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Development of object manipulation in wild chimpanzees

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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 records of stick-based foraging in over 20 years of continuous observations. Using cross-sectional data, we found evidence for social learning in that young individuals preferentially played with and explored materials manipulated by their mothers. 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 other tool materials, which were all used throughout adulthood. Overall, young chimpanzees initially explored and played unselectively with any object found in the environment before becoming increasingly influenced by their mothers' goal-directed object manipulations.

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 nonhuman primates, especially chimpanzees, *Pan troglodytes*, which 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 material 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 & Laland, 2005; Galef et al., 1998; 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, Weir, Rutz, Wimpenny, & Kacelnik, 2007; Holzhaider, Hunt, Campbell, & Gray, 2008; Tebbich & Bshary, 2004; Visalberghi & Limongelli, 1994) based on an understanding of the affordances of objects, surfaces, actions and spatial relations (Limongelli, Boysen, & Visalberghi, 1995). Whatever the underlying mechanisms, there is consensus that the acquisition of proficiency must be based on a developmental period of exploratory activity (Chevalier-Skolnikoff, 1989; Hayashi, Takeshita, & Matsuzawa, 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, which has become 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. Boesch & Boesch, 1990; McGrew, 1974; Sanz & Morgan, 2007; Teleki, 1974; Watts, 2008). There is no obvious ecological or genetic explanation for the surprising lack of stick use in the Sonso community, which is

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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) (Appendix Tables A1–A4; Gruber, Muller, Strimling, Wrangham, & Zuberbühler, 2009; Reynolds, 2005).

A number of hypotheses have been proposed for the lack of stick use. First, Budongo Forest may be unusual in its lack of cyclic food scarcities, which might prevent chimpanzees from inventing new foraging techniques (the necessity hypothesis: Gruber, 2013; Gruber et al., 2012). Indeed, the home range of the Sonso community is characterized by a high diversity of tree species that produce chimpanzee foods, especially if compared to two other Ugandan communities in nearby Kibale Forest (Kanyawara and Ngogo), both of which use sticks (Gruber et al., 2012). One historical scenario is that Sonso chimpanzees originally used sticks as tools, but that environmental changes led to increased food availability and diversity, which then caused a loss of this behaviour in the Sonso community (Gruber, 2013). Chimpanzee cultures, in other words, are determined not only by the ability to innovate and socially learn, but also by the propensity to lose behavioural elements if they are no longer required. The ability to innovate has recently been confirmed for the Sonso chimpanzees by the sudden appearance and social spread of a new sponging tool (Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Lamon, Neumann, Gruber, & Zuberbühler, 2017).

Differences in tool use are found not only between groups but also between closely related species and may originate early during ontogeny. Koops, Furuichi, Hashimoto, (2015); Koops, Furuichi, Hashimoto, & van Schaik, (2015), for instance, argued that the main reason for the striking difference in tool use frequency between chimpanzees and their closest relative, bonobos, *Pan 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. 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 additional role in the acquisition of tool use (Hirata & Celli, 2003; Inoue-Nakamura & Matsuzawa, 1997; Lind & Lindenfors, 2010; Lonsdorf, 2006; van Schaik, Deaner, & Merrill, 1999). For example, Humle, Snowdon, and Matsuzawa (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 mother's 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 developmental patterns (Lonsdorf, 2017). For example, at Kalinzu, Uganda, immature males showed higher rates of playful object manipulations than immature females (Koops, Furuichi, Hashimoto, & van Schaik, 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- and sex-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, Walkup, and Beck (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 for the proper and effective orientation of the tool'. We defined a goal-directed object manipulation as an action on an object (tool) or substrate (prototool) to achieve a purpose, which is terminated when the action's outcome meets the purpose (see Appendix Table A1). We defined a nongoal-directed object behaviour as an action, often repetitive, on an object lacking any clear function or purpose. These object manipulations typically consisted of solitary play or mere exploration. Using exploratory data analysis, we were interested in (1) how object manipulation rates, object choice and goal-directed use of materials were affected by age and sex and (2) what social factors influenced the choice of materials manipulated by the nonadults.

METHODS

Ethical Note

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

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 semideciduous tropical forest at a mean altitude of 1100 m. 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, seven subadult females, three subadult males, 15 juvenile females, three juvenile males, two infant females and two infant males, 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). 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.

Study Subject and Data Collection

Behavioural data were collected between January 2013 and February 2015 (153 days) using continuous focal sampling on 37 individuals (six infants (one female, five males), 10 juveniles (seven females, three males), four subadults (three females, one male) and 17 adults (11 females, six males); see Appendix Table A5). Ages were calculated using the date of the last focal sampling. Infants, juveniles and subadults were categorized as nonadults. Object