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Reproductive inequality among males in the genus *Pan*

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Reproductive inequality, or reproductive skew, drives natural selection,
but has been difficult to assess, particularly for males in species with pro-
miscuous mating and slow life histories, such as bonobos (*Pan paniscus*)
and chimpanzees (*Pan troglodytes*). Although bonobos are often portrayed
as more egalitarian than chimpanzees, genetic studies have found high
male reproductive skew in bonobos. Here, we discuss mechanisms likely
to affect male reproductive skew in *Pan*, then re-examine skew patterns
using paternity data from published work and new data from the Kokolo-
pori Bonobo Reserve, Democratic Republic of Congo and Gombe National
Park, Tanzania. Using the multinomial index (M), we found considerable
overlap in skew between the species, but the highest skew occurred
among bonobos. Additionally, for two of three bonobo communities,
but no chimpanzee communities, the highest ranking male had greater
siring success than predicted by priority-of-access. Thus, an expanded
dataset covering a broader demographic range confirms that bonobos
have high male reproductive skew. Detailed comparison of data from
Pan highlights that reproductive skew models should consider male–
male dynamics including the effect of between-group competition on incen-
tives for reproductive concessions, but also female grouping patterns and
factors related to male–female dynamics including the expression of
female choice.

This article is part of the theme issue 'Evolutionary ecology of
inequality'.

1. Introduction

Given that natural selection results from differential reproductive success, factors
affecting the distribution of reproduction constitute a central issue for under-
standing social evolution [1]. Disparities in individual physical condition,
access to resources, social status and social relationships can lead to inequality
in reproduction, also known as reproductive skew [2]. Across societies, the
degree of inequality in lifetime reproductive success varies from low, such as
in cooperatively breeding greater ani (*Crotophaga major*) [3], to high, such as
in eusocial naked-mole rats (*Heterocephalus glaber*) [4] and mound-building termites

(*Macrotermes*) [5], in which many individuals assist the reproduction of one fertile pair. Efforts to establish a unified theory of reproductive skew depend on long-term field data from species living in a broad range of societies. Such data have been difficult to obtain, however, particularly for males in species with internal fertilization, promiscuous mating, and slow life histories, including our closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).

In a strictly promiscuous mating system, where males and females mate indiscriminately, equal access to reproductive opportunities can theoretically occur. In practice, however, the distribution of paternities often deviates from an equal distribution owing to competition and conflicting interests within and between the sexes [6–10], as observed in a broad range of species, including rock iguanas (*Cyclura nubila caymanensis*) [11], acorn woodpeckers (*Melanerpes formicivorus*) [12], tree sloths (*Bradypus variegatus* and *Choloepus hoffmanni*) [13], buffy flower bats (*Erophylla sezekorni*) [14], spotted hyaenas (*Crocuta crocuta*) [15], white-faced capuchins (*Cebus capucinus*) [16], Barbary macaques (*Macaca sylvanus*) [17] and yellow baboons (*Papio cynocephalus*) [18]. This in turn shapes male and female reproductive strategies [19]. On one hand, males seek to increase reproductive success through strategies including contest competition with other males, sperm competition, efforts to constrain female mating behaviour with sexual coercion, and infanticides [20–22]. On the other hand, females compete among themselves for resources to enhance offspring survival while trying to obtain benefits from males such as good genes, paternal care, and help in resource acquisition [20–22]. The interplay of these strategies makes it difficult to assess the relative importance of different factors affecting male reproductive success across species [6,17,23].

The various models proposed to explain male reproductive skew generally focus on the ability of males to monopolize reproductive opportunities with females [24,25] and to control reproductive activities of other males [1,7,26–30]. The priority-of-access (PoA) model [31] provides a useful heuristic for the expected distribution of paternities in a given multi-male, multi-female group. This model assumes that males queue for reproductive opportunities based on their competitive ability and the availability of fertile females at a given point in time. Deviations from this expected distribution can arise when dominant males cannot control reproductive access to sexually receptive females [27] or when they permit reproduction by other males [32]. Explaining such deviations require theoretical models that focus on the ultimate reasons for group formation, including fitness benefits that males may gain from group-living even if low-ranking [33].

The limited-control and concession models seek to explain variation in male reproductive skew across species, considering the ultimate reasons for low-ranking males to stay in a group. Under the limited-control model, the highest ranking male does not have complete control over the reproductive activities of other males and females, which may result in low-ranking males gaining reproductive opportunities [7,26–29]. Empirical evidence supports this model across taxa including acorn woodpeckers [12], American crows (*Corvus brachyrhynchos*) [34], meerkats (*Suricata suricatta*) [35], spotted hyaenas [15], mandrills (*Mandrillus sphinx*) [36], rhesus macaques (*Macaca mulatta*) [17] and mountain gorillas (*Gorilla gorilla beringei*) [37].

Alternatively, the concession model assumes that the highest ranking male controls reproduction in the group and permits reproduction by lower ranking males in exchange for social benefits [1,7,26,27,30]. This model was originally developed to explain reproductive skew in eusocial insects, where dominant queens control reproduction by destroying eggs laid by subordinate queens [32]. Cooperatively breeding species such as dwarf mongooses (*Helogale parvula*) provide some empirical evidence to support this model, as dominant individuals apparently concede a share of reproduction to subordinates to entice their cooperation in offspring rearing [38]. Nevertheless, in many group-living species, it may rarely be the case that top-ranking males sufficiently control reproductive access to females that concessions need to be invoked. As noted above, top-ranking males appear to lack complete control over reproductive opportunities in a broad range of species. However, even without complete control, these males may still benefit by conceding some of the reproduction which they can control in exchange for other benefits [33,39]. The reproductive concession and the limited-control models can, therefore, be difficult to distinguish.

