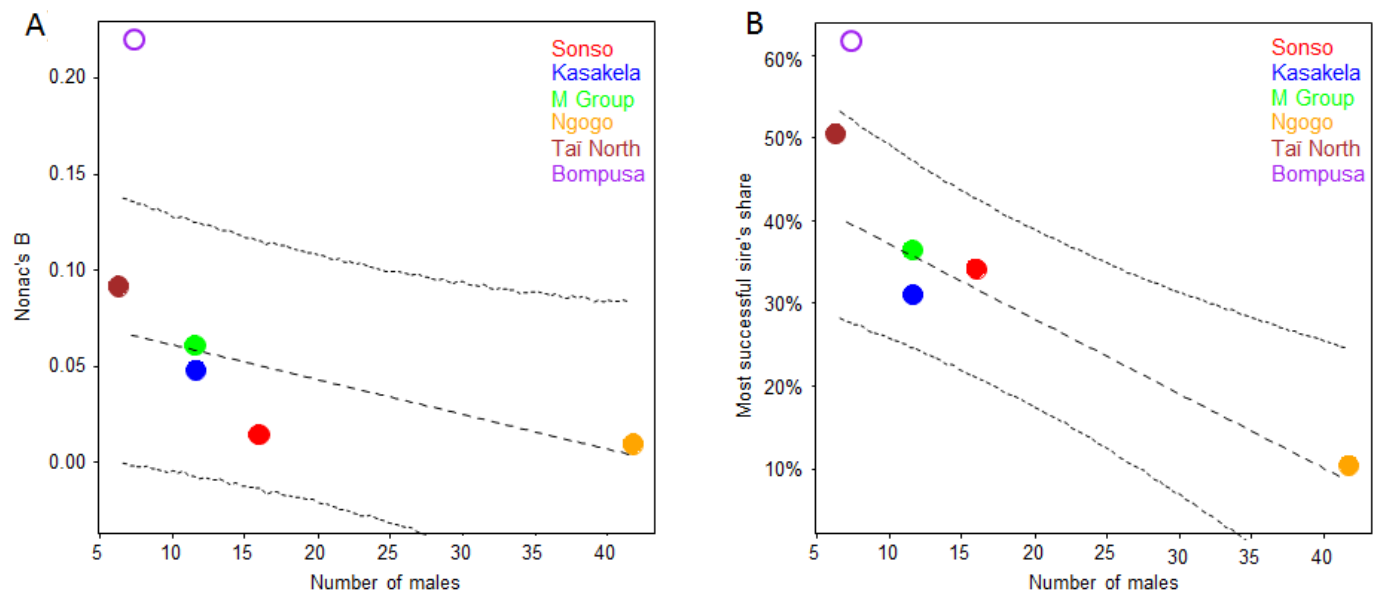**Supplemental information**

Male reproductive skew is higher in bonobos than chimpanzees

Martin Surbeck, Kevin E. Langergraber, Barbara Fruth, Linda Vigilant, Gottfried Hohmann
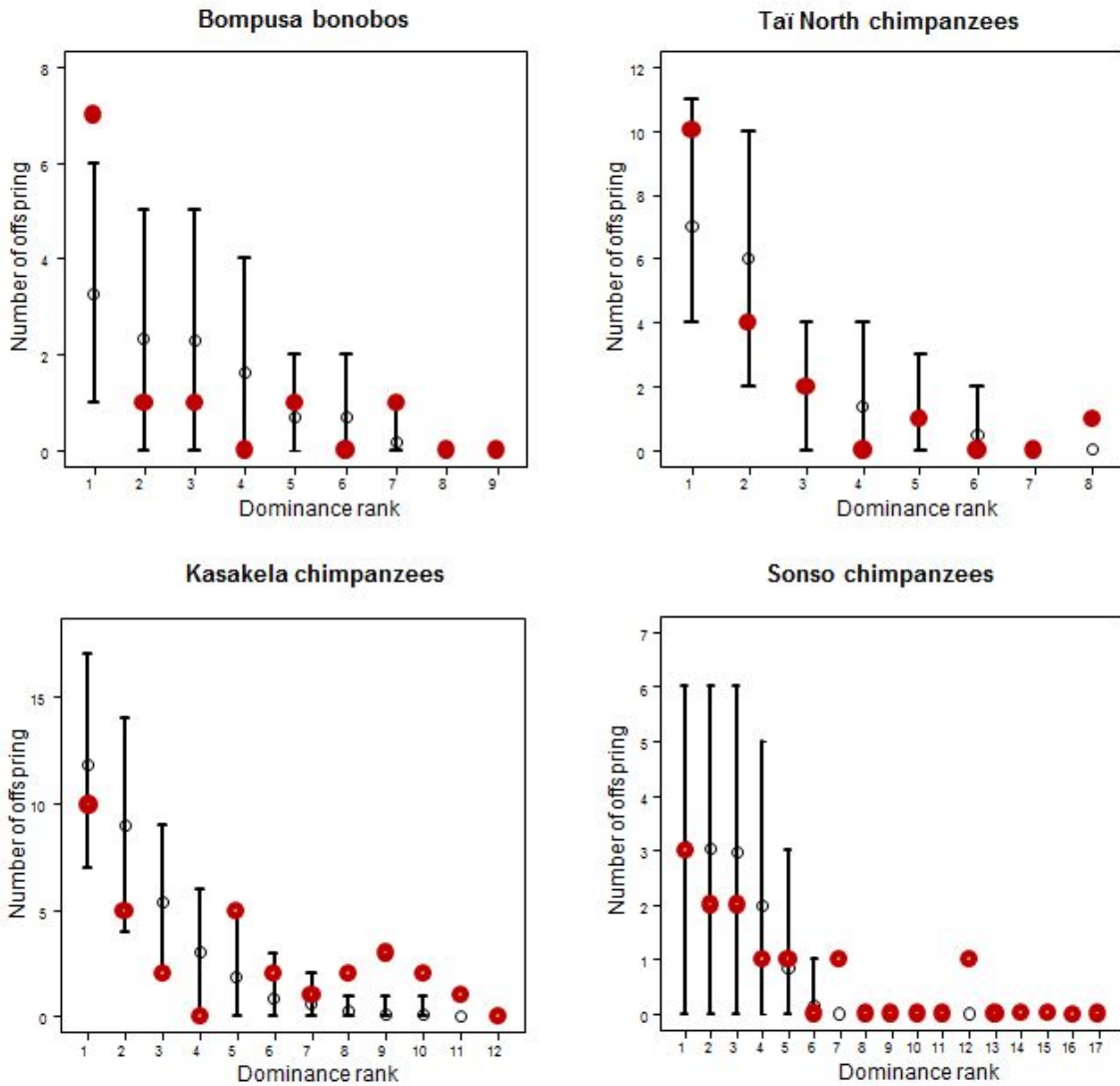
Figure S1

 Legend Figure S1:

Relationship between the number of males during conception and the strength of reproductive

skew in chimpanzees and bonobos measured as A) Nonac's *B*-index and B) the most successful

sire's share of reproduction. Filled dots indicate the values of 7-year periods across different

chimpanzee groups; the thick spotted line indicates the model estimate for the relationship in

chimpanzees and the thin spotted line indicates the 95% confidence intervals of the model

predictions. The bonobo value is depicted as an open circle.

Figure S2

Legend figure S2:

Relationship between the number of offspring and male dominance rank in one bonobo and the three chimpanzee groups for which data on female sexual swelling sizes at the probable time of conception were available. Open circles indicate expected values based on the priority-of-access model and horizontal lines indicate the 95% confidence intervals. Red circles represent the actual values based on paternity analysis.

Supplemental Experimental Procedures

Genetic and paternity analyses

We considered as potential sires all males $\geq$ 9 years at the estimated month of conception. We calculated conception month by subtracting the mean gestation length of bonobos (230 days; [S1]) from the date the newborn was first seen. Paternity was assigned at 95% confidence levels in the likelihood-based CERVUS 3.0 parentage analyses program [S2] using 