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Development of object manipulation in wild chimpanzees

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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 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.

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*), 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 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, 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; C. E. 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., McGrew 1974; Teleki 1974; Boesch & Boesch 1990; Sanz & 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 A1) (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 characterised 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 not only determined by the ability to innovate and socially learn, but also by the propensity to loose 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 not only found between groups but also been closely related species and may originate early during ontogeny. 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. 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 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 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 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 A1). We defined a non-goal-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 (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 of materials manipulated by the non-adults.

MATERIALS AND 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 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): 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 (6 infants (1F, 5M), 10 juveniles (7F, 3M), 4 subadults (3F, 1M) and 17 adults (11 F, 6 M) see Table A2). Ages were calculated using the date of the last focal sampling. Infants, juveniles and subadults were categorized as non-adults. 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. Data were recorded on an all occurrence basis and whenever possible documented on video (Panasonic HC-X909 camcorder; see Table A1 for a comprehensive definition). 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 A1). Manipulations were identified as either 'goal-directed' or 'non-goal directed' (for definitions see Table A1).

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. We also fitted the interaction between age and sex to account for the possibility that there might be sex differences in how age affects manipulation rates. 37 individuals contributed data to the model (N=22 females; N=15 males; age range: 0.4 to 52 years). After fitting the full model (i.e. including the interaction term), we tested this model against a null (intercept-only) model using a likelihood ratio test (LRT, Dobson, 2002). If this revealed a significant difference, we explored the full model by comparing the full model against a reduced model from which the interaction term was removed (Forstmeier & Schielzeth, 2011). If the interaction term was not significant, we tested the main effects of sex and age.

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 above, we also fitted the interaction between age and sex. 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). As above, we first tested the full model against a null (intercept-only) model, and only if this revealed significance then tested the interaction term and main effects.

Choice of material

First, we explored the rate of object manipulations across materials for adults and non-adults. In this analysis we treated age as a categorical variable, i.e. non-adults (<160 months, infants, juveniles and subadults) or adults (≥160 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 (see figure 3). The goal was to investigate the potential social and individual learning mechanisms by which non-adult subjects 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 (*N*= 51 = 17 subjects x 3 material categories) (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 (square-root transformed) as predictor and one model contained subject sex as predictor variable. Four more models addressed the potential influence of the social environment. Specifically, we distinguished mothers as potential demonstrators from non-maternal demonstrators. In the models regarding maternal demonstrators, 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. In particular, young chimpanzees might be more attentive to absolute exposure (approximate time mother spends manipulating) or relative exposure (approximate proportion of time mother spends with each material). We had to exclude three individuals (FA, KX and OK3) because we were unable to collect systematic object manipulation data from their mothers. 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 the subject's 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. To quantify non-maternal influences, we then weighted the non-maternal adults mean proportions and rates of object manipulations by every subject's association with all the non-maternal adults. In this way we obtained a subject- and material-specific measure of how much each subject was potentially exposed to object manipulations by non-maternal adults. The last model represented a conceptual null model and consisted only of the material as 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, manipulate leaves more than woody vegetation.

We then ranked the models, using an information-theoretic approach (Burnham & Anderson, 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 was 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).

RESULTS

Object manipulation rates

The full model (manipulation rates are a function of age, sex and their interaction) was significantly different from the null model (likelihood ratio test: $\chi^2_3 = 29.64$, $P < 0.0001$). There was no significant interaction between age and sex in object manipulations rates (LM: N=37, β±SE = -0.03 ± 0.05, LRT: $\chi^2_1 = 0.52$, $P = 0.4710$), so we removed the interaction.

We found that manipulation rates decreased with age (LM: N=37, β±SE = -0.11 ± 0.02, LRT: $\chi^2_1 = 18.85$, $P < 0.0001$, **Error! Reference source not found.**, table A3) and that males manipulated objects significantly more than females, regardless of age (LM: N=37, β±SE = 0.63 ± 0.28, LRT: $\chi^2_1 = 5.04$, $P = 0.0247$, **Error! Reference source not found.**, table A2 and A3).

Goal-directedness

The full model (probability of manipulating objects in goal-directed ways is a function of age, sex and their interaction) was significantly different from the null model (LRT, $\chi^2_1=72.45$, $P<0.0001$). There was no significant interaction between age and sex in goal-directedness of object manipulations (GLMM, β±SE = 0.03 ± 0.32, LRT: $\chi^2_1 = 0.01$, $P = 0.9252$), so we removed the interaction.

