of young individuals emulating adult feeding tool use" (p. 4). However, it is well known that chimpanzees also use leaves in other contexts, particularly body care (Sanz & Morgan, 2007; Whiten et al., 1999). Moreover, leaf-sponging is a universal behaviour, observed in all the chimpanzee communities across Africa. Even though I could not find any published catalogue of tool use in the Kalinzu community, it is highly probable that the chimpanzees use also leaves in such contexts. Thus, young Kalinzu chimpanzees may not be influenced by foraging tool use regarding their leaf manipulation, yet they very likely observed adults using leaves for other purposes.

Overall, my research showed that young Sonso chimpanzees were not selective regarding the type of material they played with. However, the materials selected for tool use were significantly influenced by the mothers' choices of tools used in different contexts. Consequently, the mothers' choice of tool types appears to determine her offspring's choices of play material (Table 2.1).

Chimpanzee mothers are very tolerant towards their infants and, undoubtedly, this plays a major role in their learning process (Matsuzawa et al., 2001), suggesting that chimpanzee mothers are the primary role models for the acquisition and spread of cultural behaviour. Similar findings were shown in a study on Aka pygmies, foragers living in the tropical forests of the Central African Republic and the Republic of the Congo (Hewlett, Barry & Cavalli-Sforza, 1986). The authors of the study were interested in the cultural transmission of foraging techniques, childcare skills, and group-oriented activities, such as hut building. They found that the parents (father and mother) were the primary contributors to the cultural spread of these behaviours. According to one of their models (Cavalli-Sforza & Feldman, 1981), this predominantly vertical transmission pattern (parent-child) is responsible for the relatively slow change, but also high variation within and between members of a population. Interestingly, the patterns reported in this human population are similar to what has been seen in the Sonso chimpanzee community, in which individuals also rely mostly on vertical transmission for transmission of foraging skills (Figure 3.3). Equally relevant is that the tool repertoires of different chimpanzee communities across Africa do not seem to change much over time, with archaeological data further supporting this claim (e.g. Mercader et al., 2007; Mercader, Panger, & Boesch, 2002).

To conclude, social learning plays a major role in how young chimpanzees learn to focus on relevant objects, which then facilitates acquiring tool-related behaviour, but this takes place mainly between kin (Boesch & Boesch-Achermann, 2000; Fragaszy et al., 2013; Humle et al., 2009; Lamon et al., 2017; Lind & Lindenfors, 2010; Lonsdorf, 2006; McGrew, 1992). This is well illustrated by the two first studies of this thesis, which add to the growing body of knowledge on the importance of mothers as demonstrators in tool use acquisition and more generally in animal social learning (Jaeggi et al., 2010; Lind & Lindenfors, 2010; Sargeant & Mann, 2009; van de Waal, Bshary, & Whiten, 2014). These findings should be taken more in account when studying social learning strategies in chimpanzees. Indeed, research on social learning strategies and more specifically on the "Who" strategy (Laland, 2004), tend to focus mainly on the identity and characteristics of demonstrator and observer such as skill competence, rank, age, affiliation (i.e. time spent grooming, time spent in proximity) or social tolerance (e.g. Bonnie & de Waal, 2006; Horner, Proctor, Bonnie, Whiten, & de Waal, 2010), but rarely on family ties (e.g. Biro et al., 2003). This lack of captive studies on the influence of the mothers may come from the restricted numbers of mother-dyads in captivity. Thus, field research has made an important contribution to this topic.

Overall, the importance of vertical transmission can explain the variability between individuals in the community regarding moss-sponging but can also, to a certain extent, explain the high temporal stability of chimpanzee technology in general, as well as their small tool repertoires if compared to humans.

