

Female monopolizability promotes within-community killing in chimpanzees

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Abstract

Male chimpanzees (*Pan troglodytes*) defend group territories and sometimes kill members of rival communities – a pattern often compared to human warfare¹⁻³. Male chimpanzees also sometimes kill grown males from their own community⁴⁻⁹. Such within-community killings are puzzling, as they reduce the coalition strength needed to win inter-community contests^{5,10}. Here we examine the contexts of within-community killing using data from two neighboring communities at Gombe National Park, Tanzania, as well as published data from other long-term chimpanzee study sites. At Gombe, more killing occurred within the smaller Mitumba community, where fertile females were more monopolizable. Attackers increased their share of mating and paternity following known and inferred killings. Other factors proposed to explain such killings, including the degree of intercommunity threat, male-biased sex ratios, high population density, or generalized aggression, did not explain the high rates of killing in Mitumba. Comparing across study sites, the best predictor of within-community killing was an index of the degree to which fertile females can be monopolized by the highest ranking male¹¹. Our findings therefore support the hypothesis that within-community killing is a strategy to eliminate reproductive rivals that is more likely to pay off when fertile females are more easily monopolized.

Main Text

Killing males from rival communities can provide male chimpanzees with clear reproductive benefits, including improved access to feeding territory for themselves, their mates, and offspring¹²⁻¹⁴. Within-community killing of males, on the other hand, is puzzling, because these males can provide benefits, such as increasing the chances of winning inter-community contests^{8,15} and expanding territory¹⁴. Previous studies have hypothesized that within-community killing in chimpanzees is (1) a non-adaptive byproduct of generalized aggression⁷; (2) a consequence of decreased inter-community threat^{5,7,9}; or (3) the result of reproductive competition intensified by male-biased operational sex ratios^{4-5,9}. Previous analysis also indicates that killing in chimpanzees occurs more frequently at high population densities⁸. Here, we test these hypotheses, as well as a fifth: within-community killings function to eliminate rivals, which is more likely to benefit attackers when females are few in number, and thus more readily monopolized. Evolutionary game theory predicts that fatal fighting should be most likely when the value of a contested resource is large relative to expected future payoff¹⁶. Thus, when a large share of reproductive opportunities is at stake, males should be more willing to engage in fatal fighting. The share of reproductive opportunities available depends on the degree to which fertile females can be monopolized by the highest-ranking male. Nunn¹¹ proposed an index of monopolizability, which is higher when females are few in number and/or cycle asynchronously¹¹. Nunn found that this index predicted traits associated with contest competition in male primates better than the operational sex ratio¹⁷. Following this logic, we propose that in groups with many males and females, killing rival males is unlikely to benefit attackers, because the degree to which the remaining females can be monopolized remains low. In smaller groups, however, killing rivals can enable attackers to greatly increase their share of reproductive opportunities.

We tested these hypotheses using data from the Mitumba (median = 3 males, 9 females ≥ 12 years old) and Kasekela (median = 12 males, 23 females ≥ 12 years old) communities at Gombe (1997–2018). During this study period, we infer that fighting among males led to 5 deaths in Mitumba and 1 in Kasekela (Table S1). The killings in Mitumba began in 2004, when alpha male Vincent was injured in a fall. During the subsequent three months, Vincent avoided the other two adult males of Mitumba, Rudi and Edgar, but when these two males encountered Vincent in December 2004, they attacked and killed him. In January 2005, Edgar's 8.2 year-old brother Ebony was found dead with injuries consistent with attack by chimpanzees. Circumstantial evidence indicates Ebony was likely killed by a Mitumba male, as most of the Kasekela males were under observation 2.5 km away at the likely time of Ebony's death. Rudi then became alpha male, but Edgar challenged Rudi repeatedly, severely injuring Rudi in 2007. Edgar became alpha male in 2008. Rudi disappeared in 2013; as he had not recently been injured, and also was positive for SIVcpz, we infer that he died from disease. Edgar injured three other males in severe attacks: Forest (2012), Apple (2015), and Fansi (2017). Forest and Apple disappeared soon after the attacks; we infer they died from injuries inflicted by Edgar. In 2017, observers found Edgar displaying near Fansi's freshly killed body; we infer Edgar was the killer. In Kasekela, one male, Kris, disappeared after an attack by the alpha male, Ferdinand; we infer Kris died from the resulting injuries. Controlling for population size in the manner commonly used for homicide data (killings per year per 100,000 individuals^{18,19}) yields rates of 2859 (Mitumba) and 242 (Kasekela) killings per 100,000 weaned males per year, much higher than the median rate across long-term chimpanzee studies, which is 0 (Table S2).

Ranging and male coalition strength

We examined both the potential costs and benefits of killing males from one's own community. We began by exploring the impact of male coalition size on effectiveness in competition for territory. Mitumba had a smaller home range than Kasekela (1997-2016, $n=20$ years; Mitumba: median=5.13 km², range=3.51–8.03; Kasekela: median=16.5 km², range= 10.9–19.4). The Mitumba community's range size increased when they had more adult males relative to the number of males in the neighboring community (Pearson correlation; $t=2.6$, $df=18$, $n=20$, $p=0.02$, $r=0.52$, 95% CI=0.11–0.79) but Kasekela's did not ($t=1.42$, $df=18$, $n=20$, $p=0.17$, $r=0.32$, 95% CI=-0.15–0.67; Figure S1), probably because when Kasekela chimpanzees lost range to Mitumba, they were able to expand their range to the south at the expense of the declining Kalande community²⁰. Kasekela's annual range center shifted south by 585 m during the study period (1997: 9482903 m N; 2016: 9482318 m N; UTM 35S). The annual locations of the two communities' range centers were positively correlated (Pearson Correlation, $t=2.74$, $df=18$, $n=20$, $p=0.01$, $r=0.54$, 95% CI=0.13–0.79), indicating that Kasekela shifted southward to avoid Mitumba chimpanzees as the number of mature males in Mitumba increased.

We examined use of the 'contested area,' which we defined as the area of overlap in range used by each community over the study period, using 99% minimum convex polygons (Figures S2-3). The proportion of time that chimpanzees spent in the contested area each year increased with increasing number of males for Mitumba (Pearson correlation, $t=5.3$, $df=18$, $n=20$, $p<0.01$, $r=0.78$, 95% CI=0.51–0.91; Figure S4), but not for Kasekela (Pearson correlation, $t=-0.4$, $df=18$, $n=20$, $p=0.70$, $r=-0.09$, 95% CI=-0.51–0.37). Both

Mitumba and Kasekela used the contested area more in years when they had a higher ratio of males in their community to males in the neighboring community (Pearson correlation; Mitumba, $t=5.7$, $df=18$, $n=20$, $p<0.01$, $r=0.80$, 95% CI=0.55–0.92; Kasekela, $t=3.9$, $df=18$, $n=20$, $p<0.01$, $r=0.68$, 95% CI=0.34–0.86; Figure S4). Thus, having more males improved access to territory. To be adaptive, within-community killing of males would need to provide killers with sufficient benefits to offset the costs resulting from reduced coalition size.

