

# Bonobo but not chimpanzee infants use socio-sexual contact with peers

Vanessa Woods · Brian Hare

Received: 18 August 2010 / Accepted: 2 November 2010  
© Japan Monkey Centre and Springer 2010

**Abstract** Bonobos have been observed to use socio-sexual behavior at higher frequency than chimpanzees. Little is known about the developmental influences that shape this behavior in bonobos. We compared the social sexual behavior of wild-born bonobo ( $n = 8$ ) and chimpanzee ( $n = 16$ ) infants in an experimental feeding test. Subjects of both species were orphans of the bushmeat trade living at sanctuaries in peer groups. During the experiment, chimpanzee infants never had socio-sexual interactions with one another. In contrast, bonobo infants had socio-sexual interactions significantly more than the chimpanzee infants and more often when food was presented. During these socio-sexual interactions, bonobo infants did not show a preference for heterosexual partners or genital–genital positioning that is reproductive in adults (e.g. a dorso–ventral posture). These findings suggest that the socio-sexual behavior previously observed in various captive and wild bonobos is species-typical. Wild-born bonobos originating from a large geographical range develop this behavior long before puberty and without the need for adults initiating such behavior or acting as models for observational learning. Meanwhile, chimpanzee infants of the same age with similar rearing history show no signs of the same socio-sexual behavior. Results are interpreted regarding hypotheses for the evolution of bonobo psychology.

**Keywords** Bonobo · Chimpanzees · Development · Infant · Socio-sexual behavior

## Introduction

Bonobos and chimpanzees are closely related genetically and in many ways behaviorally. The two species split from a common ancestor around 1 million years ago, both live in fission–fusion societies, with fruit making up the largest portion of their diet (Boesch et al. 2002; Won and Hey 2005; Furuichi et al. 2008). However, while these two species are highly similar, there are also important behavioral and psychological differences between them. In dyadic food-sharing experiments bonobos are more tolerant when feeding than chimpanzees—even voluntarily sharing food in some contexts (Hare et al. 2007; Hare and Kwetuenda 2010). Bonobo aggression does not reach the level of severity observed in chimpanzees with no case of lethal aggression ever observed (Wrangham 1999). This profile, in part, has led to the suggestion by some that bonobos evolved from a more chimpanzee-like ancestor because of selection against aggression (Wrangham and Pilbeam 2001; although see de Waal and Lanting 1997 who suggest a bonobo-like ancestor of both Pan species). Consistent with this hypothesis is the observation that in anticipation of a contest over monopolizable food resources bonobo males show an increase in cortisol, or a passive coping style, while chimpanzee males show an increase in testosterone that is consistent with high-power motive (Hohmann et al. 2008; Wobber et al. 2010a). However, perhaps no behavioral contrast between these two species has received more attention than the differences between the two species' sexual behavior.

There are now a number of captive and field studies that have found significant differences between the sexual

---

V. Woods · B. Hare  
Department of Evolutionary Anthropology,  
Duke University, Durham, NC 27705, USA

B. Hare (✉)  
Center for Cognitive Neuroscience,  
Duke University, Durham, NC 27705, USA  
e-mail: b.hare@duke.edu

behavior of the bonobo and chimpanzee. First noted in the Hellabrunner Zoo in Germany and studied more systematically at Yerkes, captive bonobos were seen frequently copulating and often in a ventral–ventral position rarely observed in captive chimpanzees (Tratz and Heck 1954; Savage-Rumbaugh and Wilkerson 1978). Subsequently, research on the sexual behavior of bonobos in captivity and in the wild (particularly from the Wamba field site) has suggested that bonobos use sexual behavior outside a strictly reproductive context (Kuroda 1984; de Waal 1987). Bonobos exhibit sexual behavior outside of estrous in a variety of sexual positions and often with same-sex partners (Kano 1992). This type of sexual behavior has been hypothesized to serve an important social function in relieving social tension (Kano 1980; Kuroda 1980, 1984; Badrian and Badrian 1984; De Waal 1989; Parish 1996; Hohmann and Fruth 2000; Paoli et al. 2007; although see Hohmann et al. 2008). In addition, it has also been suggested this behavior may be used in a range of situations including reconciliation after an aggressive encounter (De Waal 1989; Hohmann and Fruth 2000), as a signal of dominance (Thompson-Handler et al. 1984; Kano 1992; Hohmann and Fruth 2000; although see Paoli et al. 2006) and as a bonding mechanism between females, reunited groupmates or even during intergroup encounters (Badrian and Badrian 1984; Kano 1989; Wrangham 1993).