We found that goal-directedness increased with age (β±SE = 1.49 ± 0.12, LRT: $\chi^2_1 = 70.38$, P < 0.0001, **Error! Reference source not found.**, table A2 and A4) and that males were more likely to manipulate objects in goal-directed ways than females, regardless of age (β±SE = 0.57 ± 0.23, LRT: $\chi^2_1 = 5.26$, $P = 0.0218$, **Error! Reference source not found.**, table A2 and A4).

Choice of material

We found that, for adults, leaves and woody vegetation were the most manipulated objects, while sticks were 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 (**Error! Reference source not found.** and table A2). The transitional age from playing and exploring sticks to ignoring sticks was around 10 years old, which corresponded to the transition to adulthood (**Error! Reference source not found.**).

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 1, for estimates and standard errors see table A5). Of these three, two suggested maternal influence of material choice of our subjects and one represented an individual feature (sex) that explained material choice (figures 5 and 6).

With regards to maternal influence, we found that, for woody vegetation, there was a positive relationship between maternal use and offspring use regardless of whether we measured maternal use as rates or proportions (figure 5). In other words, subjects whose mothers used woody vegetation at high rates or proportions also manipulated woody vegetation more often compared to other subjects. For trunks, the relationship was flat, i.e. subjects used trunks very little (table A2), regardless of maternal use of trunks, which was also infrequent (table A2). For leaves, results differed depending on whether we measured maternal use as rates or proportions. Subjects whose mothers used leaves at large proportions also used leaves at high proportions. However, subjects whose mothers used leaves at high rates used leaves at low proportions.

Regarding subject sex, we found that females used woody vegetation more than male subjects, while males used trunks and leaves more than females (figure 6).

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).

DISCUSSION

In this study, we were interested in age- and sex-related changes in ~~-directed~~ object manipulation and their possible social and non-social influences in the Sonso chimpanzee community of Budongo Forest, Uganda. This community is known for its striking absence of a key tool use behaviour seen in virtually all other 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. We also found that the relative proportions of the tool material manipulated by the non-adults varied according to sex, with males manipulating more trunk and leaves than females and females manipulating more woody vegetation than males. Finally, we found some tentative evidence for social learning in that non-adults played and explored at higher proportions some of the materials manipulated by their mothers.

Our 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-directed behaviours becoming predominant 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 and possibly participate in the understanding of object affordances, it does not automatically lead to the use of these objects as tools. Social learning, through the observation of maternal object manipulations, 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 object play and exploration behaviour. Interestingly, maternal influence seems to play a role only for material that is most often manipulated, such as woody vegetation. For material barely used by the mothers, such as trunk, no maternal influence seems to take place. 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 et al., 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 object 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, a cognitively low-level process, repeatedly identified as the main mechanism in the spread of tool use in primates (Call, Carpenter, & Tomasello, 2005; Nagell, Olguin, & Tomasello, 1993; Whiten, Horner, Litchfield, & Marshall-Pescini, 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 object manipulations in immature chimpanzees in the Kalinzu Forest Reserve, Uganda. 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. This hypothesis is partly confirmed by our result showing that immature males manipulated more trunk objects, a material essentially used by adult males to buttress- and trunk-beat. The differences regarding leaves and woody vegetation between immature females and males need further investigations because both types of material can be used in various contexts such as body care, liquid absorption, aggressive displays or mating behaviour.

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.

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TABLES

Table 1. Results of model ranking. The response variable is the proportion of material the non-adult manipulated in each of the three material categories (i.e. leaf, woody vegetation and trunk).

Model	*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

Table A1. Lists of definitions and descriptions of key concepts, material categories, manipulation contexts, types of manipulations and goal-directedness.

a) Definitions of key concepts

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 (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.).

b) Descriptions of the material categories

Material category	Description
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

c) Descriptions of the different contexts of manipulation

Manipulation contexts	Description
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
Object play/exploration	Object 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.

606 d) Descriptions of the different types of manipulations, the associated goal-directedness and

607 contexts

Manipulations	Description	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 object 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 collect water and then squeezed in mouth	Yes	Drinking
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	Object 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	Object play/exploration

