

# Atypically High Reproductive Skew in a Small Wild Chimpanzee Community in a Human-Dominated Landscape

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## Keywords

*Pan troglodytes* · Chimpanzee · Reproductive skew · Anthropogenic disturbance · Social rank

## Abstract

Social rank is positively correlated with reproductive success in numerous species, albeit demographic factors often influence those patterns. In multimale primate species, reproductive skew tends to decrease with increasing numbers of males and sexually receptive females. Alpha male chimpanzees (*Pan troglodytes*) often sire a disproportionate, though somewhat variable, percentage of offspring compared to other males. In a small community of eastern chimpanzees inhabiting a human-dominated landscape in Bulindi, Uganda, we found extraordinarily high levels of alpha male reproductive success over a 5-year period (7/8 offspring = 88%), despite the presence of multiple subordinate males. The skew exceeds that reported in other studies of chimpanzees as well as closely related bonobos (*Pan paniscus*). Our findings underscore the role of demographic and social factors in male reproductive success and also suggest that conclusions about species differences may be premature. The interaction of small community size, dispersal limitations, and male reproductive strategies like those found here may decrease genetic diversity and increase the risk of concomitant inbreeding in chimpanzee communities under strong anthropogenic pressure.

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## Introduction

Sexual selection theory predicts that males compete for access to a limited number of females [Trivers, 1972]. In many species, social rank reflects the outcomes of potentially costly competition among males, but these costs are frequently offset for high-ranking males by an increase in reproductive success [Ellis, 1995]. Nonetheless, even for dominant males high rank does not ensure complete control over reproductive opportunities. Models of reproductive skew typically focus on the demographic and social factors relevant to male reproductive success [transactional and compromise models; reviewed in Johnstone, 2000]. Demographic factors include the number of rival males and reproductive females; as these increase, the ability of the dominant male to control mating opportunities tends to decrease [Reeve et al., 1998]. In addition, social factors include the costs and benefits to dominant males of ceding opportunities to maintain group stability, garner support, or gain inclusive fitness benefits by allowing mating opportunities for subordinate males [Reeve et al., 1998]. In multimale primate species, reproductive skew typically decreases as a function of increasing numbers of males [Kutsukake and Nunn, 2006] and receptive females [Ostner et al., 2008], underscoring an important role for demographic factors in predicting the reproductive success of dominant males [Altmann, 1962].

Chimpanzees (*Pan troglodytes*) offer a useful opportunity to investigate how demographic and social factors are linked to male reproductive skew. They live in multimale/multifemale “communities” that vary in size from approximately 20 to 200 members [Sugiyama, 1999; Langergraber et al., 2017]. Sexually receptive females typically mate with multiple males [Takahata et al., 1996], and although female chimpanzee estrous cycles are asynchronous [Matsumoto-Oda et al., 2007], simultaneous sexual receptivity of multiple females commonly occurs [Goodall, 1986]. Males form a linear dominance hierarchy, with alpha males typically siring a disproportionate share of offspring [Boesch et al., 2006; Inoue et al., 2008; Wroblewski et al., 2009; Newton-Fisher et al., 2010]. Nonetheless, subordinate males also sire offspring, particularly through the use of strategies such as opportunistic mating and consortship [Constable et al., 2001]. In larger communities, alpha males may be able to exert relatively less control over mating opportunities, especially in the presence of multiple simultaneously receptive females [Boesch et al., 2006]. Male reproductive success in chimpanzee communities is therefore skewed, but variably so.

In contrast, closely related bonobos (*Pan paniscus*) are characterized by lower rates of male aggression and relatively higher female social ranks, which could be expected to lead to lower reproductive skew as compared to chimpanzees. Intriguingly, however, two recent studies found higher levels of reproductive skew in bonobos than in chimpanzees [Surbeck et al., 2017; Ishizuka et al., 2018]. Possible explanations for this particularly high skew include maternal support of sires, female choice acting to enhance the reproductive success of desirable males, and high group cohesion leading to few opportunities for lower-ranking males to exert alternative strategies such as consortship or sneaky copulation. However, to date there are relatively few studies on male reproductive success in bonobos, and additional research is necessary to confirm that these purported species differences [Surbeck et al., 2017; Ishizuka et al., 2018] are not merely an artefact of having insufficient data to represent the range of variation present in these species.