Although many studies have examined the sexual behavior of bonobos, few have allowed for direct quantitative comparisons between the sexual behavior of bonobos and chimpanzees. Therefore, debate remains regarding the degree to which the sexual behavior of bonobos and chimpanzees actually differs. Most notably Stanford (1998) argued that captive populations were not representative of species-typical behavior and that comparisons between the two species should focus on their behavior in non-provisioned wild groups. Stanford (1998) argued that 95% of bonobo mating behavior occurred during estrus, similar to chimpanzees, and that the Mahale chimpanzees have a higher copulation rate than the Wamba bonobos. Moreover, he suggested that larger group size with multiple estrous females could account for cases where copulation rates were higher in bonobos than chimpanzees. However by focusing on copulations, Stanford (1998) misses the fact that only bonobos exhibit socio-sexual behavior regardless of reproductive state and with same-sex partners (de Waal 1987, 1992, 1998). A recently conducted experimental comparison of semi-free ranging, age-sex matched bonobos and chimpanzees with highly similar rearing histories again found bonobos showed significantly more socio-sexual behavior than chimpanzees (Hare et al. 2007) providing further evidence that previous demonstrations were not an artifact of zoo life or demographic skew in previous comparisons (de Waal 1987, 1992, 1998).

Another way to identify any significant differences in the two species' sexual behavior is to study the development of their sexual behavior. To date, only a few studies have examined the development of sexual behavior in bonobos in comparison to chimpanzees. Although infant bonobos as young as 1 year old have been seen to rub genitals, this is typically observed occurring with adults (Kano 1980; Kuroda 1984; Thompson-Handler et al. 1984; de Waal 1987) and may not be used by infants to regulate social relationships (Hashimoto 1997). This might suggest that if bonobos' socio-sexual behavior differs from that of chimpanzees—it may be largely a product of adults initiating and guiding such contact. If high-levels of socio-sexual behavior observed in adult bonobos is simply an artifact of captivity then zoo bonobos may slowly acquire this behavior through years of social learning. Indeed, the only direct comparison between infants of the two species found that the rates of non-copulatory mounts did not differ in infants—supporting the slow acquisition of this behavior (de Lathouwers and van Elsacker 2006).

Therefore, we designed a simple experiment to compare the development of socio-sexual behavior of bonobos and chimpanzees. Given, the concern that some researchers have expressed about the validity of studies in captivity we took advantage of two unique populations of wild-born ape infants living in peer-groups at ape orphanages. Not only do individuals from both species have nearly identical rearing histories, but they have spent little time in captivity. Crucially, because they live in peer-groups their behavior in the experiment cannot be influenced by adult behavior. Based on a range of observational and experimental studies from captivity and the wild, we predicted that bonobo infants have a predisposition to use socio-sexual behavior at a higher rate than age-sex matched chimpanzee infants—particularly in a feeding context. Alternatively, if the two species did not differ or both showed low levels of sexual behavior in infancy it would support the hypothesis that any differences observed in the sexual behavior of adult bonobos is likely to be acquired during development through interactions with older bonobos (i.e. through participation or observation learning).

## Methods

We collected data at the nursery groups of two ape orphanages in Africa. The bonobo nursery was located at Lola ya Bonobo sanctuary just outside Kinshasa in the Democratic Republic of Congo, and the chimpanzee nursery was located at the Jane Goodall Institute's Tchimpanza Chimpanzee Rehabilitation Center near Pointe Noire, Republic of Congo. The bonobos and chimpanzees orphans come to the sanctuary from throughout the Congo

Basin (Andre et al. 2008). In direct comparisons between mother-reared chimpanzees and bonobos and those that arrived at the sanctuaries as orphans all measures suggest orphans are very healthy psychologically. Orphan chimpanzees and bonobos at the sanctuaries show little, if any, aberrant behavior and have similar basal cortisol levels and cognitive performance compared with mother-reared apes of the same species (Wobber and Hare 2010).