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

Table A2. List of subjects, their object manipulations and their time in sight

ID	Age (month)	Age class	Sex	Leaf	Stick	Woody vegetation	Trunk	Others	Total	Goal directed	Time in sight
FA	87	non-adult	F	9	3	25	0	0	37	29	383
FK	180	adult	M	10	0	8	7	0	25	22	360
HR	48	non-adult	F	1	3	2	0	2	8	4	440
HT	432	adult	F	5	0	0	0	0	5	4	306
HW	252	adult	M	21	0	22	17	0	60	57	243
HY	90	non-adult	F	10	2	17	0	0	29	18	522
JN	360	adult	F	5	0	6	0	0	11	10	273
JS	90	non-adult	M	3	1	5	1	0	10	8	559
KB	83	non-adult	F	6	10	25	1	3	45	26	598
KC	85	non-adult	M	16	4	21	7	1	49	30	452
KF	11	non-adult	M	30	13	16	8	4	71	6	218
KH	64	non-adult	F	10	7	6	0	4	27	11	406
KJ	19	non-adult	M	10	10	24	2	7	53	10	203
KL	420	adult	F	1	0	4	1	0	6	5	371
KL8	5	non-adult	M	8	2	16	0	7	33	0	218
KN	192	adult	F	3	0	4	0	1	8	5	526
KR	155	non-adult	F	1	0	1	0	1	3	2	426
KS	136	non-adult	M	5	0	0	1	0	6	6	381
KT	254	adult	M	5	0	5	2	0	12	8	215
KU	420	adult	F	2	0	0	0	0	2	2	344
KW	396	adult	F	5	0	1	1	0	7	7	377

KX	73	non-adult	F	6	5	10	2	1	24	8	476
KZ	238	adult	M	2	0	3	0	0	5	4	279
MB	59	non-adult	M	17	5	36	1	9	68	40	299
MI	71	non-adult	F	6	17	17	1	1	42	15	469
MK	408	adult	F	3	0	1	0	0	4	4	420
ML	468	adult	F	2	0	2	1	0	5	5	249
MS	276	adult	M	0	0	5	4	0	9	9	363
NB	624	adult	F	7	0	1	0	0	8	8	441
NK	384	adult	M	6	0	4	0	0	10	9	323
NT	123	non-adult	F	7	7	30	0	14	58	32	468
OK3	5	non-adult	M	20	6	20	0	3	49	3	203
RF	74	non-adult	F	6	0	5	0	1	12	8	537
RH	600	adult	F	3	0	0	0	0	3	3	333
RM	135	non-adult	F	7	3	6	1	0	17	14	390
RS	204	adult	F	6	0	5	0	1	12	10	286
RY	16	non-adult	M	6	4	15	1	24	50	7	222

Age was calculated from the date of the last focal sampling.

Table A3. Results from object manipulation rate analysis. The table shows parameter estimates and standard errors for the full model (including interaction) and for the final model (from which the interaction was removed).

	full model (β±SE)	final model (β±SE)
intercept	1.86±0.46	2.04±0.37
age	-0.09±0.03	-0.11±0.02
sex (female versus male)	1.01±0.62	0.63±0.28
age : sex (interaction)	-0.03±0.05	

Table A4. Results from goal directedness GLMM. The table shows parameter estimates and standard errors for the full model (including interaction) and for the final model (from which the interaction was removed).

	full model (β±SE)	final model (β±SE)
intercept	-6.30±1.32	-6.41±0.58
age	1.47±0.29	1.49±0.12
sex (female versus male)	0.43±1.43	0.57±0.23
age : sex (interaction)	0.03±0.32	

Table A5. Detailed model results of the model ranking. Shown are parameter estimates and standard errors, and the table is ordered in the same ways as table 1, i.e. according to model weights. The models differed only with regards to which variable was the test predictor of interest, which is shown in the first column (see also table 1).

Model/test predictor	Corresponding model weight	Intercept	material (woody vegetation)	material (trunk)	test predictor	test predictor : woody vegetation (interaction term)	test predictor : trunk (interaction term)
Mother's rates	0.803	-0.55±0.19	0.23±0.20	-2.58±0.37	-0.64±0.20	0.92±0.25	0.67±0.44
Sex	0.165	-1.24±0.17	1.06±0.20	-3.14±0.60	0.29±0.22	-0.55±0.26	1.36±0.65
Mother's proportion	0.022	-1.27±0.24	0.98±0.24	-1.85±0.40	0.22±0.22	0.14±0.30	-0.18±0.48
Null (material only)	0.008	-1.07±0.11	0.73±0.13	-2.09±0.23			
Age	0.002	-1.08±0.11	0.80±0.13	-2.12±0.25	-0.02±0.11	0.24±0.13	-0.10±0.23
Non-maternal adults proportions	0.000	-1.51±0.75	1.15±0.76	-0.44±3.93	0.39±0.64	0.77±1.15	0.62±3.40
Non-maternal adults rates	0.000	-0.98±0.45	0.64±0.45	-0.61±1.69	-0.09±0.48	0.12±0.54	1.31±1.31

FIGURES

Figure 1. Rates of object manipulation as a function of age and sex. Rates represent the number of object manipulations per time in sight (h) for each subject (*N*=37). The blue (male) and red (female) solid lines represent the fitted model, with confidence intervals (dashed lines).

Figure 2. Goal-directed object manipulation 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 over all the manipulations for each of the 37 individuals.