5.3 Low-fidelity transmission processes and the consequences on cultural evolution

Humans are said to acquire new tool-related behaviours mainly through imitation and teaching, with verbal instructions enhancing considerably the transmission (Morgan et al., 2015). In chimpanzees, this social influence is mostly indirect, in the sense that models have very rarely been observed acting on objects with the apparent intention to solicit the attention of the observers (Bard & Vauclair, 1984). Additionally, evidence for active teaching (that is, active information donation (Fogarty, Strimling, & Laland, 2011)) in chimpanzees is missing, apart from a few anecdotes that have not been backed by more systematic studies (Boesch, 1991). Data from this and other studies suggest that social learning and social influence are mainly in terms of observational learning, where mothers elicit object play and acquisition of tool use, just by manipulating objects in front of their offspring (Lind & Lindenfors, 2010; Lonsdorf, 2006). Additionally, experimental studies have shown that chimpanzees rely mostly on low-fidelity processes, like stimulus enhancement or emulation, but very rarely on imitation or teaching when acquiring novel behaviours from others (e.g. Call, Carpenter, & Tomasello, 2005; Nagell, Olguin, & Tomasello, 1993; Tennie, Call, & Tomasello, 2003).

Although evidence for teaching in nonhuman animals is rare, there are various studies that have provided relevant data (Caro & Hauser, 1992; Franks & Richardson, 2006; Raihani & Ridley, 2008; Thornton & McAuliffe, 2006). An influential working definition for teaching in animals was proposed by Caro and Hauser (1992) as followed: "An individual actor **A** can be said to teach if it modifies its behavior only in the presence of a naive observer, **B**, at some cost or at least without obtaining an immediate benefit for itself. **A**'s behavior thereby encourages or punishes **B**'s behavior, or provides **B** with experience, or sets an example for **B**. As a result, **B** acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all." (p. 153). It is worth noting that this definition is mainly in terms of costs and benefits but does not refer to any underlying *intention* of the tutor to facilitate the pupil's learning.

As said, teaching in wild chimpanzees has been claimed by Boesch (1991), which consisted of two events during nut-cracking: the first one was a mother changing the position of a nut on the anvil during her son's struggling cracking attempts. The second event was another mother receiving a hammer from her daughter, who was unable to use it correctly. The mother then handled the hammer slowly in the correct position in front of her daughter watching, a behaviour that was interpreted as an ostensive teaching demonstration for the daughter. As always, it is impossible to use such anecdotal observations for anything else than generating hypotheses, but so far no systematic study from any other chimpanzee community has provided data in support of the teaching hypothesis. A possible reason for the lack of teaching in chimpanzee tool use is that their tool technology is simple and can be acquired without complex forms of social learning including teaching (Moore & Tennie, 2015).

Indeed it has been hypothesised that for teaching to emerge subjects may have to employ complex forms of tool use (Kline, 2015).

Recently, it has been claimed that the transfer of a manufactured tool from an individual to another, often from the mother to the offspring, can be regarded as a case of teaching since it fulfils the three criteria stated above (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016). But such behaviour mostly occurred after the "pupil" begged for the "tutor's" tool. I personally observed several times this kind of tool transfer (moss and leaf sponges) from mothers to their infants, something that has also been reported by other researchers studying wild chimpanzees (Fragaszy et al., 2013; Lonsdorf, 2006; Pruetz & Lindshield, 2011). Although interesting, these cases can be subjected to simpler explanations, for instance that tool transfers were triggered by insistent begging. The action of giving up the tool (or food) may thus solely result from the desire of the donor to stop the harassment, and not from a desire to teach, and has been interpreted as "sharing under pressure" (Musgrave et al., 2016). This interaction is therefore purely egoistic on the part of the tool-user, yet beneficial for the beggar, who does not have to manufacture the tool itself and very likely learn some features of the tool at the same time.

Overall, thus, the current literature does not provide any conclusive cases of teaching in chimpanzees, a transmission process likely to play a major role in the capacity for cumulative culture. This absence may also explain the high stability of tool repertoires and lack of cultural evolution in this species. However, this does not mean that chimpanzees are not able to show some basic cultural changes, as demonstrated in my third study, but the lack of high-fidelity transmission may prevent them from reaching high levels of complexity in tool use, like the ones found in human societies. On the other hand, earliest human lithic tool use did not appear until about 2.6 million years ago (Semaw, 2000), but remained largely unchanged for almost 700,000 years when the Oldowan hand-axe technology changed to more complex Acheulean tools (Laland & Hoppitt, 2003; Morgan et al., 2015).

