Nested Male Reproductive Strategies in a Tolerant Multilevel Primate Society

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Abstract

Male reproductive success varies within populations. Models explaining reproductive skew largely emphasize dominance, yet the determinants of male reproductive success in egalitarian societies remain poorly understood. Using nine years of behavioral and genetic data from five parties, we investigated male reproductive monopolization in wild Guinea baboons (*Papio papio*), an egalitarian multilevel society with one-male "units" nested within "parties" and low male-male contest competition. Genetic analyses showed 93% of the 71 infants were sired by the female's "unit male", with rare extra-unit paternities consistent with limited control models. Within parties, reproduction was shared among multiple unit males, resulting in low reproductive skew, with top males siring 23-40% of offspring, well below levels in hierarchical species. Female takeovers were rare, suggesting male restraint. Reproductive success, assessed as the number of unit females, was positively associated with dominance ratings, yet males with average ratings held the largest units. Prime-age predicted reproductive success better than dominance. In conclusion, male Guinea baboons' reproductive success is shaped less by dominance than by age and stable associations with females, who play an active role in inter-sexual relationships. These results emphasize the need to move beyond frameworks focused solely on dominance-based mechanisms and to consider species-specific social organization.

Significance statement

Current theoretical models of male reproductive success often focus on dominance and males' ability to monopolize access to females. Yet, less is known about the determinants of reproductive success in societies with egalitarian male relationships, such as the multilevel society of wild Guinea baboons. Using nine years of behavioral and genetic data from five groups ("parties"), we show that unit males almost always sire their unit's offspring. However, at the party level, male reproductive skew is low. Reproductive success is better predicted by prime-age than dominance and appears to result from long-term associations with females, likely shaped by female choice. Our results highlight the need to examine diverse social systems to understand the evolution of reproductive strategies beyond dominance-centered models.

Introduction

Because reproductive opportunities are limited, individuals often compete for access to mates, leading to considerable variation in reproductive success. Several theoretical models have been proposed to explain patterns of reproductive skew, the unequal distribution of reproductive success. Limited control models (or 'Tug-of-war') suggest that reproductive skew results from reproductive contests between dominant and subordinate individuals, which impose costs to group productivity (Reeve et al., 1998). These models acknowledge that dominant individuals cannot fully monopolize reproductive opportunities, primarily due to the high costs of competition (Kutsukake & Nunn, 2006; Reeve et al., 1998). Consistent with this view, the 'priority of access model', developed for primates, posits that higher-ranking males have priority in mating (S. A. Altmann, 1962). Since only one female can be monopolized at a time, the distribution of reproductive success is affected by the number of males and receptive females at a given point in time (Carnes et al., 2011; Cowlishaw & Dunbar, 1991). Several studies have demonstrated that estrus synchrony limits the success of male monopolization in primates, highlighting how breeding seasonality and the number of females in a group influence male reproductive skew (Carnes et al., 2011; Kappeler & Port, 2008; Ostner et al., 2008). Transactional models, in contrast, assume that reproduction can be controlled and suggest that males share reproduction through concessions or restraint to maximize group stability and mutual benefits (Clutton-Brock, 1998; Johnstone & Cant, 1999; Keller & Reeve, 1994). The magnitude of concession or restraint is determined by kinship and other social and ecological factors (Emlen et al., 1998).

Variations in the degree of male-male contest competition and dispersal patterns influence the outcomes of conflicts over reproduction. In societies where direct male competition is reduced and hierarchies are less strictly enforced, males may engage in reproductive cooperation through alliances and bonds that provide both indirect and direct fitness benefits (e.g., Bray et al., 2016; Chowdhury et al., 2015). Male-philopatric societies, characterized by higher relatedness among males, are expected to have low to moderate levels of reproductive skew, most likely due to kin-based alliances and cooperation among males (discussed in Strier et al., 2011). A striking example is the patrilocal society of northern muriquis (*Brachyteles hypoxanthus*) where aggressive competition between males is virtually absent and male reproductive skew extremely low (Strier et al., 2011). Bonobos (*Pan paniscus*) also live in male philopatric societies, yet high-ranking males successfully monopolize a large share of reproduction, with the most reproductively successful male siring up to 62% of offspring (Surbeck et al., 2017). Interestingly, reproductive skew in bonobos exceeds that of chimpanzees (*Pan troglodytes*), a closely related species that also lives in fission-fusion patrilocal societies but presents more frequent and intense aggression between males (Surbeck et al., 2017). In chimpanzees, reproductive skew was lower but varied substantially between communities, likely reflecting environmental and demographic factors (Bray et al., 2016). The stronger association between dominance rank and reproductive success in male bonobos, despite less intense mate competition, has been attributed to greater group cohesiveness, which may facilitate monopolization, and to female choice for high-ranking males in these female-dominated societies (Surbeck et al., 2017).

In many mammals male age also plays a key role in shaping reproductive monopolization, as it is linked to physical maturation, body size, and the development of sexually selected traits (Hollister-Smith et al., 2007). In most species, subadults have lower reproductive success compared to adults (Kuester et al., 1995; Widdig et al., 2004) and prime-age males, being at their peak physical condition and highest rank (Hollister-Smith et al., 2007), have higher reproductive success compared to other age classes (Widdig et al., 2004). In some species, however, older males can be equally or even more successful. In African elephants (*Loxodonta africana*), for example, male rank depends on body size, and males grow throughout much of their lives (Poole, 1989), with older males having markedly elevated paternity success (Hollister-Smith et al., 2007).

Male reproductive success depends not only on the ways males attempt to gain access to mates, but also on female behavior. In spotted hyenas (*Crocuta crocuta*), where females typically dominate males, dominance and direct competition among males have little effect on male reproductive success, which is primarily affected by female mate choice (Engh et al., 2002). In vervet monkeys (*Chlorocebus pygerythrus*), where females exhibit co-dominance, females mate with multiple males and can resist mating attempts, influencing reproductive monopolization (Minkner et al., 2018). In several species, including some in which males are dominant over females, female preference for males that provide support and protection is associated with

variation in male reproductive success (Arseneau et al., 2015; Haunhorst et al., 2017; Kulik et al., 2012; Ostner et al., 2013; Städele et al., 2019).

To date, the determinants of male reproductive success in egalitarian societies – characterized by low levels of contest competition, shallow dominance hierarchies, and high social tolerance – remain less well understood. To fill this knowledge gap, we investigated male reproductive monopolization in wild Guinea baboons (*Papio papio*), a male philopatric species living in a multilevel society with egalitarian relationships among males and relatively high female leverage (Dal Pesco et al., 2022; Kalbitzer et al., 2015; Patzelt et al., 2014). The base of the society consists of 'units' comprising one reproductively active 'primary' male (hereafter 'unit male'), associated females, and their offspring (Goffe et al., 2016). Several units form stable groups called 'parties', where males maintain strong bonds and display a high degree of social tolerance (Dal Pesco et al., 2021b, 2022). Bachelor males may associate with one or several unit males and are integral to the party cohesion (Dal Pesco et al., 2021b).