Figure 3. Rates of object manipulation across materials and age classes. Rates represent the number of object manipulations per time in sight (h) for each material category and the two age-classes (192 object manipulations from 17 different adults, and 691 object manipulations from 20 different non-adults). Other material consisted of stone, flower, mud insect channel, moss, bark, soil, sawdust, thorn and termite mount. Thick lines represent medians and the box around them quartiles. The whiskers comprise the most extreme points within 1.5 times the inter-quartile range away from the quartiles.

Figure 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.

Fig 5. Proportion of materials manipulated by non-adult subjects as a function of material and maternal behaviour. The figure shows the model results and confidence intervals for the three materials considered and separated by the type of maternal behaviour considered (maternal rates of manipulation of a given material versus maternal proportion of manipulated objects) (see table 1 and table A5.

Fig 6. Sex differences in manipulation of different materials by non-adult subjects. The figure shows model estimates and confidence intervals (see table 1 and table A5).

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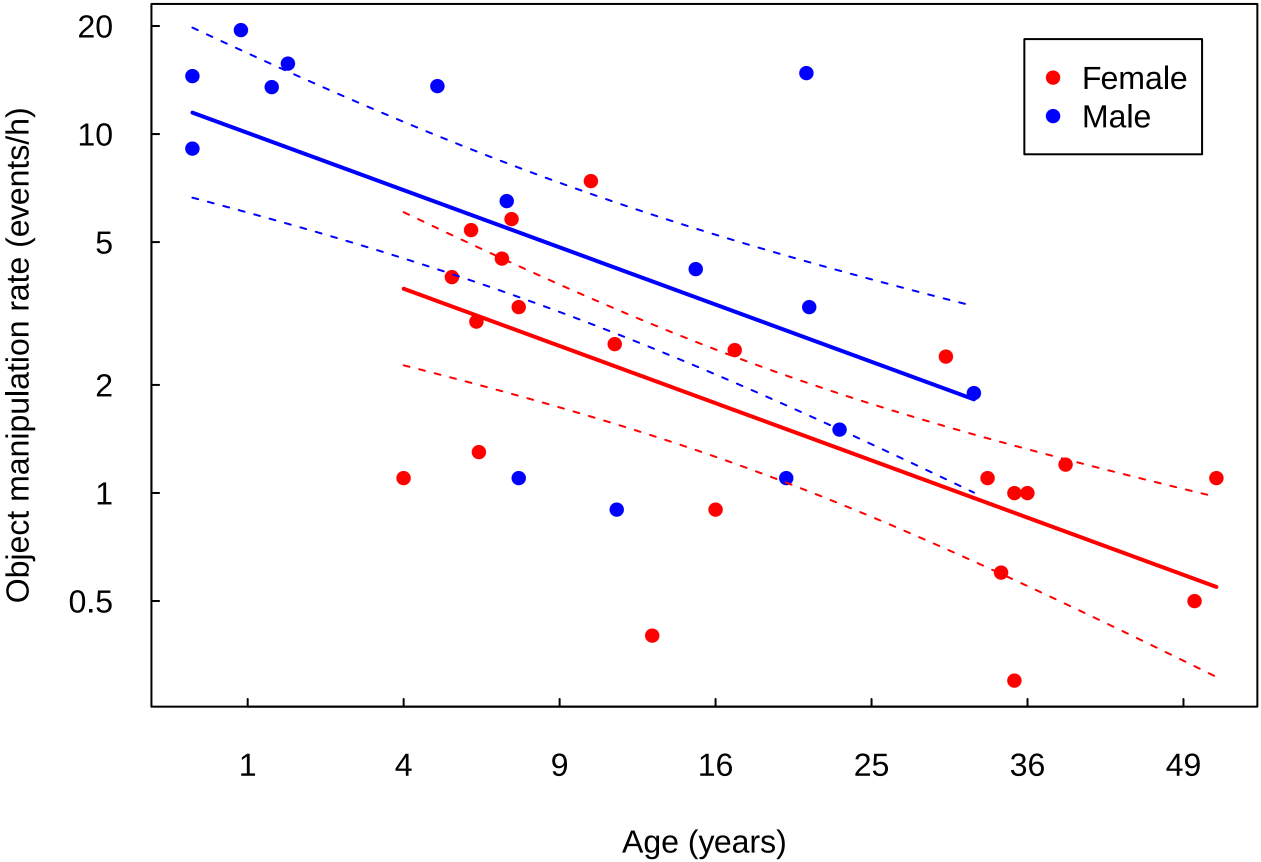
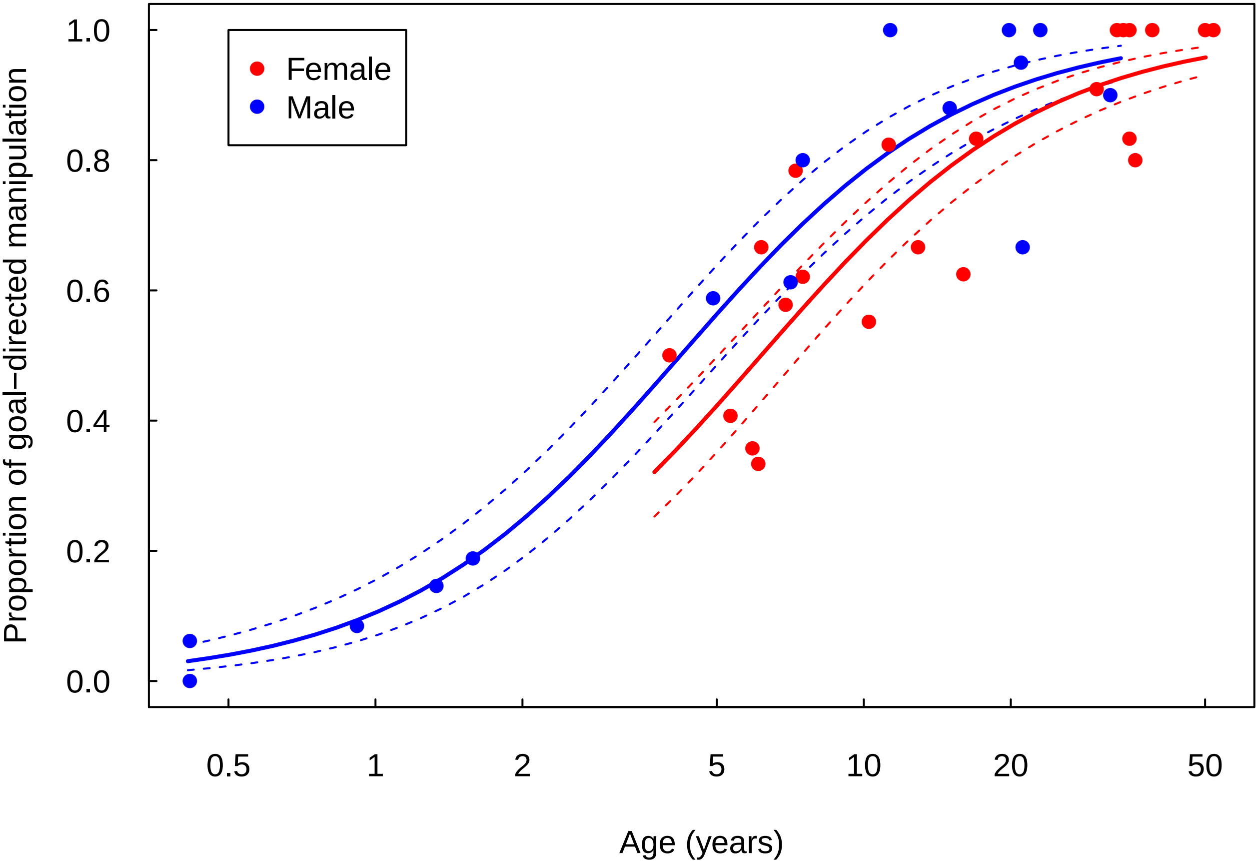
Figure

