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ORIGINAL PAPER

Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa

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Abstract We currently have little understanding of the influence of learning opportunity, whether social or environmental, and maternal role on tool-use acquisition in young wild chimpanzees. This study aims to fill this gap by focusing on the acquisition of ant-dipping among chimpanzees of Bossou, Guinea. Ant-dipping is a hazardous tool-use behaviour aimed at army ants (*Dorylus* spp.). Bossou chimpanzees target these ants both at nests (high risk) and trails (low risk) and employ two techniques to consume them: direct mouthing and pull-through. We present data for 13 mother–offspring pairs (1–10 years old). Mothers with young $\leq$5 years old dipped significantly more often at trails than at nests, thus minimizing the risk posed to themselves and their young. Infants thus benefited from better conditions to observe and practice ant-dipping. Mothers also varied greatly in their percent time spent ant-dipping and offspring differed in their learning opportunity. Our results suggest that high opportunity young started to observe and perform ant-dipping sooner and were better at ant-dipping than low opportunity young. Although mothers and weaned offspring correlated positively in their percent time spent dipping and proficiency, they did not match in technique used or tool length. Finally, we propose that the learning trajectory of young may predict individual and sex differences in adulthood. This study demonstrates the important role of mothers and learning opportunity in the acquisition of a hazardous tool-use behaviour and suggests that chimpanzee material culture is a product of a complex interaction between social processes and ecological factors.

Keywords Ant-dipping · Chimpanzee · Culture · Learning · Sex difference · Tool use · Development

Introduction

A greater appreciation for local behavioural differences between groups or populations of animals ranging from fish to cetaceans has stimulated investigations into the prevalence of culture and a wealth of studies of social learning among non-human animals (Fragaszy and Perry 2003). Due to the difficulties in controlling for alternative genetic or ecological explanations in field settings, most studies have favoured controlled experiments in captivity. These studies have identified possible social learning mechanisms, ranging from local enhancement to more cognitively complex, high fidelity transmission processes such as imitation (Whiten and Ham 1992). However, there is a growing consensus that most social learning observed in animals does not fit such clear categories and that learning may best be described as socially biased learning, a process that is

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coupled with individual experience and mediated by exposure to the activities and/or behaviours of others (Galef and Laland 2005).

In this context, Coussi-Korbel and Fragaszy (1995) proposed that social tolerance and opportunities for close behavioural coordination in space and time with group members could explain many of the underlying species differences in their propensity for learning socially. Many studies have shown that social dynamics among group members are more important than cognitive ability or phylogenetic status in predicting social learning. Individuals in more egalitarian and tolerant social groups are more likely to learn socially and exhibit behavioural homogeneity (examples reviewed in Fragaszy and Visalberghi 2004). As an extension to this hypothesis, van Schaik (2003) proposed that individual differences observed within population or groups of animals can be explained by differential opportunities for socially biased learning during ontogeny. They provided supporting evidence for this hypothesis in explaining tool-use variation for feeding within populations of wild orang-utans (*Pongo pygmaeus abelii*).

For most mammalian species, mothers are the primary mediating agent canalizing young's exposure to novel behaviours. This mother–offspring association is particularly prolonged among great ape species, such as the orang-utan or the chimpanzee (*Pan troglodytes*). For the first 5 years of life and beyond, the majority of a chimpanzee infant's social interactions are with its mother (McGrew 1977). Since offspring and their mothers travel together almost exclusively for up to 8–10 years, the mother remains the primary source of information during an extensive period beyond weaning rarely matched in other primates (Goodall 1967; Pusey 1983, 1990). This prolonged association ensures that young are exposed to all of the mother's feeding and social activities. Therefore, in species like the chimpanzee, the mother is likely to influence her offspring's opportunities for learning a given behaviour (van Schaik 2003).

Based on predictions from social learning models (Laland 2004), copying others is a valuable strategy when individual trial and error learning is costly in terms of time or risk. We can predict that for immature individuals, opportunity for socially biased learning is likely to play a significant role in skill acquisition when young are faced with learning complex and/or hazardous behaviours. Chimpanzees regularly demonstrate complex foraging skills, including the use of tools. These complex behaviours usually present marked variations between, as well as within communities, and often require young several years to perfect (e.g. Inoue-Nakamura and Matsuzawa 1997). However, few studies have focused on the development of tool use among wild chimpanzees and fewer still have explored in detail the influence of the mother's behaviour on her offspring's acquisition of complex skills (Matsuzawa 1994; Inoue-Nakamura and Matsuzawa 1997; Matsuzawa et al. 2001; Biro et al. 2003; Lonsdorf 2005, 2006). Such studies are essential in helping us better understand the mind of the chimpanzee (Matsuzawa 2009).

The general consensus is that active teaching by the mother or any other knowledgeable member of the community is rare. Indeed, active demonstration and assistance in canalizing an immature animal's acquisition of a complex tool-use behaviour, such as nut cracking, have rarely been observed (Boesch 1991; Inoue-Nakamura and Matsuzawa 1997; Matsuzawa et al. 2001), and has not been recorded in the context of termite fishing at Gombe (Lonsdorf 2005). Instead, through a process termed education by master-apprenticeship (Matsuzawa et al. 2001), the apprentice (the naive young) acquires these complex skills through repeated observations of the master, and the master, in turn, exhibits high levels of tolerance for the close proximity of the apprentice.

In contrast to the above mentioned tool-use skills, we explored here instead the acquisition of a hazardous tool-use task, known as ant-dipping among the chimpanzees (*P. troglodytes verus*) of Bossou, Guinea. Bossou chimpanzees dip on army ants of three epigaeic species (these forage on the ground and in the vegetation and have conspicuous nests) and two intermediate species (these only forage on the ground and have less conspicuous underground nests) both at nests or trails (Humle and Matsuzawa 2002; Yamakoshi and Myowa-Yamakoshi 2003). These ants are readily available in the relatively small home range of this community and therefore we can assume that the ecological opportunity for ant-dipping is the same for all members of the community. Ant-dipping requires the manufacture and use of a stick or stalk of vegetation as a tool to gather army ants (*Dorylus* spp). Ant-dipping typically involves a chimpanzee holding the tool between its index and middle finger and performing a back and forth movement of the tool, to stimulate the ants to attack the tool. Ants that climb the tool are then ingested. The reliance on a tool for ant-dipping has been proposed as a more efficient and less painful strategy for harvesting these biting ants (McGrew 1974).