Understanding male reproductive skew in our two closest living relatives, chimpanzees and bonobos, is challenging owing to their long lives and low reproductive rates. Both species live in multi-male, multi-female communities [40–44] with: (i) fission–fusion dynamics, in which individuals travel in subgroups (parties) that can vary in size and composition throughout the day [41,42,45]; (ii) female-biased dispersal [41,44,46,47]; (iii) promiscuous mating [41,46,48]; and (iv) female signalling of fertility though sexual swellings [49–51]. Bonobos are commonly considered to be more peaceful and egalitarian than chimpanzees [42,52,53]. Consistent with this notion, one study based on mating behaviour found bonobos to have low reproductive skew [23]. However, studies using genetic paternity data revealed that bonobos at LuiKotale [54,55] and Wamba [56] have high reproductive skew, even higher than that reported for both eastern (*Pan troglodytes schweinfurthii*: Gombe, Mahale, Kibale and Budongo) and western (*Pan troglodytes verus*: Taï) chimpanzees [54]. However, the sample reported for bonobos remains small (12 population-years in bonobos compared to 41 population-years in chimpanzees) [54].

In this review, we will first consider potential mechanisms underlying reproductive skew in *Pan*. Second, we re-examine reproductive skew in *Pan* using existing and new data for bonobos ($n = 27$ population-years) and chimpanzees ($n = 91$ population-years). Third, we re-evaluate the mechanisms underlying reproductive skew in *Pan* and consider the broader consequences of our findings.

2. Mechanisms underlying reproductive skew in *Pan*

In many species, including fig wasps [57], wire-tailed manakins (*Pipra filicauda*) [58], greater sage-grouse (*Centrocercus urophasianus*) [59], Weddell seals (*Leptonychotes weddellii*) [60], elephant seals (*Mirounga leonine*) [61], feral horses (*Equus ferus caballus*), plains zebras (*Equus quagga*) [62] and red deer (*Cervus elaphus*) [63], high male reproductive skew results from intense contest competition between males. Contrary to the common portrayal of bonobos as peaceful, in both

bonobos [55,64–67] and chimpanzees [68–74], more aggressive, high-ranking males obtain more mating success than less aggressive, low-ranking males. Nonetheless, dominance status does not completely predict male reproductive success in *Pan*, requiring the consideration of additional mechanisms [28,75,76].

(a) Mechanisms operating under reproductive concession

(i) Importance of male coalitionary aggression and opportunities for extra-community paternities

High-ranking males can gain fitness benefits from reproductive concessions when their reproductive success depends on the support of coalition members, as in wire-tailed manakins (*Pi. filicauda*) [58], bottlenose dolphins (*Tursiops aduncus*) [77] and lions (*Panthera leo*) [78]. Male chimpanzees defend a group territory, which serves as a feeding territory for themselves, their mates and their offspring; females reproduce faster when territory size is larger [79]. Males depend on support from other males to patrol territory boundaries and exclude outside males from mating with resident females [76,80,81], and to attack and kill extra-community members [82–86]. Within communities, males may also rely on support from allies to achieve high status and gain mating opportunities [28,75,87,88]. With their strictly hostile inter-community interactions and strong cooperative outgroup defence, male chimpanzees reduce opportunities for within-community females to reproduce with extra-community males.

Unlike male chimpanzees, male bonobos rarely provide agonistic support to other males [89], and mostly rely on individualistic strategies during conflict within [66,67,89] and between communities [90,91]. Thus, high-ranking male bonobos may have little motivation to concede reproductive opportunities, which should increase reproductive skew (table 1). Moreover, without strong coalitions among males, interactions among neighbouring bonobo communities are more relaxed; males and females can spend many hours associating with extra-community individuals [52,90,92–94], creating opportunities for males to sire offspring in other communities. Such opportunities can result in further inequalities in lifetime reproductive success, particularly if they correlate with dominance rank (table 1).

(b) Mechanisms operating under limited-control

(i) Social cohesion and female gregariousness

Although variation in social cohesion occurs across chimpanzee communities (Budongo [95]; Gombe: [96–98]; Kanyawara: [99,100]; Mahale:[101]; Ngogo [102,103]; Taï [69,104,105]), bonobos generally appear to travel in larger [106–111] and more cohesive parties [104,112] than chimpanzees, with females being more gregarious in the former [106,109,112]. The mean bonobo party size contains 27–51% of all community members (*n* = 2 communities), compared to only 9–20% for chimpanzees (*n* = 8 communities) [106]. Increased female social cohesion may allow male bonobos to monitor the reproductive status and activity of maximally tumescent females more effectively, potentially leading to higher male reproductive skew in bonobos than chimpanzees (table 1).

In chimpanzees, the more dispersed ranging patterns of females may provide opportunities for consortships whereby a male and female travel together, away from others [71,76,113,114]. Insofar as lower ranking males use consortships to evade control by higher ranking males, consortships should reduce reproductive skew (table 1).

