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## A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the *Pan* lineage

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Chimpanzees, *Pan troglodytes*, are the most sophisticated tool-users among all nonhuman primates. From an evolutionary perspective, it is therefore puzzling that the tool use behaviour of their closest living primate relative, the bonobo, *Pan paniscus*, has been described as particularly poor. However, only a small number of bonobo groups have been studied in the wild and only over comparably short periods. Here, we show that captive bonobos and chimpanzees are equally diverse tool-users in most contexts. Our observations illustrate that tool use in bonobos can be highly complex and no different from what has been described for chimpanzees. The only major difference in the chimpanzee and bonobo data was that bonobos of all age–sex classes used tools in a play context, a possible manifestation of their neotenus nature. We also found that female bonobos displayed a larger range of tool use behaviours than males, a pattern previously described for chimpanzees but not for other great apes. Our results are consistent with the hypothesis that the female-biased tool use evolved prior to the split between bonobos and chimpanzees.

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Chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*, are particularly relevant for investigations into the origins of the human mind. The two species shared a common evolutionary history until very recently, and their current phenotypic similarities and differences have been the cause of much debate (Stanford 1998; Wrangham & Pilbeam 2001). One particularly relevant topic concerns tool use. Wild chimpanzees have shown a notable array of population-specific tool use behaviours (Goodall 1986; Whiten et al. 1999), a manifestation of their ‘material culture’ (McGrew 1992). Only a small number of comparable observations of bonobo tool use have been made in the wild (Kano 1982; Ingmanson 1996; Hohmann & Fruth 2003), suggesting that bonobos might differ from chimpanzees and humans in this fundamental way (McGrew 1998).

However, a number of isolated reports have described captive bonobos as rather skilful tool-users (Jordan 1982; Toth et al. 1993; Gold 2002). Additionally, the two species do not differ in significant ways in terms of manipulation skills and motor sequences (Takeshita & Walraven 1996). In terms of the underlying cognitive abilities, interpretations are contradictory. One study found that tool use in

bonobos was not based on a profound understanding of physical causation (Helme et al. 2006), in contrast to chimpanzees (Limongelli et al. 1995; Mulcahy & Call 2006a). However, bonobos, similarly to orang-utans, *Pongo pygmaeus*, have been shown to be capable of saving tools for future use (Mulcahy & Call 2006b) and a more recent report concluded that captive bonobos have the same understanding of the functional properties of tools as all other great apes (Herrmann et al. 2008). Thus, the most recent results appear to describe bonobos as having equal tool-using capabilities as chimpanzees.

Reports from the wild suggest a potentially interesting pattern. In terms of context, chimpanzee tool use occurs mostly during feeding and acquisition of difficult foods (such as hard-shelled fruits or concealed insects; McGrew 1992). In contrast, bonobo tool use has been observed mainly in social situations, such as communication and play, but also during cleaning or as protection from rain (Ingmanson 1996), a pattern also seen in captivity (de Waal 1986). Currently, however, it is not possible to draw any firm conclusions. Chimpanzees are well known for their group- and population-specific behavioural differences (e.g. Whiten et al. 1999; Crockford et al. 2004) and, crucially, some chimpanzee groups hardly use tools in the wild, despite decades of long-term observations (Reynolds 2005). The small captive population of bonobos and the difficulties of obtaining data from the wild may thus be largely responsible for the reported species differences in the wild. For instance, the most extensive study of chimpanzee

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culture was based on long-term data from seven different field sites (Whiten et al. 1999) while comparable data for bonobos were only from two sites (Hohmann & Fruth 2003). Long-term studies with chimpanzees have shown that females are more accomplished tool-users during food acquisition, a fact with some implications for theories of human evolution (McGrew 1979; Marlowe 2005; Byrne 2007; Pruetz & Bertolani 2007). So far, no comparable findings have been reported for bonobos, possibly because of the lack of observations in the wild. It is therefore unknown whether the female bias seen in chimpanzees is a species-specific peculiarity or whether it is present in both species.

In this study, we compared the tool use behaviour of captive chimpanzees and bonobos at various sites. For chimpanzees, we relied on the extensive catalogue compiled by Beck (1980), which we complemented with more recent data. For bonobos, we combined the published records (Savage 1976 as quoted in Beck 1980; Jordan 1982; Gold 2002) with our own data collected from five groups at four locations. We were particularly interested in potential sex differences in tool use, whether there were idiosyncratic tool use behaviours, and to what extent there was flexibility in tool use.

## METHODS

### Subjects

We collected data from five bonobo groups, housed at San Diego Zoo and San Diego Wild Animal Park, U.S.A., Lola ya Bonobo, DRC, and Twycross Zoo, U.K. (two groups). Group sizes ranged from five to 22. Age class categories were derived from Goodall (1986) simplified to four stages: infants (0–5 years), juveniles (childhood to early adolescence), subadults (late adolescence) and adults. Individuals were considered adults if they were either fully grown or had already given birth. All bonobos were able to witness tool use behaviour of humans on numerous occasions and interactions with human caretakers were not uncommon. This was particularly true at Lola ya Bonobo where caretakers feed them daily using plastic bottles and demonstrated to individuals from a young age how to break open nuts.

### Study Sites

#### San Diego Zoo

Data were collected from the bonobos at San Diego Zoo between January and April 2008 with permission from the Animal Care Management at San Diego Zoo following approval by its IUCAC committee. The group consisted of three adult females, two adult males, one subadult female, one juvenile male and one juvenile female. The group was housed in a 560 m<sup>2</sup> outdoor area, connected to a heated indoor housing facility, which consisted of one large room (136 m<sup>2</sup>) and four smaller rooms (55 m<sup>2</sup> each), which also served as sleeping areas at night. Individuals were unable to pass between the indoor and outdoor enclosures during the day. The composition of the Zoo group was managed with an attempt to simulate a fission–fusion social system. Individuals were usually fed in a group setting three to four times per day, both indoors and outdoors, with a diet of roughly equal proportions of ape biscuits and cereals, vegetables, green leaf vegetables and fruits (approximately 25 types of food per week). Water was freely available. Individuals were also given additional enrichment feeds (such as ice lollies and seeds) several times per week. An artificial termite mound in the outdoor enclosure, filled daily with honey and human baby food, provided additional enrichment.

#### San Diego Wild Animal Park

Data were collected at San Diego Wild Animal Park between January and April 2008, with permission from the Animal Care

Management at San Diego Wild Animal Park and approval by its IUCAC committee. The group consisted of three adult females, three adult males, one subadult female and one juvenile female. The group was housed in an approximately 3000 m<sup>2</sup> outdoor area, connected to a heated indoor housing facility, which consisted of one large room (47 m<sup>2</sup>) and four smaller rooms (40 m<sup>2</sup> each) serving as sleeping areas at night. Individuals were unable to pass between the indoor and outdoor enclosures during the day. The group spent the entire observation time together. Individuals were usually fed in a group setting three to four times per day, both indoors and outdoors, with a diet of roughly equal proportions of ape biscuits and cereals, vegetables, green leaf vegetables and fruits, approximately 25 different types of food per week. Water was freely available. Individuals were also given separate supplementary enrichment feeds (such as ice lollies and seeds) several times per week.