Given the scarce occurrence of decided agonistic interactions between males, previous analyses have failed to estimate male dominance hierarchies with any certainty (Dal Pesco et al., 2021b), raising the possibility that rank is of little utility in describing male-male relationships. Alternatively, existing methods (Sánchez-Tójar et al., 2018) may not have been able to estimate reliable dominance hierarchies under such conditions. To address these two possibilities directly, we employed novel statistical methods that explicitly incorporate uncertainty during the estimation of individual dominance ratings ('ranks') and utilize such ratings, along with their associated uncertainty, as predictors in our modeling approach. Estimating dominance ranks, ratings, and hierarchies is challenging, especially when few decided interactions were recorded (due to low interaction rates and/or low observation effort) and/or under conditions of low hierarchy steepness (Sánchez-Tójar et al., 2018). With this novel approach, we aimed for a more nuanced understanding of social and reproductive dynamics in this species.

We used long-term data on wild Guinea baboons collected over nine years from five social groups (parties) to investigate the extent of male reproductive skew and the link between male rank and age and their reproductive success. Party was used as our group unit because males aggregate and interact the most at this social level (Dal Pesco et al., 2021b; Patzelt et al., 2014). We first established paternity for all genotyped offspring. Considering the high investment of unit males in stable year-round associations with their females and the high mating fidelity (99% of observed copulations, Goffe et al., 2016), we predicted high paternity certainty (i.e., unit males should sire the offspring of their associated females). We then assessed reproductive skew by quantifying the share of reproduction among all co-resident males at the party level. Given the multi-level social organization of the species, the presence of male kin in the party, and the occurrence of male-male social tolerance and bonds, we hypothesized that the balance between competition and cooperation is shifted towards male cooperation, resulting in low reproductive skew. Lastly, we modeled the effects of age and rank on male reproductive success using a custom Bayesian model based on Elo-ratings. Given that Guinea baboons exhibit low rates of overt male-male competition, we predicted that male rank would have a modest linear effect on reproductive success. We further predicted that males in their prime age have a higher reproductive success than subadult males or males past their prime.

Material and methods

Study species

Guinea baboons live in multilevel societies with female-biased dispersal and high spatial tolerance within and between different social levels (reviewed in Fischer et al., 2017). The basal level comprises 'units' composed of a 'primary' male (i.e., unit male), typically 1-6 associated females, and their offspring (Dal Pesco et al., 2022; Goffe et al., 2016). Male-female associations remain stable throughout the various stages of female reproductive cycle and can last from weeks to several years (Goffe et al., 2016, unpublished data). Females play an active role in inter-sexual relationships and have comparatively high levels of spatial and social freedom (Goffe et al., 2016). Males are predominantly philopatric and associate in stable groups called 'parties' composed of several units and bachelor males (Dal Pesco et al., 2021b; Patzelt et al., 2014). Bachelor

males are an integral part of the party and can be associated with one or multiple units, affording them limited social access to females in the units (Dal Pesco et al., 2021b). At the party level, males establish strong and lasting bonds with other males, relying on them for mutual support during aggressive events (Dal Pesco et al., 2022). Strong ties between males, however, are not linked to increased reproductive success. On the contrary, with an increasing number of females in their unit, males tend to decrease the time they spend socializing with other males (Dal Pesco et al., 2022). Finally, several parties form a 'gang,' and several gangs share largely overlapping home ranges (Ohrndorf et al., 2025; Patzelt et al., 2014). The rate of aggression between Guinea baboon males is lower than in other Papio species and their dominance hierarchies were previously described as "non-significant" (Kalbitzer et al., 2015) and characterized by intermediate/low steepness (Dal Pesco et al., 2021b).

Study subject and study site

We used data collected over nine years (2014-2022) on wild Guinea baboons at the CRP Simenti field station in Niokolo-Koba National Park, Senegal (Fischer et al., 2017). We initially worked with three habituated parties (5, 6, 9) within the Simenti Guinea baboon community, which consists of around 400 individuals. Party 6 split into two parties, 6I and 6W, in 2020. Ultimately, we entered five party IDs into our analyses (see supplementary table A1 for details). We confined all our analyses to within-party interactions, following previous studies on the same population (Dal Pesco et al., 2021b; e.g., Dal Pesco et al., 2022). We conducted behavioral observations on all males in the study parties, starting from the time they first attained the age classification of large subadult, approximately 8 years old (n = 48). At that age, they may already be associated with females and hold their unit (see Dal Pesco et al., 2022). For each study year, we assigned males to one of two age categories. Sexually mature and fully developed individuals were categorized as prime-age. Individuals not yet fully developed, as well as old males, were classified as non-prime-age. For males who switched from non-prime to prime-age or vice versa in the same study year, the category with the longer duration (higher number of days) was chosen for that year. We collected data using customized electronic forms, which were operated on Pendragon 7.2 software, and were accessed via Samsung Note 2 and 3, as well as Gigaset GX290 Plus handheld devices. On each observation day, we recorded census data encompassing demographic information (including births, deaths, dispersal/migration, and presence/absence), health status, and female reproductive state (see Goffe et al., 2016). We collected 20-minute continuous focal follows (J. Altmann, 1974), ensuring a balance between subjects and the time of day. During these focal follows, we continuously recorded the focal animal's activity (movement, feeding, resting, and socializing) and all social behaviors (e.g., approaches, retreats, supplants, aggression, grooming, contact-sits, and greetings) involving the focal subject. Instances of aggression, coalitionary support, copulation, and grooming were also recorded on an ad libitum basis.

Reproductive success: number of females

We recorded unit composition and female unit transfers on each observation day. Daily unit composition was established based on previous observations showing that females interact more with their unit males (Goffe et al., 2016). We thus based our assessment of unit composition on copulations, grooming bouts, contact-sit bouts, greetings, and aggression events between each female and all males in the same party (see Dal Pesco et al., 2022). To account for unit size variation due to female transfers and demographic changes, we used daily unit size within each study year to calculate the modal number of associated females per male and year (i.e., the most frequent unit size value), following Dal Pesco et al. (2022). The daily unit size for bachelor males was, by definition, zero.

Reproductive success: genetic and paternity analyses

We used genetic data collected over eight years (2014-2021) to evaluate male paternity, reproductive skew, and the proportion of offspring sired by males of the five study parties. Dal Pesco et al. (2022) used a subset of genetic data collected from two parties from 2014 to 2017 to investigate the fitness benefits of male-male

sociality. Here, we added demographic and genetic data collected over an additional four years (2018-2021; see supplementary table A2).