Rates of male aggression

If within-community killings occurred as a byproduct of overall higher rates of aggression, then these rates should be higher in Mitumba than in Kasekela. However, controlling for individual identity and observation time, Kasekela and Mitumba males did not differ in their rate of aggression, considering either all aggressive acts (mixed Poisson regression, $\beta=0.64$, 95% CI=-0.31–1.55, $z=1.43$, $p=0.152$), or only instances of higher-cost aggression (chasing and/or physical contact: mixed Poisson regression, $\beta=-0.30$, 95% CI=-0.98–0.42, $z=-0.90$, $p=0.37$; Table S3). Even Edgar, who was observed attacking four of the five victims in Mitumba, nonetheless did not have an exceptionally high rate of aggressive behavior overall (Figure S5). These findings indicate that the higher rate of killings in Mitumba did not result from simply from a higher rate of aggression in that community. Moreover, in the observed case, Edgar and Rudi continued attacking Vincent until he was dead, suggesting that killing was intentional. The many wounds found on Fansi's freshly killed body also appear consistent with intentional rather than accidental killing.

Intercommunity threat

If within-community killings resulted from chimpanzees being faced with a low level of intercommunity threat, then we would expect (1) that more within-community killings would occur in the community facing a lower level of inter-community threat and (2) that within-community killings would occur more often in years with few intercommunity incursions. The Mitumba chimpanzees faced a high level of intercommunity threat, as they had a smaller range than Kasekela (1997–2016; t -test, $t=21.0$, $df=30.8$, $n_{KK}=n_{MT}=20$ years, $p<0.01$, 95% CI= 9.96–12.11, $d=6.64$) and fewer males to defend it (1997–2018; t test, $t=20.3$, $df=41.0$, $n_{KK}=n_{MT}=22$ years, $p<0.01$, 95% CI= 7.57–9.26, $d=6.12$; Figure S6). Kasekela had a nearly 4:1 numerical advantage over Mitumba (median male ratio=3.67, range=1.80–7.00). Kasekela males killed infants from Mitumba in 1993 (Rejea²¹) and 2005 (Andromeda²²), and likely killed an adolescent male in 2002 (Rusambo²¹), while Kasekela suffered a single inter-community killing in 2004 (Patti⁸). The mean rate at which individuals died from intercommunity killing was higher in Mitumba (404 victims per year per 100,000 individuals) than Kasekela (175 victims per year per 100,000 individuals), though this difference was not statistically significant; t -test, $t=-0.75$, $df=28.6$, $n_{KK}=n_{MT}=22$ years, $p=0.46$, 95% CI=-851.47–393.16, $d=-0.23$). As a finer scale metric of intercommunity threat, we examined the number of days per year when Kasekela males traveled north of a major ridge between the communities (Figure S2; median=13.5 days/year, range = 0–99). Within-community killing did not occur more often in

Mitumba in years when Kasekela males crossed this boundary less frequently (Poisson regression; $\beta=0.016$, 95% CI=-0.03–0.04, $z=0.91$, $n=20$ years, $p=0.36$).

Population density

We previously found that high population density correlated with higher rates of killing overall (including within- and between-communities)⁸. If within-community killings occur due to increased competition for resources resulting from high population density, such killings should occur more often in more densely populated communities. Population density was greater in Mitumba than Kasekela (1997-2016, Mitumba mean=4.91, Kasekela mean= 3.40, t-test, $t=-5.37$, $n_{KK}=n_{MT}=20$, $df=31.2$, $p<0.01$, 95% CI=-2.09–-0.94, $d=-1.70$). However, the years in which within-community killings took place did not have higher population density than years with no killings (1997-2016, Mann-Whitney U, $U=88$, $n_0=36$, $n_1=4$, $p=1$, $A=1$).

Operational sex ratio

Previous studies have suggested that within-community killings in chimpanzees occur when a highly male-biased operational sex ratio increases intensity of competition among males^{4,5,9}. However, we found that the operational sex ratio was less male-biased in Mitumba than Kasekela (1997-2018; Mitumba mean=10.52; Kasekela mean=14.92; t-test, $t=4.18$, $df=41.9$, $n_{KK}=n_{MT}=22$ years, $p<0.01$, 95% CI=2.27–10.52, $d=1.26$, Figure S6).

Monopolizability

Following Nunn¹¹, we propose that the intensity of competition among males is best predicted, not by operational sex ratio, but by the degree to which males can monopolize fertile females. When many females are present, the probability that only one female is fertile – and is thus monopolizable by the top-ranking male – decreases. We calculated predicted annual monopolizability of fertile females for both communities and compared these with observed values determined via observations of female sexual swelling (Figure S7, Table S4). Predicted and observed monopolizability were positively correlated (linear regression, $\beta=1.41$, 95% CI=1.01–1.81, $t=7.11$, $p<0.01$, $R^2=0.60$). Each day, Mitumba had fewer cycling, parous females than Kasekela (Mitumba mean=1.05; Kasekela mean=5.90; t-test, $t=173.43$, $df=8137.1$, $n_1=n_2=6574$ days, $p<0.01$, 95% CI= 4.80–4.91, $d=3.03$; Figure 1) and as a result, Mitumba exhibited a greater proportion of days with only one female observed mating ($X^2=23.59$, $df=1$, $p<0.01$, $\Phi=0.05$; Figure S8).

Attackers are those listed in Table S1 as known or inferred attackers in fatal cases. Non-attackers are all other mature males (i.e., those that were observed mating in periods before and after violent events). Error bars represent one standard deviation of uncertainty.