All subjects were orphans between 2 and 4 years old. There were no adult apes in the nursery groups, nor did the infants have any contact with adult apes. The nursery groups were supervised during the day by between 2 and 4 human caretakers and the apes slept in groups of 2 and 3 in night boxes in the night buildings. Each nursery group spent the day in a forested enclosure of approximately one acre.

The composition of the bonobo nursery group is listed in Table 1. One additional bonobo orphan (Lomela) arrived shortly before the start of the study and was not included because she was recovering from the trauma of her capture (she was malnourished at the time) and did not show any sexual behavior. All the other infants had arrived at the

sanctuary between 2 and 3 years of age and at least 6 months before the start of the study. The composition of the chimpanzee nursery group was four 2 years old (2 female, 2 male), six 3 years old (3 female, 3 male), and six 4 years old (4 female, 2 male). There were no significant differences in the age of the two samples (mean age: bonobos = 3.38; chimpanzee = 3.125, independent *t* test,  $p > 0.7$ ). Subjects were not food-deprived in any way for the purpose of this test.

At both the bonobo and chimpanzee nursery groups the first experimenter (E1) arrived in the nursery and waited 10 min before beginning observations. This allowed the infants time to habituate to the presence of the experimenter who did not interact with them. At both sanctuaries infants in the nursery groups were cared for by human staff and had frequent visits by other staff. During the test only the infants' surrogate mothers were present (2 men at Tchimpounga and 2–4 women at Lola ya Bonobo). Once the 10-min period had elapsed, for 30 min E1 recorded all occurrences of the three most frequently observed types of socio-sexual behavior seen in pilot observations:

**Table 1** Sex, age, number of partners each infant had at least one socio-sexual interaction with out of the total possible partners, and the number of same-sex or opposite partners subjects had at least one socio-sexual interaction with

	Sex (f/m)	Age (years)	Number of partners	Same-sex partners	Opposite-sex partners
Lodja	Female	4	4/7	1/3	3/4
Tchilenge	Female	4	6/7	3/3	3/4
Muanda	Female	3	3/7	2/3	1/4
Sake	Female	2	3/7	2/3	1/4
Louzi	Male	4	3/7	3/3	1/4
Vanga	Male	3	6/7	3/3	3/4
Iyolo	Male	4	4/7	3/3	2/4
Boyoma	Male	3	5/7	3/3	2/4
Means	4/4	3.4	60.7%	83.33%	50%
Manisa	Female	2	0/16	0/16	0/16
Pounga	Female	2	0/16	0/16	0/16
Kudia	Female	3	0/16	0/16	0/16
Kuiza	Female	3	0/16	0/16	0/16
Zimbana	Female	3	0/16	0/16	0/16
Louise	Female	4	0/16	0/16	0/16
Ngoro	Female	4	0/16	0/16	0/16
Tambikissa	Female	4	0/16	0/16	0/16
Tchivingina	Female	4	0/16	0/16	0/16
Kaoko	Male	2	0/16	0/16	0/16
Ultimo	Male	2	0/16	0/16	0/16
Baliele	Male	3	0/16	0/16	0/16
Lusingu	Male	3	0/16	0/16	0/16
Podive	Male	3	0/16	0/16	0/16
Ulengue	Male	4	0/16	0/16	0/16
Lufino	Male	4	0/16	0/16	0/16
Means	9/7	3.13	0%	0%	0%