13 autosomal microsatellite loci genotyped from DNA derived from noninvasively collected feces, as recently described [S3]. Methods of genetic and paternity analyses for the five chimpanzee communities were similar and are described in the original publications: North group in Tai National Park, Ivory Coast, [S4]; Kasakela group in Gombe Stream National Park, Tanzania, [S5, S6]; Sonso group in Budongo Forest Reserve, Uganda, [S7, S8]; M group in Mahale Mountains National Park, Tanzania [S9]; Ngogo group in Kibale National Park, Uganda [S10–S12].

Measuring reproductive skew

We compared skew in bonobos with that in chimpanzees using identical time periods (i.e., 7 years and 12 years) because the extent of reproductive skew can be strongly affected by the period over which it is calculated. For example, in a group of 5 males where each male monopolizes reproduction in any given year, reproductive skew will be complete when calculated 5 times on a yearly basis, but absent if calculated only once for the whole 5-year period. Comparing skew over multiple chimpanzee community time periods also reduces the possibility that the observed differences result from chance temporal effects. For example, the long-term, underlying skew distribution of two communities may be identical, but if one was sampled during a period where the same male held the alpha position and the other when the

alpha male happened to change, the observed skew distributions would be very different. The alpha male did not change during the 7-year period in bonobos. However, reproductive skew was higher in bonobos than in the five chimpanzee 7-year periods where the alpha position also was constant (Table 1).