During 2014-2021, 110 infants were born within the study parties, of which 71 were sampled successfully for genetic analysis (supplementary table A4). To conduct the parental analysis, we utilized fecal samples from all focal males (from approximately 8 years old) and sexually mature females (from approximately 5.5 years old) who were members of the study parties during the period of interest. We accounted for a 6-month gestation period (see supplementary table A2). Although the average gestation length in our population is around 5.5 months, we used 6 months to include longer pregnancies, which also occur in this dataset. Since we did not know at which age sperm would be viable in our population, and given that in other baboon species, even relatively young males have been documented to sire offspring (Zinner et al., 2006), we also included all males between 6 and 8 years of age. Ultimately, we sampled 54 males (98% sampling success, with all unit males present at the time of conception sampled) and 68 females (85% female sampling success, with all observed mothers sampled). In addition, to rule out potential cases of paternity outside of the study parties or errors in our maternity assessment, we collected fecal samples from 50 males and 13 females belonging to the other habituated parties within our study population.

We assessed individual allelic variation using a panel of 24 autosomal microsatellite markers (Dal Pesco et al., 2021a; also see Patzelt et al., 2014). The methods employed in genetic sample collection, storage, DNA extraction, and genotyping are described in Dal Pesco et al. (2021a). All loci demonstrated polymorphism, with an average allele number of 4.5 (range = 2-7; sd = 1.4); no locus showed signs of null alleles or departures from Hardy-Weinberg Equilibrium (see supplementary table A3).

The paternity analysis was performed using the software Cervus (v. 3.0.7, Kalinowski et al., 2007), employing the methodologies described in detail by Dal Pesco et al. (2021a). The mother's identity was recorded during field observations and verified using a maternity likelihood analysis with the acceptance criterion of identification as candidates with zero mismatches. All mothers were confirmed with zero mismatches. Subsequently, we employed the trio likelihood approach, leveraging the known identity of the mother to determine the most probable father (supplementary table A4). A male was considered the sire of an offspring if he was assigned as the most likely father, had a maximum of one mismatched allele, and the confidence level for the assignment exceeded 95% (using the 'strict' criterion).

Reproductive skew and unit males' reproductive success

For each genotyped offspring born between 2014 and 2021 (n = 71), we checked the unit association of the mother at the time of conception. Then we calculated the percentage of offspring sired by each unit male. For two offspring, we did not know with which male the female was associated before they joined our study groups, resulting in 69 offspring for which we could determine whether the unit male sired the offspring (see supplementary table A4).

To measure male monopolization at the party level, we calculated the percentage of offspring sired by the most successful male within each party over the eight years. Initially, we calculated this percentage using only the offspring sired within the party for which paternity was genetically assessed (n= 70, one case of extra-party paternity was excluded). Based on high paternity certainty (see results), we assigned the unit male at the time of conception as the most likely father for offspring without genetic data. We then repeated the calculation, including all offspring sired within the party (n = 109).

To investigate male reproductive skew at the party level, we used all offspring with assigned paternity in the study parties (n = 70). One offspring was sired by a male of another party (see supplementary table A4). We included all focal males associated with the study parties over the eight years, extending from six months before the start to six months before the end of each study party's observation period to account for gestation time (supplementary table A2). This dataset comprised 45 males (note that one male was counted twice due to a party transfer). Although Party 6 split into Parties 6I and 6W in 2020, we combined them for the reproductive skew analysis and for calculating the share of offspring sired by the most successful male, because the split occurred near the end of genetic data collection and sample sizes were too small for separate analyses. All other analyses treated these parties separately after the split.

We calculated reproductive skew using the Multinomial Skew Index (M index, Ross et al., 2020, see supplement section "Reproductive skew" for details about implementation and interpretation). This index can be fitted in a Bayesian framework and therefore results in a posterior distribution of M. In contrast to the widespread B index (which can still be calculated from M), M is unconstrained. An M value equal to zero indicates that reproduction is distributed as expected for a random multinomial model where rates of reproductive success are equal. An M value above zero indicates a positive skew of reproduction. An M value below zero indicates that the share of reproduction within the group is more equal than expected under a random multinomial model (Ross et al., 2020). The share of reproduction is not different from chance when the confidence interval includes zero. The M index accounts for group demographic changes, allowing us to include demographic information regarding male presence, and is not biased by differences in sample or group size (Ross et al., 2020). We also calculated M for the total monopoly and equal sharing scenarios (Nonacs, 2000) to assess where these values fall in relation to the observed indices (see supplement section "Reproductive skew").

Dominance hierarchy

We evaluated the male dominance hierarchy using ad libitum and focal data on within-party male-male aggressive behaviors that occurred during the nine-year study period. This included all threats, lunges, chases, physical fights, displacements/supplants, avoidance, and unprovoked submissions. We excluded interactions without a decided winner/loser outcome. We also excluded all interactions that followed one or more polyadic interactions within the same aggression event, as the outcome could still be influenced by previous coalitionary behavior. In cases where multiple interactions occurred between dyads during the same aggression event, we only considered the most intense interaction. We included 714 interactions in the rank calculation (median = 33.5 per male, range = $1 - 90$). We assessed male rank within parties by estimating Bayesian Elo-ratings (Goffe et al., 2018, see supplementary subsection "Elo-ratings" for a full methodological description).

Modeling reproductive success as a function of age and rank

We modeled the modal number of females a male had in his unit in a given calendar year. Our data set comprised 190 data points (male-years), with 48 male subjects. Males who switched party association within a calendar year were assigned to the party in which they resided the longest. Males were present between 1 and 9 years (median = 3). We modeled the modal number of females a male had in his unit in a given year as a Poisson process with a log-link. As predictors, we used a male's Elo-rating (at the end of a given calendar year), age, and the interaction between Elo-rating and age. We fit the model in a Bayesian framework in Stan (Gabry et al., 2023; Stan Development Team, 2023), which allowed us to combine Bayesian estimation of Elo-ratings with our model of interest on the number of females. This approach allowed us to utilize the full posteriors of Elo-ratings as a predictor variable. A detailed model description can be found in the supplementary section "Modelling reproductive success".

Results

Reproductive skew and unit males' reproductive success

We were able to estimate paternity for all 71 sampled offspring. Of these, 67 offspring were sired by adult males, while four different subadult males sired the remaining four offspring. Of the 69 offspring for which we could determine the identity of the unit male at the time of conception, 64 (93%) were sired by that male. The remaining five offspring were sired by an adult male from a different party (same gang) whose social association with the mother had ended six months before conception and by four subadult males belonging to the same party (see supplementary table A4). All extra-unit paternities occurred between August and November, corresponding to the middle or late rainy season, or shortly thereafter, when the vegetation is

dense and visibility is poor (not only for the observers but most likely also for the baboons). For all extra-unit paternity cases, we examined whether any other unit females were cycling simultaneously during the conception period. For the four cases for which we had these data, the unit male had two females cycling at the same time during the conception period.