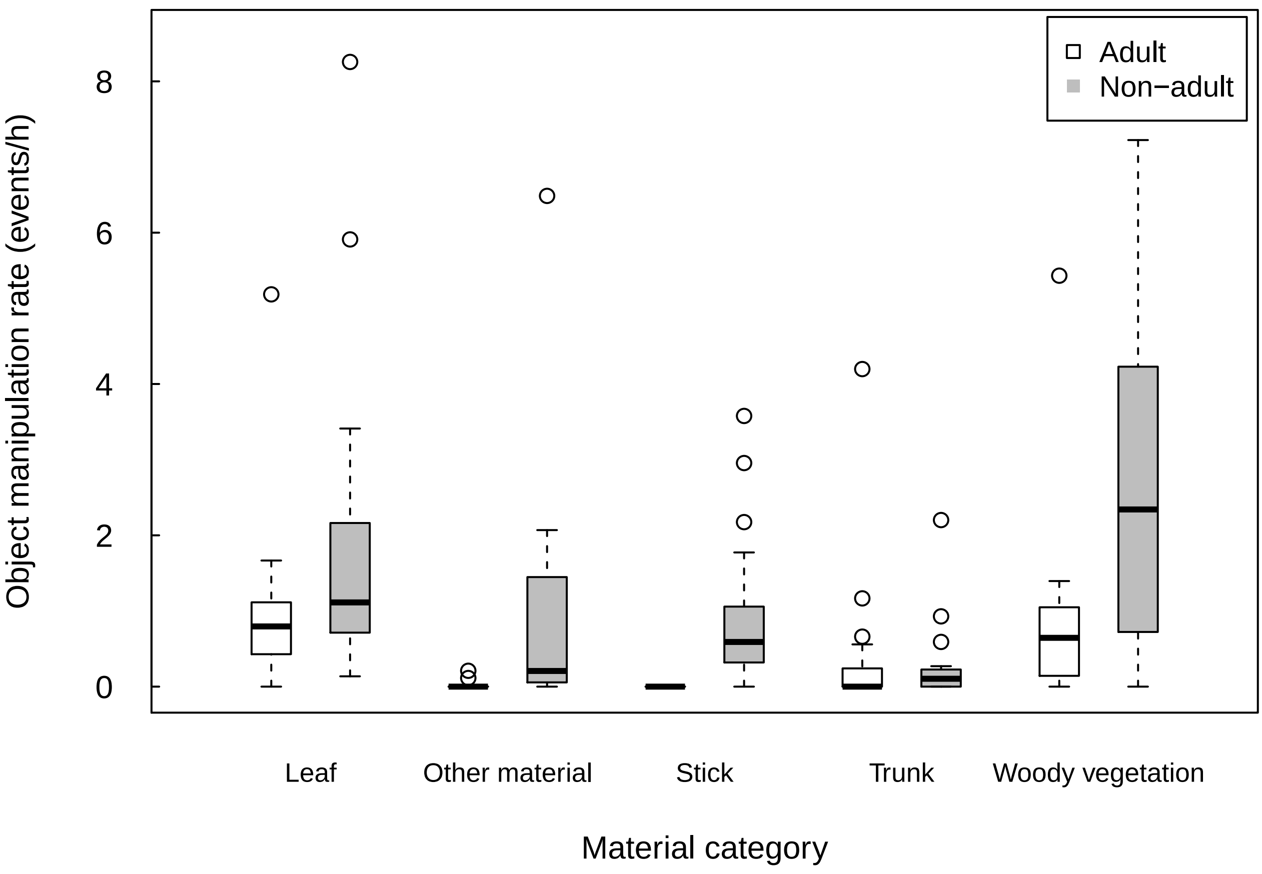


Female
Male
20
10
5
2
1
0.5
Object manipulation rate (events/h)
1
4
9
16
25
36
49
Age (years)