Reproductive consequences for attackers

Known and suspected attackers from both communities increased their share of observed mating following severe within-community attacks (Figure 2, Figure S9; Binomial glmm, Attack Order*Attacker, $\beta=0.62$, 95% CI=0.42–0.81, $z=6.2$, $p<0.01$). Paternity data also indicated that community size affected the extent to which attackers gained benefits from intra-community killing (Figure 3). In the small Mitumba community, the alpha male sired 80% of infants born in Mitumba, but only 18% of infants born in Kasekela (1997-2018). In 2002, Mitumba had three adult males: alpha-male Vincent, Rudi, and Edgar. Genetic data indicate that prior to Vincent’s killing, he sired 66.7% ($n=4$) of Mitumba infants with known paternity while Rudi and Edgar sired only one infant each (16.6%). After killing Vincent in December of 2004, Rudi and Edgar increased their share of paternity ($X^2=8.19$, $df=2$, $p=0.016$, $\Phi=0.74$; Figure 3A). In 2009, Kasekela’s alpha-male, Ferdinand, similarly increased his share of conceptions after attacking Kris, an adult male who subsequently disappeared. Ferdinand’s share of paternities increased from before his attack on Kris (6.3%, $n=2$) to after (15.4%, $n=2$); however, this change was not statistically significant ($X^2=0.16$, $df=1$, $p=0.70$, $\Phi=0.15$; Figure 3B). Both Mitumba attackers fathered more infants than all but three Gombe males (Figure 3C-D), making them exceptionally successful even after taking into account the death of Andromeda (sired by Edgar), whose killing by Kasekela males might have been averted if Vincent had survived. After Rudi died, Edgar obtained 72% of observed matings (Figure S9A). Edgar likely has sired even more offspring; 14 Mitumba infants remain un-genotyped, with only one conceived before Rudi’s death.

Cross-site analysis

Using the Gombe data presented here, together with published data from long-term chimpanzee field sites⁸ (Table S5), we employed an information-theoretic model selection approach to test which of three factors best predicted rates of within-community killing: operational sex-ratio, population density, and monopolizability. The best model included only monopolizability (model weight $w = 0.70$), and only for monopolizability did the 95% confidence interval of the model-averaged parameter value exclude zero (Table 1). These results support the view that within-community killing of male chimpanzees results from male reproductive competition^{4-5,9}, and that monopolizability provides a better predictor than sex ratios. High monopolizability of fertile females can make it worthwhile for males to eliminate rivals.

Table 1. Summary of information-theoretic model averaging: within-community killings of weaned males.

| Model | Intercept | Monopolizability | Operational Sex Ratio | Population Density | K | Δ_i | w_i |
|--------------------------|-----------|------------------|-----------------------|--------------------|---|------------|-------|
| 1 | -9.65 | 4.64 | | | 2 | 0.00 | 0.70 |
| 2 | -11.49 | 6.59 | -0.05 | 0.22 | 4 | 2.80 | 0.17 |
| 3 | -5.97 | | | | 1 | 4.49 | 0.07 |
| 4 | -6.47 | | | 0.12 | 2 | 5.96 | 0.04 |
| 5 | -6.19 | | 0.02 | | 2 | 6.90 | 0.02 |
| Model-Averaged Parameter | -9.50 | 5.03 | -0.04 | 0.21 | | | |
| 2.5% | -14.26 | 0.26 | -0.15 | -0.06 | | | |
| 97.5% | -4.75 | 9.80 | 0.07 | 0.47 | | | |

Conclusions

In summary, we found that within-group killings of male chimpanzees occurred most frequently when fertile females were most readily monopolized. Because killing male group members reduces ability to hold territory, such killings must be offset with substantial reproductive benefits to be adaptive. Our findings indicate that this is most likely to be the case in small communities. Nonetheless, such killings of males have been observed in larger communities with many females, such as Ngogo⁵, Mahale⁷, and Budongo⁴. Other factors likely affect both the benefits and the costs of killing, such as relative fighting ability. Attackers often target young or injured individuals, suggesting that chimpanzees attack when they can do so at low risk to themselves.

That within-community killing occurs even during times of intense inter-community threat challenges a widespread explanation for the evolution of cooperation in humans. Following Darwin²³, Alexander²⁴ and others have proposed that within-group cooperation in humans co-evolved with between-group competition. Bowles²⁵ developed this idea further in the parochial altruism hypothesis: intense competition between groups selects for increased cooperation within groups. However, chimpanzees and human hunter-gatherers experience similar rates of between-group killing¹⁹. High rates of between-group killing thus appear insufficient to promote the high levels of within-group cooperation observed in human societies.

Methods

Animal Subjects

We report data generated from non-invasive observational studies of chimpanzees at Gombe National Park, Tanzania (4°40'S 29°38'E). Long-term researchers at Gombe Stream Research Centre, employed by the Jane Goodall Institute, collected behavioral data. Gombe encompasses a 35.69 km² strip of land along the shore of Lake Tanganyika that is home to 3 communities of chimpanzees. Researchers conducted nearly daily focal follows of individual chimpanzees, recording party composition and location at 15-minute intervals while maintaining a continuous record of feeding behavior¹⁵. Researchers recorded all observed occurrences of selected behaviors, including aggression, mating, and intercommunity interactions. Observers documented the reproductive state of all adult females seen each day, based on the size of ano-genital sexual swellings.

Data

Killings

We examined evidence for all reported cases of within-community killing at Gombe for the Mitumba and Kasekela communities (1997–2018). Following Wilson et al.⁸, we rated killings to be 'observed' if observers directly witnessed a within-community attack leading to death, and 'inferred' if the victim disappeared following one or more severe within-community attacks, or if compelling evidence indicated that the individual was killed by chimpanzees (such as a body found with multiple bite wounds, and/or skeletal trauma consistent with a chimpanzee attack). For this analysis, we did not include cases that were only suspected to be killings. For cases that were not directly observed, we considered them to be within-community killings only if circumstantial evidence sufficiently ruled out intercommunity attacks or other causes of injury.

To investigate whether chimpanzees who kill community members benefit following lethal attacks, we identified which individuals were involved in each attack. For all cases, we used documentation of attack records to identify individuals involved in each killing. For observed cases, we classified all individuals observed attacking the killed chimpanzee as 'attackers'. For disappearances preceded by within-community attacks, we considered individuals observed attacking the victim leading up to their disappearance as attackers. For other inferred cases, we used circumstantial evidence to identify likely attackers given sightings surrounding the incident. For all cases, we categorized all remaining adult males in the community as non-participants.

Demographics: As part of the long-term study, researchers documented demographic events, including births, deaths, immigrations and emigrations. Using these data, we calculated annual community size and composition using all individuals known to be alive on 01 Jan of each year (1997–2018). For this study, we considered all individuals 12 years of age and older as 'adults' (old enough to participate in intercommunity fighting and reproductive competition). For each year for each community, we calculated the 'male ratio': the number of males in the focal community divided by the number of males in the neighboring community.