If we exclude the one extra-party paternity, the remaining 70 offspring had 20 different fathers, indicating that reproduction is shared at the party level. Almost half of the large subadult and adult males of the study parties (47%) sired at least one offspring. The number of sired offspring per male during the study period ranged from 0 to 8 (mean = 1.56; sd = 2.23). When we considered all offspring sired within the party, irrespective of whether they were genotyped or not, the 109 offspring had 27 different fathers, with 60% of males siring at least one offspring (mean = 2.42, sd = 3.09, range = 0-11).

The percentage of offspring sired by the most successful male within each party ranged from 23% to 40% over the eight-year study period (average across parties 29%) when considering only offspring for which paternity was genetically assessed; in two of the three parties, two or three males tied as the most successful. When including all offspring, this percentage ranged from 24% to 33% (average across parties 28%), and each party then had a single most successful male. The expected share under random paternity (i.e., assuming all males have equal probability of siring each offspring), given the number of candidate males per party, would range between 6% and 11% (average across parties 7%), indicating that the observed shares are modestly higher than expected by chance.

The reproductive skew, measured within parties using the multinomial index, was close to zero, with posterior medians ranging from 0.29 to 0.5 for the three parties (table 1). The 89% credible intervals overlapped zero for all parties, indicating that the share of reproductive benefit within parties (i.e., sired offspring in the study parties) did not differ from chance in an obvious way (figure 1). For all parties, the point estimate for the total monopoly scenario was well outside the credible intervals (table 1), providing strong evidence that reproduction is not monopolized. The point estimate for the equal share scenario was just outside the confidence interval ranges for all parties (table 1), indicating that reproduction is not entirely shared equally.

Table 1: Reproductive skew assessed by the multinomial index (M) in three parties of Guinea baboons. We investigated reproductive skew for all focal males and all offspring present/born between 2014 and 2021 with assigned paternity in our three study parties.

party	males	sires	offspring	monop	equal	$M_{\text{post. median}}$	89% CI
5	9	5	20	7.61	-0.90	0.35	-0.40 – 1.57
6	18	10	28	16.39	-0.94	0.50	-0.46 – 2.03
9	18	6	22	16.22	-0.95	0.29	-0.85 – 2.13

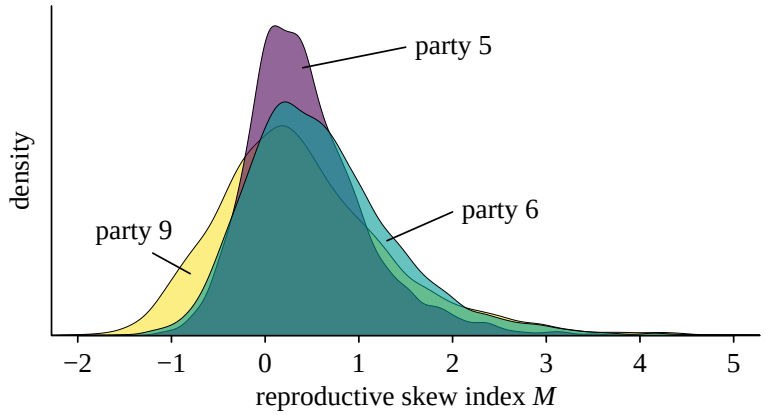

Figure 1: Full posterior distributions of the reproductive skew index for three Guinea baboon parties (5, 6, and 9).

Modeling reproductive success as a function of age and rank

We found a positive relationship between a male's Elo-rating in a given year (figure 2) and the mode number of females a male was associated with in that year (figure 3, table 2, see supplementary figure A6 for result visualization by party). The positive relationship between rank and reproductive success was only visible in prime-aged males. In contrast, for non-prime aged males, the association between rating and number of females was virtually flat (see figure 2 for a visualization of Elo-rating ranges by age). Reproductive success was not biased in favor of the highest-ranking males. Indeed, middle-ranking males held the largest units (4-6 females), and some of the top-ranking males had no units or units with only 1 to 2 females. Across males and years, the average mode of the number of associated females was 1.78 (n = 148 male-years, sd = 1.42, range = 0-6) for prime-aged males and 0.14 (n = 42 male-years, sd = 0.42, range = 0-2) for non-prime-aged males. Of the 148 male-year observations for prime-aged males, only 24% had a mode number of females of zero (n = 20 males). Non-prime-aged males typically had no females and there were only five observations where non-prime-aged males had any females; these were large subadult males.

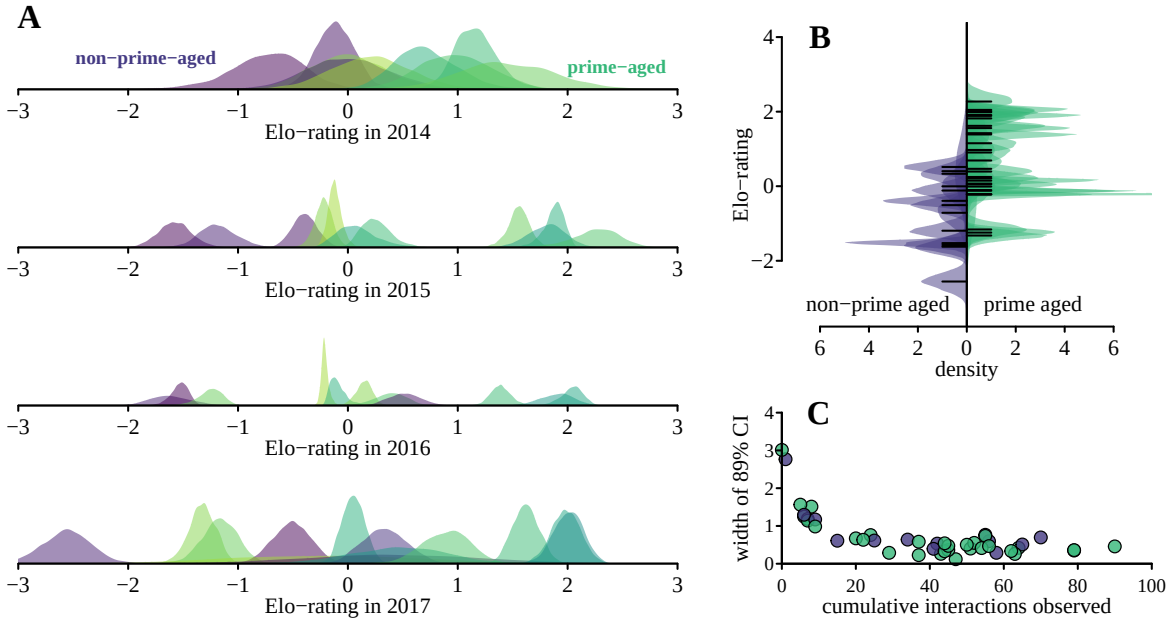

Figure 2: Bayesian Elo-rating. We assessed male rank within parties using a modified Bayesian Elo-rating approach that yields ratings as posterior distributions instead of conventional point estimates. In our downstream model of reproductive success, we make use of these full posteriors as predictors, thereby carrying forward the uncertainty from rank estimation. The three panels illustrate this approach for a sub-sample of four years and one study party (party 6). Panel A represents the individual dominance ratings and associated posteriors at the end of each calendar year. Panel B shows the range of rating posteriors across age classes. Panel C illustrates how uncertainty in the rating estimates typically decreases with increasing numbers of interactions.