The first eight subjects are the bonobos followed by the 16 chimpanzees

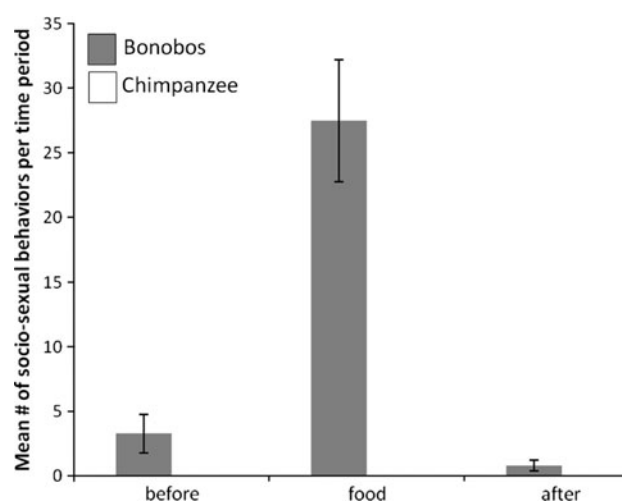
1. ventral–ventral: bonobos touch each other's genital areas together while facing each other;
2. dorso–ventral: one bonobo touches its genital area to back of another's genital area;
3. reverse ventral–ventral: one bonobo lays dorsally while the other faces away from its partner touching its genital region together while laying ventrally or standing.

E1 noted the dyad and position used in each socio-sexual bout (a bout ended when a dyad were no longer physically touching). After this 30-min period, a second experimenter brought a plastic box with preferred food into the nurseries (at both sanctuaries this consisted of 10–12 bananas, 4–5 mangoes, 3–4 avacados, and an entire sliced pineapple and papaya; the larger chimpanzee nursery received proportionally more food) and E1 again recorded the dyad and position of all socio-sexual behavior observed. Finally, after 30 min the food box and any remaining food was removed from the nursery and E1 recorded the infants' socio-sexual behavior in the same way as before. Ten experimental sessions were conducted with each species within a 1-month period at each of the sanctuaries.

All data were coded live by the first author during the ten experimental sessions. Two of these days the second author coded subjects' behavior independently of the main coder. Reliability was assessed by comparing the identity of the pair in each dyad during each socio-sexual bout as observed by the two experimenters on each of the 2 days. The identity of the dyads and the frequency of the bouts were highly correlated on both days (day 1:  $r = 0.940$ ,  $p < 0.001$ ; day 2:  $r = 0.987$ ,  $p < 0.001$ ). The main analysis was conducted at the level of the individual using ANOVA to test for main effects and interactions between species and test time period on the frequency of socio-sexual behavior. Meanwhile one-way ANOVA was used to examine within a species which type of partner or position was preferred. Post-hoc comparisons were conducted using Bonferroni correction when necessary. All tests are two tailed unless otherwise specified and results were analyzed using SPSS 18.

## Results

Univariate ANOVA with species and time period as variables revealed a significant effect of species ( $F(1, 72) = 83.5$ ,  $p < 0.001$ ) and session ( $F(2, 72) = 55.09$ ,  $p < 0.001$ ) and a significant interaction between the two variables ( $F(2, 72) = 55.09$ ,  $p < 0.001$ ; Fig. 1). Post hoc analysis further revealed there was significantly more socio-sexual behavior in bonobos than in chimpanzees in



**Fig. 1** The mean number ( $\pm$ SEM) of occurrences of socio-sexual behavior for each infant bonobo and chimpanzee in each of the three 30-min time periods of the experiment

**Table 2** The mean number ( $\pm$ standard deviation) of occurrences of socio-sexual behavior exhibited in the time period when food was present by the three different types of bonobo dyads based on sex

	Ventral–ventral	Dorso–ventral	Reverse ventral–ventral
Female–female	0.4 (0.7)	0.0 (0.0)	2.5 (4.0)
Male–male	1.33 (2.33)	0.833 (1.17)	1.3 (2.16)
Female–male	0.85 (1.79)	0.85 (1.63)	1.3 (2.5)

the 30-min period when food was present than in the period before or after the food was present ( $p < 0.001$ , Bonferroni corrected).