We calculated two complementary, widely used measures of male reproductive skew. The Nonac's binomial skew (B) considers the reproductive success of all candidate sires, and is the only such index that adjusts for differences among individuals in length of group membership. It is calculated as the difference between the observed and expected variance in paternity success, where the expected variance reflects a situation where every male has an equal probability of fathering any given offspring, which is calculated as the variance of the binomial distribution [S13]. The B-index thus not only reflects the underlying skew distribution, but also how likely the observed distribution was to have arisen by chance. Therefore, even when the underlying skew distributions are identical, more productive groups (i.e., more offspring paternities) and larger groups (i.e., more candidate sire males) will have higher B values than less productive and smaller groups, because the observed skew distributions are less likely to have resulted from random processes [S13]. Considering that both productivity and community size in bonobos were at the low end of the range of chimpanzees (Table 1), this lends support to our claim that the underlying skew distribution was indeed higher in bonobos than chimpanzees.

Our second measure of skew, the most successful sire's share of reproduction, is mathematically unrelated to differences between groups in productivity and size and is unaffected by the absence of unidentified/ungenotyped males who did not reproduce. However, it ignores variation in reproductive success among all but the most successful male.

All calculations of reproductive skew for each community considered males ≥10 years as candidate sires. We excluded years 1995-2002 at Taï North because anthropogenic and other diseases and poaching reduced the number of candidate sire to 2-3 males, which is a demographic scenario that probably did not frequently occur in the long-term evolutionary history of chimpanzees.

Reproductive skew and number of males

We ran two simple linear mixed models on the chimpanzee data to determine if bonobos had higher reproductive skew values than expected for a chimpanzee community with a similar number of males. Our two response variables were our two measures of reproductive skew, and our predictor variable was the average number of males ≥10 years alive in the community at the time of the conception. Random differences between communities may impact how the fixed effects influenced reproductive skew. To account for this, we incorporated the random slopes of fixed effects within communities in the model [S14]. The units of analysis were non-overlapping 7-year time periods. We therefore extracted from each community all possible sets of consecutive but non-overlapping 7-year-periods. For example, for the Ngogo community there are six different sets of two non-overlapping 7-year time periods (1996-2002 and 2003-2009, 1997-2003 and 2004-2010, 1998-2004 and 2005-2011, 1999-2005 and 2006-2012, 2000-2006 and 2007-2013, 2001-2007 and 2008-2014), as well as one single 7-year time period not represented in the preceding list (2002-2008). We ran each of our two models 392 times, which is the number of all possible combinations of these non-overlapping 7-year time periods across all chimpanzee groups, and averaged the results.

We generated 95% confidence intervals for the predicted values of both measures of reproductive skew for a given a number of males in the community using a parametric bootstrap. More specifically, we first conducted 100 independent bootstraps of the model estimates from each combination of non-overlapping 7-year blocks. Secondly, based on each bootstrapped model's estimates of the intercept, fixed effect and residual standard deviation, we generated a bootstrap of the response values. Finally, we examined where the observed reproductive skew value in bonobos fell in relation to the 95% confidence intervals for the predicted values in chimpanzees, which were generated from these 39,300 bootstrap responses (Figure S1).

Male dominance ranks

We determined bonobo male dominance rank during the month of conception using Elo-ratings (15) of the outcomes of decided agonistic interactions [S16], which we converted into monthly ordinal rankings (r). Details for determining ordinal rankings in chimpanzees are described in the original publications (Tai North: [S4]; Sonso: [S8]; Kasakela: [S5]; Ngogo: [S12]). To account for the fact that the same ordinal rank (r) could have different meanings depending on male group size (e.g., a male with a rank of 5 is very low-ranking in a group of 5 males, but very high-ranking in a group of 35 males), we calculated standardized dominance ranks (R) that accounted for the number of males aged ≥10 years in the community(n_m) with the following formula: $R = (n_m-r)/(n_m-1)$ [S17].

To compare the strength of the relationship between male dominance rank and reproductive success in chimpanzees and bonobos, we calculated 95% confidence intervals for the average standardized rank of sires through bootstrapping using the same procedure as described above for the most successful sire's share of reproduction [S12]. Unlike our comparisons of reproductive skew, where we parsed the data into 7 year periods, here we used

all of paternities in each community for which the corresponding dominance rank data were available (Bonobos: N = 13; Taï North = 13; Sonso = 13; Kasakela = 33; Ngogo = 109; M Group = 10).

