Published in final edited form as:

Curr Biol. 2017 July 10; 27(13): R640–R641. doi:10.1016/j.cub.2017.05.039.

Male reproductive skew is higher in bonobos than chimpanzees

Martin Surbeck[1,6], **Kevin E. Langergraber**[2,3,6], **Barbara Fruth**[4,5], **Linda Vigilant**[1], and **Gottfried Hohmann**[1]

[1]Primatology Department, Max Planck Institute for Evolutionary Anthropology, Leipzig, 04103, Germany

[2]School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85281, USA

[3]Institute of Human Origins, Arizona State University, Tempe, AZ 85281, USA

[4]Centre for Research and Conservation, Royal Zoological Society of Antwerp; 2018 Antwerp, Belgium

[5]School of Natural Sciences and Psychology Liverpool John Moores University, Liverpool, L3 3AF, United Kingdom

The two closest living relatives of humans, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), share many traits that are common in humans but rare in other mammals, including societies with high fission–fusion dynamics, male philopatry, female dispersal and extensive social bonding among unrelated individuals [1]. The major difference between these two species is that male aggression is more frequent and intense in male-dominated chimpanzees than in bonobos, where the highest-ranking individuals are female [1]. One potential explanation is that because periods of female sexual receptivity and attractiveness are more extended in bonobos [2], males compete less intensely for each mating opportunity. This would reduce the strength of selection for traits that lead to success in direct contest competition between males and in sexual coercion of females, thus increasing the potential for female choice [3]. Accordingly, it has been predicted that the influence of male dominance rank on reproductive success and the extent of male reproductive skew should be lower in bonobos than in chimpanzees [1]. Although relevant for understanding the evolution of the unusual levels of egalitarianism and cooperation found in human hunter-gatherers [4], comparativ analyses in the genus *Pan* have been limited by the scanty paternity data available for wild bonobos [5]. Here, we show using the largest sample of paternity data available that, contrary to expectation, male bonobos have a higher reproductive skew and a stronge relationship between dominance rank and reproductive success than chimpanzees.

Correspondence to: Martin Surbeck; Kevin E. Langergraber.

[6] Co-first authors

Supplemental Information including experimental procedures and one table can be found with this article online at http://dx.doi.org/10.1016/j.cub.2017.05.039.

The authors have no financial conflicts of interest that influence the results or interpretations contained in this paper.

We compared skew in bonobos using paternities for 13 offspring conceived in the seven years between 2007 and 2013, the time period for which we sampled all potential sires, in the Bompusa community of bonobos at LuiKotale, Democratic Republic of the Congo. Skew was calculated from published paternity data from 41 temporally overlapping 7-year time periods in five chimpanzee communities, which represented a total of 191 paternities occurring over 70 independent chimpanzee community-years (Table 1). Nonac's binomial skew (B) index [6], where –1 indicates an equal distribution of reproduction, 0 a random distribution, and 1 total monopolization by one individual, was higher in bonobos (0.22) than in any chimpanzee period (range: –0.03–0.14, mean: 0.03; Table 1). The percentage of paternities achieved by the most reproductively successful male was also higher in bonobos (62%) than in any chimpanzee 7-year period (range: 7–56%, mean = 26%; Table 1). We also calculated skew in bonobos after extending the analysis to a 12-year period (2002–2013) where we had a larger sample of genotyped offspring ($n = 24$) but lacked genotypes from an estimated one to three candidate sire males present at the beginning (2002 – 2006). Even if we assume that all 3 offspring with unassigned paternity were sired by different ungenotyped males, the B-index was still higher in bonobos (0.083) than in all but two of 24 12-year periods in chimpanzees (range = -0.010–0.123, mean = 0.028; Table 1). Additionally, the most successful male's share of reproduction, which is unaffected by the presence of ungenotyped males, was higher in bonobos (39%) than in all but 1 of 24 chimpanzee 12-year periods (range = 6–41%, mean = 20%; Table 1).

Comparative research in group-living primates indicates that male reproductive skew is high when the number of competing males is low [7]. However, this does not appear to explain why skew was higher in bonobos than chimpanzees. Although we found that the chimpanzee periods with skew values most similar to those of bonobos also had a small average number of males present at the time of each conception (Table 1), both the B-index and the most successful male's share of reproduction for bonobos were outside the 95% confidence intervals of the model prediction for a chimpanzee community with the same number of competing males (Supplemental information).