To further explore the role of demographic and social variation on patterns of reproductive skew in *Pan*, we studied a small community (18–22 individuals) of eastern chimpanzees (*P. t. schweinfurthii*) at Bulindi, Uganda. This community contained a total of 5 males and 8 females of reproductive age during the study period, making it among the smaller habituated chimpanzee study sites. These individuals live in a human-dominated landscape characterized by small, unprotected riparian forest fragments amid farms and villages [McLennan, 2013], and are further constrained by a limited and likely decreasing ability to disperse to other communities in the region [McCarthy et al., 2018]. Using behavioral and genetic data, we determined the paternity of all surviving offspring conceived and born between 2012 and 2016 to assess patterns of male reproductive success and their potential consequences for the conservation of this exemplar of a small chimpanzee community.

## Methods

### *Study Area and Subjects*

The Bulindi chimpanzee community inhabits a farm-forest mosaic in Hoima District, western Uganda, between the Budongo and Bugoma Forests (1°29'N, 31°28'E) [McLennan, 2013]. Bulindi is one of at least nine chimpanzee communities inhabiting this human-dominated landscape, which is populated by an estimated 260 or more chimpanzees [McCarthy et al., 2015]. The Bulindi chimpanzee community was studied initially from 2006 to 2008 [McLennan and Hill, 2010]. During this time, the chimpanzees were mostly unhabituated to researcher presence [McLennan and Hill, 2010] and community size was estimated at 30 or more individuals, including 6 identified mature males, at least 8 mature females, and numerous infants and juveniles [McLennan, 2010].

Data collection resumed in 2012, and the chimpanzees were fully habituated by 2015 [Cibot et al., 2019; McLennan et al., 2019]. During the period 2012–2016, all community members were individually identifiable and the community had declined to between 18 and 22 individuals, including a total of 5 mature males (range per year: 0–1 adolescents and 2–3 adults, see online suppl. Table S1 for age estimates; see [www.karger.com/doi/10.1159/000508609](http://www.karger.com/doi/10.1159/000508609) for all online suppl. material) and a total of 8 mature females (range per year: 0–2 adolescents and 5–6 adults). Although precise maturational transitions are difficult to pinpoint in chimpanzees [Alberts, 2012], reproductive maturity typically occurs around age 10 and is generally defined by the onset of adult-sized sexual swellings in females and by the descent of the testes in males [Boesch and Boesch-Achermann, 2000]. This age also corresponds to the youngest age at which a wild male chimpanzee has been known to sire offspring [Boesch et al., 2006].

Since the resumption of data collection in 2012, there has been a single socially dominant (alpha) male, Sylvester (SL). Based on observational data, he is thought to have achieved alpha rank around the time data collection resumed [unpublished data]. In this study, we considered all mature males as putative fathers and as competitors for reproductive access. Among females, up to 3 were sexually receptive (i.e., with a maximal swelling of the anogenital region) at any given time during the period since 2012 [McLennan et al., 2019], though female cycle data were not available continuously throughout this time.

### *Genetic Analysis*

We collected fresh fecal samples from chimpanzees at Bulindi during 2017. We collected samples only when individual identity could be confirmed, and collected up to five samples per individual to allow us to compare genotypes and confirm identities. Samples were stored at room temperature in the field for up to 8 months using the two-step ethanol-silica method described in Nsubuga et al. [2004]. Samples were then shipped to the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, where they were stored at 4 °C prior to extraction. DNA was extracted and amplified at 15 microsatellite loci including amelogenin, used for sex determina-