Ant-dipping is a risky behaviour since army ants are highly gregarious and mobile prey, and can readily inflict painful bites to chimpanzees. However, the risk may vary depending on the lifestyle of ants, i.e. epigaeic or intermediate, and whether dipping is targeted at nests or trails. Although dipping at nests provides a greater ant harvest per unit time, dipping at nests poses a greater risk to the chimpanzees due to the greater gregariousness and/or aggressiveness of ants in this context (Humle 2006; Möbius et al. 2008). Bossou chimpanzees adopt specific behavioural strategies to circumvent these risks, by either (1) positioning themselves more often above ground when dipping at nests than trails or (2) using longer tools particularly when dealing with ants at nests and with epigaeic species at nests, since these species are faster and have larger mandibles than intermediate species (Humle and Matsuzawa 2002; Humle 2006; Schöning et al. 2008). Bossou chimpanzees demonstrate two main techniques when consuming army ants off the tool: (1) direct mouthing, whereby the tool is directly pulled sideways through the lips and (2) pull-through, whereby the length of the tool is pulled through the closed fingers of the free hand, thus bringing the ants to the mouth (McGrew 1974) (see S1 and S2 in Electronic Supplementary Material for examples of both techniques). We found that the pull-through technique was almost exclusively associated with tools >50 cm long, whereas tools ≤50 cm were solely associated with direct mouthing.

Whereas previous studies of ant-dipping have focused on the micro-ecological factors influencing variations in this behaviour within and between communities, we investigated the influence of socially biased learning on the acquisition of ant-dipping by young. First we hypothesized that mothers would act as the prime models to their offspring, especially during the formative years of acquisition of this hazardous tool-use skill. Second, we explored whether mothers varied in their time spent ant-dipping and in the context in which they dipped, i.e. nest or trail and hypothesized that young who benefitted from more opportunity to learn ant-dipping would start observing and acquire the skill sooner, and would be more skilled and proficient in the skill than others of the same age. Finally, we hypothesized that mothers and offspring would match in technique and tool length employed. Since individual variation may also reflect sex differences in the propensity to use tool (Uehara 1986; Goodall 1986; McGrew 1992; Lonsdorf 2005), whenever possible, we also systematically tested potential sex differences in all measured variables relating to learning or performing ant-dipping efficiently.

Method

Study site

Bossou (7°39′N and 8°30′W) is situated in south-eastern Guinea, West Africa, 6 km from the foot of the Nimba Mountains on the border with Côte d'Ivoire and Liberia. A small community of chimpanzees (*P. troglodytes verus*) inhabits the forest surrounding the village. This community of wild chimpanzees has been habituated to observers, without provisioning, and has ranged in size between 12 and 23 individuals ever since 1976 (Sugiyama 1981, 1999; Matsuzawa 2006). It currently numbers 13 individuals. Small hills 70–150 m high covered in primary and secondary forest constitute the core area of the Bossou chimpanzee community. At the foot of the hills, cultivated or abandoned fields and secondary, riverine and scrub forests form a patchy mosaic for ca. 6 km in all directions. For further details refer to Sugiyama (1999), Matsuzawa et al. (2001) and Humle and Matsuzawa (2001, 2004).

Subjects and data collection

Ant-dipping is seasonal at Bossou and primarily observed during rainy season months (April–October). We focused our observations during the peak of the rainy season. Between August–October, 1997, July–September, 1999 and 2000 and June–September, 2001, a total of 32 ant-dipping sessions were recorded. Fourteen were video-recorded (12 h), while 18 could not be video-recorded, either due to poor visibility conditions or the brief duration of the session. Between June 2003–March 2004 and July–September 2005 and 2006, an additional 57 ant-dipping sessions were recorded, including 40 that were video-recorded (24 h) and 17 that were observed but could not be video-recorded. We defined a session as a period during which at least one chimpanzee was engaged in ant-dipping. The session terminated when the last remaining chimpanzee of the subgroup ended dipping. Session duration ranged from 8 s to 2 h 6 min 26 s, lasting on average 27 min 10 s (SE = ±4 min 28 s). Between 1997 and 2006, we gathered data on ant-dipping on 13 offspring (≤10 years old: 7 females and 6 males) (Table 1), as well as an additional adult male offspring aged 17 in 1997 and seven mothers.

After each session, we systematically recorded the dipping context, nest or trail, and measured the length (cm) of recovered tools which we assigned to their user whenever possible. Based on video observations focusing on the instant a tool was newly manufactured until it was discarded, only 3.4% (6 out of 177 tools) were actually modified in length during their use, so we can conclude that the length of the recovered tools reflected well their functional length. Tool assignment required the consensus of a minimum of two observers. We assigned a tool to its user 48.5% of a total 189 tools recovered between 1997 and 2001, and 79.2% of a total of 265 tools recovered between 2003 and 2006. Between 2003 and 2006, we systematically sampled the species of *Dorylus* targeted for subsequent taxonomic identification by C. Schöning, an expert in *Dorylus* (*Anomma*) taxonomy (Schöning et al. 2005; Kronauer et al. 2007). During this period, we also recorded the exact time that each individual was seen dipping and observed during daily follows. From these data, we calculated individual time spent ant-dipping as a percentage of total observation time for that individual during any given period. Age of acquisition was defined as when the young successfully harvested ants using a tool it had manufactured on its own at least 3 times during a single session (*sensu* Lonsdorf 2006).