(ii) Female reproductive synchrony

Female reproductive synchrony can hinder reproductive monopolization by high-ranking males [23,25,115], decreasing male reproductive skew. In primates, sexual swellings appear to have evolved as a female strategy to attract mating effort from many different males, thereby confusing paternity and reducing infanticide risk [115–118]. While both bonobos and chimpanzees exhibit sexual swellings, the extent to which females synchronously display full tumescence differs between the two species. Compared to chimpanzees, female bonobos: (i) resume swelling sooner after giving birth [49,51,64,119–122]; (ii) have longer maximally tumescent phases and greater variation in their duration; and (iii) therefore, spend a larger proportion of their interbirth intervals maximally tumescent [49,116,119,120,123]. Hence, for a given number of females, at any given time, more females display full tumescence in bonobos than chimpanzees [52,124]. Because bonobo swellings signal ovulation less reliably, monitoring and mate-guarding females seem more difficult and costly for male bonobos, reducing male reproductive skew compared to chimpanzees [55] (table 1).

(iii) Additional cues of ovulation

In mammals, males also rely on other signals to infer female reproductive status and fecundability. This includes the use of olfactory cues by males in Djungarian hamsters (*Phodopus campbelli*) [125], ring-tailed lemurs (*Lemur catta*) [126] and cotton-top tamarins (*Saguinus oedipus*) [127]; the use of female vocal signals in grey mouse lemurs (*Microcebus murinus*) [128] and Barbary macaques [129]; and detection of female behavioural changes in rhesus macaques [130] and long-tailed macaques (*Macaca fasciularis*) [131]. Reproductive skew may then be increased, insofar as high-ranking males are better able to act on this information than low-ranking males. Chimpanzees in captivity use olfactory cues to obtain information about social relationships [132], suggesting they may be able to use them to detect ovulation [133], but whether either species of *Pan* does, in fact, do so remains untested.

(iv) Importance of female alliance

In some species, females may cooperate with kin to combat male aggression and harassment (rhesus macaques: [134,135]; olive baboons: [136]; also review by Smuts [137]). Strikingly, in bonobos, females form coalitions with unrelated females; this strategy may have evolved to counter sexual coercion and/or infanticide by males [52,138,139]. One of the key behaviours facilitating female social bonding in bonobos is genito-genital rubbing, which often involves maximally tumescent females [140,141]. Having a full swelling, therefore, may increase a female's value as a social partner [104,142]. Thus, although sexual swellings presumably originated as a reproductive signal to males [99], they may also serve as a signal to attract affiliation and coalitionary support among females. This may in turn restrict males'

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Table 1. Predicted effects of different mechanisms that may drive variation in male reproductive skew in *Pan*.

model	mechanism	type of relationship affected	predicted effect on skew	which species expected to have higher skew
reproductive concessions	reduced importance of male coalitionary aggression decreases the need to reward allies with reproductive concessions	male–male	increase	bonobos
	with little cooperative outgroup defence, increased opportunities for extra- community paternities	male–male	unclear	unclear
limited-control	increased social cohesion and female gregariousness increase monopolizability of females by top-ranking male	female–female	increase	bonobos
	lower number of females per community increases monopolizability of females by top-ranking male	female–female	increase	bonobos
	more apparent female reproductive synchrony	female–female	decrease	chimpanzees
	reduced infanticide risk reduces female need to distribute paternity certainty across many males	male–female	increase	bonobos
	additional cues of ovulation (e.g. odour) improves male ability to detect fertile females and control reproduction	male–female	increase	unclear
	increased importance of female alliances reduces males' ability to control reproduction	female–female; male–female	unclear	unclear
	reduced male sexual coercion	male–female	unclear	unclear
	increased potential for expression of female mate preference	male–female	unclear	unclear
	increased influence of mothers on sons' reproductive behaviour	male–female	unclear	unclear
	low number of males per community increases the ability of high-ranking males to monitor the activities of low-ranking males	male–male	increase	bonobos
	within-community relatedness between sexes and inbreeding avoidance	male–female	decrease	unclear

reproductive control and increase females' ability to express their mate preferences; the resulting effect on male reproductive skew would depend on female preferences (see below).

(v) Male sexual coercion and female mate preference

While males commonly seek to control female reproductive activities, females have their own goals and preferences. Females can seek out preferred mating partners and avoid or resist advances by non-preferred males. Among chimpanzees, females face the risk of sexual coercion by males [69,74,76,143–147], and the extent to which females can exercise mate choice remains disputed [116,146,148,149]. However, whether sexual coercion increases male reproductive skew depends on which males use this strategy. While high-ranking male chimpanzees may coerce females to restrict their mating activity [74,114,145], lower ranking males also coerce females, including during consortships, when males threaten and attack females if they do not follow [71,76,114].

By contrast, female bonobos commonly outrank even the highest ranking males [52,139] and they do not appear to experience sexual coercion by males [67,139,150]. Thus, female bonobos probably have a greater capacity to act on their preferences than do female chimpanzees [151,152].

Factors that guide female preferences may affect male reproductive skew differently. Females can use male dominance status as a cue of genetic quality [153–155], in which case increased female choice would increase male reproductive skew, such as in Verreaux's sifakas [156] and white-faced capuchins [16], reaching an extreme in species with a lek mating system [157], such as in black grouse (*Lyrurus tetrix*) [158] and wire-tailed manakins (*Pi. filicauda*) [58]. Alternatively, if females base their choice on male traits that do not necessarily depend on dominance rank, such as the provisioning of resources, paternal care or other services, increased expression of female choice could reduce male reproductive skew. In spotted hyaenas, where females are dominant over males, females can express their preferences and tend to mate with immigrant males that are typically lower ranking than natal resident males, potentially to ensure genetic diversity in their offspring [15]. In bonobos, females both affiliate and copulate more with high-ranking than low-ranking males [66], suggesting that female preferences combine with competition among males to increase male bonobo reproductive skew [146] (table 1).