#### Lola ya Bonobo

Data were collected at the Lola ya Bonobo sanctuary in Kinshasa between September and November 2008 and between August and November 2009, with permission from 'Les Amis des Bonobos du Congo' (ABC) Scientific Committee and its Scientific Coordinator. Lola ya Bonobo is a facility for orphan bonobos usually seized from the bush meat and pet trade. All data were collected in 'Group 1', which consisted of six adult females, three subadult females, three adult males, three subadult males and three juvenile males. Four infants were also present but their interactions with tools were not taken into account. The group was housed in a 10 ha outdoor enclosure during the day and in a subdivided indoor facility at night. We only conducted observations when bonobos were visible in the open, nonforested areas of the enclosure (along the perimeter of the enclosures; approximately 15% of the total enclosure area). Despite this relatively small area, the bonobos spent most of their time on it (50–60% of daytime; Z. Clay, unpublished data), mainly because food was provisioned there. However, we cannot rule out that other tool use took place in the forested areas where observations were not possible. Individuals were fed a seasonal selection of fruits in the morning and vegetables in the afternoon, approximately 6 kg per individual per day, as a scatter feed to the entire group. At midday, bonobos were provided soy drink, enriched with honey, maize and vitamins, by a caregiver using a bottle. Additional enrichment food, such as bananas, peanuts and seasonal fruits, were provided once or twice per day. Bonobos had access to water from lakes and streams during the day. In addition to edible enrichment, bonobos were given enrichment items, such as plastic bottles and fruit shells, and they had free access to the large forested areas.

#### Twycross Zoo

A fourth set of data was collected at Twycross Zoo from March to July 2009 from two separate groups, following approval from the Twycross Zoo Research Coordinator and Zoo Management Committee and in compliance with the ethical guidelines set out by the British and Irish Association of Zoos and Aquariums (BIAZA). The first group consisted of two adult males, two adult females and one subadult female. The second group consisted of three adult females, one adult male, one subadult male and one juvenile female. The two groups were housed separately in one indoor building (124 m<sup>2</sup>) composed of two identically designed heated indoor facilities. On each side of the building, the housing facilities for each group were composed of one main 'day room' (62 m<sup>2</sup>) and three off-show 'feeding rooms' (22 m<sup>2</sup>). The two bonobo groups shared the outdoor enclosure (588 m<sup>2</sup>) through temporal separation, with one group typically having access in the morning, and the other one in the afternoon. Both groups were fed a range of fruits and vegetables twice per day (typically four types of fruits and six to nine types of vegetables) in a scatter feed in either their outdoor or indoor enclosure. Water was freely available; milk and cordial were

provided several times per day. In addition, bonobos received regular enrichment feeds, such as seeds or frozen juice blocks, as well as access to a diverse array of edible branches and enrichment materials (some edible, such as seed boxes, and some inedible, such as clothing/papers). Once or twice per week, bonobos were also provided additional feeds of live yoghurt, egg, cheese and bread. In both groups, an artificial termite mound was present in the indoor enclosure, although they were not used during the time of this study.

#### Data Compilation and Analyses

At all four facilities, tool use was recorded on an all occurrence basis by T.G. and Z.C. during focal animal observations (Altmann 1974). At Lola, observation time was balanced across individuals (each day, one individual was selected and followed from 0800 to 1630 hours), which enabled us to conduct systematic comparisons between species and between individuals. At San Diego Zoo, San Diego Wild Animal Park and Twycross Zoo, observation time was unequal, so the data were only used to compile tool use catalogues, which were combined with the already published records (Savage 1976; Jordan 1982; Gold 2002). Data for wild bonobos were compiled from the published records (Ingmanson 1996; Hohmann & Fruth 2003). The tool use catalogue used to compare the two species was largely based on Beck's (1980) compilation because it still represents the most up-to-date published catalogue for captive chimpanzees. Newer catalogues only exist for wild populations (Whiten et al. 2001). Minor modifications in terminology and classifications were necessary to facilitate comparisons. We included all contexts and behaviours described by Beck's original list to enable the broadest possible comparison between the two species (Table 1; see Appendix Table A1 for definitions, descriptions and page numbers used by Beck 1980).

Any report or observation of distinct tool use behaviour in captive bonobos or wild chimpanzees was taken as an indication that this behaviour was present. Unfortunately, it was not possible to compare frequency data in a systematic way, mainly because some of the published records did not provide them. Data were collected by T.G. (San Diego, Lola) and Z.C. (San Diego, Lola, Twycross) according to Beck's (1980) descriptions (Table 1).

An interobserver reliability test was conducted in which the two observers independently coded 21 video clips containing tool use behaviours of bonobos at Lola ya Bonobo. The featured tool use behaviours represented 18.5% of the entire tool catalogue recorded at Lola performed by 10 different individuals (group 1:  $N = 8$ ; group 2:  $N = 2$ ). Reliability in tool classification and recognition of individuals was perfect at 100% with no disagreements or omissions.

We used the results of the surveys to determine whether there were systematic differences in tool use behaviour both between the two species (chimpanzee versus bonobo) and between habitats (wild versus captivity). For this analysis, we determined whether or not a tool use behaviour (i.e. each line in Table 1) was present in the four groups (wild chimpanzees, wild bonobos, captive chimpanzees, captive bonobos). To enable systematic comparisons, we removed all tool use behaviours that could not have occurred naturally (e.g. if they were part of a specific experiment). We then conducted Pearson chi-square tests to compare the diversity of tool use behaviours in each of the four groups and to determine whether species membership or habitat had significant effects on the observed proportion relative to all possible tool use behaviours. In a second analysis, we compared the two species in captivity per context. This way, we were able to rule out that the effects were due to unequal contributions by some contexts in terms of the number of observed tool use behaviours. We were unable to carry out this analysis with wild populations since the bonobo tool set was too small to do statistics.

To investigate whether there were systematic sex and age differences in bonobo tool use, we analysed data collected at Lola ya Bonobo.

Using univariate analyses of variance, we compared individuals in terms of their contributions to the catalogue both for tool use behaviours and tool-related behaviours (e.g. using a hard surface to crack a fruit). Data collection started after both observers were able to identify individuals without difficulties. Experienced field assistants were always present and could be consulted if there were doubts.

For each individual we entered sex (male versus female) and age class (adult versus nonadult) as fixed factors and tool variety (the total number of different tool use behaviours produced by the individual) as the dependent variable. One female (MM) was excluded from these analyses because she was raised by humans before coming to the sanctuary at the age of 18. We first determined the general effect of sex and age class on the total number of observed tool use behaviours, and then conducted the same analysis per context. All statistical tests were two tailed and conducted with SPSS for Windows Release 17.0 (SPSS Inc., Chicago, IL, U.S.A.).

## RESULTS

### Species Differences

Following Beck (1980), we discriminated 63 different tool use behaviours in 14 contexts, each containing one to nine actions (mean  $\pm$  SD =  $2.7 \pm 2.4$ ; Table 1). Direct comparisons between chimpanzees and bonobos, both in the wild and in captivity, were possible over 52 behaviours. Eleven tool use behaviours had to be excluded because they involved contexts that were not available to captive individuals (e.g. hunting, rainstorms) or because they were not spontaneous, but artificially elicited as part of other ongoing behavioural experiments (see italic fields, Table 1).

We first compared the four data sets in terms of overall differences in tool use in the four groups (wild chimpanzees, captive chimpanzees, wild bonobos, captive bonobos). Of the 52 tool use behaviours, captive chimpanzees produced 47, wild chimpanzees 44, captive bonobos 42 and wild bonobos eight. Comparisons revealed an overall effect of species ( $\chi^2_1 = 37.01$ ,  $P < 0.001$ ) and habitat ( $\chi^2_1 = 30.14$ ,  $P < 0.001$ ). However, when analysing the tool use behaviour of the two species separately, we found no differences between wild and captive chimpanzees ( $\chi^2_1 = 0.79$ ,  $P = 0.37$ ), but a significant difference between captive and wild bonobos ( $\chi^2_1 = 44.53$ ,  $P < 0.001$ ). When analysing the two habitat types separately, we found no difference between captive chimpanzees and bonobos ( $\chi^2_1 = 1.95$ ,  $P = 0.16$ ) but a significant difference between wild chimpanzees and bonobos ( $\chi^2_1 = 49.85$ ,  $P < 0.001$ ). Thus, the differences reported in the previous analysis resulted from the contribution of the wild bonobos only: of all 52 tool use behaviours, only eight have so far been reported from wild bonobos (compared to 44 in wild chimpanzees). Of all 52 tool use behaviours, only seven were different in captive bonobos and chimpanzees. Of these seven, one (dental autogrooming) was not found in captive bonobos, although it has been observed in the wild.