Table 2: Summaries of estimates of primary model parameters, including 89% credible intervals. Greek letters refer to supplementary material, 13, and the three subsequent ones. The model parameters in this table represent population-level effects. Age was a binary predictor with the reference level being prime-age.

	mean	median	5.5%	94.5%	$\hat{R}$
intercept (α)	0.24	0.24	-0.03	0.49	1.00
Elo-rating (β)	0.29	0.29	0.10	0.49	1.00
age (γ)	-2.01	-2.01	-2.72	-1.34	1.00
interaction Elo-rating : age (δ)	-0.21	-0.20	-0.81	0.40	1.00

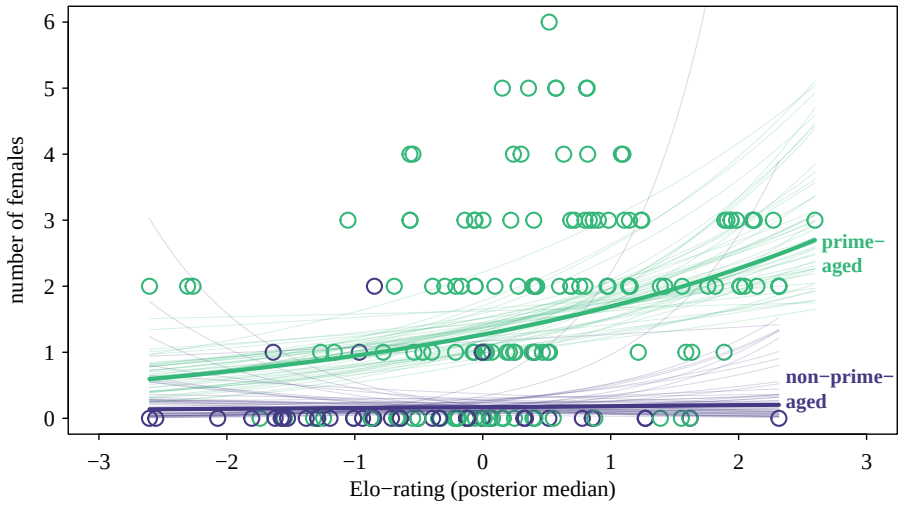

Figure 3: Count model results. The figure shows the mean predictions for the relationship between Elo-rating and the number of females, separated by age class. Alongside the mean predictions, 50 randomly selected samples show the range of uncertainty in the estimation. Circles represent the observed number of females, and Elo-ratings are plotted at the median of the posterior distribution for each male year.

Discussion

By analyzing nine years of data on wild Guinea baboons, we show that within parties, reproduction is shared between multiple males. About half of the males (47%) sired at least one offspring, resulting in low reproductive skew. The most successful males accounted for 23–40% of paternities, which is well below the levels observed in strictly hierarchical or coercive species, such as mountain gorillas living in multi-male groups (*Gorilla beringei beringei*: 85%; Bradley et al. (2005)) or yellow baboons (*Papio cynocephalus*: 81%; J. Altmann et al. (1996)). The paternity analysis revealed that 93% of the 71 infants were sired by the female's unit male, indicating that these males have high paternity certainty. This finding is in line with the observation that 99% of observed copulations occurred with the unit male (Goffe et al., 2016). Extra-unit paternities were rare and occurred when multiple females from the same unit cycled simultaneously and during periods of low visibility due to dense vegetation, when male visual control over female whereabouts was low. This constellation of factors may have limited the unit males' ability to monopolize reproduction (Carnes et al., 2011; Ostner et al., 2008; Rowell, 1988; van Schaik & van Hooff, 1983). Reproductive concessions to associated bachelors in exchange for support appear unlikely, given that bachelor associations span multiple units (Dal Pesco et al., 2021b) and that extra-unit paternities can occasionally occur across parties.

Our analysis indicates that the same social system can conform to predictions from different bodies of theory, depending on the social level. At the unit level, findings are consistent with limited control models (Clutton-Brock, 1998; Reeve et al., 1998). At the party level, in contrast, the combination of low reproductive skew, rare takeovers (Goffe et al., 2016), and little overt aggression (Dal Pesco et al., 2021b) is consistent with models of male restraint (Johnstone & Cant, 1999). This pattern resembles what Kummer described as the "respect of ownership" in hamadryas baboons (*Papio hamadryas*) (Kummer, 1968). Taken together, these findings show that in multi-level societies, different theoretical frameworks are not mutually exclusive, but rather complement each other.

While nested social levels are a key feature of multilevel and fission-fusion societies, most animal groups are also internally substructured and embedded in larger collectives that face similar ecological and social problems. Many theoretical models of reproductive skew assume that a single level within social groups represents the main arena for reproductive competition. We suggest explicitly considering and accounting for substructuring to avoid incomplete or misleading interpretations of behavioral and reproductive strategies. The effect of substructures on social behavior is not restricted to Guinea baboons: Recent experimental studies and agent-based modeling approaches in humans have shown that the permeability of group boundaries and the frequency of interactions between subgroups determine whether cooperation remains group-bound or transitions into broader collective actions (Gross et al., 2023). Cross-group interactions also shift perceptions of group membership, with individuals increasingly identifying with the collective rather than their in-group (Gross et al., 2023). Similar considerations may also apply to bonobos and dolphins, where interactions across subgroups and the permeability of social boundaries can influence patterns of cooperation, competition, and resource access (Samuni et al., 2026).

In addition to understanding evolutionary dynamics, substructuring needs to be considered in comparative research. If the effect the relevant social level has on reproductive competition is not explicitly considered, comparisons across species risk conflating fundamentally different processes. We propose that the Guinea baboon "party" constitutes the ecological equivalent to the "clan" in hamadryas baboons (Kummer, 1968), and the "group" in uni-level societies (Fischer et al., 2019).

In prime-aged Guinea baboon males, dominance ratings were positively associated with the number of females in the unit, although the association was weak. The majority of prime-aged males had one to three females. Males with average dominance ratings had the most females, while some males with above-average dominance ratings had few or no associated females. While this pattern may question the application of a linear model, the choice of the linear model was based on the theoretical considerations outlined in the introduction. Overall, male age was a stronger predictor of reproductive success than rank. Most non-prime-aged males had no associated females, while prime-aged males typically had more females across the entire range of rank ratings. These results suggest that we are missing an important component in the model, most likely female preferences.