(vi) Influence of mothers

Mothers can assist the reproductive success of their sons [159], as reported in orcas (*Orcinus orca*) [160] and northern muriquis (*Brachyteles hypoxanthus*) [161]. Although in chimpanzees, sons with mothers present have a higher rank and reproductive success [96,162–166], the impact of mothers

appears stronger and more direct in bonobos [89,167,168]. Bonobo mothers may support their sons by interrupting copulations between females and other males [168], providing agonistic support to their sons during conflict with other males [52,139]. Males may also take advantage of their mother's social ties, to monitor maximally tumescent females more effectively, and to form close associations and copulate with them [169]. Because high-ranking females often occupy high-quality food patches [170], other females potentially mate with the sons of high-ranking females in exchange for better access to food. The effect of mothers on male reproductive skew probably depends on whether it is high- or low-ranking sons that have a living mother to provide support (table 1).

(vii) Number of males
The number of males per group probably impacts the potential for male reproductive control [18,23,115,171–173]. In the Kasekela chimpanzee community at Gombe, low-ranking males sometimes do manage to sire offspring, despite PoA expectations, perhaps because males are too numerous and dispersed to be monitored effectively by the highest ranking male [76]. In this situation, the highest ranking male may focus on monitoring males that are close to him in rank [76]. Overall, we should expect male reproductive skew to be lower in communities with more males (table 1).

(viii) Relatedness
Within-community relatedness may also influence the ability of high-ranking males to control female reproduction and thus the degree of male reproductive skew, owing to female efforts to avoid inbreeding [174]. Even when they remain in their natal community, female chimpanzees frequently reject mating attempts by close male kin and generally avoid conceiving offspring with them [174]. As in spotted hyaenas [15] and white-faced capuchins [175], females with high-ranking male relatives may willingly participate in consortships and mate preferentially with lower ranking, unrelated males to avoid costs of inbreeding [71,76,113,114]. High relatedness within communities may thus reduce male reproductive skew, but only insofar as females have high-ranking male kin, because low-ranking male kin may already be excluded from mating opportunities (table 1).

3. Existing data on reproductive skew in bonobos and chimpanzees
Among the 13 mechanisms reviewed above, which potentially affect variation in male reproductive skew in *Pan*, five predict higher reproductive skew for bonobos compared to chimpanzees, whereas only one mechanism predicts higher reproductive skew for chimpanzees (table 1). The relative importance of these different mechanisms remains to be assessed. Nonetheless, while a previous analysis based on mating behaviour inferred that bonobos should have low reproductive skew [23], the introduction of genetic paternity data revealed that high-ranking males bonobos sire more offspring [55]. For example, the most successful male in the Bompusa bonobo community sired 62% of the offspring during a 7 year period, in contrast with chimpanzees, in which the most successful male sired a mean of 26% of

offspring (range: 7–56% for $n = 5$ communities) [54]. Similarly, genetic paternity data from Wamba bonobos revealed that the most successful male sired 86% and 75% of the offspring during a 4 year period for communities E1 and PE, respectively [56]. However, recent data from a small chimpanzee community at Bulindi found that the most successful male sired 88% of the offspring over a 4 year period [176], indicating that under suitable circumstances, chimpanzees can also exhibit high male reproductive skew. Thus, the extent to which male reproductive skew differs consistently between bonobos and chimpanzees warrants further investigation.

In long-lived, slowly reproducing taxa such as primates, it takes many years to obtain a clear understanding of factors affecting reproductive success [33]. For example, early studies of baboons (*Papio* spp. [18,177–183]) reported conflicting findings regarding the relationship between male rank and reproductive success. Only after many group-years of genetic paternity data had been obtained did it become clear that higher ranking males generally sire more offspring, but that over shorter time-scales factors such as demographic composition can disrupt the relationship between male rank and reproductive success [18,184]. Similarly, among mountain gorillas, researchers initially assumed the top-ranking male sired all offspring, but genetic paternity data eventually revealed reproduction by other males in groups with multiple males [17,37,184,185]. Accumulating data from different bonobo and chimpanzee populations now provide new opportunities for understanding male reproductive skew in *Pan*. We re-examine male reproductive skew in *Pan* by collating published data from Surbeck *et al.* [54], Ishizuka *et al.* [56] and McCarthy *et al.* [176] with new data from two chimpanzee communities in Gombe National Park, Tanzania, and two additional bonobo communities at the Kokolopori Bonobo Reserve, Democratic Republic of Congo. This results in a total of 91 population-years for chimpanzees and 27 population-years for bonobos, which provides greater statistical power than previous studies.

4. Methods to re-evaluate male reproductive skew in *Pan*
The PoA model uses a simple queuing model to provide a baseline of expected patterns of reproductive skew for a given number of males and fertile females. We therefore first examined the extent to which bonobos and chimpanzees followed or deviated from PoA predictions. Then we characterized and compared patterns of skew between the two species, using the multinomial index (M), the most successful sire's share, and the total number of within-community and extra-community offspring sired by identified males per year. We included only males old enough to potentially sire offspring (i.e. ≥10 years old) in all analyses, including only offspring with assigned fathers. We considered extra-community offspring as those with an identified within-community mother and an identified extra-community father. To calculate PoA, M, and the most successful sire's share, we considered only within-community offspring. Finally, we examined the effect of male demography on reproductive skew by conducting linear mixed models with M or the most successful sire's share as the dependent variable and the mean number of males per conception during the time period as the independent variable (electronic supplementary material).