We then conducted a context analysis and found that the tool use catalogue of captive bonobos and chimpanzees was identical for nine of 13 possible contexts ('Play', 'Oddness', 'Balancing', 'Propping', 'Stacking', 'Digging', 'Cleaning', 'Liquids', 'Draping'; 'Escape' was not included as no attempt was ever witnessed). In other words, all the behaviours observed in captive chimpanzees had also been observed in at least one of the captive bonobo groups. Additionally, we found no significant differences in two other contexts ('Antagonism':  $\chi^2_1 = 1.51$ ,  $P = 0.22$ ; 'Food acquisition':  $\chi^2_1 = 0.42$ ,  $P = 0.52$ ). Tool use was also observed in both captive chimpanzees and bonobos during 'Grooming', but only wild bonobos used tools during dental grooming. The only context that differed between chimpanzees and bonobos on the whole was 'Baiting' with no observations in wild or captive bonobos.

**Table 1**  
Summary of tool use behaviours observed in wild and captive chimpanzees and bonobos

Context	No.	Action	Behaviour	Chimpanzee		Bonobo					Comparison		
				Wild	Captivity	Savage 1976	Jordan 1982	Gold 2002	Ingmanson 1996	Lola ya Bonobo	Note	Captivity	
Antagonism	1	Brandishing tools	Agonistic intimidation displays	Yes	Yes		Yes				Yes	Yes	✓
			Immature Agonistic intimidation displays	Yes	Yes*					No	No rainstorm witnessed	No	x
			Sticks in rainstorm	Yes	Yes					?		?	n/a
			Wave tools against flies	Yes	No				Yes	No	Present in the wild	No	✓
			Sticks in play	Yes	Yes		Yes		Yes	No	Present in Twycross and San Diego groups	Yes	✓
	2	Dragging tools	Dragging, rolling, and/or kicking objects during display (conspecific)	Yes	Yes		Yes	Yes†	Yes	Yes	Present in Twycross and San Diego groups	Yes	✓
			Dragging, rolling, and/or kicking objects during display (heterospecific)	Yes	Yes*					No	Present in Twycross and San Diego groups	Yes	✓
			Drag branches during rainstorm	Yes	Yes					?	No rainstorm witnessed	?	n/a
			Dragging during social play	Yes	Yes†		Yes			Yes	Present in Twycross groups	Yes	✓
	3	Unaimed throwing	Unaimed throwing in arousal states	Yes	Yes	Yes			Yes	Present in Twycross groups	Yes	✓	
			Unaimed throwing in reaction to other species	Yes	Yes*					Yes	Present in Twycross groups	Yes	✓
			Unaimed throwing during social interaction	Yes§	Yes		Yes			No	Present in Twycross and San Diego groups	Yes	✓
	4	Aimed throwing	Unaimed throwing resulted from frustration	Yes§	Yes				Yes	Present in Twycross groups	Yes	✓	
			Unaimed throwing during play	Yes	Yes*		Yes		Yes	Present in Twycross groups	Yes	✓	
			Aimed throwing during agonistic interaction	Yes	Yes	Yes	Yes		Yes	Present in Twycross groups	Yes	✓	
	5	Dropping	Interspecific aimed throwing	Yes	Yes		Yes		Yes		Yes	✓	
			Interspecific aimed throwing (hunting)	Yes	X				X			X	n/a
			Aimed throwing during social play	Yes§	Yes		Yes		Yes	Present in Twycross groups	Yes	✓	
	6	Clubbing	Conspecific dropping during social play	Yes	No				No	Present in San Diego groups	Yes	✓	
			Conspecific clubbing during agonistic episodes	Yes	Yes				No		No	x	
7	Prodding or jabbing	Interspecific clubbing	Yes	Yes		Yes	Yes	No		Yes	✓		
		Social play conspecific clubbing	Yes	Yes				Yes	Present in Twycross groups	Yes	✓		
		Conspecific prodding or jabbing during agonistic contexts	Yes§	Yes		Yes		Yes	Present in Twycross groups	Yes	✓		
8	Tree pounding	Interspecific prodding or jabbing	Yes§	Yes				Yes		Yes	✓		
		Insect or animal spearing	Yes**	Yes				No		No	x		
9	Frustration pounding	Pound on tree buttresses (or equivalent) during agonistic displays	Yes	Yes*				Yes	Present in Twycross and San Diego groups	Yes	✓		
		Pound on objects after unsuccessful attempts	X††	Yes				?		?	n/a		
Grooming	1	Dental grooming	Dental allogrooming	No	Yes				No		No	x	
			Dental autogrooming	Yes	Yes††			Yes	No	Present in the wild	No	x	
2	Grooming	Interspecific grooming	No	Yes			Yes	Yes	On dogs and humans	Yes	✓		
		Self-grooming using tools	Yes††	Yes			Yes	Yes		Yes	✓		
Escape	1	Escape enclosure	Use of sticks as pitons to escape enclosure	X	Yes				?	No attempt of escape witnessed	?	n/a	
Play	1	Infant Termite fishing	Insert and probe in mounds or nests of termites (or equivalent)	Yes	Yes				Yes	Present in Twycross and San Diego groups	Yes	✓	
			Pound objects on others for playful purpose	Yes*	Yes				Yes	Present in Twycross groups	Yes	✓	
			Exploration with stick	Yes§	Yes				Yes		Yes	✓	
Oddness/ Inaccessibility	1	Using tool when reluctant to touch with hand or inaccessible	Touching inhabitual objects	Yes	Yes		Yes		?		Yes	✓	
			Interspecific touching	Yes§	Yes				Yes	Present in San Diego groups	Yes	✓	
Balancing and climbing	1	Secure object	Secure object (e.g. suspended food)	No	Yes		Yes		?		Yes	✓	
			Playful balancing	No	Yes				Yes	Present in Twycross groups	Yes	✓	
Propping and climbing	1	Secure suspended food	Secure suspended food	No	Yes			Yes	?		Yes	✓	
			Escape enclosure propping	X	Yes		Yes		?		?	Yes	✓

Stacking	1	Access to suspended lures or extended vision	Gain access to suspended lures or to extended vision	No	Yes	Yes	?		Yes	✓
	2	Escape enclosure stacking	Escape enclosure stacking	X	Yes		?	No attempt of escape witnessed	?	n/a
Food acquisition	1	Termite fishing	Insert and probe in mounds or nests of termites	Yes	Yes	Yes	X	Present in Twycross and San Diego groups	Yes	✓
	2	Ant Dipping	Perforate termite mound Dipping for fossorial ants Dipping for arboreal ants	Yes	X		X	No termite mound in captivity	X	n/a
	3	Wild: Honey fishing. Captivity: Artificial fishing	Insert tool and probe in bee/artificial nest	Yes	Yes		? +	No ant trail observed in zoos	?	n/a
	4	Reaching food or object	Reaching and retrieving food lures or objects	Yes	No		? +	No ant trail observed in zoos	?	n/a
	5	Opening tough rinds or shells	Nut cracking Hard-shell fruit cracking	Yes	Yes		X	Present in Twycross and San Diego groups	Yes	✓
	6	Leverage or enlargement of openings	Nut cracking Hard-shell fruit cracking Nest opening	Yes	Yes	Yes	Yes	Present in Twycross groups	Yes	✓
Digging	7	Ant wiping	Ant wiping	Yes	No		?	Present in Twycross groups	Yes	✓
	1	Digging	Digging	Yes	Yes		Yes	Present in Twycross groups	Yes	✓
Cleaning	1	Cleaning body	Cleaning body, wound or menses	Yes	Yes	Yes	Yes	Never eat what is excavated	Yes	✓
	2	Cleaning surface	Cleaning outer space	X	Yes	Yes	Yes	Present in Twycross groups	Yes	✓
Liquids	1	Water sucking	Insert tool into concavities or plain water and suck water from it	Yes	Yes	Yes	No	Present in Twycross groups	Yes	✓
	2	Leaf sponging	Leaf sponging	Yes	Yes		No	Present in the wild§§ and Twycross groups	Yes	✓
	3	Fluids absorbing	Fluids absorbing	Yes	No		No	Present in Twycross and San Diego groups	No	✓
	4	Containers	Fluid container	Yes	Yes	Yes	Yes	Present in Twycross and San Diego groups	Yes	✓
Baiting	1	Baiting	Using any kind of object to lure them within reach	No	Yes		No	Present in Twycross and San Diego groups	No	×
Draping	1	Draping	Draping objects on one's body	Yes	Yes		Yes	Present in Twycross and San Diego groups	Yes	✓