Because only the bonobos ever exhibited any socio-sexual behavior we conducted a number of follow-up analyses specifically examining the pattern of this behavior in this species. One-way ANOVA examining the use of each of the three positions in each of the three time periods revealed that the infant bonobos' use of each position differed between the time periods (ventral–ventral:  $F(2, 21) = 51.7$ ,  $p < 0.001$ ; dorso–ventral:  $F(2, 21) = 17.7$ ,  $p < 0.001$ ; reverse ventral–ventral:  $F(2, 21) = 11.1$ ,  $p = 0.001$ ). Post-hoc tests revealed that the infant bonobos used each sexual position more often when food was available than before or after its presence ( $p < 0.01$ , Bonferroni corrected).

Univariate ANOVA with socio-sexual position and sex of each dyad (female–female, male–male, female–male) as factors did not reveal any significant main effects or interactions ( $p < \text{NS}$ ; Table 2). Likewise univariate ANOVA with socio-sexual position and make-up of the dyad (heterosexual or homosexual) again revealed no significant main effects or interactions ( $p < \text{NS}$ ). Finally,

one-way ANOVA examining the frequency of use of each socio-sexual position within the time period where food was available did not show significant preference for one socio-sexual position over the other (although there was a tendency,  $p < 0.09$ ).

Examination of the choice of partners of each subject showed that bonobos had significantly more socio-sexual partners than chimpanzees ( $t(2) = 13.58$ ,  $p < 0.001$ , independent  $t$  test). In addition, examining the choice of partners of each bonobo when having socio-sexual interactions shows that they had more same-sex partners than opposite-sex partners ( $t = 2.78$ ,  $df = 7$ ,  $p < 0.03$ , paired sample  $t$  test; see Table 1).

## Discussion

These results support the hypothesis that bonobos have a predisposition to use socio-sexual behavior in ways not observed in chimpanzees. Even as infants, bonobos use socio-sexual behavior, whereas the same behavior is completely absent in chimpanzee infants. Bonobos used a range of socio-sexual behavior with a range of partners, including positioning that is non-reproductive and frequently with same-sex partners. Consistent with what has been observed in adult bonobos in captivity and the wild, infant bonobos show a high frequency of socio-sexual behavior when food is present. Taken together with previous studies showing a relationship between socio-sexual behavior and feeding (Kuroda 1980; Kano 1980; de Waal 1987; Paoli et al. 2007), these findings suggest that socio-sexual behavior in bonobos serves some function during social feeding that is not closely tied to reproduction.

The results do not support the prediction that bonobo behavior serves an exclusively reproductive function as has previously been implied (Stanford 1998). Instead even wild-born prepubescent infants have same-sex socio-sexual interactions in positions that do not mimic positions used by adults for reproduction. Moreover, it clearly does not take years of exposure with adults to develop this type of sexual behavior. Most of these infants would have been rarely venturing off their mothers before the traumatic capture that eventually led them to the sanctuary. They would have had limited opportunity to learn such behavior through interactions with adults, given their poor motor control at the age they arrived at the sanctuaries. So the sexual behavior observed cannot be dependent on a gradual learning process facilitated by interactions with adults or by close observation of such behavior. In addition, although this experiment took place in a captive setting all of the infants from both species were wild-born (and from a far-ranging set of locals within the bonobos natural range). Therefore, the socio-sexual behavior we observed cannot be because of a

lifelong stay in captivity or because the subjects were from only one local in the Congo basin. Finally, the socio-sexual behavior is unlikely to be an aberration caused by the acute trauma of their capture or their captive setting because the infants almost exclusively exhibited socio-sexual behavior when food was presented in the feeding test. This suggests that these infants are using this behavior in species-typical ways that have been observed in wild and captive individuals across a variety of studies.