Table 1 Summary of the frequency of video-recorded ant-dipping sessions for which individual's presence was confirmed by age class for each offspring ≤10 years old

Name	Sex	Age (years)										Total sessions
		0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	
Joya	Female	10 (11)	3 (5)									13 (16)
Jimato	Male	8 (8)	X	X	X							8 (8)
Fokaye	Male	–	2 (2)	2 (2)	0 (0)	X	X					4 (4)
Veve	Female	–	–	4 (4)	X	X	X					4 (4)
Peley	Male	0 (0)	1 (1)	0 (1)	–	2 (2)	0 (1)	2 (6)	4 (5)			9 (16)
Jeje	Male	–	1 (3)	1 (3)	1 (8)	–	11 (11)	1 (1)	16 (16)	9 (9)		40 (51)
Fanle	Female	–	0 (0)	0 (0)	0 (0)	–	1 (2)	0 (0)	4 (4)	8 (12)		13 (18)
Juru	Female	–	–	–	0 (7)	–	2 (3)	4 (4)	4 (4)	–	X	10 (18)
Poni	Male	–	–	–	–	0 (0)	–	0 (0)	0 (0)	0 (0)	4(4)	4(4)
Nto	Female	–	–	–	–	0 (0)	–	1 (2)	0 (3)	3 (3)	–	4 (8)
Yolo	Male	–	–	–	–	–	3 (6)	–	2 (2)	1 (3)	3 (3)	9 (14)
Vuavua	Female	–	–	–	–	–	3 (5)	–	1 (1)	2 (2)	2 (4)	8 (12)
Fotaiu	Female	–	–	–	–	–	2 (5)	–	2 (3)	2 (2)	–	6 (10)
Total		18 (19)	6 (10)	7 (10)	1 (15)	2 (2)	22 (33)	8 (13)	33 (38)	25 (31)	9 (11)	132 (183)

The number in parentheses indicates the total number of sessions (video-recorded plus ad libitum observations) where presence of individual was confirmed

"X" individual no longer present in the community, "–" data not available for this age class for that individual, "empty cells" represent age classes not covered by data set

We analysed the videos using Observer XT 6.0 (Noldus Information Technology). Each video session was coded by TH. A second coder analysed a set of 12 randomly chosen sessions, yielding a mean inter-observer reliability of 96.4 ± 0.5%. The major behaviours recorded were (1) dip duration per dip, (2) number of failed dips (as in dips yielding no ants), (3) tool length [based on actual tool length data or estimated as ≤50 or >50 cm (*sensu* Humle and Matsuzawa 2002)], (4) technique employed to consume ants from the tool (direct mouthing or pull-through), (5) time spent dipping, (6) time spent observing mother or other social models ant-dipping, i.e. the time that the gaze and attention of the young is on an individual's ant-dipping activity, (7) time spent performing other behaviours, e.g. play or grooming.

Data analysis

For analyses concerning frequency of sessions under different contexts, i.e. nest or trail, we combined all ad libitum and video data; otherwise all data are based on video analysis. For those analyses involving measures based on dips, i.e. percent error and dip duration, we only considered subjects for whom we had gathered data on a minimum of 20 dips for the condition(s) being analysed. The number of offspring varied each year as a result of death, birth, disappearance or absence of data for that subject during that particular study period (Table 1). Therefore, for analyses concerning the effect of learning opportunity, sex and age class on percent time spent observing others or dipping during a given session or on measures of performance such as dip failure (i.e. percent error), we used general linear mixed models (GLMMs) with SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA). The use of GLMMs allowed us to control for repeated measures on the same individual and the fact that we had mothers with multiple offspring in the data set. When a significant interaction between main effects emerged, we used Bonferroni correction in our post hoc analysis to account for multiple comparisons with $\alpha^* = \alpha/c$ (c is the number of comparisons performed). We used individual means based on individual session means for each age class considered unless otherwise specified. All standard errors were calculated based on individual means. As appropriate, we systematically checked the data for normality using a normality probability plot and a Kolmogorov–Smirnov test. If the data deviated significantly from normality, we used non-parametric rather than parametric statistics. All tests were two-tailed, and significance level was set at $\alpha < 0.05$. For all independent samples t tests, we employed the Levene's test to test for equality of variances and adjusted the degrees of freedom if equality of variances could not be assumed.

The mean inter-birth interval for Bossou female chimpanzees is 4.6 years, or 5.1 years if cases in which the previous infant had died within its first 3 years were excluded (Sugiyama 1994). For analyses involving comparisons between mothers with dependent young versus adult females with weaned young, we set weaning at 5 years. A cut off point of 10 years old was chosen to approximate the age when females exhibit their first oestrous and males reach puberty (Pusey 1983). For tests performed comparing mothers with offspring (≤5 years old) and mothers with offspring (>5 years old) or tool length for offspring ≤5 years old and more than >5 years old, we excluded the data set for offspring for which we obtained data across both age classes to avoid repeated measures. In addition, we considered only a single average data point for each mother with multiple offspring for each age class considered to avoid issues of pseudo-replication (Hurlbert 1984). When analysing time spent ant-dipping over total time observed, we calculated the time for mothers for the period during which her offspring was present in the community, as some offspring disappeared or died during the course of this study. Since these data were available only between 2003 and 2006, we used mothers' mean percent observation time spent ant-dipping across field seasons to categorize offspring (0–10 years old) into either high and low opportunity young (see below).

Results

Mothers as prime models for their offspring

Young ≤5 years old only dipped for army ants during sessions when their mother also dipped. Young between 5 and 10 years old dipped on average in 61.8% (SE = ±5.5%; range 46.6–100.0%) of the same sessions as their mother. In addition, adult females with dependent young (≤5 years old) spent significantly more sessions ant-dipping alone with their offspring without the presence of any other community member than adult females with weaned young (5–10 years old) (mothers with ≤5 years old: $X \pm \mathrm{SE} = 63.6 \pm 3.2\%$; range 58.2–69.7%, $N = 3$; mothers with weaned young: $X \pm \mathrm{SE} = 12.8 \pm 6.5\%$; range 0–33.3%, $N = 5$; independent samples t test: $t_6 = 5.701$, $P < 0.001$). Finally, during ant-dipping, young (≤5 years old) spent significantly more time observing their mother than other members of the community than weaned young (5–10 years old) (≤5 years old: $X \pm \mathrm{SE} = 92.1 \pm 3.0\%$; range 86.9–100.0%, $N = 4$; 5–10 years old: $X \pm \mathrm{SE} = 34.6 \pm 2.7\%$; range 0–66.1%, $N = 7$; independent samples t test: $t_9 = 4.722$, $P = 0.001$).