To calculate skew, we included bonobo communities from three sites in the Democratic Republic of Congo: Bompusa from Luikotale [54] ($n = 13$ paternities), E1 from Wamba ($n = 7$ paternities) [56], and Ekalakala and Kokoalongo from Kokolopori ($n = 20$ paternities) (this study). For PoA, M, and the most successful sire's share, we included all individuals that were conceived between 2016 and 2019 in Ekalakala ($n = 5$ paternities) and Kokoalongo ($n = 8$ paternities). For the total number of offspring sired by each male per year, we included data from 2013 to 2019 for Ekalakala ($n = 7$) and included five extra-community paternities (Ekalakala: $n = 4$; Kokoalongo: $n = 1$). For the most successful sire's share, we also included PE from Wamba ($n = 4$ paternities) [56].

For chimpanzees, we included six communities for eastern chimpanzees (*Pan t. schweinfurthii*): Ngogo, Kibale National Park, Uganda ($n = 109$ paternities); Sonso, Budongo Forest, Uganda ($n = 13$ paternities); Bulindi, Uganda ($n = 7$ paternities) [176]; M-group, Mahale National Park, Tanzania ($n = 11$ paternities); and Kasekela and Mitumba from Gombe National Park, Tanzania ($n = 75$ paternities) (this study); and one community of western chimpanzees: North, Taï, Côte d'Ivoire ($n = 13$ paternities) [54] (electronic supplementary material, table S2).

For Gombe chimpanzees, we included genotyped individuals born between 1985 and 2017 ($n = 62$ paternities) in Kasekela and between 2004 and 2013 ($n = 13$ paternities) in Mitumba.

(a) Priority-of-access model

Using data on female reproductive states and demography, we calculated the expected distribution of paternities ($n = 75$ for chimpanzees, $n = 13$ for bonobos) based on male dominance rank and the number of maximally tumescent females available at a given time in two chimpanzee communities (Kasekela and Mitumba) and two bonobo communities (Ekalakala and Kokoalongo), with 95% confidence intervals (CIs) for each rank. We also included PoA calculations from Surbeck *et al.* [54] for the Bompusa bonobo community, and Taï North and Sonso chimpanzee communities [59]. Deviations from PoA expectations imply the operation of other mechanisms besides male dominance rank and female reproductive synchrony.

(b) Comparing bonobo and chimpanzee reproductive skew

(i) The multinomial index

Many studies have used Nonac's binomial index (B) to measure reproductive skew [16,17,54,56,58,186–188]. However, this measure is sensitive to factors including community size (e.g. number of potential sires), productivity (e.g. number of paternities) and the time of presence of each sire during the period of observation [189]. To overcome these limitations, Ross *et al.* [189] introduced the multinomial index, M, which is insensitive to community size, sample size, mean reproductive success, and age-structure, allowing for better comparisons of skew across populations and species. M can be calculated using Nonac's B and remains robust to the factors previously cited through the conversion [189]. We report M below and Nonac's B in the electronic supplementary material.

Because apes reproduce slowly, and changes in male rank and demography each year can affect estimates of skew, we

calculated M for each community using an overlapping set of time windows, moving at 1 year increments. We chose 7-year windows when possible, to maximize comparability with previous studies [54]. However, for four communities, only 4 years of data were available. For communities with several periods, we calculated the mean M across all overlapping 7-year periods.

To examine species differences in skew, we calculate 95% CIs for M for chimpanzees for a given mean number of males per conception using a parametric bootstrap. Since we did not have sufficient data to calculate these intervals for bonobos, we inferred species differences by visually inspecting whether estimates of M for bonobos fell outside the 95% CIs for chimpanzees. We used linear mixed models with M as the dependent variable, and the mean number of males per conception as the independent variable, with a random intercept for the community and a random slope for the mean number of males within each community. Ideally, we would also control for the number of maximally tumescent females, but these data were not available for seven communities. From the results of these models, we generated 100 bootstrap samples to obtain the 95% CIs (electronic supplementary material).

(ii) Most successful male's share of reproduction

As an additional measure of male reproductive skew, we examined the proportion of offspring sired by the most successful male in the community. This measure is independent of differences in size and productivity between communities and is not affected by the absence of unidentified/ungenotyped males who did not reproduce [54]. Along with the data used to calculate M, we added data from the PE bonobo community where information about the most successful sire's share of reproduction was available (chimpanzees: $n = 228$ conceptions; bonobos: $n = 37$ conceptions; electronic supplementary material, table S2). As with M, we generated 95% confidence intervals for a given mean number of males per conception in chimpanzees (figure 2*b*; electronic supplementary material).

(iii) Total number of offspring sired by each male per year

The striking differences in inter-community relationships between chimpanzees and bonobos can strongly affect male reproductive opportunities. Specifically, the hostile relationships between chimpanzee communities limit opportunities for males to sire offspring with extra-community females, whereas the more tolerant inter-community interactions of bonobos provide opportunities for extra-community mating. Therefore, we examined the number of within- and extra-community paternities obtained by each individual male in the Kokolopori bonobo communities and the Gombe and Bulindi chimpanzee communities. We could assign extra-community paternities because we obtained genetic samples from multiple communities (electronic supplementary material).