**Table 1.** Paternity analysis results for offspring conceived and born during SL's alpha tenure (2012–2016)

Offspring			Mother	Assigned father		
ID	sex	YOB	ID	ID <sup>a</sup>	rank	Comp. <sup>b</sup>
GG	F	2013	LL	NA	beta <sup>c</sup>	4
RO	M	2013	MN	SL	alpha	4
MK	M	2013	MD	SL	alpha	4
AL	M	2014	TD	SL	alpha	4
MA <sup>d</sup>	F	2016	MD	SL	alpha	4
KS	M	2016	JM	SL	alpha	4
LC	F	2016	MN	SL	alpha	4
WD	F	2016	LL	SL	alpha	3

YOB, year of birth. <sup>a</sup>NA indicates that paternity analysis did not yield a paternity assignment with >95% confidence. <sup>b</sup>Number of male competitors present in the Bulindi community at the approximate date of conception. <sup>c</sup>Rank is beta if KT, the only unsampled male who was present in the community at the time of conception, was confirmed as father. <sup>d</sup>This paternity was published previously in Cibot et al. [2019].

tion [Bradley et al., 2001]. Further details of these methods are provided in the online supplementary material.

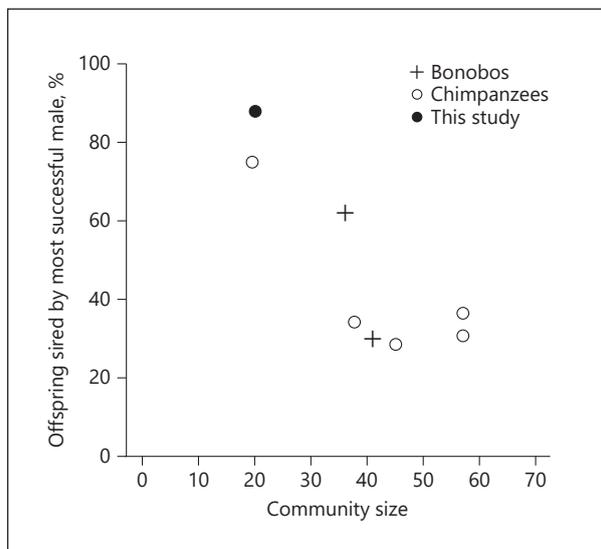
We supplemented these genotypes with additional genotype data generated from samples collected during 2012–2013 for members of this community using the same approach [McCarthy et al., 2015]. These additional genotypes provided the only genetic data for 3 individuals deceased at the time of sample collection in 2017, and provided data used to create consensus genotypes for 14 additional chimpanzees. The resulting consensus genotypes were 97% complete for 25 chimpanzees, including 8 offspring conceived and born between 2012 and 2016, 4 candidate fathers, and 8 candidate mothers. Candidate parents included all individuals who appeared reproductively mature during the study period.

#### *Parentage Analysis*

We conducted parentage analyses using a likelihood-based method in CERVUS 3.0.7 [Kalinowski et al., 2007]. First we conducted a maternity analysis to confirm all pedigree-assigned maternities, i.e., to verify mother-offspring pairs known through years of observed behavioral association. This analysis included 8 candidate mothers, all of which were sampled, and confirmed maternities for all 8 offspring with >99% confidence.

Next we conducted a paternity analysis for the same offspring using mothers confirmed in the maternity analysis. We estimated a total of 6 candidate fathers, which included 4 sampled mature males (estimated proportion sampled = 0.67), 1 mature male who was known to be present during this period but disappeared before being sampled (KT), and 1 additional potential sire via extragroup copulation. Extragroup copulation occurs infrequently in eastern chimpanzees [<5%; Wroblewski et al., 2009] and is probably especially unlikely given the lack of neighboring chimpanzee communities near Bulindi (the minimum distance to the nearest community is about 8 km across a human-dominated landscape), but we conservatively factored in the potential for its occurrence. All resulting paternities were assigned with >99% confidence. Paternity for 1 offspring was published previously [Cibot et al., 2019], while all remaining paternities were newly assigned in the current study. Further details of the maternity and paternity analyses are provided in the online supplementary material. We compared reproductive skew at Bulindi, assessed as the proportion of offspring sired by the most successful male, to published values from other studies of chimpanzees and bonobos. These studies are comparable, relying on a similar