Maternal variation in dipping context

Mothers with young ≤5 years old dipped significantly more often at trails than nests than did adult females with weaned young (mothers with ≤5 years old: $X \pm \mathrm{SE} = 94.7 \pm 3.9\%$; range 87.1–100.0%, $N = 3$; mothers with weaned young: $X \pm \mathrm{SE} = 55.4 \pm 6.0\%$; range 36.4–69.3%, $N = 5$; independent samples t test: $t_6 = 4.617$, $P = 0.004$) (Fig. 1). We could not perform a within-subjects analysis of this pattern due to the small sample size ($N = 2$) of mothers for which data were available for both conditions (Jire and Pama). The data on these two mothers was, nevertheless, in the same direction, indicating that mothers may change their dipping context depending on the age of their offspring (Fig. 1).

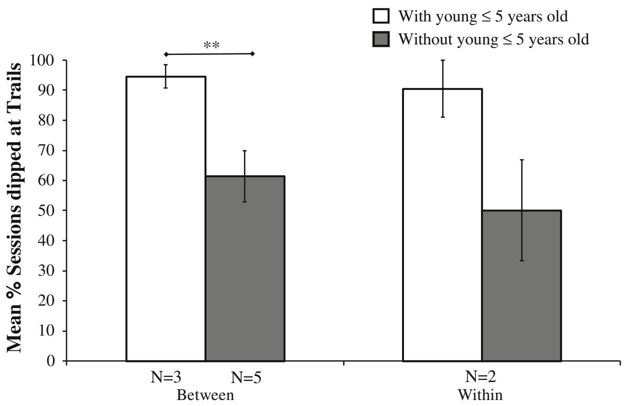

Fig. 1 Mean percentage of sessions between 1997 and 2006 study periods that mothers with unweaned (≤5 years old) versus weaned young (5–10 years) spent ant-dipping at army ants' trails. The between subjects analysis considers only a single data point per mother and excludes all offspring for which data were gathered across both age classes

Variation in time spent dipping in mothers

Mothers varied in their mean percent of observation time spent ant-dipping ($X \pm \mathrm{SE} = 0.17 \pm 0.03\%$; range 0.09–0.27%, $N = 7$). Mean percent observation time spent ant-dipping was independent of the total time that each mother was observed (Pearson correlation: $r = -0.187$, $N = 7$, $P = 0.688$), indicating that some mothers preferentially ant-dipped more than others.

Percent time spent ant-dipping over the total time observed correlated positively between mother and weaned offspring ≤10 years old (Pearson correlation: $r = 0.848$, $N = 6$, $P = 0.033$). This pattern remained significant even if we included in our sample offspring >10 years old (Pearson correlation: $r = 0.814$, $N = 8$, $P = 0.014$) (Fig. 2). Although data were available for only four young ≤5 years old, mother and young ≤5 years old also correlated positively in their percent time spent dipping over total time observed (Fig. 2). For offspring older than 5, there was no significant difference between males and females in their overall mean percent time spent ant-dipping (males: $X \pm \mathrm{SE} = 0.23 \pm 0.06\%$; range 0.08–0.43%, $N = 5$; females: $X \pm \mathrm{SE} = 0.20 \pm 0.04\%$;

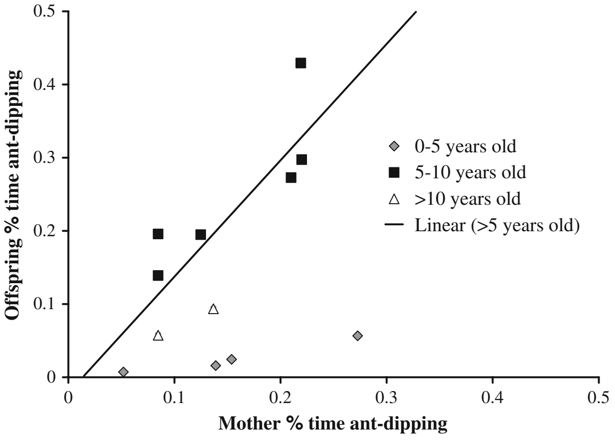

Fig. 2 Correlation between mother and offspring (>5 years old) in percentage time spent dipping over total time observed while both were present together in the community

range 0.14–0.27%, $N = 3$; independent samples t test: $t_6 = -0.301$, $P = 0.773$).

Time spent observing model

We classed offspring into two categories, depending on how much overall time their mother spent ant-dipping. Offspring classified in the high learning opportunity category ($N = 6$, 4 females and 2 males) had mothers ($N = 3$) who spent overall more than 0.2% of their activity time ant-dipping, whereas offspring in the low learning opportunity category ($N = 7$, 3 females and 4 males) belonged to mothers ($N = 4$) who spent less than 0.2% of their daily activities ant-dipping.

Although there was no significant effect of sex on time spent observing (GLMM, $N = 13$; sex: $F_{4,8} = 1.641$, $P = 0.205$), there was a significant interaction between age and learning opportunity, with high opportunity young between 0 and 2 observing ant-dipping being performed significantly more during a given session than low opportunity young (high: $X \pm \mathrm{SE} = 16.8 \pm 3.7\%$; range 13.8–20.9%, $N = 3$; low: $X \pm \mathrm{SE} = 0 \pm 0\%$; range 0%, $N = 2$; independent samples t test: $t_3 = -6.110$, $P = 0.009$, Bonferroni adjusted alpha level: $\alpha = 0.01$), whereas the reverse held for young between 4 and 6 (high: $X \pm \mathrm{SE} = 3.6 \pm 1.9\%$; range 4.3–8.4%, $N = 3$; low: $X \pm \mathrm{SE} = 11.8 \pm 2.4\%$; range 9.4–15.0%, $N = 4$; independent samples t test: $t_5 = 4.676$, $P = 0.005$, Bonferroni adjusted alpha level: $\alpha = 0.01$) (GLMM, $N = 13$; age × learning opportunity: $F_{4,8} = 11.743$, $P = 0.005$). Although the sample size of subjects per age class is small, this result suggests that offspring with more learning opportunity begin observing ant-dipping sooner than offspring with less learning opportunity