Since calculation of the most successful sire's share of reproduction does not require information about the number of males present in the community, we extended the study period for Ekalakala from 2016–2019 to 2013–2019, before the community was fully habituated. Doing so enabled us to include all successfully assigned paternities, whether the paternity was within-community (Ekalakala: $n = 7$; Kokoalongo: $n = 8$; Bulindi: $n = 8$; Kasekela: $n = 62$;
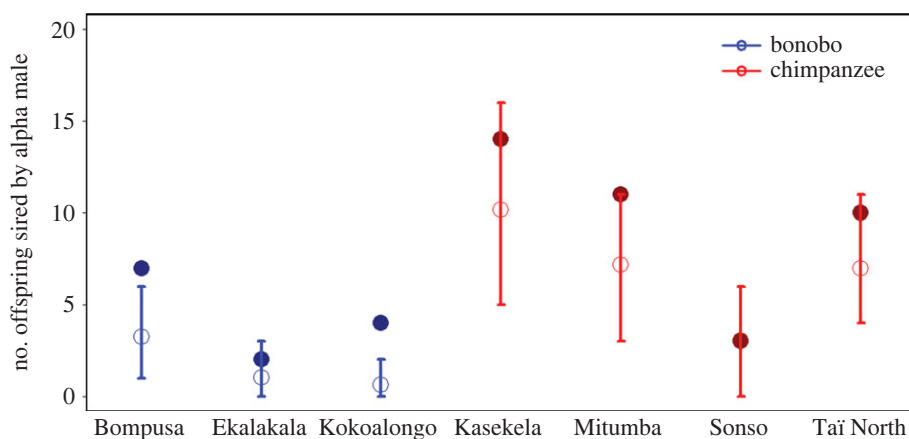
Figure 1. Observed (filled circles) versus expected (open circles) number of offspring sired by the highest ranking male in three bonobo (blue) and four chimpanzee (red) communities. The observed number is based on all infants sired by the current alpha male, rather than the number sired by any particular male. The expected total number is based on the PoA model. Error bars represent the 95% confidence intervals obtained from resampling the expected number of offspring sired by a given male 10 000 times.
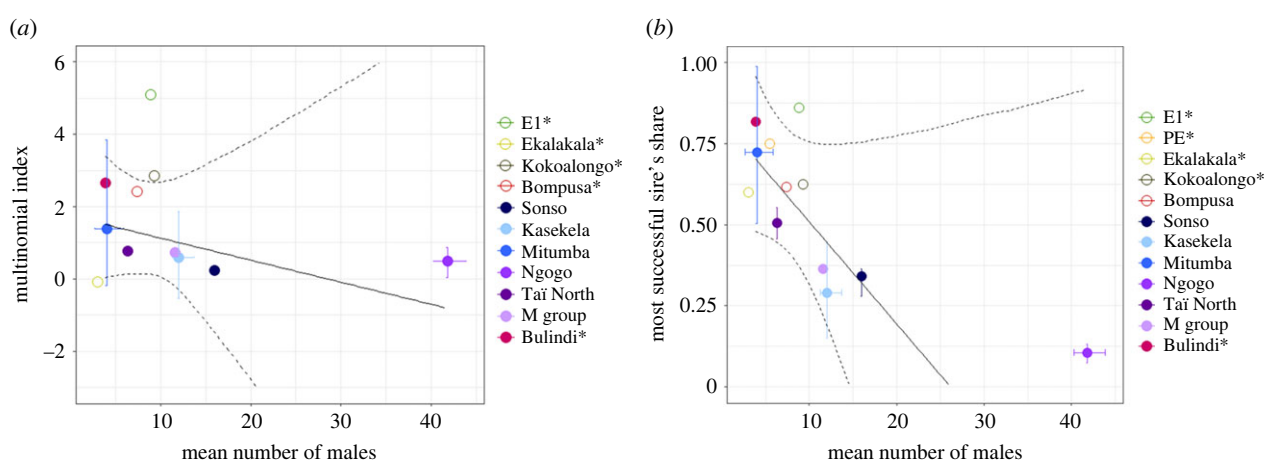
Figure 2. Male reproductive skew in bonobos and chimpanzees. (a) Relationship between the mean number of males per conception and male reproductive skew measured by the multinomial index, M. (b) Relationship between the mean number of males per conception and the most successful sire's share of reproduction. Circles indicate the mean for a given community; open circles represent chimpanzees and filled circles represent bonobos. Vertical and horizontal error bars indicate the 2.5% and 97.5%. The solid and dotted lines represent the model estimate and 95% confidence intervals, respectively, for the effect of number of males in chimpanzees. Asterisks indicate communities with only one 4-year period (electronic supplementary material, table S3).

Mitumba: $n = 13$) or extra-community (Ekalakala: $n = 4$; Kokoalongo: $n = 1$). The number of extra-community paternities may be underestimated as males may have sired offspring in other unfollowed and ungenotyped neighbouring communities.

To facilitate between-community comparison, we calculated the mean number of offspring each male sired per year, by dividing the total number of paternities for each male by the total number of years this male was observed during the respective study period.

5. New results on male reproductive skew in *Pan*

(a) Priority-of-access model

For both bonobos and chimpanzees, the highest ranking males sired the highest proportion of offspring compared to other males in the community (electronic supplementary material, figure S2). For all four chimpanzee communities but only one of the three bonobo communities, the observed proportion fell within the 95% CI of that expected by the PoA model (figure 1).

As previously reported [76], low-ranking Kasekela males (ranks 10, 12, 13 and 15 of 15) obtained more offspring than expected by the PoA model (electronic supplementary material, figure S2). Although low-ranking males also obtained more paternities than expected in Sonso (ranks 7 and 12 of 17) and Taï North (rank 8 of 8), the distribution of male reproduction more closely aligned with patterns predicted by the PoA model (electronic supplementary material, figure S2; [54,80,81]).