This experiment does not solve the puzzle regarding the social function(s) of socio-sexual behavior in bonobos. It is possible, for instance, that these infants are living in a relatively unstable social hierarchy and sexual behavior is being used when individuals become anxious, or *negatively* aroused, as a result of social uncertainty. In the experiment social uncertainty was likely to be elicited by feeding, and we did not collect data during the sessions about other forms of uncertainty (e.g. fights over objects). Perhaps, if we had developed a coding scheme for different classes of social uncertainty, we would have seen a strong relationship between the use of sexual behavior and uncertainty, irrespective of whether food was present or not. Alternatively, it may be that these infants are using this behavior when food is provided because the presence of food itself (not the social uncertainty it might create) *positively* arouses them and the excitement drives them to make social contact. In both cases, sexual behavior may be relieving anxiety but in one case it is due to social tension and in the other it is positive arousal in the presence of food. Only future research can tease out these and the many other hypotheses that have been suggested as explanations for this behavior. However, the presence of this behavior in such young infants does underscore the likelihood that such behavior is not tied to reproduction, but to social bonding or the relief of anxiety. Finally, it is important to note that the infant bonobos showed little sexual behavior outside feeding time. Moreover, while it has been suggested that in many regards bonobos are juvenilized relative to chimpanzees; this pattern of behavior in bonobos seems to actually suggest earlier onset of sexual behavior in this species (Shea 1983; Lieberman et al. 2007; Wobber et al. 2010b). If bonobos are the more derived species of *Pan*, then the selection pressure(s) that led to their evolution did not simply lead to juvenilization (e.g. bonobos develop sexual behavior before chimpanzees). Instead, it may be that selection against aggression in bonobos shaped their development so they behave *like* juveniles throughout life. To make this possible, behavior observed in chimpanzees is expressed earlier whereas other behavior is expressed later or not at all in bonobos. If true, what may unify all the changes is that they led to a pattern of development that promotes less severe forms of aggression in this species (Wrangham and Pilbeam 2001).

**Acknowledgments** Thanks to Rebeca Atencia, Lisa Pharoah, Debby Cox, Keith Brown, Claudine Andre, Valery Dhanani, Dominique Morel, Pierrot Mbonzo, and the caretakers of Tchimpounga Chimpanzee Sanctuary and Lola ya Bonobo for making this research possible. This work was performed under the authority of the Ministry of Research and the Ministry of Environment in the Democratic Republic of Congo (research permit #MIN.RS/SG/004/2009) and the Ministry of Scientific Research and Technical Innovation in the Congo Republic (research permit: 009/MRS/DGRST/DMAST). This work was approved by the Institutional Care and Use Committees at Duke University. This work was supported in part by European Research Commission Advanced Grant Agreement 233297 and by National Science Foundation grant NSF-BCS-08-27552 and NSF-BCS-25172 to B.H.