Ranging

During focal observations at Gombe, observers collected the focal target's location at 15-minute intervals. Prior to 2005, Gombe researchers recorded locations manually on maps. These were later digitized into the UTM35S coordinate system. We used these locations to calculate annual home range size for each community, using 99% minimum convex polygons (R package `adehabitatHR`)²⁷ for the years 1997–2016, during which location data had been digitized and entered into the Gombe Database. From these ranging data, we calculated the latitudinal range center for each community. Gombe is bordered to the west by Lake Tanganyika and to the east by village land. The boundary between the Mitumba and Kasekela territories runs roughly east-west, along a ridge dividing the Mitumba and Busindi stream valleys. The north-south dimension thus provides a proxy of movement relative to community boundaries. We defined the 'contested area' between the two communities as the 99% minimum convex polygon enclosing points used by both communities (1997–2016). We calculated the annual use of this contested area as the percentage of each year's location points located within the contested area. To quantify variation in annual inter-community pressure experienced by Mitumba chimpanzees, we calculated the number of days each year that Kasekela males were recorded traveling north of 9485400 N, UTM 35S, a point along the ridge dividing the two communities' ranges.

Aggression

We analyzed aggression data from focal follows of male chimpanzees conducted in Mitumba (2000–2008) and Kasekela (1997–2011) for all years within the study period for which aggression data have been extracted, cleaned, and entered into the Gombe Database. We limited analysis to aggressive acts conducted by the focal target. We classified each observed aggressive act into 4 categories of increasing severity (bristle, display, chase, contact) following published previous studies^{28–29}. 'Bristle' involved piloerection (raised hair), 'display' involved exaggerated or demonstrative movement directed at another chimpanzee, 'chase' as one individual actively pursuing another, and 'contact' as hitting, kicking, or biting from the focal target. We also combined chase and contact together as 'severe aggression' for analysis.

Density

Using annual range estimates and demographic data described above, we calculated the annual density for each community, defined as the number of chimpanzees per square kilometer. For cross-site analysis we used published density data⁸.

Mating

We analyzed all cases of observed mating between adults collected during focal follows (1997–2016). To assess whether participants in killing increased their share of matings, we calculated each male's proportion of mating relative to each within-community killing. In Mitumba, we inferred that 5 within-community killings occurred during the study period, so we identified the proportion of mating events each male participated in for 6 time periods surrounding these events. In Kasekela, only a single within-

community killing took place over the study period. To identify a comparable comparison of change in mating behavior we analyzed mating that took place 3 years before and after the within-community killing in Kasekela to match the time periods between killings in Mitumba (mean = 3.18).

Paternity

Paternity was assigned using genetic material from fecal samples. Using PCR, 11 microsatellite loci were amplified and used to match fathers with offspring (see Wroblewski et al.³⁰). Genetic sampling of offspring usually takes place after the infant has survived for two years³⁰. Over the study period, the Kasekela community had 45 assigned paternities (1997–2016), while Mitumba had 15 (1997–2015). When assessing lifetime reproductive success, we considered all paternity assignments from Gombe (n = 80).

Genotyping and paternity

This study included paternity for 69 offspring previously reported^{30–34}, and new paternities established for 11 offspring (nine in Kasekela and two in Mitumba) (Table S6). Two offspring were genotyped at 8–11 microsatellite loci following previous PCR and repeat size-based sequencing methodology (described in Walker et al.³⁴, Wroblewski et al.³⁰), while the other nine offspring, their mothers, and candidate males were genotyped at 8 of those loci using next generation sequencing-adapted PCR and amplicon sequencing (described in Barbian et al.³⁵). Paternity analysis was done by the exclusion principle and confirmed via likelihood methods using Cervus 3.0³⁶, as described by Walker et al.³⁴, conservatively including all genotyped males as candidate fathers, regardless of community residence or known dates of birth or death. For the two offspring assessed using the sized-based genotypes, candidate males included all sampled males from all three Gombe communities (Mitumba, Kasekela, and the unhabituated but monitored community of Kalande), while those newly assessed using next-generation sequence-based genotypes included all genotyped males from Mitumba and Kasekela, but not Kalande (as updated genotypes for them were not available). In both cases, however, we also simulated 90% sampling of candidate males for a conservative estimate of paternity confidence in Cervus.

Predicted Monopolizability: We calculated predicted monopolizability of mating opportunities using the following equation: $P(Y) = \frac{k!}{Y!(k-Y)!} p^Y (1 - p)^{k-Y}$, when $P(Y)$ is the probability that Y females are mating simultaneously¹¹. In this equation, k represents the number of females in the community. The probability that a given female is mating — p — is calculated based upon the following equation: $p = \frac{n*c}{B*d}$, where B is the interbirth interval, d is the breeding season length, n is the number of cycles to conception, and c is the average cycle length. We used published demographic data for each study site⁸. Chimpanzees reproduce year-round so d is always 365. For the remaining life-history traits, we used published estimates^{17,37-39} (Table S7).

If a parameter had been estimated for a specific site, we used that estimate, however if a site-specific estimate was unavailable, we used the average estimate for the subspecies. If no published estimates were available within the subspecies, we used the average estimate across all study sites. The relationship between predicted monopolizability and number of adult females thus varied across subspecies (Figure S10).

Operational Sex Ratio: We calculated operational sex ratio using demographic and life-history traits used to calculate expected monopolizability. We defined the operational sex ratio following Mitani¹⁷ using the following equation: $OSR = \frac{m*B*d}{f*n*c}$, where m is the number of adult males, B is the interbirth interval, d is the breeding season length, f is the number of adult females, n is the number of cycles to conception, and c is the average period of maximum sexual swelling per cycle. We used published estimates of these variables as explained above in our calculation of predicted monopolizability.

Observed Monopolizability

To test the validity of the predicted monopolizability estimates, we calculated two measures of observed monopolizability at Gombe, based on (1) mating and (2) sexual swellings. We defined observed monopolizability as the proportion of days on which the number of females observed mating, or with a

maximally tumescent sexual swelling, was zero or one. For each day in each community, we calculated the number of females that were observed mating, and with a full swelling. We compared these annual measures of observed monopolizabilities with predicted values for both communities. We found that predicted monopolizability estimates fit monopolizability calculated with swelling observations (linear regression, $\beta = 1.41$, 95% CI = 1.01–1.81, $t = 7.11$, $p < 0.01$, $R^2 = 0.60$) better than monopolizability calculated with mating observations (linear regression, $\beta = 0.13$, 95% CI = -0.05–0.30, $t = 7.11$, $t = 1.48$, $p = 0.15$, $R^2 = 0.06$).