(b) Comparing bonobo and chimpanzee reproductive skew

(i) The multinomial index

As indicated by the multinomial index, M, bonobos had higher male reproductive skew (mean ± s.d.: $M = 2.57 \pm 2.12$; $n = 4$ bonobo communities) than chimpanzees ($M = 0.979 \pm 0.819$; $n = 7$ chimpanzee communities; electronic supplementary material, table S2). Also, bonobos exhibited greater variation in M than chimpanzees (electronic supplementary material, figure S3a). Estimates of M for two bonobo communities, Kokoalongo and E1, exceeded the
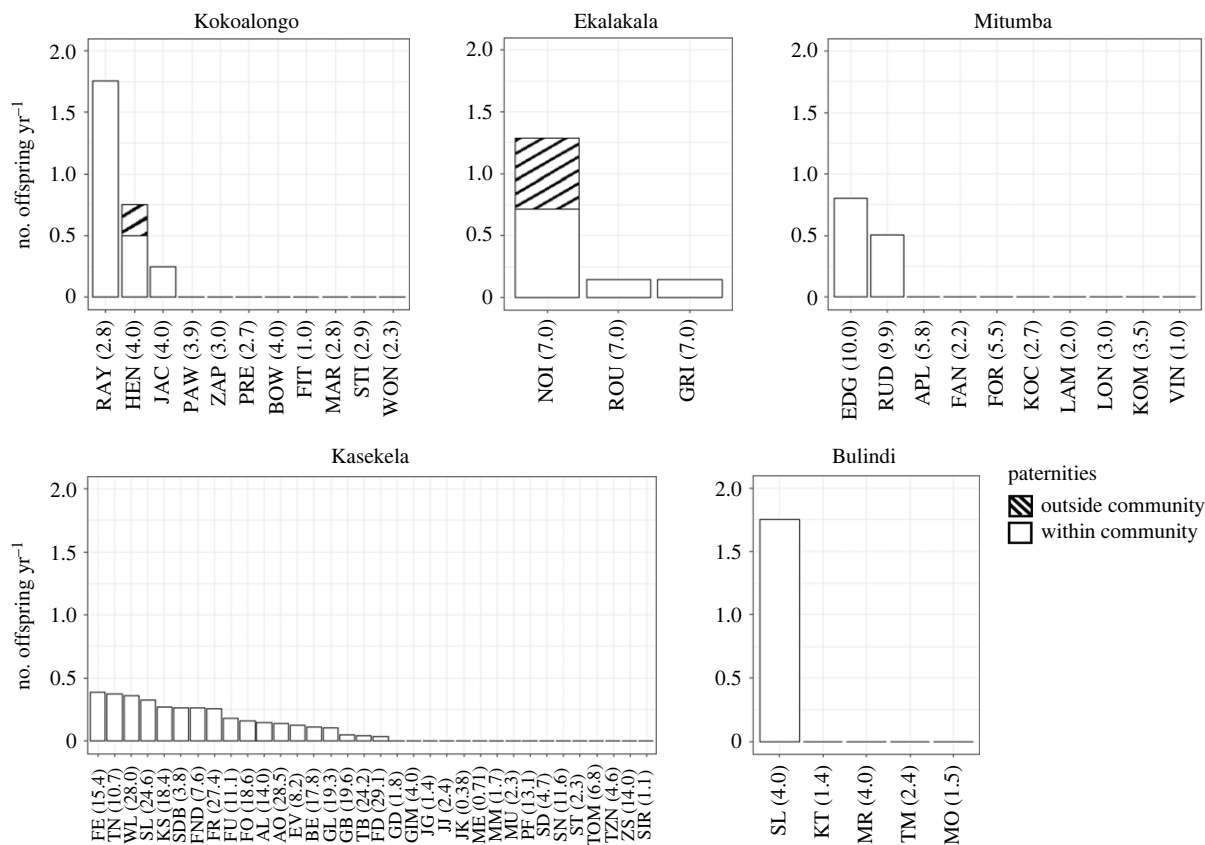
Figure 3. Number of paternities per year per male for two bonobo communities (Ekalakala and Kokoalongo) and three chimpanzee communities (Bulindi, Kasekela and Mitumba). Values in parentheses represent the number of years each male was present in the community throughout the study period.

95% CIs calculated for chimpanzees, whereas two other bonobo communities, Ekalakala and Bompusa, were within the chimpanzee range (figure 2a).

(ii) Most successful male's share of reproduction

The most successful male sired more offspring in bonobos (mean ± s.d.: 0.69 ± 0.11) than in chimpanzees (0.44 ± 0.25) (electronic supplementary material, table S3). However, only in one of the four bonobo communities (E1) did this exceed the 95% CI for chimpanzees (figure 2b).

(iii) Total number of offspring sired by each male per year

Two male bonobos sired offspring in other communities: NOI, in Ekalakala, sired three offspring in Kokoalongo and one in Fekako (a habituated neighbouring community with insufficient data to be included in this study), and HEN, in Kokoalongo, sired one offspring in Ekalakala. The distribution of male reproduction appeared more skewed in Ekalakala when we considered both within- and extra-community paternities (figure 3), as the most successful male was NOI, whose four extra-community paternities gave him a total of nine offspring (electronic supplementary material, table S2). Measures that did not include extra-community paternities—*M* and the most successful sire's share of reproduction—thus underestimated the degree of reproductive skew in this population. The only two males who sired extra-community offspring both had their mother present in the community at the time of siring (NOI and HEN).