## References

- Andre C, Kamate C, Mbonzo P, Morel D, Hare B (2008) The conservation value of Lola ya Bonobo. In: Furuichi T, Thompson J (eds) Bonobos ecology, behavior, genetics and conservation. Springer, New York, pp 303–322
- Badrian A, Badrian N (1984) Social organization of *Pan paniscus* in the Lomako Forest, Zaire. In: Susman RL (ed) The Pygmy Chimpanzee: evolutionary biology and behavior. Plenum Press, New York, pp 325–344
- Boesch C, Hohmann G, Marchant L (2002) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge
- de Lathouwers M, van Elsacker L (2006) Comparing infant and juvenile behavior in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): a preliminary study. *Primates* 47:287–293
- de Waal F (1987) Tension regulation and nonreproductive functions of sex among captive bonobos (*Pan paniscus*). *Nat Geo Res* 3:318–335
- de Waal F (1989) Peacemaking among primates. Harvard University Press, Cambridge
- de Waal FBM (1992) Appeasement, celebration, and food sharing in the two Pan species. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM (eds) Topics in primatology: vol. 1. Human origins. University of Tokyo Press, Tokyo, pp 37–50
- de Waal FBM (1998) Commentary on C. B. Stanford. *Curr Anthropol* 39:407–408
- de Waal F, Lanting F (1997) Bonobo: the forgotten ape. University of California Press
- Furuichi T, Thompson J (eds) (2008) Bonobo ecology, behavior, genetics and conservation. Springer, New York
- Hare B, Kwetuenda S (2010) Bonobos voluntarily share their own food with others. *Curr Biol* 20:R230–R231
- Hare B, Melis A, Woods V, Hastings S, Wrangham R (2007) Tolerance allows bonobos to outperform chimpanzees in a cooperative task. *Curr Biol* 17:619–623
- Hashimoto C (1997) Context and development of sexual behavior of wild bonobos at Wamba, Zaire. *Int J Primatol* 18:1–21
- Hohmann G, Fruth B (2000) Use and function of genital contacts among female bonobos. *Anim Behav* 60:107–120
- Hohmann G, Mundry R, Deschner T (2008) The relationship between socio-sexual behavioral and salivary cortisol in bonobos: tests of the tension regulation hypothesis. *Am J Primatol* 3:223–232
- Kano T (1980) Social behavior of wild pygmy chimpanzees of Wamba: a preliminary report. *Hum Evol* 9:23–260
- Kano T (1989) The sexual behavior of Pygmy chimpanzees. In: Heltné P, Marquardt L (eds) Understanding chimpanzees. Harvard University Press, Cambridge, pp 176–183
- Kano T (1992) The last ape: pygmy chimpanzee behavior and ecology. Stanford University Press, Stanford
- Kuroda S (1980) Social behavior of the pygmy chimpanzees. *Primates* 21:181–197
- Kuroda S (1984) Interaction over food among pygmy chimpanzees. In: Susman RL (ed) The pygmy chimpanzee: evolutionary biology and behavior. Plenum Press, New York, pp 275–300
- Lieberman DA, Carlo J, de Leon MP, Zollikofer CPE (2007) A geometric morphometric analysis of heterochrony in the cranium of chimpanzees and bonobos. *J Hum Evol* 52:647–662
- Paoli T, Palagi E, Borgognini Tarli SM (2006) Reevaluation of dominance hierarchy in bonobos (*Pan paniscus*). *Am J Phys Anthropol* 130:116–122
- Paoli E, Tacconi G, Borgognini T, Palagi E (2007) Influence of feeding and short-term crowding on the sexual repertoire of captive bonobos. *Ann Zool Fennici* 44:81–88
- Parish AR (1996) Female relationships in Bonobos (*Pan paniscus*) Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Hum Nat* 7:61–96
- Savage-Rumbaugh S, Wilkerson B (1978) Socio-sexual behavior in *Pan paniscus* and *Pan troglodytes*: a comparative study. *J Hum Evol* 7:3327–3344
- Shea B (1983) Paedomorphosis and neoteny in the pygmy chimpanzee. *Science* 222:521–522
- Stanford C (1998) The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. *Curr Anthropol* 39:399–407
- Thompson-Handler N, Malenky R, Badrian N (1984) Sexual behavior of *Pan paniscus* under natural conditions in the Lomako forest, Equateur Zaire. In: Susman RL (ed) The pygmy chimpanzee: evolutionary biology and behavior. Plenum Press, New York, pp 347–366
- Tratz E, Heck H (1954) Der afrikanische Anthropoide “Bonobo”, eine neue Menschenaffengattung. *Saugetierkundliche Mitteilungen* 6:1–4
- Wobber V, Hare B (2010) Psychological health in orphan bonobos and chimpanzees in African sanctuaries
- Wobber V, Wrangham R, Hare B (2010a) Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Curr Bio* 20:226–230
- Wobber V, Hare B, Maboto J, Lipson S, Wrangham R, Ellison P (2010b) Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proc Natl Acad Sci*. <http://www.pnas.org/cgi/doi/10.1073/pnas.1007411107>
- Won Y, Hey J (2005) Divergence population genetics of chimpanzees. *Mol Biol Evol* 22:297–307
- Wrangham R (1993) The evolution of sexuality in chimpanzees and bonobos. *Hum Nat* 4:47–79
- Wrangham R (1999) Evolution of coalitionary killing. *Yrbk Phys Anth* 42:1–30
- Wrangham R, Pilbeam D (2001) African apes as time machines. In: Galdikas B, Briggs N, Sheeran L, Shapiro G, Goodall J (eds) All apes great and small. Kluwer/Plenum Publishers, New York, pp 5–18