5.4 Adaptive traits related to tool use acquisition

I often observed immatures closely peering at objects manipulated by their mothers or siblings. They seemed to be strongly attracted to any object manipulations by the adults, either when it involved a tool or unusual food items, which required some specific handling before consumption, like peeling or hitting the fruit on a substrate. Similar observations were made on capuchins monkeys (Perry & Ordoñez Jiménez, 2006), with juveniles spending more time watching conspecifics eating rare food items than common food. They also spent more time watching individuals foraging on difficult-to-process food than individuals eating food requiring very basic processing or no processing at all. Thus, manipulations, which require fine-tuning handling, elicit the attention of the learners.

Learning by observing others is likely to be faster than exploring the world by mere trial-and-error. But social learning depends on sociability, to the extent that individuals with a high social propensity have more learning opportunities than less social individuals (Koops, Furuichi, & Hashimoto, 2015; Lonsdorf, 2006; van Schaik et al., 1999; van Schaik, Fox, & Fechtman, 2003; van Schaik & Pradhan, 2003). The influence of the social environment on behaviour acquisition has been called the "opportunity for social learning" hypothesis (van Schaik, 2003). As mentioned earlier (p. 7), chimpanzees may acquire tool use by a hybrid learning process, in which they first learn socially which materials are relevant as tool (stimulus enhancement) and then in which context to use it (local enhancement) before learning the required actions by individual trial-and-error learning. Consequently, traits such as exploratory tendency and persistence should help an individual to become proficient in tool-related behaviours. Using a battery of experiments, Massen et al. (2013) demonstrated that chimpanzees vary in terms of exploration tendency, tool-orientation and persistence. Interestingly, the authors further showed that these traits were associated, meaning that chimpanzees that approached objects readily were also more persistent and more likely to use tools to solve a task. These traits therefore constitute a 'syndrome', i.e., consistent covariance among the traits (Sih, Bell, Johnson, & Ziemba, 2004). Consequently, traits such as sociability, exploration tendency, tool-orientation and persistence should be developed in individuals who readily acquire tool use.

5.5 An experimental approach to cultural evolution

Cumulative culture, the process underlying cultural evolution, is a highly debated topic in non-human animals. Some researchers have argued that cumulative culture in not restricted to humans and that non-human animals possess the ability to accumulate innovations on previous knowledge and pass them on to new generations (e.g., Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Hunt & Gray, 2003; Sasaki & Biro, 2017; Vale, Davis, Lambeth, Schapiro, & Whiten, 2017; Yamamoto, Humle, & Tanaka, 2013). Others are more sceptical and point out the lack of conclusive examples for this capacity in non-human species (e.g. Laland & Hoppitt, 2003; Tennie, Call, & Tomasello, 2009). So far, most of the empirical research on cumulative culture in non-human animals comes from experiments in captivity (Claidière, Smith, Kirby, & Fagot, 2014; Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Vale, Davis, Lambeth, Schapiro, & Whiten, 2017 but see Sasaki & Biro, 2017).

As a general pattern these studies have demonstrated, so far, that animals can use previously acquired knowledge to find new solutions to a familiar task, but the studies poorly reflect natural behaviours and ecological challenges found in wild animals. Moreover, subjects have been extensively trained before being able to perform the tasks, a general concern in this type of research and tasks are often related to foraging, but in ways that rarely match natural behaviours. Finally, the motivation to learn

and the degree of access to tolerant expert models can vary greatly between captive and natural conditions (Perry & Ordoñez Jiménez, 2006).