Data for chimpanzees were from Beck (1980) and other sources (see References). Minor modifications in terminology and classifications were necessary to facilitate comparisons. Data for bonobos were taken from published studies (see References) and complemented by our own data. General contexts were divided into different functional categories ('Action'), which could be further divided into tool use variants ('Behaviour'). The next two columns describe whether wild chimpanzees and captive chimpanzees have been observed with the behaviour. The next columns describe whether the behaviour has been observed in different captive and wild bonobo studies (see text for description). Finally, the column Lola ya Bonobo sums up the observations recorded at Lola ya Bonobo sanctuary. The summary of the captive studies is given in the Captivity column. Finally a comparison between chimpanzees and bonobos in captivity is given in the last column: a tick indicates the behaviour is similarly present or absent in the captive populations of the two species, a cross indicates otherwise. Yes: behaviour present. No: behaviour not present. ?: presence of the behaviour unknown. n/a: comparison not applicable. X: settings not applicable for wild (experimental setting) or captive (hunting) animals. No: behaviours absent in the wild, maybe because of a lack of need to develop it. X: behaviours not observed because of experimental settings or natural artefacts not found in captivity. +: behaviour not observed within observation range in cleared areas but no control of the forest areas.

\* Personal observations.

† Quoting Walraven et al. (1993).

‡ E.g. Jensvold & Fouts (1993).

§ van Lawick-Goodall (1968).

\*\* Pruetz & Bertolani (2007).

†† Pounding exists during food acquisition (Yamakoshi & Sugiyama 1995).

‡‡ Goodall (1986).

§§ Hohmann & Fruth (2003).

## Sex Differences

We compared tool-related behaviours of 17 bonobos at Lola (eight females; nine males; Table 2). Following Beck (1980), we were able to compare the effects of age and sex class for 27 behaviours in seven contexts. There was no significant difference in the average number of tool use or tool-related behaviours between adult (mean  $\pm$  SD = 8.12  $\pm$  1.30) and nonadult individuals (5.89  $\pm$  1.15; ANOVA:  $F_{1,15} = 0.43$ ,  $P = 0.52$ ; Fig. 1). However, there was a significant sex effect with females showing a larger average number of behaviours (mean  $\pm$  SD = 9.37  $\pm$  1.33) than males (4.78  $\pm$  0.55; ANOVA:  $F_{1,15} = 8.15$ ,  $P = 0.014$ ; Fig. 1). We found no interaction between the two factors (ANOVA:  $F_{1,15} = 0.19$ ,  $P = 0.67$ ).

At the context level, we were able to compare 'Antagonism', 'Play', 'Food acquisition' and 'Liquids'. 'Digging' was absent in males but present in females. The sample size for 'Cleaning' was too small to allow statistical analysis; it was observed once in a male and once in a female. We found no effect of age class on any of the contexts (ANOVA: 'Antagonism':  $F_{1,15} = 4.04$ ,  $P = 0.057$ ; 'Play':  $F_{1,15} = 0.50$ ,  $P = 0.49$ ; 'Food acquisition':  $F_{1,15} = 0.009$ ,  $P = 0.93$ ; 'Liquids':  $F_{1,15} = 0.29$ ,  $P = 0.60$ ). Similarly, we found no sex effects for 'Antagonism' and 'Liquids' (ANOVA: 'Antagonism':  $F_{1,15} = 4.04$ ,  $P = 0.066$ ; 'Liquids':  $F_{1,15} = 1.36$ ,  $P = 0.26$ ), but significant effects for play and food (ANOVA: 'Play':  $F_{1,15} = 8.91$ ,  $P = 0.011$ ; 'Food acquisition':  $F_{1,15} = 8.02$ ,  $P = 0.014$ ) owing to females having a larger diversity of tool use behaviours than males (females: 'Play': mean  $\pm$  SD = 3.00  $\pm$  1.58; 'Food acquisition': 4.00  $\pm$  1.41; males: 'Play': 1.00  $\pm$  0.87; 'Food acquisition': 1.00  $\pm$  1.24). No significant interactions were found between the main factors in any context (ANOVA: 'Antagonism':  $F_{1,15} = 0.002$ ,  $P = 0.97$ ; 'Play':  $F_{1,15} = 0.50$ ,  $P = 0.49$ ; 'Food acquisition':  $F_{1,15} = 1.12$ ,  $P = 0.31$ ; 'Liquids':  $F_{1,15} = 0.73$ ,  $P = 0.41$ ).

Specific Behaviours (*Lola ya Bonobo*)

The bonobos at Lola used tools in seven general contexts. 'Play' and 'Food acquisition' were the most common ones in which tool use occurred, with nine and seven different types, respectively. We added 'Sex' as an additional context to Beck's (1980) classification, which contained two behaviours: using natural material (e.g. fruits) or artefacts (e.g. bottles) for sexual stimulation. Tool use in a sexual context was also observed in San Diego and Twycross (Z. Clay, personal observation). We also observed a number of seemingly idiosyncratic behaviours in the 'Play', 'Cleaning', 'Liquids' and 'Sex' contexts (Table 2). In the following, we describe some of these observations in more detail, because they have implications for the underlying cognitive capacities.

## 'Pretend' milk feeding

At noon, caretakers feed the bonobos soymilk through the fence using plastic bottles. The individuals usually keep the bottles and some continue to play with them, for instance by taking them over to the nearby lake and repeatedly filling them and pouring out their contents. On one occasion, a subadult female, Nioki, filled her bottle in the lake, but then brought it back to the fence where she had previously been fed by a caregiver. She then passed the bottle and her arm through the fence, aimed the bottle at herself and started pouring water into her mouth. She did not seem to ingest any of the water, but instead adopted her typical facial expression while being fed by a caretaker, as if pretending to drink soymilk.