**Fig. 1.** The relationship between community size and male reproductive success across bonobo and chimpanzee sites, including this study. Data beyond the current study come from reported values or study period means extracted from the following published findings: Sugiyama et al., 1993; Gerloff et al., 1999; Constable et al., 2001; Vigilant et al., 2001; Inoue et al., 2008; Newton-Fisher et al., 2010; Surbeck et al., 2017; Surbeck, personal communication.



age criterion for defining male sexual maturity: 10 years in the current study and 9–10 years in the other published studies, except for one study that did not report the minimum age for male inclusion [Gerloff et al., 1999].

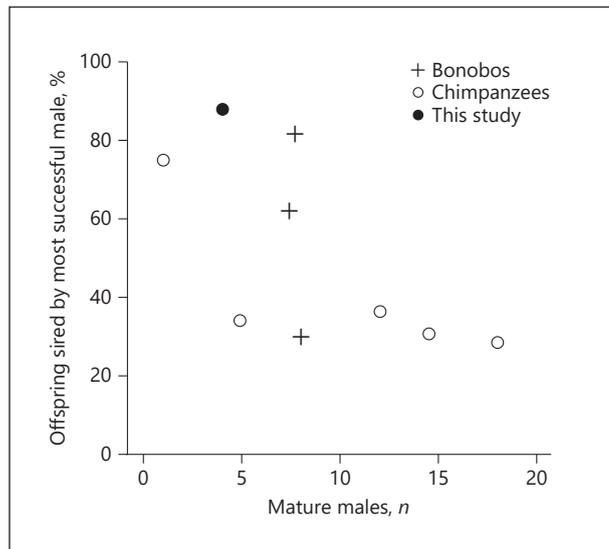
In addition to the paternity analysis for these 8 offspring, we conducted a second parentage analysis for 7 offspring born between 2005 and 2011, which included all surviving offspring born around and following the time the initial study of the Bulindi chimpanzees began, but prior to SL achieving alpha status. Due to the decline in community size over the course of this period, a number of candidate parents were no longer present in the community by the time of sampling in 2017. The estimated proportions of candidate parents sampled were therefore much lower for this period (0.6 and 0.3 for candidate mothers and fathers, respectively). Because of these differences in the parentage analysis parameters, we tested this period separately to determine whether any paternities could be confirmed even in the absence of more extensive data on male ranks and full community demography. Details of this secondary analysis are provided in the online supplementary material.

## Results

Of the 8 sampled offspring born since SL achieved alpha status, he sired 7 (Table 1). For the 8th offspring, paternity could not be assigned and the father is presumed to be high-ranking KT, the only mature male who was present in the community but not genotyped during the study period. One additional offspring was born during this period, but died before being genotyped. Based on these data, alpha male SL sired 88% of the sampled offspring. Including the unsampled offspring, he sired between 78 and 89% of all offspring born since achieving alpha rank. This degree of alpha male reproductive success exceeds that reported for other chimpanzee study sites and equals or exceeds that reported for bonobos (Fig. 1, 2).

SL was not assigned as father of any of the 7 sampled offspring born prior to 2012; instead, a minimum of 3 other males were found to have sired offspring during this time (details provided in the online supplementary material).

**Fig. 2.** The relationship between the number of reproductively mature males in a community and male reproductive success across bonobo and chimpanzee sites, including this study. Data beyond the current study come from reported values or study period means extracted from the following published findings: Sugiyama et al., 1993; Gerloff et al., 1999; Constable et al., 2001; Vigilant et al., 2001; Inoue et al., 2008; Newton-Fisher et al., 2010; Surbeck et al., 2017; Ishizuka et al., 2018.