As always, results from fieldwork are likely to change theories built from data obtained in laboratory settings, so the logical next step is to experimentally test the cumulative culture hypothesis with wild animals. The following criteria are relevant, each requiring unique data sets. First, there must be evidence that the putatively accumulated behaviour is learned socially and across generations. Second, there must be evidence that the behaviour is an improved variant of previous cultural behaviour, in term of complexity and efficiency. With chimpanzees, the main problem is the scarcity of natural innovations but also the subsequent rate of propagation (Hobaiter et al., 2014; Nishida et al., 2009). Often innovations are made by exploratory and manipulative juveniles, but these individuals are rarely copied in wild groups (Biro et al., 2003; Kendal et al., 2015 but see Watson et al., 2017), suggesting that the absence of cumulative culture may have less to do with low rates of innovations, but with low propensity of chimpanzees to copy behaviour shown by juveniles. For adults, innovations appear to be more difficult, possibly due to species-specific neophobia, conservatism, conformity, endowment effects, functional fixedness or cultural influences (Brosnan & Hopper, 2014; Gruber, 2016).

In my research, I had the unusual opportunity to study the spread of a new behaviour, moss sponging, which resembled an already existing behaviour, leaf sponging, allowing me to test some of the criteria for cumulative culture. I found that moss-sponging, indeed, fulfilled two of them, namely increased efficiency of the new variant (Figure 4.3) and its social transmission from one generation to the next (Figure 3.3). At the same time I found no evidence for an increase in complexity, insofar as moss sponges are easier to manufacture than leaf sponges and insofar as moss sponging is probably not beyond what a single individual could have invented alone (Dean et al., 2013; Tennie et al., 2009). Instead, moss-sponging may be simple enough for a chimpanzee to invent without any precursor tools, such as leaf sponges, and thus within a 'zone of latent solutions' available to any chimpanzee (Tennie et al., 2009). Nevertheless, in study 3, I showed that even if the behaviour may be easy to learn and less complex than leaf-sponging, the majority of individuals who never experienced moss-sponging did not invent it *in situ* during the experiment (Table 4.2), suggesting that (a) social learning is required for acquisition and (b) that chimpanzees are culturally conservative. Another point is that, perhaps, the current definition of cumulative culture is inadequate. For example, a diffusion-chain study on an artificial language showed that, over generations, the language became easier to learn, more structured but also less complex (in terms of a reduction in the number of distinct words) (Kirby et al., 2008), suggesting that complexity is not a necessary criterion for a cumulative culture definition. In sum, under one current definition, as put forward by *Dean et al.* (2013), moss-sponging chimpanzees do not meet all the criteria for cumulative culture (no evidence for increased complexity, beyond the possibility of individual innovation). However, if the complexity criteria is removed, then moss sponging qualifies as an example of cultural evolution in the sense that the behaviour represents

a cultural change towards more efficiency, analogous to the findings of the experimental study on artificial languages (Kirby et al., 2008).

5.6 Limitations and Perspectives

5.6.1 Methodological considerations

The three studies of my thesis offer new insights in chimpanzees' capacities and propensities in relation to object manipulation, tool use, social learning and cultural evolution. Even though progress has been made, my studies are also subject to various limitations that need to be highlighted.

One limitation concerns the approach I used to investigate the ontogeny of object manipulations. For obvious reasons, I could not collect longitudinal data on the development of object manipulation from infancy to adulthood, a period that spans over at least a decade. Instead, I used cross-sectional data collection, which is inferior compared to longitudinal data that are less prone to inter-individual variations and sampling biases resulting from underrepresentation of some age/sex classes (e.g. infant males).

Although the chimpanzees of the Sonso community are followed by researchers and field assistants on a daily basis, moss-sponging remains a rare behaviour, mostly displayed during a few months of the rainy season, when the clay pits in the swamp forests are filled with rain water and mineral suspensions become available. Although no data were collected between 2011 and 2014, I was able to use camera traps to investigate the behaviour in 2014 in substantial detail.