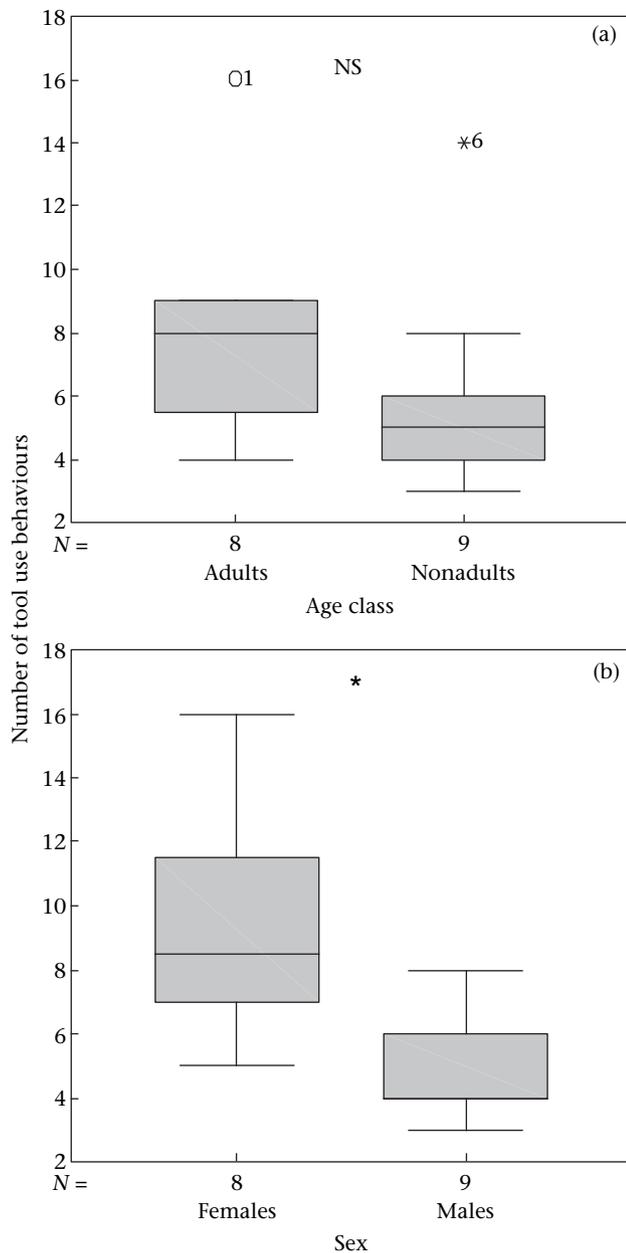
## Using fruit shells as containers

A number of times, bonobos were observed using shells of fruits (such as *Strychnos*) as containers for water or soymilk. One adult

**Table 2**  
Summary of the tool use observed at Lola ya Bonobo

Action	Behaviour	AF			SF			AM			SM			JM					
		MM	SW	OP	BD	KL	SL	NO	IS	LK	TT	MN	KW	MA	BN	MI	KG	IB	KD
Antagonism	Agonistic intimidation displays	1	1	1	1		1			1	1	1	1	1		1			
	Agonistic intimidation displays using bottle (artificial)	1	1	1	1					1	1	1	1	1	1				1
Play	Playful pounding				1				1										
	<i>Conspecific beating</i>						1												
	<i>Interspecific poking</i>						1												
	Playful balancing		1	1	1	1	1	1	1		1	1	1				1	1	1
Pretending play	Fake drinking		1	1		1	1	1									1		
	<i>Pretend milk feeding through fence</i>						1												
Playful containers	Bottle filling to play		1		1					1								1	
	<i>Pouring water in bottle submerged in lake</i>		1																
Playful rolling	<i>Using fruit (coconut) as play tool</i>						1												
	Opening tough rinds or shells	1	1	1	1	1	1	1	1			1	1	1	1	1	1	1	1
Food acquisition	Opening tough rinds or shells			1	1	1	1	1	1			1	1	1	1	1			1
	Opening tough rinds or shells	1	1	1			1					1						1	1
	Opening tough rinds or shells	1			1		1					1							1
	Opening tough rinds or shells	1	1	1	1	1			1							1			
Reaching food or object	Raking objects out of the enclosure			1			1												
Digging	Digging with stick	1		1		1	1			1									
Cleaning	Cleaning body										1								
	Cleaning surface		1																
Liquids	Containers	1				1		1											
	Bottle filling	1				1		1											
	Using human-made objects as recipients to drink	1				1	1												
	Using fruit shell as a recipient to drink	1			1	1					1					1		1	
Sex	<i>Bottle pouring into another bottle or into lid</i>		1																
	Sexual stimulation	1				1		1								1	1		
Total		2	16	9	8	8	9	14	6	5	4	5	6	4	3	4	8	3	6

See Table 1 for terminology. '1' indicates that the behaviour has been observed. AF: adult females. SF: subadult females. AM: adult males. SM: subadult males. JM: juvenile males. Italic: idiosyncratic behaviours. Infants were excluded from the analysis.



**Figure 1.** Box plots presenting the number of tool use behaviours observed at Lola ya Bonobo by age and sex. Boxes show the median with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range. In (a) the number of outliers is shown by the circle and star. In (b) the asterisk indicates  $P < 0.05$ .

female, Semendwa, was frequently observed pouring liquid between the shells, bottles and lids. This behaviour had no apparent function, and we therefore assigned it to the 'Play' context, although she sometimes used this technique to share milk with her daughter.

## DISCUSSION

### *Chimpanzee and Bonobo Tool Use*

The tool use behaviour of nonhuman primates is relevant for theories of human evolution (Washburn 1960; Parker & Gibson 1979). The natural tool use behaviour of our closest living relatives, the chimpanzees and bonobos, plays a key role in this comparison, but no systematic comparison has been conducted so far. Previous research has shown that, in terms of cognitive and physical abilities

to use tools, bonobos and chimpanzees do not differ in relevant ways (Takeshita & Walraven 1996; Herrmann et al. 2008). Our study is in line with these results by demonstrating that, in captivity, bonobos and chimpanzees do not differ in their overall diversity of tool use behaviours. Bonobos showed a large portfolio of tool use behaviours that did not differ from chimpanzees in either quantitative or qualitative terms. This conclusion is based on previously published studies and our own data from four captive facilities. Out of 52 tool use behaviours, only seven were different between captive bonobos and chimpanzees. One of them (dental autogrooming) has been observed in wild bonobos, suggesting that it is part of the species' behavioural repertoire. All contexts in which chimpanzees used tools were also found in bonobos, with only one exception ('Baiting').

The general diversity of tool use behaviours was comparable in the two species, although some differences remained in terms of context specificity and functional use. Wild chimpanzees predominantly use tools in the context of food acquisition (McGrew 1979; Boesch & Boesch 1990) while wild bonobos appear to use tools mainly for personal care (cleaning, protection from rain) and social purposes (Ingmanson 1996). Our observations at Lola ya Bonobo are in line with these observations, that is, tool use is not just used to acquire food. Instead, the biggest diversity of tool use behaviours was found in the 'Play' context. Another difference was in the use of tools for sexual stimulation, something that has been reported for orang-utans but not chimpanzees (van Schaik et al. 2003). As our study could not compare the frequency of the different tool use behaviours, it is possible that some more subtle species differences are also present in terms of usage.

Observations in the wild and in captivity have led to the hypothesis that bonobo tool use has mainly a social function (de Waal 1986; Ingmanson 1996). However, our own observations are not entirely consistent with this interpretation despite the fact that a considerable proportion of tool use was observed in the play context. Most play-related tool use in bonobos was part of solitary, not social, play. Although social games with objects have been observed in bonobos interacting with humans (Pika & Zuberbühler 2008), we did not record any shared tool use between bonobos in this context. Even though we sometimes saw two or more bonobos simultaneously playing with bottles, these activities remained solitary. One possible exception was a subadult female (Nioki), who was observed to use a stick to beat an infant playfully, while both produced laughter, an indicator of friendly motivations (Davila Ross et al. 2009). However, no exchange of gaze was observed between the two individuals, suggesting that the behaviour did not serve a joint social purpose (Tomasello et al. 2005). We frequently observed playful stick beating in solitary bonobos and this was often accompanied by a characteristic 'play face' (Palagi 2008). Solitary play is also common in bonobo infants in the wild, while social play is comparably rare (Ingmanson 1996).

Perhaps the most striking difference that emerged from this report concerned the observation that, at Lola ya Bonobo, nearly all fully grown individuals engaged in tool-based play behaviour, such as 'bottle filling', regardless of their age or social position. While young chimpanzees spend much time playing, this is not so much the case for the adults, especially the males (de Waal 1982; Goodall 1986). It has been argued that bonobos have been subjected to an evolutionary pressure towards neoteny, in that they have retained some juvenile characteristics in adulthood (Shea 1983; Wrangham & Pilbeam 2001; Wobber et al. 2010), a hypothesis also supported by our own observations. High levels of play are common in adults (Palagi 2006; Palagi & Paoli 2007) and this study shows that tools are an integral part of this behaviour. In chimpanzees, however, adult play is very rarely observed (Pellis & Iwaniuk 2000). If adult play is observed in wild groups, it does not appear to involve the use of tools (T. Gruber, personal observations).