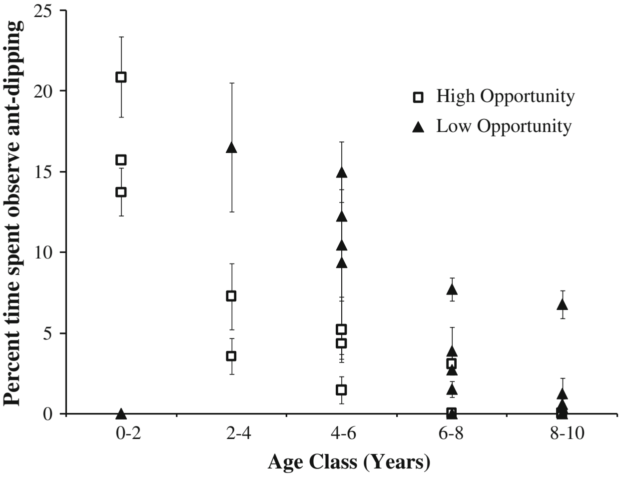

Fig. 3 Individual mean session percentage time spent observing others ant-dipping by age class for young who benefited from either high or low learning opportunity from their mothers

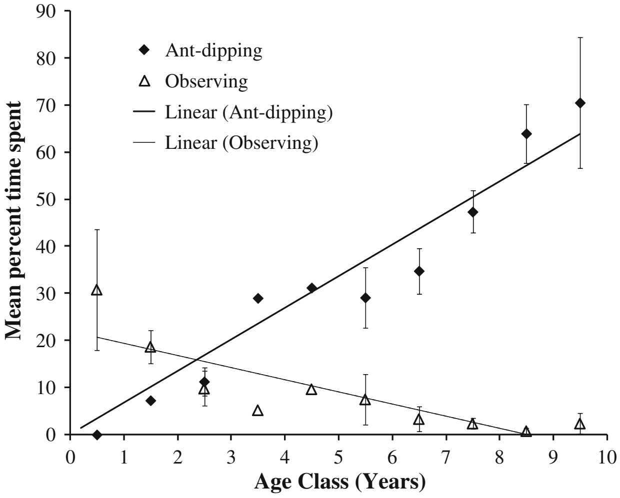

Fig. 4 Correlations with age of mean percentage time spent dipping or observing others ant-dip during a session (ant-dipping: Pearson correlation $r = 0.972$, $N = 10$, $P = 0.001$; observing: Pearson correlation $r = -0.843$, $N = 10$, $P = 0.002$)

(Fig. 3). As offspring grew older, they spent less time observing ant-dipping (Pearson correlation: $r = -0.843$, $N = 10$, $P = 0.002$) and more time engaged in ant-dipping (Pearson correlation: $r = 0.972$, $N = 10$, $P = 0.001$) (Fig. 4).

Age at first acquisition and learning opportunity

Among the five infants observed since birth, the mean age of first successful ant-dipping recorded was 29.6 months (SE = ±2.5, range 24–36 months). There was no apparent difference between females and males in the onset of ant-dipping (males: $X \pm \mathrm{SE} = 30.5 \pm 5.5$ months; range 25–36 months, $N = 2$; females: $X \pm \mathrm{SE} = 29 \pm 3.2$ months;

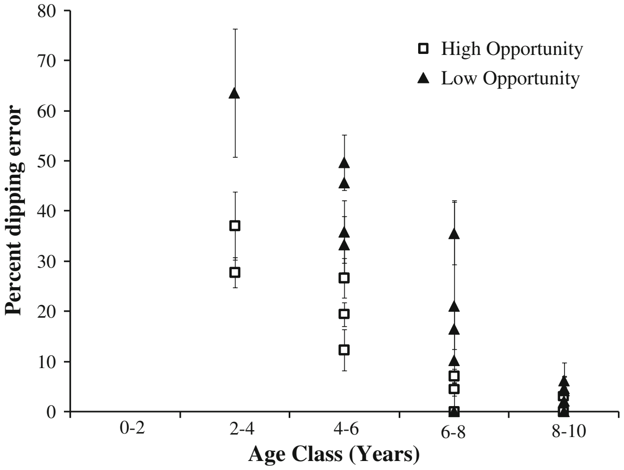

Fig. 5 Individual mean session percent dipping error by age class for young who benefited from either high or low learning opportunity from their mothers

range 24–35 months, $N = 3$; independent samples t test: $t_3 = -0.257$, $P = 0.814$). However, there was a significant difference between the onset of ant-dipping between high and low opportunity young (high: $X \pm SE = 25.7 \pm 1.2$ months; range 25–28 months, $N = 3$; low: $X \pm SE = 35.5 \pm 0.5$ months; range 35–36 months, $N = 2$; independent samples t test: $t_3 = 6.162$, $P = 0.009$).

Percentage error in dipping and opportunity learning

There was no effect of sex on percentage error in dipping (GLMM, $N = 13$; sex: $F_{4,8} = 0.533$, $P = 0.469$). However, a significant interaction emerged between age and learning opportunity, with high opportunity young between 4 and 6 performing significantly fewer dipping errors than low opportunity young (high: $X \pm SE = 17.8 \pm 2.5\%$; range 13.0–24.5%, $N = 4$; low: $X \pm SE = 42.8 \pm 2.3\%$; range 39–47%, $N = 3$; independent samples t test: $t_5 = -6.980$, $P = 0.001$, Bonferroni adjusted alpha level: $\alpha = 0.01$), whereas there was no difference beyond this age (GLMM, $N = 13$; age × learning opportunity: $F_{4,8} = 5.415$, $P = 0.037$) (Fig. 5).

Proficiency and opportunity learning

Through a series of human ant-dipping experiments (*sensu* Humle and Matsuzawa 2002 and Möbius et al. 2008), we found a significant increase in the number of ants gathered as dip duration increased, regardless of context or lifestyle of the ants. Dip duration for uninterrupted successful dips was used here as a relative measure of proficiency, i.e. the number of ants gathered per dip.