Sexual swelling data exhibited more variation than mating data and appeared a better overall measure of monopolizability. This is likely because matings last only a few seconds and can be missed, whereas swellings last many days and are readily observed. Moreover, the discrepancy between monopolizability calculated from matings versus swellings was higher for Kasekela than Mitumba, which is consistent with other evidence that Kasekela females were less monopolizable than Mitumba females.

Reproductive cycles

The calculation of observed monopolizability may overestimate actual monopolizability, because chimpanzees often travel in multiple scattered parties, while researchers generally follow a single focal target each day. Additionally, chimpanzees on consortships often appear to avoid other chimpanzees and researchers directly observe consortship pairs rarely. To capture reproductive state for all females, including those not directly observed, we calculated the daily number of cycling, parous females in Mitumba and Kasekela over a period for which complete data on female reproductive states were inferred in both communities using sexual swellings to identify reproductive cycling (1997–2014; Fig. 1). We limited this analysis to parous females. Male chimpanzees appear to prefer mating with parous females, likely because nulliparous females experience prolonged periods of adolescent subfecundity prior to their first birth⁴⁰. We excluded females that were likely to be pregnant or lactating, based on records of sexual swellings and the timing of births. We identified likely pregnancy start dates based on the end of the menstrual cycle closest to 225 days before birth. For females that had given birth, we classified them as having resumed cycling upon their first observed sexual swelling after birth. We inferred that menstrual cycles took place if females were observed with sexual swellings (at least two of them full swellings) over a 14-day window, followed by at least 5 days without a full swelling. We determined the day of detumescence as the subsequent day without a full swelling or, in the case of a gap in observation, halfway between the final observation of full swelling and the next observation.

Cross-site Analysis

We used data published by Wilson et al.⁸ for cross-site analysis, including occurrences of within-community killing, demographics, and range size. We updated numbers for Mitumba and Kasekela using data from other sections of this paper.

Statistical Tests

We conducted statistical tests in Rstudio (Version 3.6.1)⁴¹. To assess the benefits that males gain by having other male community members, we tested the impact of two measures of male coalition strength at Gombe: the raw number of adult males and the male ratio. We tested the extent to which each of these variables correlated with three measures of range use – range size, the northing of the range center (UTM 35S) and use of the contested area – using Pearson correlation tests. Range size did not correlate with raw number of males ≥ 12 years old in Mitumba (Pearson correlation; $t = 1.8$, $df = 18$, $n = 20$, $p = 0.09$, $r = 0.39$, 95% CI=-0.06–0.71) or Kasekela (Pearson correlation, $t=-0.27$, $df = 18$, $n = 20$, $p = 0.79$, $r=-0.06$, 95% CI=-0.49–0.39; Figure S1). All other test statistics are reported in the body of the paper.

To address the hypothesis that within-community killing results from generalized aggression within communities, we used GLMMs with Poisson error structure (lme4 R package⁴²) to compare rates of aggression by the targets of focal follows of males in Kasekela and Mitumba. We ran two separate regressions: one for hourly aggression rate using all instances of aggression, and another that only considered contact and chase aggression. In both regressions, we assessed the degree to which individuals differed between Kasekela and Mitumba, using individual identity as a random variable and log(focal follow duration) as an offset.

To test the hypothesis that within-community killing occurs when between-community competition is low, we compared Kasekela and Mitumba using multiple metrics of between-community threat. Using two-tailed t-tests, we compared male ratio and range size of the two communities using annual measures (1997–2016). We also used a two-tailed t-test to compare the per capita rate of inter-community killings experienced by each community. We used a Poisson regression to assess whether within-community killing was more likely in years when Kasekela traveled north of 9485400 N, UTM 35S, less frequently.

To assess the possibility that population density drives within-community killing, we used a two-tailed t-test to compare annual population density in Mitumba and Kasekela (1997–2016). To further examine the connection between killing rate and population density, we used a Mann-Whitney U test to compare population in density in years during which within-community killing occurred and other years.

To assess the possibility that operational sex-ratios affect rates of within-community killing, we used a two-tailed t-test to compare annual operational sex ratios in Mitumba and Kasekela.

We then assessed the relationship between the monopolizability of mating opportunities and within-community killing rate. We used a two-tailed t-test to compare the annual mean number of cycling, parous females present in Mitumba and Kasekela. Using all observed mating events, we calculated the daily number of females observed mating. We tested whether the proportion of days with one female observed mating differed between Kasekela and Mitumba using a chi-squared test.

To assess reproductive gains that males experienced following within-community kills, we used both mating observations and paternity assignments. For Mitumba, we binned these mating events around within-community killings. We conducted a GLMM with a binomial error structure (lme4 R package⁴²) to assess whether attackers increased their share of matings following an attack, controlling for attack

identity and individual identity. We classified individuals as suspected attackers or non-attackers and tested whether there was a non-zero coefficient for the interaction between attacker and time period relative to the attack. We compared lifetime individual reproductive success across communities, defined as the sum of all assigned paternities over an individual's lifetime. To test for an impact on reproductive shares surrounding killing, we used a chi-squared test to compare the distribution of reproductive success in Mitumba before and after Rudi and Edgar killed Vincent, the alpha male. We also conducted a chi-squared test to compare the share of reproductive success of Ferdinand in Kasekela before and after he attacked Kris, who is inferred to have died from the resulting injuries.

To investigate which factors best explained the number of within-community killings of weaned males per community on a larger scale, we used killing and demographic data published from 18 chimpanzee communities at long-term study sites⁸. Using information-theoretic model selection procedures⁴³, we examined a set of *a priori* specified models based on three hypotheses: operational sex-ratio, density, and monopolizability. All models were Poisson regressions with the number of within-community killings observed or inferred in each community as the dependent variable, and the log(weaned male years) as an offset. Here, we consider 'weaned male years' to be the product of the average number of weaned males (≥ 3 years old) multiplied by the years of demographic data reported. We included five models in our model set: one for each hypothesis, a null model, and a full model. Using the AICcmodavg R package⁴³, we identified model-averaged parameters weighted by the fit of each model to identify non-zero coefficients.

Ethics Statement:

Research at Gombe National Park was conducted with approval from the Tanzania Wildlife Research Institute and the Tanzania Commission for Science and Technology. This research follows guidelines set forth by the University of Minnesota IACUC; data collection involves observation of natural behaviors.

Declarations

Author Contributions

Conceptualization: M.L.W., A.P.M. Formal Analysis: A.P.M., D.C.M., N.D., S.F., M.L.W. Investigation: E.E.W., E.B., R.S.R., B.H.H. Data Curation: A.E.P., E.B. Writing- Original draft preparation: A.P.M., M.L.W. Writing-reviewing and editing: E.E.W., A.E.P., Visualization: A.P.M., S.F., M.L.W. Project Administration: B.H.H., M.L.W., D.C.M. Funding Acquisition: B.H.H., A.E.P., M.L.W.