Flexibility is a key characteristic of higher cognitive capacities, something that has been repeatedly demonstrated in chimpanzees

(Bruner 1972; Tomasello & Call 1997). We found a number of seemingly idiosyncratic behaviours by some individuals at Lola, some of which were intriguingly complex. An interesting example was the use of fruit shells or skins as containers. These items were not treated as fruits, but as items with specific functional properties as tools (e.g. pepper, Jordan 1982). Another interesting example concerned the sequential use of two tools, part of the daily routine for the female Semendwa during which she used lids (*Strychnos* shells) or plastic bottles to transfer water between the different containers. Finally, Nioki's 'pretend soymilk feeding', seen by two observers (T.G., Z.C.), is equally noteworthy and could be a case of pretence play. Although we cannot rule out that Nioki, as well as other individuals who engaged in similar behaviour, did not ingest some of the water, most was pouring out of their mouths and they often adopted a play face during the act, raising doubts that they were interested in the functional aspect of the behaviour. Second, in Nioki's case, she first passed her arm with the container through the fence, thereby reproducing the movement patterns of the daily soymilk feeding events (see Appendix Fig. A1). Had she just been interested in drinking, these actions could not be explained. These observations illustrate that bonobos are no different from chimpanzees in terms of the flexibility associated with the behaviour, especially in the play context (Jensvold & Fouts 1993). In line with recent experimental studies (Mulcahy & Call 2006b; Herrmann et al. 2008), our observations support the hypothesis that the cognitive mechanisms responsible for this flexibility are shared by both species and have most likely evolved prior to their split about 1 million years ago (Won & Hey 2005).

#### Female bias in tool use in the *Pan* genus

Another key finding of our study concerned the sex differences in bonobo tool use behaviour. Similar to chimpanzees (McGrew 1979; Boesch & Boesch 1990), we found that bonobo females were more avid tool-users, compared to males, and that they were using a larger diversity of tools. At Lola ya Bonobo, females displayed a larger range of tools or tool-related behaviours during food acquisition and play than males, although both sexes used tools in all contexts apart from one. Only females used sticks to dig in the mud. To date, no such bias has been found in wild orang-utans (Fox et al. 2004; C. van Schaik, personal communication), the only other skilful ape tool-users in the wild. Data on gorillas, *Gorilla gorilla*, whether in the wild (Breuer et al. 2005; Wittiger & Sunderland-Groves 2007) or in captivity (reviewed in Lonsdorf et al. 2009), are too limited to draw conclusions. Apart from apes, a female bias in tool use has also been found in dolphins (*Tursiops* sp.: Mann & Sargeant 2003). One explanation for the female bias is that mothers and daughters tend to remain close until late adolescence in both chimpanzees (Lonsdorf et al. 2004) and dolphins (Mann 2009), while sons become independent earlier and are thus less exposed to their mothers' skills.

In wild chimpanzees, the acquisition of tool use behaviour in infants appears to be partly socially learned from the mother (Lonsdorf 2005), suggesting that similar processes may be at work in bonobos. At Lola ya Bonobo, bonobos typically arrive as orphans at a very young age, suggesting that they have had only very limited previous exposure to their biological mother and any of her acquired skills. At Lola, newly arriving infants are first looked after by humans, before integration into one of the groups where they are sometimes cared for by an existing group member. During this process, male and female infants are equally exposed to various tool use behaviours of their human and conspecific caretakers, indicating that the observed sex bias in bonobo tool use behaviour cannot be explained with differences in rearing conditions. More likely, female infant bonobos are more receptive to tool-using models, more motivated to interact with artefacts, or they are simply more patient. We also found that female bonobos employed a larger number of techniques to solve one particular problem than

males (e.g. opening a hard-shelled fruit), suggesting that they were better able to dissociate means from their ends.

One can only speculate about the functional significance of the observed sex difference in the *Pan* genus. Perhaps females have evolved more sophisticated tool skills owing to the higher nutritional demands of pregnancy and infant care. If social learning plays a key role, the long periods of proximity with the mother, characteristic for both species, are likely to be important. Whether female-biased tool use was shared with a common ancestor with modern humans is difficult to decide and further conclusions will obviously depend on ecologically valid observations in the wild, ideally from different groups facing different ecological constraints (McGrew 1989).

#### Great Apes' Tool Use in the Wild

In our analysis, wild bonobos differed considerably from captive groups and from chimpanzees in captivity and the wild. We can think of two main lines of explanation. First, bonobos may have lost tool use in the wild, not because they are cognitively incapable but because all relevant food sources can be acquired without the help of artefacts (McGrew et al. 1997: hypothesis 8; Hohmann & Fruth 2003). This hypothesis has also been put forward to explain the lack of tool use in the Sonso chimpanzees of Budongo forest (Gruber et al. 2009, 2010). Although chimpanzees are capable tool-users, it is also relevant to point out that some groups only have very small repertoires with infrequent use (Reynolds 2005). Second, it is also possible that tool use in wild bonobos has simply been underestimated because long-term observations are absent and because the number of studied groups is still small (Hohmann & Fruth 2003). Before firm conclusions can be made, more data on bonobo and gorilla tool use are needed, beyond the existing records (bonobos: Kano 1982; Ingmanson 1996; Hohmann & Fruth 2003; gorillas: Breuer et al. 2005; Wittiger & Sunderland-Groves 2007). Studies that focus on the cognitive abilities underlying tool use are equally relevant. In one of them, gorillas performed as well as bonobos, but both species did not appear to understand the causality of the task while a chimpanzee and two orang-utans appeared to do so (Mulcahy & Call 2006a). Although this finding matches with the current dichotomy in ape tool use in the wild, there are other studies that found no cognitive differences or limitations in other aspects of tool use. For example, both gorillas and orang-utans are able to represent relevant aspects of experimental tool tasks (Mulcahy et al. 2005), while both bonobos and orang-utans are able to plan ahead by saving tools for a specific future use (Mulcahy & Call 2006b). Finally, there does not seem to be a profound difference between the great apes in their ability to represent the functional properties of tools (Herrmann et al. 2008). Overall, the data are more compatible with the hypothesis that both gorillas and bonobos are able to develop a large portfolio of tool use in the wild, but that the environment prevents this development. Comparing the impact of habitat differences on the development of tool use in all apes is likely to provide progress, as are data on populations that spend much time on the ground or forage in open savannah-type habitats (e.g. Myers-Thompson 2002). Habitat type and use, in other words, are likely to play a key causal role in the emergence and maintenance of tool use in wild ape populations.