Mothers varied in their dip duration. Dip durations for mothers at trails were significantly longer than at nests (trail: $X \pm SE = 32.3 \pm 4.8$ s; range 17.9–47.4 s, $N = 5$; nest: $X \pm SE = 14.5 \pm 1.4$ s; range 11.1–17.9 s, $N = 5$; paired samples test: $t_4 = -4.415$, $P = 0.012$). The ranked dipping duration of mothers was significantly positively correlated between nests and trails (Pearson correlation: $r = 0.900$, $N = 5$, $P = 0.037$). Mothers, who dipped for shorter durations at nests, also performed shorter dips at trails and vice versa. To account for overall differences in dip duration between contexts, i.e. nest or trail, we analysed both contexts separately.

Dip durations for young ≤5 years old were significantly briefer than for those aged 5–10 years old when dipping at trails, the only condition for which we had sufficient data on young ≤5 years old (0–5 years old: $X \pm SE = 6.8 \pm 0.9$ s; range 5.3–9.4 s, $N = 4$; 5–10 years old: $X \pm SE = 31.2 \pm 4.6$ s; range 13.8–58.6 s, $N = 8$; independent samples t test: $t_{10} = -3.605$, $P = 0.005$). Considering only offspring >5 years old, offspring and mothers correlated positively in their dip duration in both contexts (nest: Pearson correlation $r = 0.876$, $N = 6$, $P = 0.022$; trail: Pearson correlation $r = 0.883$, $N = 7$, $P = 0.008$) (Fig. 6).

High opportunity young between 5 and 10 years old dipped for longer durations than low opportunity young of the same age class (Fig. 6). Although this pattern was significant when ant-dipping occurred at trails (independent

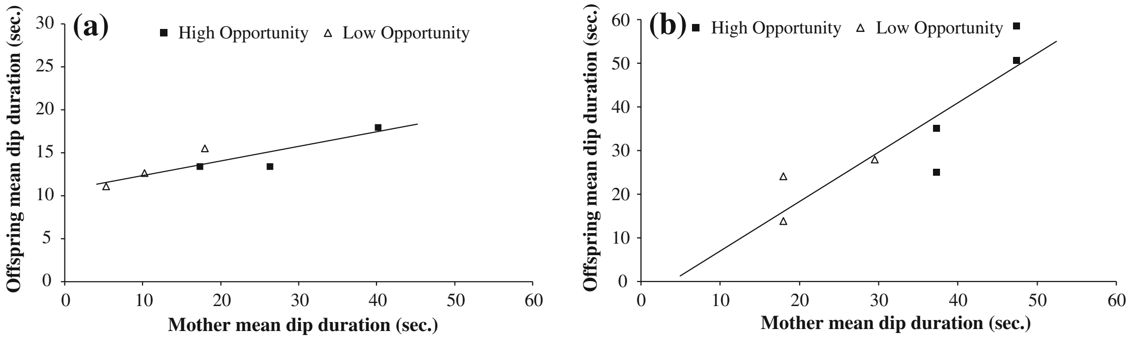

Fig. 6 Correlation between mother and offspring in their mean dip duration for successful and uninterrupted dips

Table 2 Frequency of total recorded dips and percentage of direct mouthing versus pull-technique performed by each Bossou chimpanzee while employing a tool >50 cm long since 1997

Individual	Sex	Birth: month/year	Total no. dips	% Direct mouthing	% Pull-through
Fana	**Female**	**Adult in 1976**	**12**	**100**	**0**
Fanle	Female	Oct-1997	120	63	38
Foaf	Male	Late 1980	57	39	61
Fotaiu	Female	Middle 1991	47	87	13
Jire	**Female**	**Adult in 1976**	**173**	**100**	**0**
Juru	Male	Nov-1993	138	78	22
Jeje	Male	Dec-1997	71	99	1
Nina	**Female**	**Adult in 1976**	**27**	**100**	**0**
Nto	Female	Early 1993	5	60	40
Pama	**Female**	**Adult in 1976**	**10**	**100**	**0**
Peley	Male	Apr-1998	55	7	93
Poni	Male	Feb-1993	8	88	13
Velu	**Female**	**Adult in 1976**	**47**	**100**	**0**
Vuavua	Female	Middle 1991	34	26	74
Yo	**Female**	**Adult in 1976**	**252**	**96**	**4**
Yolo	Male	Middle 1991	142	74	26
Kai	**Female**	**Adult in 1976**	**11**	**100**	**0**
Tua	Male	Adult in 1976	69	97	3

In 'Individual' column, offspring are indented below their mother whose name is bolded

samples *t* test: $t_7 = -2.049$, $P = 0.008$), it showed no significant effect at the nest (independent samples *t* test: $t_4 = -2.205$, $P = 0.092$). High learning opportunity young between 5 and 10 years old were relatively more proficient ant-dippers, particularly at trails, than low learning opportunity young of the same age class.

Tool length and technique

Since tool length varied depending on ant-dipping condition and lifestyle of the ants (Schöning et al. 2008), we analysed tool length between mother and offspring for condition and lifestyle considered separately and for pairs from whom we had gathered at least five tools each that we knew they had manufactured on their own. We only had sufficient data to analyse intermediate species at trails. Offspring ≤5 years old used significantly shorter tools than offspring older than 5 years old (Tukey HSD: $P = 0.002$) or mothers (Tukey HSD: $P = 0.012$) (0–5 years old: $X \pm \mathrm{SE} = 20.5 \pm 4.9$ cm; range 12.5–29.4 cm, $N = 3$; 5–10 year old: $X \pm \mathrm{SE} = 37.9 \pm 0.9$ cm; range 35.5–41.3 cm, $N = 6$; mothers: $X \pm \mathrm{SE} = 34.3 \pm 2.7$ cm; range 24.5–41.0 cm, $N = 5$; ANOVA: $F_{2,11} = 10.689$, $P = 0.003$). Since young ≤5 years old dipped with significantly shorter tools, we excluded them from the subsequent analysis. We found no correlation in mean tool length between mothers and offspring >5 years old (Pearson correlation: $r = -0.203$, $N = 6$, $P = 0.699$). We could not explore the effect of opportunity learning on tool length matching between mother and offspring since we had too few subjects. However, the two young in our sample that belonged to the high opportunity group matched their mothers more than the other four young in the sample.