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Data Availability: Summary data used in this analysis are available in the Dryad data repository with the identifier <https://doi.org/10.5061/dryad.bcc2fqzbf>. We do not provide access to the raw data used in some of these analyses, as these represent a substantial fraction of the long-term data from Gombe, which are not publicly available at this time because of multiple ongoing studies, but are available from the corresponding author on reasonable request.

Code Availability: R code used for data analysis is available in the Dryad data repository with the identifier <https://doi.org/10.5061/dryad.bcc2fqzbf>.

References

1. Goodall, J. *The Chimpanzees of Gombe: Patterns of Behavior*. (Belknap Press of Harvard University Press, 1986).
2. Wrangham, R. W. & Peterson, D. *Demonic Males: Apes and the origins of human violence*. (Houghton Mifflin Company, 1996).
3. Wilson, M. L. & Glowacki, L. Violent cousins: Chimpanzees, humans and the roots of war. in *Chimpanzees and Human Evolution* (eds. Muller, M. N., Wrangham, R. W. & Pilbeam, D.) (Harvard University Press, 2017).
4. Fawcett, K. & Muhumuza, G. Death of a wild chimpanzee community member: possible outcome of intense sexual competition. *Am. J. Primatol.* **51**, 243–247 (2000).
5. Watts, D. P. Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* **25**, 507–521 (2004).
6. Williams, J. M. *et al.* Causes of death in the Kasekela chimpanzees of Gombe National Park, Tanzania. *Am. J. Primatol.* **70**, 766–777 (2008).
7. Kaburu, S. S. K., Inoue, S. & Newton-Fisher, N. E. Death of the alpha: within-community lethal violence among the chimpanzees of the Mahale Mountains National Park. *Am. J. Primatol.* **75**, (2013).
8. Wilson, M. L. *et al.* Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature* **513**, 414–417 (2014).

9. Pruett, J. D. *et al.* Intragroup Lethal aggression in West African chimpanzees (*Pan troglodytes verus*): inferred killing of a former alpha male at Fongoli, Senegal. *Int. J. Primatol.* (2017). doi:10.1007/s10764-016-9942-9
10. Mitani, J. C. Cooperation and competition in chimpanzees: current understanding and future challenges. *Evol. Anthropol.* **18**, 215–227 (2009).
11. Nunn, C. L. The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* **46**, 1–13 (1999).
12. Williams, J. M., Oehlert, G. W., Carlis, J. V. & Pusey, A. E. Why do male chimpanzees defend a group range? *Anim. Behav.* **68**, 523–532 (2004).
13. Pusey, A. E., Oehlert, G. W., Williams, J. M. & Goodall, J. Influence of ecological and social factors on body mass of wild chimpanzees. *Int. J. Primatol.* **26**, 3–31 (2005).
14. Mitani, J. C., Watts, D. P. & Amstler, S. J. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Curr. Biol.* **20**, 507–508 (2010).
15. Wilson, M. L., Kahlenberg, S. M., Wells, M. & Wrangham, R. W. Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Anim. Behav.* **83**, 277–291 (2012).
16. Enquist, M. & Leimar, O. The evolution of fatal fighting. *Anim. Behav.* **39**, 1–9 (1990).
17. Mitani, J. C., Gros-Louis, J. & Richards, A. . Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *Am. Nat.* **147**, 966–980 (1996).
18. Wilson, M. & Daly, M. Competitiveness, risk taking, and violence: the young male syndrome. *Ethol. Sociobiol.* **6**, 59–73 (1985).
19. Wrangham, R. W., Wilson, M. L. & Muller, M. N. Comparative rates of violence in chimpanzees and humans. *Primates* 14–26 (2006). doi:10.1007/s10329-005-0140-1
20. Rudicell, R. S. *et al.* Impact of simian immunodeficiency virus infection on chimpanzee population dynamics. *PLoS Pathog.* **6**, (2010).
21. Wilson, M. L., Wallauer, W. R. & Pusey, A. E. New cases of intergroup violence among chimpanzees in Gombe National Park , Tanzania. **25**, (2004).
22. Kirchhoff, C. A. *et al.* Infanticide in chimpanzees: taphonomic case studies from Gombe. *Am. J. Phys. Anthropol.* 1–15 (2017).
23. Darwin, C. *The Descent of Man, and Selection in Relation to Sex.* (John Murray, 1871).
24. Alexander, R. D. *The Biology of Moral Systems* (1987). doi:10.4324/9780203700976
25. Bowles, S. Group competition, reproductive leveling, and the evolution of human altruism. *Science.* **314**, 1569–1572 (2006).

Methods References

27. Calenge, C. The package ‘adehabitat’ for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**, 516–519 (2006).

28. Bygott, J. D. Agonistic behavior, dominance and social structure in wild chimpanzees of the Gombe National Park. in *The Great Apes* (eds. Hamburg, D. A. & McCown, E. R.) 405–428 (Benjamin/Cummings Pub. Co., 1979).
29. Muller, M. N. & Wrangham, R. W. Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Anim. Behav.* **67**, 113–123 (2004).
30. Wroblewski, E. E. *et al.* Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Anim. Behav.* **77**, 873–885 (2009).
31. Constable, J. L., Ashley, M. V., Goodall, J. & Pusey, A. E. Noninvasive paternity assignment in Gombe chimpanzees. *Mol. Ecol.* **10**, 1279–1300 (2001).
32. Gilby, I. C. *et al.* Fitness benefits of coalitionary aggression in male chimpanzees. *Behav. Ecol. Sociobiol.* **67**, 373–381 (2013).
33. Feldblum, J. T. *et al.* Sexually coercive male chimpanzees sire more offspring. *Curr. Biol.* **24**, 2855–2860 (2014).
34. Walker, K. K. *et al.* Chimpanzees breed with genetically dissimilar mates. *R. Soc. Open Sci.* **4**, (2017).
35. Barbian, H. J. *et al.* CHIIMP: An automated high-throughput microsatellite genotyping platform reveals greater allelic diversity in wild chimpanzees. *Ecol. Evol.* **8**, 7946–7963 (2018).
36. Kalinowski, S. T., Taper, M. L. & Marshall, T. C. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**, 1099–1106 (2007).
37. Emery Thompson, M. Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): methodological considerations and the role of hormones in sex and conception. *Am. J. Primatol.* **67**, 137–158 (2005).
38. Deschner, T. & Boesch, C. Can the patterns of sexual swelling cycles in female Tai chimpanzees be explained by the cost-of-sexual-attraction hypothesis? *Int. J. Primatol.* **28**, 389–406 (2007).
39. Jones, J. H., Wilson, M. L., Murray, C. & Pusey, A. Phenotypic quality influences fertility in Gombe chimpanzees. *J. Anim. Ecol.* **79**, 1262–1269 (2010).
40. Muller, M. N., Thompson, M. E. & Wrangham, R. W. Male chimpanzees prefer mating with old females. *Curr. Biol.* **16**, 2234–2238 (2006).
41. R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
42. Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, (2015).
43. Burnham, K. P., Anderson, D. R. & Huyvaert, K. P. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**, 23–35 (2011).
44. Mazerolle, M. M. J. Package 'AICcmodavg'. (2020). Available at: <https://cran.uib.no/web/packages/AICcmodavg/AICcmodavg.pdf>.