Male reproductive skew was higher in bonobos than chimpanzees because high-ranking bonobo males more effectively monopolized reproduction. The average standardized dominance ranks of sires was higher in bonobos (0.81) than in four out of five chimpanzee communities (mean = 0.77, range = 0.65–0.91). According to the priority-of-access model, the influence of male dominance rank on reproductive success decreases with the degree of estrous synchrony: when one female is maximally tumescent, the alpha male will sire her offspring, when two females are simultaneously maximally tumescent, the alpha and beta male will each sire one offspring, and so on [7,8]. However, the average number of maximally tumescent females at each conception was actually higher in bonobos (mean = 4.9, range = 1–9) than in chimpanzees (mean = 3.8, range = 1–11). In addition, in bonobos, but in none of the chimpanzee communities, the alpha male sired significantly more offspring than expected under the priority-of-access model (Supplemental information). Thus, lower estrous synchrony among females does not appear to explain the stronger influence of dominance rank on male reproductive success in bonobos than in chimpanzees.

If not an effect of the numbers of competing males or simultaneously receptive females, how did high-ranking males more effectively monopolize reproduction in bonobos than chimpanzees? One possibility is that higher levels of male aggression in chimpanzees actually decrease reproductive skew. Although rank and sexual coercion are positively correlated in male chimpanzees, coercion by low-ranking males may also result in paternities that are unavailable for low-ranking bonobos [9]. Within-group infanticide also appears to be absent in bonobos. The need to confuse paternity through promiscuous mating may thus lower for female bonobos. Rather, the low levels of sexual coercion and the comparatively higher dominance of female bonobos may allow them to selectively mate with high-ranking males during periods when they are likely to conceive, thereby gaining ‘good genes’ or some other benefits [10]. A further, non-exclusive possibility is that the more cohesive society of bonobos, with parties consisting of a higher proportion of the total community, makes it easier for high-ranking males to monopolize reproduction, as it limits the use of alternative mating strategies that low-ranking male chimpanzees use, such as sneaky copulation or consortship. In addition to conducting paternity studies in other bonobo groups to establish the generality of our results, an important area of future research will be to collect the detailed behavioral data necessary for evaluating the specific ways in which male competition and female choice interact to result in the large rank effects and high reproductive skew reported here. A clearer understanding of the phylogenetic building blocks and functional mechanisms underlying the evolution of the social and mating systems of humans is likely to emerge as a consequence.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

Thanks to C. Rowney and A. Nicklisch for performing genetics lab work, to R. Mundry for statistical advice, to P. L. Hooper and two reviewers for helpful comments. The Congolese wildlife authority (ICCN) gave permission to conduct field research and export fecal samples for genotyping. Funding for bonobo field and genetics research was provided by the Max Planck Society, the National Geographic Society and the Wenner-Gren Foundation. M.S. was partially supported by SNF K.E.L. is supported by NIH RO1AG049395 and Arizona State University President's Strategic Initiative Fund.

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Table 1

Overview of male reproductive competition in one bonobo (bold) and five chimpanzee communities over 7-year and 12-year time periods

	Species	Community	Time period	Number of time periods	Average number of males per conception[a]	Number of paternities[a]	Nonac's *B* index[a]	Most successful sire's share[a] [%]	Average rank of sires (95% C.I.)
7-year periods	Bonobos	Bompusa	2007–2013	1	7.4	13	0.22	62	0.81 (0.63–0.95)
	Chimpanzees	Taï North	1987–1994	2	6.3 (6.1–6.5)	10.5 (10–11)	0.09 (0.07–0.11)	51 (45–56)	0.77 (0.60–0.91)
	Chimpanzees	Kasakela	1985–2011	21	11.6 (11.3–12.3)	12 (8–16)	0.05 (-0.03–0.14)	31 (13–45)	0.65 (0.53–0.76)
	Chimpanzees	M group	1999–2005	1	11.6	11	0.06	36	0.91 (0.84–0.97)
	Chimpanzees	Sonso	1993–2002	4	16.0 (15.7–16.2)	11 (11–11)	0.01 (0.01–0.02)	34 (27–36)	0.80 (0.66–0.91)
	Chimpanzees	Ngogo	1996–2014	13	41.8 (40.2–43.9)	42 (30–54)	0.01 (0–0.02)	11 (7–13)	0.66 (0.62–0.71)
12-year periods	Bonobos	Bompusa	2002–2013	1	-	23	0.08	39	-
	Chimpanzees	Ngogo	1996–2014	8	-	72.3 (62–80)	0.01 (0.00–0.01)	7 (6–8)	-
	Chimpanzees	Kasakela	1985–2011	16	-	20.7 (15–25)	0.04 (-0.01–0.12)	27 (16–41)	-

[a] values represent the average across all time periods for each group and the values in brackets indicate the range of values of all time periods for each group.