Since at Bossou the pull-through technique was almost exclusively associated with tools greater than 50 cm (Humle and Matsuzawa 2002), we considered only data for tools >50 cm in analysing patterns of the techniques used. Among eight mother–offspring pairs only one mother (Yo) was ever observed pulling-through, and mothers were significantly less likely to adopt the pull-through technique than their offspring (Wilcoxon signed ranks test: $T = 0$, $N = 7$, $P = 0.02$, Table 2). Of all 18 individuals of the community observed using tools greater than 50 cm whilst ant-dipping, 6/7 of the older adult females (>13 years old) were never observed pulling-through, whereas all other members of the community whether young >5 years old or adult males used the pull-through technique along with direct mouthing technique when using tools >50 cm.

We never observed young ≤5 years old manufacturing and using a tool greater than 50 cm long. All young ≤5 years old only performed the direct mouthing technique. As shown above, compared to young >5 years old, young ≤5 years old spent in duration and proportionally significantly more time observing their mothers than other models and experienced ant-dipping sessions primarily alone alongside their mother. As a result young ≤5 years old rarely had the opportunity to observe others perform the pull-through technique or to dip at nests, a context also significantly associated with the pull-through technique at Bossou (Humle and Matsuzawa 2002; Humle 2006).

Discussion

Maternal role in influencing offspring's learning opportunities

Young ≤5 years old performed ant-dipping only during sessions when their mother also dipped. Mothers with dependent young also dipped significantly more frequently alone than mothers with young between 5 and 10 years old, emphasizing the importance of maternal influence during the first 5 years. The mother was the prime model and target of observation during ant-dipping for young ≤5 years old, whereas young between 5 and 10 years of age observed more the ant-dipping of activities of other members of the community, although at this later age, young spent altogether less time observing others perform ant-dipping.

Some mothers preferentially specialized on ant-dipping compared to other mothers. Mothers who ant-dipped more, therefore, provided greater opportunity for observation and practice for their young. We found no sex bias between high and low opportunity young. Young >5 years old correlated positively with their mother in their percent observation time spent ant-dipping. The correlation was also positive for young ≤5 years old. Similarly to Lonsdorf (2005) with termite fishing, the time dedicated to ant-dipping during a given session increased with age, while time spent observing decreased.

Risk and socially biased learning

Ant-dipping is a behaviour requiring a high degree of controlled manual coordination and dexterity and presenting a high degree of risk in its performance, especially at nests where the ants are more gregarious and are defending their colony. Mothers with young ≤5 years old dipped significantly more often at trails than nests. Although the yield per unit time at trails is lower than at nests (Möbius et al. 2008), mothers appeared to make this trade-off which minimized the risk posed to themselves and their young. Whether intentional or not, mothers thus facilitated skill acquisition in their offspring by providing them with safer conditions to observe at close range ant-dipping being performed and to eventually practice ant-dipping themselves.

Role of opportunity learning on observation, age of acquisition, performance and proficiency

Although our sample size of subjects is small, our results suggest that young with greater learning opportunity began observing ant-dipping and acquired the behaviour sooner than young with less learning opportunity. Although, we could not show that early observation influenced the onset of the behaviour, based on our understanding of the importance of observation in the acquisition of other complex behaviours and the onset of independent feeding during ontogeny in chimpanzees and other primate species (e.g. chimpanzees: Inoue-Nakamura and Matsuzawa 1997; Lonsdorf 2005; cottontop tamarins, *Saguinus oedipus*: Joyce and Snowdon 2007), observation of the behaviour was likely vital in acquisition alongside the opportunity to practise the behaviour under less risky conditions.

Our findings also suggest that young with greater learning opportunity performed fewer dipping errors, especially between 4 and 6 years old, than low opportunity young. Differential experience during formative years may explain this result, since, by age 6, there was no discernable difference in dipping error between high and low opportunity young. Dip duration for young ≤5 years old was significantly shorter than for older offspring. Assuming that dip duration was a good measure of proficiency, this result indicates that it takes several years for young to acquire the proficiency of adults. Young between 5 and 10 years old with greater learning opportunity demonstrated longer dip durations compared to low opportunity young. Dip duration was positively correlated between mother and offspring, revealing for the first time in chimpanzees a significant relationship in proficiency in a tool-use skill between mother and offspring. Since mother and offspring time spent ant-dipping were positively correlated, the similarity in their proficiency might be the result of experience. Since ant-dipping is seasonal and relatively rare, experience is likely to play a very important role in determining competence level. Such an effect of experience on learning has been demonstrated in a captive study comparing performance in a raking tool task between enculturated and semi-enculturated chimpanzees (Furlong et al. 2008).

Finally, practice and greater exposure to ant-dipping positively influenced the learning trajectory and skill level reached by young, confirming the importance of the education by master-apprenticeship process in tool-use acquisition by young (Matsuzawa et al. 2001) and of the socially biased learning opportunities provided especially by the mother during ontogeny. Lonsdorf (2005) also found that young females at Gombe spent more time watching others termite-fish than males, and were more precocious in acquiring and performing termite fishing. Although Lonsdorf (2006) found no overall correlation between mother's and offspring's proficiency, by age 2.5 years, there were extreme differences in skill level among young that positively related to the amount of time mothers spent alone or with their family, a predictor of the amount of time mothers spent termite fishing.