## Discussion

In the small Bulindi chimpanzee community, alpha male SL sired 88% of sampled offspring during the first 5 years of his tenure. This particularly high reproductive success may have resulted from several factors. SL has frequently been observed actively mate-guarding sexually receptive females [unpublished data] and it is clear that since his alpha tenure began, SL's reproductive strategies resulted in near monopolization of paternities despite the presence of 3–4 mature males at the time of each offspring's conception. SL's reproductive control may have been aided by high community cohesion at Bulindi [unpublished data], leaving reduced chances for sneaky copulation by subordinate males. Although calculating male reproductive success is prone to stochastic variation based on sample size and the temporal window of analysis, our 5-year study period approximates the average tenure length for alpha male chimpanzees (e.g., mean = 5.4 years) [Bray et al., 2016], making it adequate for comparisons with other studies of alpha male reproductive patterns.

This finding extends a broader pattern observed across numerous chimpanzee study sites, whereby the number of male competitors (and, more broadly, community size) is negatively associated with the alpha male's share of sirings (Fig. 1, 2). Similarly, Boesch et al. [2006] found support for the role of demographic factors in reproductive skew. In their study, as in ours, a decrease in community size was associated with an increase in alpha male reproductive success. Though limited paternity data were available for Bulindi from 2005 to 2011 as community size declined, we confirmed that at least 3 males sired offspring during this time, suggesting a shift in patterns of reproductive success with declining size.

We also found that reproductive skew was higher than levels reported at bonobo study sites. Despite recent findings indicating that bonobos have higher reproductive skew than chimpanzees [Surbeck et al., 2017; Ishizuka et al., 2018], we confirmed the

potential for very high reproductive skew in a small chimpanzee community. Thus, our findings suggest that it may be premature to conclude that reproductive skew is generally higher in bonobos than chimpanzees, and that more data from a larger sample of bonobo and chimpanzee communities under various demographic conditions are needed to ascertain whether a species difference exists in reproductive skew.

These results have strong conservation implications for the Bulindi chimpanzee community and others like it. Genetic diversity in a wild animal population can decrease when the number of individuals reproducing decreases [Frankham, 1996], and Bulindi has experienced sharp declines in community size, with approximately one-third of the members disappearing between 2008 and 2012, including disappearances associated with anthropogenic factors [unpublished data]. Though chimpanzees are not usually hunted for meat in Uganda, increasing human pressure including habitat loss [Junker et al., 2012], snare hunting [Reynolds, 2005], crop protection methods [McLennan et al., 2012], and anthropogenic disease transmission [Scully et al., 2018] pose a serious threat to their survival. In human-disturbed habitats like this one, reduced population size can also result in inbreeding depression [Keller and Waller, 2002], and this threat can be compounded by reproductive strategies leading to an even higher level of male reproductive skew, as illustrated by our findings. Further, dispersal is a potential means of reducing the risk of inbreeding [Pusey, 1987], but habitat loss may decrease the likelihood of female dispersal [McCarthy et al., 2018], thereby heightening inbreeding risk. Given the tendency for great apes to inhabit increasingly human-altered habitats [Hockings et al., 2015], there is great practical value in understanding how demographic changes, reproductive strategies, and dispersal patterns may interact to influence genetic diversity in remaining populations. Conservation approaches can be best informed by considering the potential relationships among these factors amidst the backdrop of rapidly changing great ape habitats.

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## **Statement of Ethics**

The data presented in this study were collected entirely noninvasively and required no contact with the study subjects. The study was approved by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology.

## **Conflict of Interest Statement**

The authors have no conflict of interest to declare.

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## Author Contributions

M.S. McCarthy performed laboratory analyses, analyzed the data, and wrote the manuscript. J.D. Lester performed laboratory analyses and assisted in data analysis. M. Cibot collected samples and data for analysis and contributed to project conception. L. Vigilant oversaw genetic analysis and provided expertise in the study design and analysis. M.R. McLennan collected and exported samples and data for analysis, supervised field data collection, and contributed to project conception. All authors contributed to manuscript revisions and approved the submitted version.

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