Figures

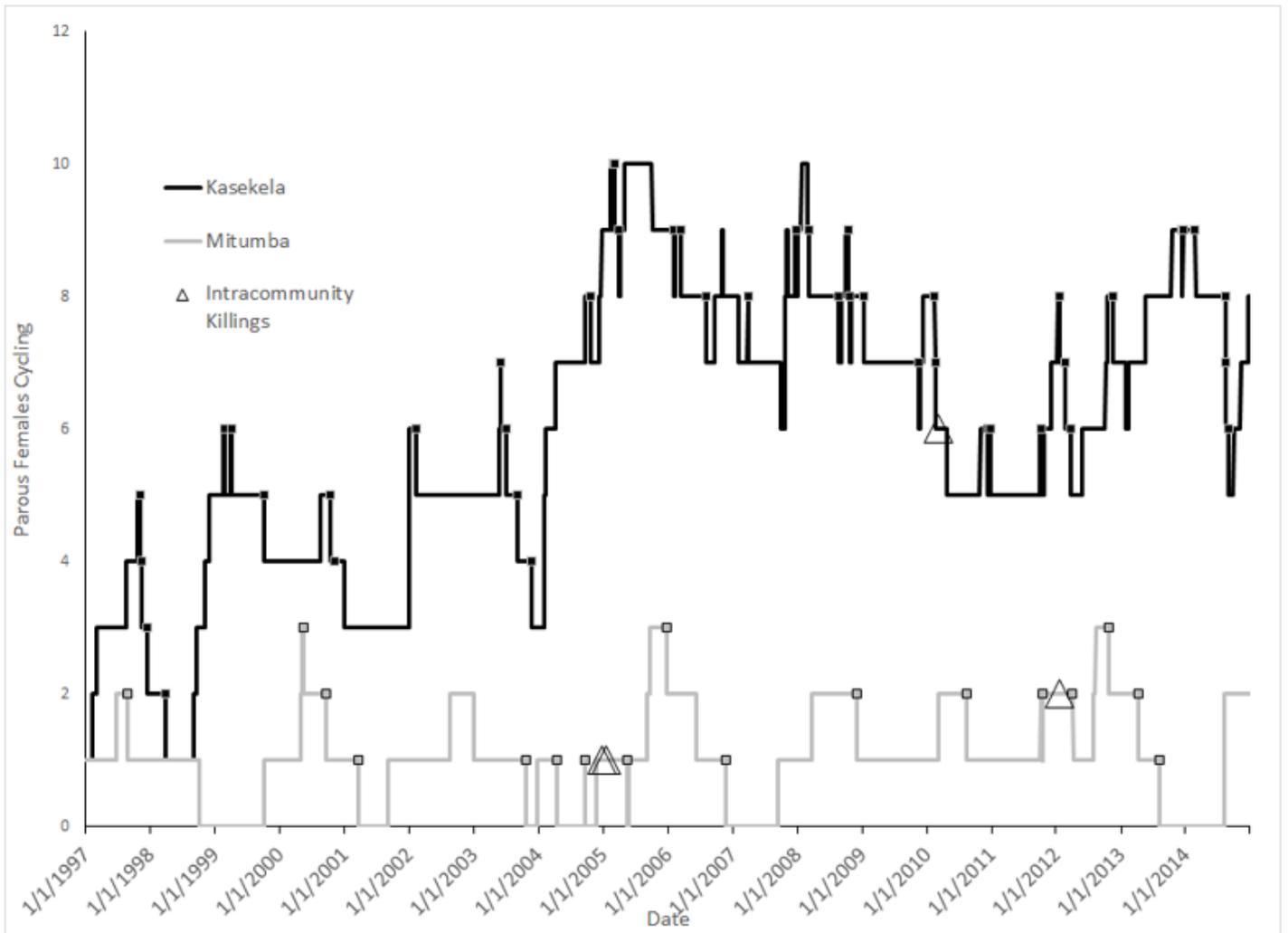


Figure 1

Timeline of cycling, parous females in Mitumba and Kasekela, showing the daily number of parous, cycling (neither pregnant nor lactating) females in Mitumba and Kasekela. Mitumba consistently had fewer of these high value mates and more instances of within-community killing.