Females may prefer males that are more tolerant and affiliative, socially compatible, or better fathers (Goffe et al., 2016; Rosenbaum et al., 2018), even when these males hold average dominance ranks. Familiarity might provide another plausible explanation, as females might prefer to remain with males they already know well, while the composition of females within a unit may further influence mate choice. Male physical condition and developmental trajectories, such as the transition speed to adulthood, may serve as critical cues for females. Males typically establish their unit during the final stages of subadulthood, and most prime-aged males are unit males. Males then gradually lose their associated females as they transition from late prime to old age (Dal Pesco et al., 2022). Lifetime reproductive success thus likely depends on the total number of female-years a male accumulates. More data on complete male life-histories will be needed to test this assertion.

Maximizing the number of female-years aligns with patterns observed in other primate multi-level societies. The underlying behavioral strategies, however, can differ substantially between species. In hamadryas baboons, male access to females is most often achieved via coercive tactics and enforced proximity, which are thought to have evolved due to their direct fitness benefits (Evans, 2024; Swedell & Schreier, 2009). Male hamadryas baboons protect their units through both direct contest competition during takeovers and alliances with follower males, which are exclusively associated with their unit (Chowdhury et al., 2015). In these male-philopatric societies, followers are thought to diminish the likelihood of extra-unit paternity and benefit from indirect fitness benefits and/or the possibility of future succession (Chowdhury et al., 2015). In snub-nosed monkeys (*Rhinopithecus roxellana*), cooperative defense of females occurs across units. Unrelated unit males join forces against satellite males, who, in turn, cooperate in takeover attempts (Qi et al., 2017; Xiang et al., 2014). In geladas (*Theropithecus gelada*), the most successful unit males are those that associate with follower males, benefitting from their support (Snyder-Mackler et al., 2012). These follower males, in turn, gain reproductive opportunities, making geladas one of the few examples supporting transactional concession models in primates (Snyder-Mackler et al., 2012; but see Port et al., 2018). In conjunction, depending on ecological conditions, evolutionary history, and dispersal patterns, different processes may lead to similar-looking outcomes at the level of social structure.

Dominance rank has long been used as a proxy for competitive ability and mating access in group-living mammals (Ellis, 1995), yet our results show that substantial variation in male reproductive success cannot be explained solely by dominance-based monopolization or overt contest competition. Even among prime-aged males, individuals with similar rank differed markedly in reproductive outcomes, such that key components of fitness variation remain unaccounted for. This extends beyond Guinea baboons. Alternative pathways to reproductive success, including the role of female spatial and social preferences, long-term social relationships, and coalitionary dynamics, have been reported for other species (e.g., Arseneau et al., 2015; Engh et al., 2002; Kulik et al., 2012; Minkner et al., 2018). While alternative pathways may remain obscured in despotic societies, expanding the mechanisms considered in reproductive skew models reduce the risk of overlooking key sources of fitness. These implications are not only limited to egalitarian societies. Even in species with clear dominance hierarchies, such as Barbary macaques (*Macaca sylvanus*), yellow baboons (*Papio cynocephalus*), and chimpanzees, reproductive outcomes can be shaped by rank, coalitionary support, or female mating behavior rather than rank alone (Bulger, 1993; Feldblum et al., 2021; Städele et al., 2019; Wroblewski et al., 2009; Young et al., 2013). In this sense, our results do not represent an exception to prevailing theory; rather, they reveal where current theoretical models are incomplete. Incorporating these dynamics into comparative analyses may help reconcile inconsistent relationships between rank and fitness across taxa.

Our study underscores the importance of considering uncertainty when estimating social features, such as dominance scores. By conventional standards (e.g., Sánchez-Tójar et al., 2018), our observed interaction networks were too sparse to reliably estimate individual dominance ratings as point estimates (see Dal Pesco et al., 2021b),raising the question of what group members can infer from such rare agonistic interactions. Here, we built on recent advances in Bayesian modeling of interaction data (e.g., Goffe et al., 2018; Neumann & Fischer, 2023, 2025), which explicitly incorporate uncertainty and allow estimates to become more precise as observation records accumulate. We extended this approach by implementing a custom Stan model that directly incorporates dominance ratings and their associated uncertainty as a predictors in our statistical model of reproductive success. This approach enabled us to retain and model the uncertainty in Elo-rating, one of the two key predictors in our model, which decreases as the number of observed interactions per

individual increases (see panel C in figure 2), rather than relying on point estimates. The key advantage of this approach is that predictors associated with uncertainty provide a more honest reflection of the underlying variable, which is the foundation of measurement error models (McElreath, 2020).

In summary, dominance and fighting ability play only a limited role in Guinea baboons' mating outcomes. We hypothesize that reproductive success is primarily influenced by long-term male-female associations rather than by male dominance, coercion, or coalition-based competition. Males strike a balance between competitive ability and social investment toward females, making them more attractive partners. Unlike other multilevel primate societies, where male reproductive success is achieved through aggression or strategic alliances (Chowdhury et al., 2015; Qi et al., 2017; Swedell & Schreier, 2009), Guinea baboons exhibit a system that revolves around social tolerance and female choice. Our results underscore the need to move beyond dominance-based frameworks when studying reproductive skew, highlighting the role of female choice in shaping male reproductive success and the importance of considering species-specific social organizations when evaluating reproductive strategies. We suggest that two levels of reproductive strategies exist within the Guinea baboon society: limited control within units and restraint among males at the party level. Considering the effects of substructuring on social dynamics constitutes an exciting and challenging avenue for future research.

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Supplementary materials for Nested Male Reproductive Strategies in a Tolerant Multilevel Primate Society

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Study parties and subjects

Table A1: Overview of behavioral observation periods for each study party

Party	Start	End
9	2014-04-01	2020-04-12
5*	2016-01-01	2022-12-31
6	2014-04-01	2020-03-31
6I*	2020-04-01	2022-12-31
6W*	2020-04-01	2022-12-31

* Covid-19 Gap: no data from 2020-04-13 until 2020-11-29

Table A2: Overview of periods of available demographic and genetic data for each study party. The columns offspring start/end indicate the periods in which newly born offspring were assessed; the columns parents start/end indicate the periods used to establish the presence of subadult females/males in the study parties as potential mothers/fathers. Note that parental presence was assessed taking into account gestation time; thus, we considered the period starting from six months before the "offspring start" date and ending six months before the "offspring end" date.