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## References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.
- Beck, B. B. 1980. *Animal Tool Use*. New York: Garland Press.
- Boesch, C. & Boesch, H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatologica*, **54**, 86–99.
- Breuer, T., Ndoundou-Hockemba, M. & Fishlock, V. 2005. First observation of tool use in wild gorillas. *PLoS Biology*, **3**, 2041–2043.
- Bruner, J. 1972. The nature and uses of immaturity. *American Psychologist*, **27**, 687–708.
- Byrne, R. W. 2007. Animal cognition: bring me my spear. *Current Biology*, **17**, R164–R165.
- Crockford, C., Herbinger, I., Vigilant, L. & Boesch, C. 2004. Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology*, **110**, 221–243.
- Davila Ross, M., Owren, M. J. & Zimmermann, E. 2009. Reconstructing the evolution of laughter in great apes and humans. *Current Biology*, **19**, 1106–1111.
- Fox, E. A., van Schaik, C. P., Sitompul, A. & Wright, D. N. 2004. Intra- and inter-populational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology*, **125**, 162–174.
- Gold, K. C. 2002. Ladder use and clubbing by a bonobo (*Pan paniscus*) in Apenheul Primate Park. *Zoo Biology*, **21**, 607–611.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.
- Gruber, T., Muller, M. N., Strimling, P., Wrangham, R. W. & Zuberbühler, K. 2009. Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Current Biology*, **19**, 1806–1810.
- Gruber, T., Reynolds, V. & Zuberbühler, K. 2010. The knowns and unknowns of chimpanzee culture. *Communicative and Integrative Biology*, **3**, 1–3.
- Helme, A. E., Call, J., Clayton, N. S. & Emery, N. J. 2006. What do bonobos (*Pan paniscus*) understand about physical contact? *Journal of Comparative Psychology*, **120**, 294–302.
- Herrmann, E., Wobber, V. & Call, J. 2008. Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, **122**, 220–230.
- Hohmann, G. & Fruth, B. 2003. Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology*, **44**, 563–571.
- Ingmanson, E. J. 1996. Tool-using behavior in wild *Pan paniscus*: social and ecological considerations. In: *Reaching into Thought: the Minds of Great Apes* (Ed. by A. E. Russon, K. A. Bard & S. T. Parker), pp. 190–210. Cambridge: Cambridge University Press.
- Jensvold, M. L. A. & Fouts, R. S. 1993. Imaginary play in chimpanzees (*Pan troglodytes*). *Human Evolution*, **8**, 217–227.
- Jordan, C. 1982. Object manipulation and tool-use in captive pygmy chimpanzee (*Pan paniscus*). *Journal of Human Evolution*, **11**, 35–59.
- Kano, T. 1982. The use of leafy twigs for rain cover by the pygmy chimpanzees of Wamba. *Primates*, **19**, 187–193.
- van Lawick-Goodall, J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, **1**, 161–311.
- Limongelli, L., Boysen, S. T. & Visalberghi, E. 1995. Comprehension of cause–effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **109**, 18–26.
- Lonsdorf, E. V. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, **70**, 673–683.
- Lonsdorf, E. V., Everly, L. E. & Pusey, A. E. 2004. Sex differences in learning in chimpanzees. *Nature*, **428**, 715–716.
- Lonsdorf, E. V., Ross, S. R., Linick, S. A., Milstein, M. S. & Melber, T. N. 2009. An experimental comparative investigation of tool use in chimpanzees and gorillas. *Animal Behaviour*, **77**, 1119–1126.
- McGrew, W. C. 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use. In: *The Great Apes* (Ed. by D. A. Hamburg & E. McCown), pp. 441–463. Menlo Park, California: Benjamin/Cummings Publishing Company.
- McGrew, W. C. 1989. Why is ape tool use so confusing? In: *Comparative Socioecology: the Behavioural Ecology of Humans and Other Mammals* (Ed. by V. Standen & R. A. Foley), pp. 457–472. Oxford: Blackwell Scientific.
- McGrew, W. C. 1992. *Chimpanzee Material Culture: Implication for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew, W. C. 1998. Comment to Stanford, 1998. *Current Anthropology*, **39**, 411.
- McGrew, W. C., Ham, R. M., White, L. J. T., Tutin, C. E. G. & Fernandez, M. 1997. Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology*, **18**, 353–374.
- Mann, J. 2009. Tool use in dolphins. *Australasian Science*, **October**, 20–22.
- Mann, J. & Sargeant, B. 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In: *The Biology of Traditions: Models and Evidence* (Ed. by D. M. Fragaszy & S. Perry), pp. 236–266. Cambridge: Cambridge University Press.
- Marlowe, F. W. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology*, **14**, 54–67.
- Mulcahy, N. J. & Call, J. 2006a. Apes save tools for future use. *Science*, **312**, 1038–1040.
- Mulcahy, N. J. & Call, J. 2006b. How great apes perform on a modified trap-tube task. *Animal Cognition*, **9**, 193–199.
- Mulcahy, N. J., Call, J. & Dunbar, R. I. M. 2005. Gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) encode relevant problem features in a tool-using task. *Journal of Comparative Psychology*, **119**, 23–32.
- Myers-Thompson, J. A. 2002. Bonobos of the Lukuru Wildlife Research Project. In: *Behavioural Diversity in Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. F. Marchant), pp. 61–70. Cambridge: Cambridge University Press.
- Palagi, E. 2006. Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): implications for natural social systems and inter-individual relationships. *American Journal of Physical Anthropology*, **129**, 418–426.
- Palagi, E. 2008. Sharing the motivation to play: the use of signals in adult bonobos. *Animal Behaviour*, **75**, 887–896.
- Palagi, E. & Paoli, T. 2007. Play in adult bonobos (*Pan paniscus*): modality and potential meaning. *American Journal of Physical Anthropology*, **134**, 219–225.
- Parker, S. T. & Gibson, K. R. 1979. A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences*, **2**, 367–408.
- Pellis, S. M. & Iwaniuk, A. N. 2000. Adult–adult play in primates: comparative analyses of its origin, distribution and evolution. *Ethology*, **106**, 1083–1104.
- Pika, S. & Zuberbühler, K. 2008. Social games between bonobos and humans: evidence for shared intentionality? *American Journal of Primatology*, **70**, 207–210.
- Pruetz, J. & Bertolani, P. 2007. Savanna chimpanzees (*Pan troglodytes verus*) hunt with tools. *Current Biology*, **17**, 412–417.
- Reynolds, V. 2005. *The Chimpanzees of the Budongo Forest: Ecology, Behaviour, and Conservation*. Oxford: Oxford University Press.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. O. 2003. Orangutan cultures and the evolution of material culture. *Science*, **299**, 102–105.
- Shea, B. T. 1983. Paedomorphosis and neoteny in the pygmy chimpanzee. *Science*, **222**, 521–522.
- Stanford, C. B. 1998. The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. *Current Anthropology*, **39**, 399–420.
- Takeshita, H. & Walraven, V. 1996. A comparative study of the variety and complexity of object manipulation in captive chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). *Primates*, **37**, 423–441.
- Tomasello, M. & Call, J. 1997. *Primate Cognition*. New York: Oxford University Press.
- Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences*, **28**, 1–17.
- Toth, N., Schick, K. D., Savage-Rumbaugh, E. S., Sevcik, R. A. & Rumbaugh, D. M. 1993. Pan the tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science*, **20**, 81–91.
- de Waal, F. B. M. 1982. *Chimpanzee Politics*. New York: Harper.
- de Waal, F. B. M. 1986. Imaginative bonobo games. *Zoos*, **59**, 6–10.
- Walraven, V., van Elsacker, L. & Verheyen, R. F. 1993. Spontaneous object manipulation in captive bonobos (*Pan paniscus*). In: *Bonobo Tidings: Jubilee Volume on the Occasion of the 150th Anniversary of the Royal Zoological Society of Antwerp*. Antwerp: Royal Zoological Society of Antwerp.
- Washburn, S. 1960. Tools and human evolution. *Scientific American*, **203**, 63–75.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999. Cultures in chimpanzees. *Nature*, **399**, 682–685.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 2001. Charting cultural variation in chimpanzees. *Behaviour*, **138**, 1481–1516.
- Wittiger, L. & Sunderland-Groves, J. L. 2007. Tool use during display behavior in wild Cross River gorillas. *American Journal of Primatology*, **69**, 1307–1311.
- Wobber, V., Wrangham, R. W. & Hare, B. 2010. Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, **20**, 226–230.
- Won, Y. & Hey, J. 2005. Divergence population genetics of chimpanzees. *Molecular Biology and Evolution*, **22**, 297–307.
- Wrangham, R. W. & Pilbeam, D. 2001. Apes as time machines. In: *All Apes Great and Small: African Apes* (Ed. by B. M. F. Galdikas, N. Briggs, L. K. Sheeran, G. L. Shapiro & J. Goodall), pp. 5–18. New York: Plenum/Kluwer.
- Yamakoshi, G. & Sugiyama, Y. 1995. Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behavior. *Primates*, **36**, 489–500.