Estrous synchrony and departure from the priority-of-access model

For each paternity we determined the number of maximally tumescent females present in the community on the estimated month of conception. For chimpanzees, these data were available from three communities: Taï North: [S4], Sonso: [S8], and Gombe: [S5]. In order to determine if alpha males sired significantly more offspring than expected under the predictions of the priority of access model, we generated 95% confidence intervals for the expected number of paternities for males of each ordinal dominance rank. For each offspring, we randomly assigned paternity to one of the males belonging to those ranks the priority-of-access model predicts will sire an offspring given the number of maximally tumescent females present in the community at the time of conception. For example, if there were four maximally tumescent females, we randomly assigned the conception to one of the males ranked 1-4. We repeated this procedure 10,000 times to obtain a distribution from which we drew our 95% confidence intervals. If the observed number of offspring sired by males of a given rank was outside the 95% confidence interval, this rank sired significantly more or significantly less offspring than expected by chance (Figure S2).

Author Contributions

Conceptualization: M.S., K.E.L., L.V., G.H.,

Methodology: K.E.L., L.V.

Formal Analysis: M.S.

Funding Acquisition: M.S., K.E.L., B.F., G.H.,

Resources: L.V., B.F., G.H., K.E.L

Writing – Original Draft: M.S., K.E.L., G.H.

Writing – Review & Editing: L.V.

Supplemental References

S1.   Drews, B., Harmann, L. M., Beehler, L. L.Bell, B., Drews, R. F., and Hildebrandt, T.B.
       (2011). Ultrasonographic monitoring of fetal development in unrestrained bonobos (*Pan
       paniscus*) at the Milwaukee County Zoo. Zoo Biol. *30*, 241–253.

S2.   Kalinowski, S. T., Taper, M.L., and Marshall, T.C. (2007). Revising how the computer
       program cervus accommodates genotyping error increases success in paternity
       assignment. Mol. Ecol. *16*, 1099–1106.

S3.   Moscovice, L.R., Douglas, P. H., Martinez-Iñigo, L., Surbeck, M., Vigilant, L., and
       Hohmann, G. (2017). Stable and fluctuating social preferences and implications for
       cooperation among female bonobos at LuiKotale, Salonga National Park, DRC. Am. J.
       Phys. Anthropol. *0*, 1–15.

S4.   Boesch, C., Kohou, G., Nene, H., and Vigilant, L. (2006). Male competition and paternity
       in wild chimpanzees of the Taï forest. Am. J. Phys. Anthropol. *130*, 103–115.

S5.   Altmann, S.A. (1962). A filed study of the sociobiology of rhesus monkeys, Macaca

mulatta. Ann. N. Y. Acad. Sci. *102*, 338–435.

S5.   Wroblewski, E.E., Murray, C. M., Keele, B.F., Schuhmacher-Stankey, J. C., Hahn, B. H., and Pusey, A. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. Anim. Behav. *77*, 873–885.

S6.   Feldblum, J.T., Wroblewski, E. E., Rudicell, R.S., Hahn, B. H., Paiva, T., Cetinkaya-Rundel, M., Pusey, A., and Gilby, I. (2014). Sexually coercive male chimpanzees sire more offspring. Curr. Biol. *24*, 2855-2860.

S7.   Langergraber, K.E, Rowney, C. Crockford, C. Wittig, R., Zuberbühler, K., and Vigilant, L. (2014). Genetic analyses suggest no immigration of adult females and their offspring into the Sonso community of chimpanzees in the Budongo Forest Reserve, Uganda. Am. J. Primatol. *76*, 640–648.

S8.   Newton-Fisher, N.E., Thompson, M.E., Reynolds, V., Boesch, C., and Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. Am. J. Phys. Anthropol. *142*, 417–428.

S9.   Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O., and Nishida, T. (2008). Relatedness in wild chimpanzees: influence of paternity, male philopatry, and demographic factors. Am. J. Phys. Anthropol. *137*, 256–262.

S10.   Langergraber, K.E., Mitani, J.C., and Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. Proc. Natl. Acad. Sci. USA *104*, 7786–7790.

S11.   Langergraber, K., Mitani, J., and Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). Am J Primatol *71*, 840–851.

S12.   Langergraber, K.E., Mitani, J.C., Watts, D.P., and Vigilant, L. (2013). Male-female socio-spatial relationships and reproduction in wild chimpanzees. Behav. Ecol. Sociobiol. *67*,

861–873.

S13. Nonacs, P. (2000). Measuring and using skew in the study of social behavior and evolution. Am. Nat. *156*, 577–589.

S14. Schielzeth, H., and Forstmeier, W. (2008). Conclusions beyond support: overconfident estimates in mixed models. Behav. Ecol. *20*, 416–420.

S15. Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., and Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. *82*, 911–921.

S16. Vervaecke, H., de Vries, H., van Elsacker, L. (2000). Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). Int. J. Primatol. *21*, 47–68.

S17. Muller, M.N., Thompson, M.E., Wrangham, R.W. (2006). Male chimpanzees prefer mating with old females. Curr. Biol. *16*, 2234–2238.