Party	Offspring_Start	Offspring_End	Parents_Start	Parents_End
9	2014-01-01	2020-04-12	2013-07-01	2019-10-12
5	2016-01-01	2021-12-31	2015-07-01	2021-07-01
6	2014-01-01	2020-03-31	2013-07-01	2019-09-30
6I*	2020-04-01	2021-12-31	2019-10-01	2021-07-01
6W*	2020-04-01	2021-12-31	2019-10-01	2021-07-01

* This party split from party 6

Genetic and paternity analysis

Table A3: **Characteristics of the 24 microsatellite loci used to estimate paternity** (calculated using the genotypes of all males, females and offspring included in the analysis; $n = 256$)

Loci		Alleles		Heterozygosity			NAFE		Null alleles
Locus ID	Locus No	Allele range	No Alleles	He	Ho	HWE*	Brookfield	Chakraborty	Null alleles Presence
D6s264	Locus1	94 – 98	3	0.521	0.506	0.891	0.010	0.015	no
D7s503	Locus2	152 – 166	6	0.756	0.784	0.213	−0.016	−0.018	no
D12s375	Locus3	165 – 181	5	0.742	0.753	0.793	−0.006	−0.007	no
D3s1766	Locus4	195 – 203	3	0.283	0.301	0.462	−0.014	−0.032	no
D14s306	Locus5	165 – 177	4	0.540	0.556	0.942	−0.010	−0.014	no
D1s533	Locus6	187 – 203	5	0.617	0.668	0.201	−0.031	−0.039	no
D2s1329	Locus7	212 – 228	5	0.628	0.595	0.794	0.021	0.027	no
D2s1326	Locus8	251 – 263	4	0.421	0.413	0.953	0.006	0.010	no
D10s611	Locus9	133 – 141	3	0.566	0.591	0.157	−0.016	−0.021	no
D8s1106	Locus10	144 – 160	5	0.467	0.494	0.951	−0.018	−0.028	no
D17s791	Locus11	166 – 172	4	0.571	0.602	0.443	−0.020	−0.026	no
D6s501	Locus12	172 – 192	6	0.691	0.749	0.075	−0.034	−0.040	no
D17s1290	Locus13	195 – 207	4	0.474	0.498	0.759	−0.016	−0.024	no
D6s311	Locus14	228 – 230	2	0.362	0.351	0.632	0.008	0.015	no
D5s1457	Locus15	124 – 136	4	0.374	0.398	0.785	−0.017	−0.031	no
D8s505	Locus16	147 – 151	2	0.285	0.282	0.810	0.002	0.005	no
D10s1432	Locus17	158 – 170	7	0.745	0.707	0.305	0.022	0.026	no
D5s820	Locus18	179 – 199	6	0.770	0.730	0.051	0.023	0.027	no
D3s1768	Locus19	169 – 213	6	0.554	0.541	0.083	0.009	0.012	no
D7s2204	Locus20	228 – 248	6	0.724	0.695	0.030	0.017	0.021	no
D1s207	Locus21	133 – 135	2	0.495	0.510	0.720	−0.010	−0.015	no
D4s243	Locus22	147 – 167	6	0.638	0.649	0.005	−0.006	−0.008	no
D1s548	Locus23	192 – 208	5	0.738	0.718	0.294	0.011	0.014	no
D21s1142	Locus24	226 – 246	6	0.697	0.722	0.464	−0.015	−0.018	no
Mean			4.5	0.569	0.575	0.492	−0.004	−0.006	
SD			1.5	0.151	0.149	0.339	0.017	0.022	
Min			2.0	0.283	0.282	0.005	−0.034	−0.040	
Max			7.0	0.770	0.784	0.953	0.023	0.027	

He= expected heterozygosity; Ho= observed heterozygosity; HWE= Hardy-Weinberg equilibrium (* note that p-value was corrected for multiple testing with the Bonferroni adjustment, $\alpha = (0.05/24) = 0.00208$)); NAFE= null alleles frequencies estimators calculated based on Brookfield (1996) and Chakraborty et al. (1992) and presence of null alleles.

Table A4: **Results of the paternity analysis for offspring born during the study period (2014-2021) in the study parties.** Samples and genotypes were available for a total of 71 offspring, while for the other 39 offspring no genetic information were available (see the column 'Offspring sampling'). Results from the paternity analysis conducted with Cervus 3.0 (version 3.0.7; Kalinowski et al., 2007). Nmis indicates number of mismatches; Trio LOD indicates the scores of the logarithm of the likelihood ratio; trio Delta is defined as the difference in LOD scores between the most likely and the second most likely candidate father. The confidence level of the Cervus paternity assignments was set to 95% ('strict' criterion) and all statistical confidence on paternity assignment were higher than 95%. An asterisk in the most likely father column indicates fathers that were not the unit holder at the time of conception. In particular, one asterisk indicate a father belonging to the same party and two asterisks a father belonging to a different party of the same gang. For two offspring the unit holder at time of conception was unknown (scored as NA) due to data gaps and the covid pandemic.