Socially biased learning and sex differences

Several studies across a range of species have revealed sex differences in performance of socially learned tasks (reviewed in Choleris and Kavaliers 1999). Chimpanzees are no exception and sex differences among adults have been demonstrated in time spent foraging for insects with the aid of tools (termite fishing at Gombe: McGrew and Tutin 1979; ant-fishing at Mahale, Tanzania: Hiraiwa-Hasegawa 1989), time spent hunting mammalian prey (e.g. Gombe: McGrew and Tutin 1979) or nut-cracking efficiency (Taï, Côte d'Ivoire: Boesch and Boesch 1981, 1984). Females surpassed males in all contexts, except for hunting, which was performed predominantly by adult males. McGrew and Tutin (1979) and Uehara (1986) suggested that females at those sites needed to spend more time foraging on insects with tools to compensate for their relative reduced protein gain through the consumption of mammalian prey. Bossou females and males >11 years percent showed no sex difference in time spent dipping (females: $X \pm SE = 0.12 \pm 0.03\%$; range 0.01–0.3 s, $N = 9$; males: $X \pm SE = 0.11 \pm 0.06\%$; range 0.01–0.3 s, $N = 4$; independent samples t test: $t_{11} = 0.871$, $P = 0.871$). Hunting for mammalian prey at Bossou is rare compared to other study sites and is a solitary activity with no sex bias (T. Humle, unpublished data). Males at Bossou may need to forage on insects as much as females do to obtain an equivalent protein intake. This observation provides indirect support for the "protein balance" hypothesis proposed by McGrew and Tutin (1979) and Uehara (1986). However, to truly validate this hypothesis, we would need to more carefully evaluate protein intake, whether through hunting or insectivory, between sexes across these different field sites.

An alternative hypothesis, similar to one proposed by van Schaik (2003) for individual differences, is that sex differences among adults reflect differences in learning trajectory during ontogeny. We found no sex differences in the percent observation time spent, performance (percentage error and dip duration) or in the age of acquisition of young. In contrast, Lonsdorf (2005) found sex differences in the development of termite fishing skills at Gombe. These results appear to mirror the presence or absence of sex differences among adults in these respective tool-use tasks at each site. Nevertheless, these differing results may be due to small samples of subjects at both sites and more data are needed to confirm such a pattern. However, our results also indicate that mothers and adult offspring positively correlated in percent observation time spent ant-dipping, further providing further support for this hypothesis. If substantiated, the lack of sex difference in the development of ant-dipping compared to termite fishing may be due to the characteristics of the behaviours. Ant-dipping is more hazardous and occurs under more variable contexts than termite fishing, thus possibly requiring both male and female young to pay attention, observe and practice this tool-use behaviour in order to reduce the risk of getting bit. Finally, we need more studies across sites and species to satisfactorily test this hypothesis, as well as the role of constraints posed by the behaviours themselves in explaining sex differences observed among adults.

Socially biased learning opportunity and culture

Culture has been operationally defined to encompass behaviours that are socially transmitted within and between generations in groups and populations of a species (Parker and Russon 1996; Laland and Hoppitt 2003). Despite the importance of micro-ecological influences on ant-dipping, we have shown here that early observation and the opportunity for observation and practice, especially provided by the mother, are potential key determinants of acquisition, performance and proficiency during development. If some sophisticated social learning was at work, we might have expected matching between mothers and offspring in tool length or technique used. However, unlike termite fishing at Gombe, where young females matched the functional tool length of their mother, young >5 years old at Bossou failed to match the tool length of their mother under similar dipping context targeted at species with the same lifestyle. However, high learning opportunity young matched the average tool length of their mother more than low learning opportunity young. To confirm any consistency in this pattern, we would require further data on more subjects and across more contexts. Nevertheless, we provide some support for van Schaik (2003) proposal that degree of exposure and opportunities for learning play a key role in determining individual variation within populations or communities of animals. We will need data on these young's performance and competence as adults to completely validate this hypothesis.

Young ≤5 years old manufactured and used significantly shorter tools than young >5 years old or adults. Since at Bossou, direct mouthing was correlated with the use of short tools (Humle and Matsuzawa 2002), as predicted, these young only performed the direct-mouthing technique when consuming ants. Therefore, for dependent young we could not test matching between mother and offspring in technique. Only one mother >13 years old ever exhibited the pull-through technique when using tools greater than 50 cm long, whereas all young >5 years old and all adult males exhibited this technique. Therefore, young could not acquire this technique through observations of their mother. Young between 5 and 10 years old, however, spent proportionally more time observing other members the community and ant-dipped more in the presence of others than young ≤5 years old. These young between 5 and 10 years old therefore had the opportunity to observe others use the pull-through technique with tools greater than 50 cm long. It is thus possible that this technique was acquired through observation of others. Marshall-Pescini and Whiten (2008) suggested in an experimental study requiring captive chimpanzees to dip and probe for honey employing two techniques that young chimpanzees become ‘stuck’ on a technique they initially learn. They concluded that chimpanzees were constrained in exhibiting cumulative cultural evolution. However, our findings among young wild chimpanzees do suggest otherwise, as young >5 years old learned to adopt the pull-through after first performing the direct mouthing as infants.

This still does not explain why so few adult females employ the pull-through technique. It is possible that all Bossou chimpanzees are able to acquire and perform the pull-through technique. However, adult females may be more competent at direct mouthing, especially when using long tools and dipping under risky contexts, than other community members who may thus rely occasionally on the presumably safer pull-through technique (Boesch and Boesch 1990). This hypothesis warrants further investigation, especially since Hrubesch et al. (2008) have evidence for an influence of competence level on individual specialization within a group of captive chimpanzees faced with solving a complex foraging task.

Ant-dipping at Bossou is displayed by all able-bodied members of the community and is perpetuated from one generation to the next. Moreover, some chimpanzee communities do not exhibit ant-dipping, although army ants are available and stick- or stalk-tool uses have been observed in other contexts at most of these sites (Humle and Matsuzawa 2002; Schöning et al. 2008). Our study has revealed the importance and relevance of maternal and other social influences through socially biased learning opportunities on the acquisition of ant-dipping. Our results corroborate evidence that simple social-mediation and tolerated coordination in time and space are as important for behavioural maintenance and transmission as the capacity for sophisticated social learning mechanisms (e.g. cottontop tamarins: Humle and Snowdon 2008). We conclude that although ant-dipping behaviour does reflect to some extent local behavioural responses to prey characteristics and behaviour, it is and remains a good example of culture in chimpanzees.

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