6. Discussion

Based on data accumulating from long-term field studies, we found considerable variation in reproductive skew within and between communities of both *Pan* species. Overall, bonobos exhibited greater variation in *M*, an improved measure of reproductive skew, than chimpanzees. The estimates for *M* exceeded the 95% CI for chimpanzees for two out of three bonobo communities, and the estimate for the most successful sire's share exceeded the 95% CI for chimpanzees for one of five bonobo communities. However, we also found that the two species overlapped in all three measures of male reproductive skew (*M*, the most successful sire's share, and the total number of paternities per male per year). As has been found for other species [17,37,184,185], longer term data thus provide a more nuanced picture of male reproductive skew in *Pan*.

Despite the common perception of bonobos as more peaceful than chimpanzees [42,52,53], several studies report that males of both species compete over access to maximally tumescent females (bonobos: [55,64–67,90]; chimpanzees: [68–74]). Aggression among males thus drives reproductive inequality in both species.

The number of males in the community may also affect male–male competitive dynamics and thus reproductive skew. Although the number of males did not have a statistically significant effect on skew in our dataset, we note that among chimpanzees, skew was the highest in communities with few males, and lower in communities with many males (figure 2; electronic supplementary material). More data are needed, even for chimpanzees, to ensure a sufficient sample size to assess demographic effects with confidence.

The hypothesis that high reproductive synchrony among female bonobos should result in low reproductive skew [55] is supported by the quantitative PoA predictions (electronic supplementary material, figure S2). However, the highest ranking male achieved more paternities than expected in two of the three bonobo communities. We, therefore, must consider additional mechanisms to explain male reproductive skew in bonobos. One such mechanism involves higher gregariousness among females, which allows male bonobos to monitor and monopolize females more effectively. Additionally, male bonobos appear to have fewer incentives to concede reproduction than male chimpanzees, given the reduced importance of male coalitions for intergroup competition in bonobos. Supporting this view, in chimpanzees, but not bonobos, low-ranking males sire more offspring than expected. However, this pattern could also result from the more limited control possible in the larger, more dispersed communities of chimpanzees; distinguishing among these alternatives poses a formidable challenge [28].

While distinguishing between limited control and concessions remains challenging, confirmation that bonobos have a relatively high reproductive skew supports the view that reproductive concessions may relate to the intensity of between-group competition. In humans, researchers have proposed that 'reproductive levelling' (i.e. low male reproductive skew) evolved because intense between-group aggression selected for more cooperation within groups [190,191]. The contrast between bonobos and chimpanzees is consistent with this hypothesis, though additional mechanisms should also be considered. For example, Chapais [192] has argued that polygyny declined in hominins after the invention of deadly weapons increased the costs of competition among males and decreased variance in competitive ability [192].

Differences in male–female dynamics between the two species may additionally influence reproductive skew. When considering the physiological mechanisms underlying reproductive competition between males [193], bonobos and chimpanzees show different patterns of associated changes in testosterone levels [66,194]. Male chimpanzees have higher aggression rates and testosterone levels in the presence of maximally tumescent females [194]. By contrast, high-ranking male bonobos, who are more aggressive to other males but also more affiliative towards females, do not have higher testosterone levels in the presence of maximally tumescent females [66]. As heightened testosterone levels during male mate competition generally indicate the relevance of aggression in securing reproductive success [193,195], other factors besides male–male aggression, such as male–female affiliative interactions that are potentially suppressed by high testosterone levels [66], may affect male reproductive skew in bonobos.

Male reproductive skew depends not just on competition among males, but also on relationships between males and females, and female choice. Studies of other species have found that males can gain mating opportunities by forming close associations with females [181,196,197] and by caring for offspring [181,196–199]. Female bonobos probably have more agency in the expression of mate choice owing to their high status [52,139] and strong female alliances [52,138,139]. Because female bonobos tend to affiliate and mate with high-ranking rather than low-ranking males, female preferences probably contribute to higher skew in bonobos than chimpanzees. Female choice can also explain

the occurrence of extra-community paternities in bonobos and other species including superb fairy-wrens (*Malurus cyaneus*) [200], blue tits (*Parus caeruleus*) [201], dwarf mongooses [202], black howler monkeys (*Alouatta caraya*) [203], ring-tailed lemurs [204], rhesus macaques [17], long-tailed macaques [131] and toque macaques (*Macaca sinica*) [205].

In bonobos, the strongest relationship between males and females involves mothers and sons. Interestingly, both males that sired extra-community offspring had a living mother present in their community. Bonobo mothers actively support their son's mating attempts with extra-community females during inter-community encounters (L. Cheng 2018, personal observation). However, the actual mechanism by which maternal presence positively influences a male's reproductive success within and across communities needs further investigation.

Our results confirm that substantial reproductive skew can emerge among males in species with promiscuous mating. While bonobos have long been characterized as peaceful and egalitarian [42,52,53], with lower reproductive skew [23,206] than chimpanzees, the accumulation of additional paternity data provides a more nuanced view of the competitive dynamics in reproductive contexts in *Pan*.

In summary, bonobo males have higher reproductive skew than expected based on degree of reproductive synchrony among females. Detailed comparison of factors promoting reproductive skew in *Pan* highlights that models of reproductive skew should consider the effect of between-group competition on incentives for reproductive concessions, as well as factors beyond those related to male–male dynamics, such as female grouping patterns and factors related to male–female dynamics including the expression of female choice.

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