## APPENDIX

**Table A1**

Beck's (1980) classification of tool use behaviours per context with associated page numbers

Context	No.	Page	Action	Behaviour	Description
Antagonism	1	79	Brandish tools	Agonistic intimidation displays	Wild: chimpanzees brandish or wave uprooted tools at others, human observers, animals (live or model), own mirror images. Captivity: at conspecifics, humans, animals (live or model)
				Immature agonistic intimidation displays	Once brandished twigs towards a young female in a miniaturized version of adult male display
				Sticks in rainstorm	Brandish sticks during explosive episode of excitement and animated locomotion triggered by a rainstorm
	2	80	Dragging tools	Wave tools against flies	Wave boughts to disperse swarming flies
				Sticks in play	Brandish sticks during play
				Dragging, rolling, and/or kicking objects during display	Conspecific dragging, rolling, and/or kicking objects during display in the presence of conspecifics
				Dragging, rolling, and/or kicking objects during display	Heterospecific dragging, rolling, and/or kicking objects during display in the presence of baboons
	3	81	Unaimed throwing	Drag branches during rainstorm	Expression of general excitement rather than of social agonism
				Dragging during social play	Dragging
				Unaimed throwing in arousal states	Throw without aiming during intraspecific agonistic charging displays and rain dances, or when frustrated by unsuccessful attempts to gain access to incentives such as estrous females
				Unaimed throwing in reaction to stimuli	Throw without aiming during model or playback experiments or in the presence of other species (baboons, goat, mongoose). Captivity: in the presence of hippopotamus
				Unaimed throwing during social interaction	Throw without aiming during agonistic charging displays in the presence of conspecifics and humans
	4	82	Aimed throwing	Unaimed throwing resulted from frustration	Throw without aiming when frustrated from unsuccessful attempt to reach food
				Unaimed throwing during play	A variety of objects are thrown without aiming during play
				Aimed throwing during agonistic interaction	During fights, aim and throw tools at conspecifics
5	83	Dropping	Interspecific aimed throwing	Wild: throwing objects at other species. Captivity: throwing sticks at other species such as humans, a tiger and dogs; and at fear-producing stimuli such as reptile models	
			Interspecific aimed throwing (hunting)	Throwing sticks at other species during predation	
6	84	Clubbing	Aimed throwing during social play	Aimed throwing during social play	
			Interspecific dropping	Wild: drop branch when descent from trees is blocked by humans or in presence of a leopard model. Captivity: drop tool on human	
7	85	Prodding or jabbing	Conspecific dropping during social play	Drop branch on conspecifics during social play	
			Conspecific clubbing during agonistic episodes	Club or hit conspecifics during agonistic episodes	
8	100	Tree pounding	Interspecific clubbing	Club or hit another species	
			Social play conspecific clubbing	Club each other during play	
9	100	Frustration pounding	Conspecific prodding or jabbing during agonistic contexts	Prodding or jabbing during agonistic contexts	
			Interspecific prodding or jabbing	Prodding or jabbing other species during agonistic contexts	
8	100	Tree pounding	Insect spearing	Spear insects with lengths of straw	
			Pound on tree buttresses during agonistic displays	Pound on tree buttresses (or other noisy object) during agonistic displays	
9	100	Frustration pounding	Pound on objects after unsuccessful attempts	Pound on objects after unsuccessful attempts	
			Pound on objects after unsuccessful attempts	Pound on objects after unsuccessful attempts	
Grooming	1	91	Dental grooming	Dental allogrooming	
			Dental autogrooming	Scrape at or probe in the other's teeth	
2	91	Grooming	Interspecific grooming	Scrape at or probe in one's teeth	
			Self-grooming using tools	Probe in different body parts of another species	
Escape Play	1	91	Use of sticks as pitons to escape enclosure	Self-grooming using tools	
			Use of sticks as pitons to escape enclosure	Use of sticks as pitons to escape enclosure	
2	100	Playful pounding	Insert and probe in mounds or nests of termites	Insert and probe in mounds or nests of termites	
			Insert and probe in mounds or nests of termites	Insert and probe in mounds or nests of termites	
3	101	Playful exploration	Pound objects on others for playful purpose	Pound objects on others for playful purpose	
			Pound objects on others for playful purpose	Pound objects on others for playful purpose	
Oddness/ Inaccessibility	1	94	Exploration with stick	Pry in crevices	
			Using tools when reluctant to touch with hand	Use of sticks to probe inhabitational, fear producing and potentially dangerous objects	
Balancing and climbing	1	95	Touching inhabitational objects	Use of sticks to probe another species	
			Interspecific touching	Use of stick to secure food	
2	95	Playful balancing	Secure object (e.g. suspended food)	Use of pole for playful purpose	
			Playful balancing	Use of pole for playful purpose	

**Table A1** (continued)

Context	No.	Page	Action	Behaviour	Description
Propping and climbing	1	96	Secure suspended food	Secure suspended food	Use of stick to secure food with the topmost tip of the stick or pole placed against a vertical surface
	2	97	Escape enclosure propping	Escape enclosure propping	Use of tool as ladder with the topmost tip of the stick or pole placed against a vertical surface to escape the enclosure
Stacking	1	97	Gain access to suspended lures or to extended vision	Gain access to suspended lures or to extended vision	Stack objects and climb them so as to reach inaccessible goals
	2	98	Escape enclosure stacking	Escape enclosure stacking	Stacking objects to be able to escape
Food acquisition	1	85	Termite fishing	Insert and probe in mounds or nests of termites Perforate termite mound	Insert and probe in mounds or nests of termites
	2	87	Ant Dipping	Dipping for fossorial ants	Use stick to perforate termite mounds Pull and scrape out handfuls of soil which stimulates massed active aggression by the soldiers. The ape then selects and/or modifies a branch and inserts it into the nest
	3	89	Wild: honey fishing. Captivity: artificial fishing	Dipping for arboreal ants Insert tool and probe in bee/artificial nest	Insert tool in the nest holes in trunks and branches Insert tool and probe in bee/artificial nest
	4	93	Reaching food or object	Reaching and retrieving food lures or objects	Using tools or a series of tools to reach and retrieve food or object
	5	98	Opening tough rinds or shells	Nut cracking Hard-shell fruit cracking	Using a rock to smash open nuts on rocks or trees Using a rock to smash open hard-shell fruits on rock or trees
	6	100	Leverage or enlargement of openings	Nest opening	Use stick to open or separate nest from branches or enlarge openings or open sturdy boxes containing bananas
	7	102	Ant wiping	Ant wiping	Use a clump of leafy boughs to wipe ants
Digging	1	101	Digging	Digging	Digging
	1	102	Cleaning body	Cleaning body, wound or menses	Cleaning body to wipe blood, feces, urine, ejaculate, sticky food residues and juices, water, mud
Liquids	2	103	Cleaning cages	Cleaning outer space	Cleaning cages
	1	90, 103	Water sucking	Insert tool into concavities containing water or plain water and suck from it	Insert tool into concavities containing water or plain water and suck from it
	2	103	Leaf sponging	Leaf sponging	Insert masses of leaves and use them as sponges to absorb the water
	3	103	Fluids absorbing	Fluids absorbing	Sponges to absorb residual fluids and brain tissue from the skull of victims, or fruits
Baiting	4	103	Containers	Fluid container	Using any kind of tool as a recipient
	1	104	Baiting	Baiting	Using any kind of object to bait animals to lure them within reach
Draping	1	104	Draping	Draping	Draping objects on one's body



**Figure A1.** 'Pretend' soymilk drinking by a subadult female (Nioki) at Lola ya Bonobo. Half an hour after the end of the 'soymilk feeding', the female carried an empty bottle, used previously by the caretaker, to the nearby lake, filled it with water, and then brought it back to the fence. She then passed the bottle through the fence and poured water into her mouth without ingesting any, while adopting the 'milk-feeding' facial expression, as if pretending to drink soymilk. Drawing: Jason Zampol.