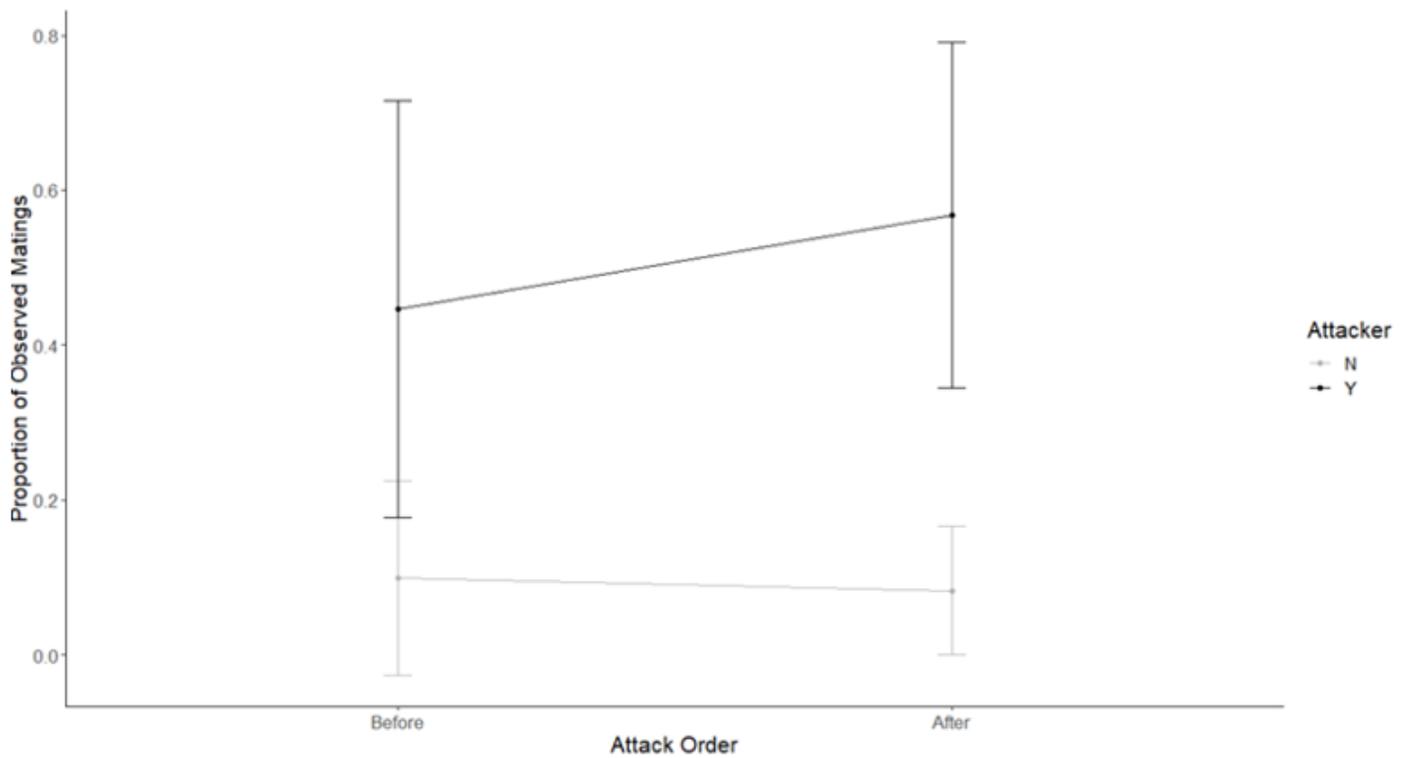


Figure 2

Mating success for attackers and non-attackers before and after 5 known or inferred killings in Mitumba and 1 inferred within-community killing in Kasekela. Attackers are those listed in Table S1 as known or inferred attackers in fatal cases. Non-attackers are all other mature males (i.e., those that were observed mating in periods before and after violent events). Error bars represent one standard deviation of uncertainty.

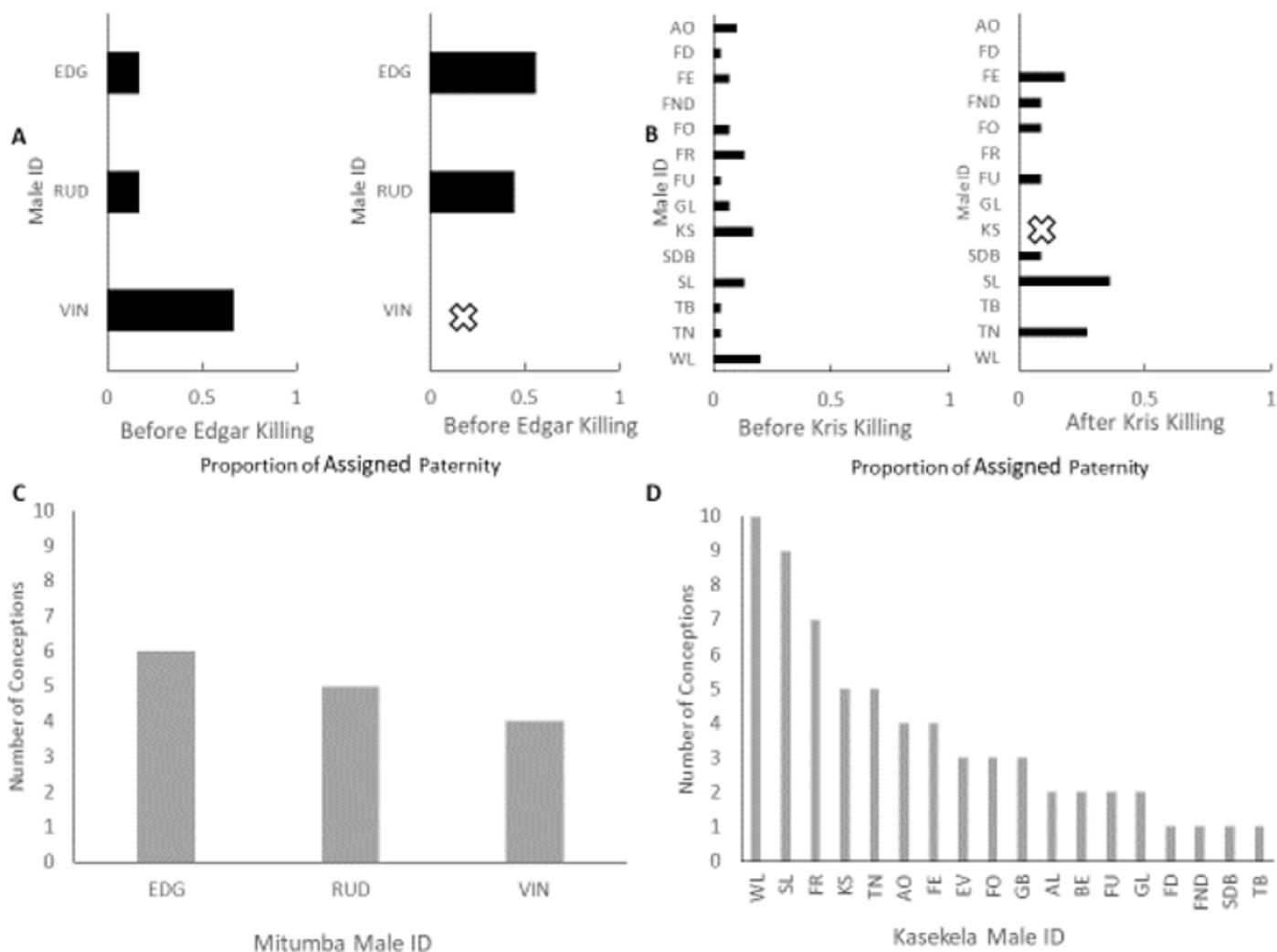


Figure 3

Male reproductive success at Gombe. The proportion of offspring sired by males before and after the killing of (A) Vincent (Mitumba) and (B) Kris (Kasekela). The lifetime reproductive success of males in (C) Mitumba and (D) Kasekela, as determined by genetic analysis.

Supplementary Files

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