Figure

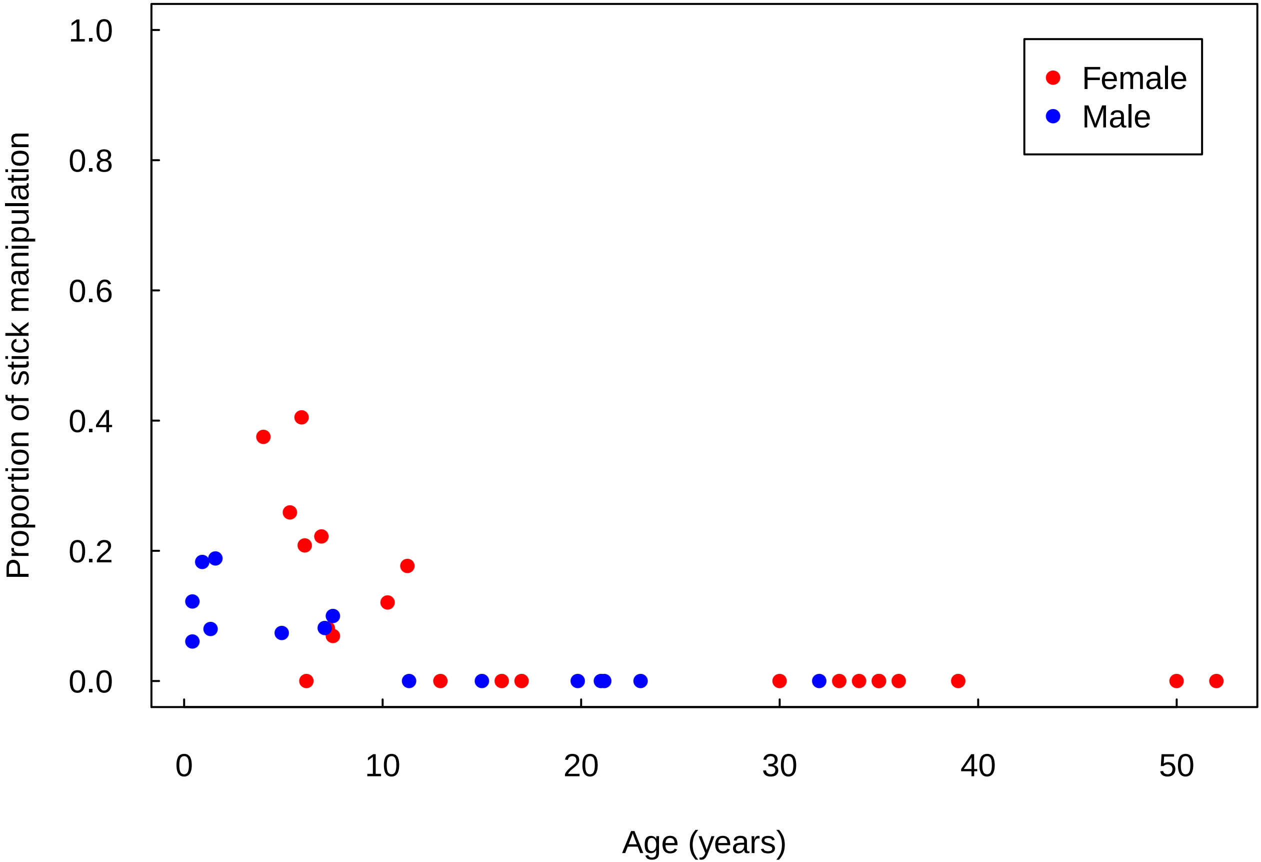

Female
Male
Proportion of goal−directed manipulation
1.0
0.8
0.6
0.4
0.2
0.0
0.5
1
2
5
10
20
50
Age (years)

Figure



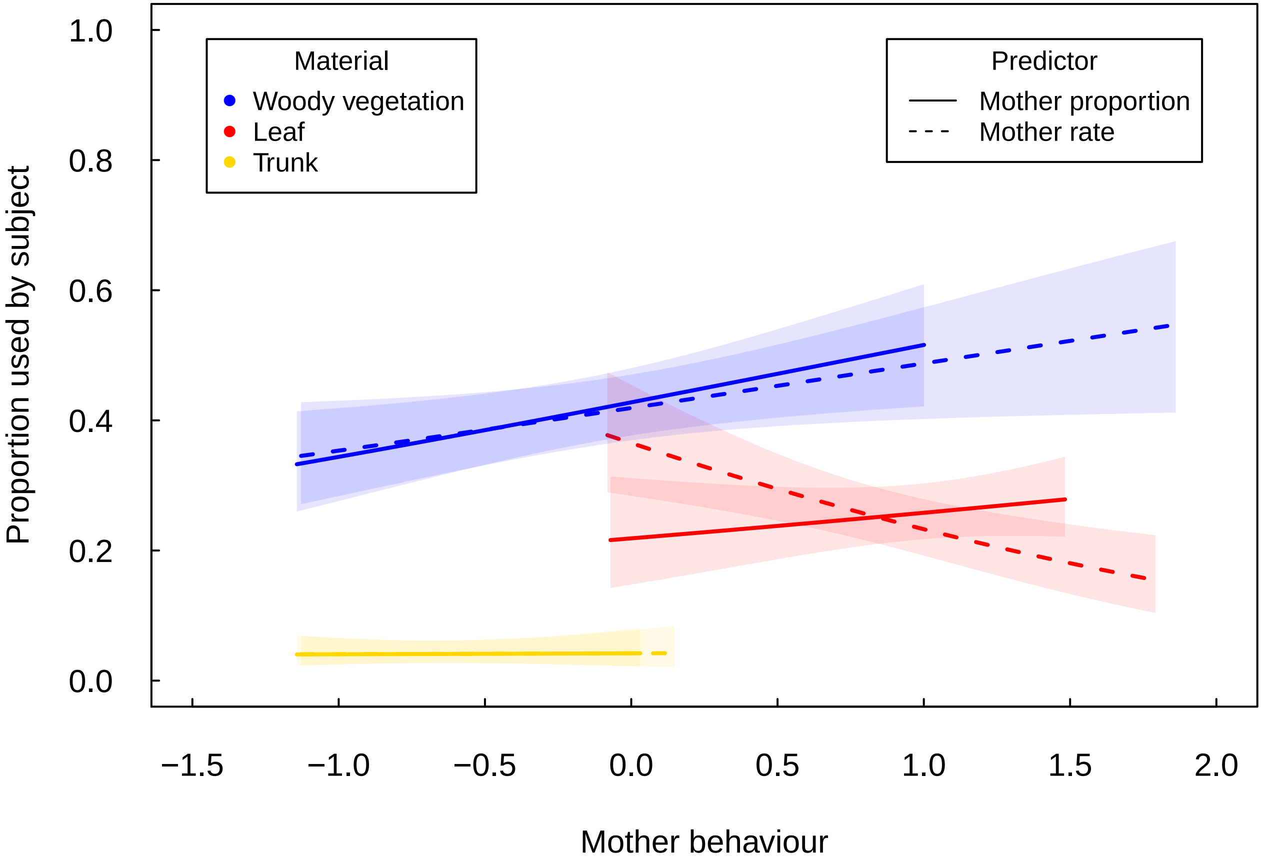
Adult
Non−adult
Object manipulation rate (events/h)
0
2
4
6
8
Leaf
Other material
Stick
Trunk
Woody vegetation
Material category