Yet, my study on the transmission mechanism following the emergence of the tool variant is based on only a snapshot of the situation in 2014. Ideally, camera traps would have been installed at the clay pits since the emergence of the new behaviour. These data would have provided information on the time of acquisition of the behaviour for the individuals who acquired it after 2011 and would have offered a better understanding of the role of mothers and other members of the matrilines regarding the transmission. Network based diffusion analyses would have therefore been possible to use. Although this would have provided essential data, moss sponging was not completely restricted to clay pits, as mentioned in study 3 (p. 64), but was observed on five occasions outside of the original context, (n=2 tree holes; n=3 stagnant water puddles). This fact complicates matters as the behaviour could have been observed and acquired at places other than clay pits.

5.6.2 Future research

As mentioned, a longitudinal approach would be ideal to study the ontogeny of tool use, suggesting that following individuals from birth to adulthood, using the same methodology to collect data on object manipulation, as presented in study 1, would be ideal. Along with data on manipulations, further data on models are needed. Several studies have investigated the models used by immatures (e.g. Bard & Vauclair, 1984; Hirata & Celli, 2003; Lonsdorf, 2006) but it is not clear how the influence of the model depends on the type and context of the behaviour, such as foraging, mating or body care. Do chimpanzees, like humans (Hewlett, Barry & Cavalli-Sforza, 1986), change their models depending on the type of behaviours they try to acquire? To answer this question, data should be collected on 1) the time a learner spent watching models, 2) the models' identity and 3) the type of behaviour the model is displaying.

To further investigate the role of object play as a precursor to tool use, I would suggest to collect data allowing to test whether there is a negative correlation between the frequency of play with a specific material and the time of acquisition of the tool use related to this material.

Last but not least, to test if moss-sponging qualifies as a cumulative cultural behaviour, and fulfils the key criteria, a future study should test experimentally if leaf-sponging knowledge is required to learn moss-sponging. To do so, we should have chimpanzees totally naïve to leaf-sponging and train half of them to leaf-sponge (test group) in a water source out of reach of their mouth. The rest of the group (control group) should be given other tools to get water (e.g. cups). The chimpanzees of the test group that have acquired the leaf-sponging behaviour, should then be tested to acquire water from a more complex device requiring this time moss-sponging. If moss-sponging is built on leaf-sponging, then these chimpanzees should be able to find the moss-sponging solution, whereas chimpanzees that have never been trained to leaf-sponge (control group) should not find the moss-sponging solution and should fail to retrieve the water.

Although laboratory studies continue to produce new insights into the different aspects of animal culture, such as the social learning mechanisms involved, the underlying physical cognition abilities and the capacity for cumulative culture, it is now important to allocate more effort and resources to test these aspects in the wild. Indeed, in chimpanzees, which are the most prolific and versatile tool users in non-human animals, it is still unclear to which extend social learning is involved in the acquisition of seemingly cultural behaviours. As mentioned earlier (p.7 and 85), a hybrid form of learning may underlie the acquisition of cultural behaviours, but if this is correct then what are the respective contributions of asocial and social learning? What kind of information is exactly provided by demonstrators and which aspects need to be learned individually, i.e. reinvented each time, by new practitioners? Does the context of a behaviour influence the type of social learning involved in the acquisition? For example, do cultural social behaviours require high-fidelity transmission, whereas

cultural foraging behaviours can already be transmitted through low-fidelity transmission? The exact level of implication of social learning and the different mechanisms according to context have to be better understood and investigated in wild chimpanzees. Furthermore, clear and unequivocal cases of cumulative culture in non-human species are still lacking. The question is whether this absence is due to the comparatively restricted timeframe since this topic is systematically investigated in captivity and in the wild or whether cumulative culture is indeed uniquely human. Work on archaeological artefacts might be an interesting approach for studying the evolution of animal tool users' technology. Finally, despite considerable effort to protect the chimpanzees across Africa, their natural habitats are under growing threat and relentlessly shrinking. Following the adage "necessity is the mother of invention", chimpanzees might be able to escape the threat of extinction if their abilities for cultural evolution are sufficiently strong to invent new and adaptive behaviours to survive in their increasingly disturbed habitats.

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