Figure



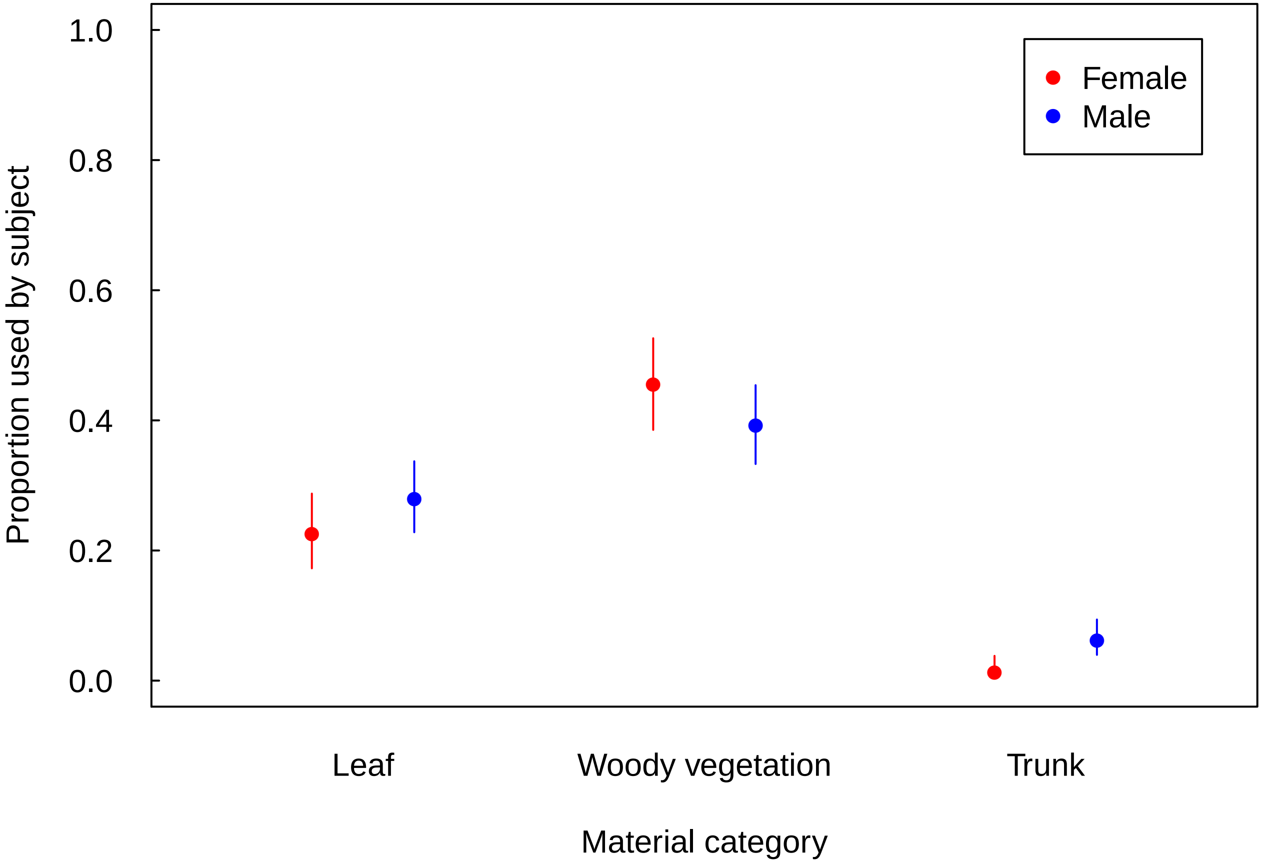
Female
Male
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of stick manipulation
0
10
20
30
40
50
Age (years)

Figure



Material
Woody vegetation
Leaf
Trunk
Predictor
Mother proportion
Mother rate
1.0
0.8
0.6
0.4
0.2
0.0
Proportion used by subject
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
Mother behaviour

Figure


Female
Male
1.0
0.8
0.6
0.4
0.2
0.0
Proportion used by subject
Leaf
Woody vegetation
Trunk
Material category

***Animal welfare note**

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).