Party	Off-spring	Date of birth	Mother	Mother genetically confirmed	Off-spring sam-pling	Most likely fa-ther	Unit holder at time of conception	N_{mis}	Trio LOD	Trio Delta	Conf-level
6	O1	2014-01	F10	Y	Yes	M17*	M20	0	1.4e+15	1.3e+15	>95%
9	O2	2014-03	F27	Y	Yes	M11	M11	0	1.1e+15	1.5e+14	>95%
6	O3	2014-04	F11	Y	Yes	M35	M35	0	1.6e+15	1.6e+15	>95%
6	O4	2014-06	F26	Y	Yes	M20	M20	0	1.0e+15	1.0e+15	>95%
6	O5	2014-07	F19	Y	Yes	M35	M35	0	1.0e+15	2.7e+13	>95%
9	O6	2014-07	F41	Y	Yes	M42	M42	0	1.2e+15	1.2e+15	>95%
9	O7	2014-08	F16	Y	Yes	M49	M49	0	1.2e+15	6.7e+14	>95%
9	O8	2014-09	F47	Y	Yes	M05	M05	0	1.2e+15	7.0e+11	>95%
6	O9	2014-09	F44		No		M51		NA	NA	
9	O10	2014-10	F14	Y	Yes	M11	M11	1	6.7e+14	6.7e+14	>95%
9	O11	2014-10	F29		No		M62		NA	NA	
6	O12	2015-01	F45	Y	Yes	M51	M51	0	1.2e+15	9.8e+14	>95%
9	O13	2015-02	F28	Y	Yes	M49	M49	0	9.0e+14	9.0e+14	>95%
9	O14	2015-03	F39	Y	Yes	M31	M31	0	1.4e+15	1.4e+15	>95%
9	O15	2015-04	F12	Y	Yes	M31	M31	0	1.4e+15	1.2e+15	>95%
9	O16	2015-05	F23		No		M62		NA	NA	
9	O17	2015-05	F40	Y	Yes	M63**	M49	0	8.5e+14	8.5e+14	>95%
6	O18	2015-05	F44	Y	Yes	M51	M51	0	1.2e+15	4.1e+14	>95%
6	O19	2015-05	F46	Y	Yes	M35	M35	0	1.2e+15	1.1e+15	>95%
6	O20	2015-06	F3	Y	Yes	M28	M28	0	1.2e+15	1.2e+15	>95%
9	O21	2015-07	F27		No		M05		NA	NA	
6	O22	2015-07	F7		No		M56		NA	NA	
9	O23	2015-08	F31	Y	Yes	M62	M62	0	1.0e+15	8.9e+14	>95%
9	O24	2015-12	F43	Y	Yes	M05	M05	0	6.7e+14	6.7e+14	>95%
5	O25	2016-03	F2	Y	Yes	M38	M38	0	1.4e+15	1.4e+15	>95%
5	O26	2016-03	F32	Y	Yes	M43	M43	0	1.3e+15	1.3e+15	>95%
9	O27	2016-04	F29	Y	Yes	M62	M62	0	1.6e+15	1.6e+15	>95%
9	O28	2016-05	F15	Y	Yes	M05	M05	0	9.7e+14	9.1e+14	>95%
6	O29	2016-05	F26		No		M20		NA	NA	
6	O30	2016-05	F10	Y	Yes	M15*	M20	0	1.3e+15	1.3e+15	>95%
9	O31	2016-05	F8	Y	Yes	M62	M62	0	1.2e+15	9.6e+14	>95%
9	O32	2016-05	F25	Y	Yes	M31	M31	0	1.6e+15	1.6e+15	>95%
6	O33	2016-05	F19		No		M35		NA	NA	
6	O34	2016-06	F7	Y	Yes	M21	M21	0	1.1e+15	1.4e+14	>95%
9	O35	2016-07	F16	Y	Yes	M49	M49	0	1.4e+15	1.4e+15	>95%
6	O36	2016-07	F11	Y	Yes	M35	M35	0	8.9e+14	8.9e+14	>95%
9	O37	2016-07	F33	Y	Yes	M62	M62	0	1.1e+15	1.1e+15	>95%
9	O38	2016-08	F41		No		M42		NA	NA	
6	O39	2016-08	F45	Y	Yes	M17	M17	0	1.4e+15	5.3e+14	>95%
9	O40	2016-09	F14		No		M42		NA	NA	
9	O41	2016-09	F47	Y	Yes	M05	M05	0	1.3e+15	1.3e+15	>95%
6	O42	2017-02	F46		No		M59		NA	NA	
5	O43	2017-02	F48	Y	Yes	M43	M43	0	9.4e+14	9.1e+14	>95%
5	O44	2017-02	F20	Y	Yes	M38	M38	0	1.2e+15	1.2e+15	>95%
9	O45	2017-03	F40	Y	Yes	M49	M49	0	1.1e+15	1.1e+15	>95%
6	O46	2017-03	F44	Y	Yes	M28	M28	0	1.1e+15	1.1e+15	>95%
9	O47	2017-03	F12		No		M31		NA	NA	
6	O48	2017-03	F3	Y	Yes	M28	M28	0	1.3e+15	1.3e+15	>95%

Table A4 – continued from previous page

Party	Off-spring	Date of birth	Mother	Mother genetically confirmed	Off-spring sam-pling	Most likely fa-ther	Unit holder at time of conception	N_{mis}	Trio LOD	Trio Delta	Conf-level
5	O49	2017-03	F37	Y	Yes	M10*	M27	0	1.3e+15	1.0e+15	>95%
9	O50	2017-05	F28	Y	Yes	M49	M49	0	1.1e+15	1.1e+15	>95%
9	O51	2017-05	F23		No		M62		NA	NA	
5	O52	2017-05	F17		No		M38		NA	NA	
5	O53	2017-06	F13		No		M08		NA	NA	
9	O54	2017-06	F21	Y	Yes	M31	M31	0	1.2e+15	1.2e+15	>95%
6	O55	2017-07	F22		No		M21		NA	NA	
9	O56	2017-09	F31		No		M62		NA	NA	
5	O57	2017-09	F32		No		M43		NA	NA	
6	O58	2017-11	F46	Y	Yes	M55	M55	0	1.4e+15	1.4e+15	>95%
9	O59	2018-01	F43		No		M05		NA	NA	
6	O60	2018-03	F10		No		M21		NA	NA	
5	O61	2018-04	F13	Y	Yes	M08	M08	0	1.3e+15	1.3e+15	>95%
9	O62	2018-04	F25		No		M42		NA	NA	
5	O63	2018-05	F4	Y	Yes	M08	NA	0	1.6e+15	1.6e+15	>95%
9	O64	2018-05	F16		No		M49		NA	NA	
6	O65	2018-06	F35	Y	Yes	M15	M15	0	9.1e+14	9.1e+14	>95%
6	O66	2018-07	F11	Y	Yes	M21	M21	0	8.6e+14	4.4e+14	>95%
9	O67	2018-08	F29	Y	Yes	M62	M62	0	1.3e+15	1.3e+15	>95%
5	O68	2018-08	F32		No		M43		NA	NA	
5	O69	2018-10	F1	Y	Yes	M08	M08	0	1.2e+15	1.2e+15	>95%
9	O70	2018-10	F12		No		M31		NA	NA	
9	O71	2018-11	F47	Y	Yes	M05	M05	0	1.1e+15	1.1e+15	>95%
6	O72	2018-11	F44	Y	Yes	M28	M28	0	1.2e+15	8.6e+14	>95%
6	O73	2018-11	F22		No		M21		NA	NA	
5	O74	2019-01	F2	Y	Yes	M38	M38	0	1.3e+15	1.3e+15	>95%
6	O75	2019-02	F42		No		M04		NA	NA	
5	O76	2019-04	F20		No		M38		NA	NA	
5	O77	2019-04	F9		No		M55		NA	NA	
6	O78	2019-06	F30	Y	Yes	M61*	M28	0	1.4e+15	1.4e+15	>95%
6	O79	2019-06	F10	Y	Yes	M21	M21	1	1.1e+15	5.4e+14	>95%
5	O80	2019-07	F5	Y	Yes	M10	M10	0	1.7e+15	1.7e+15	>95%
6	O81	2019-07	F38	Y	Yes	M21	M21	0	1.1e+15	6.8e+14	>95%
5	O82	2019-07	F48	Y	Yes	M43	M43	0	1.1e+15	7.5e+14	>95%
5	O83	2019-07	F37		No		M16		NA	NA	
5	O84	2019-10	F46	Y	Yes	M55	M55	0	9.5e+14	9.5e+14	>95%
9	O85	2020-02	F8		No		M53		NA	NA	
6	O86	2020-02	F42		No		M04		NA	NA	
9	O87	2020-02	F28		No		M02		NA	NA	
6	O88	2020-02	F35		No		M04		NA	NA	
9	O89	2020-02	F40		No		M40		NA	NA	
9	O90	2020-02	F21		No		M31		NA	NA	
5	O91	2020-02	F13	Y	Yes	M08	M08	0	8.4e+14	7.3e+14	>95%
5	O92	2020-03	F36		No		M55		NA	NA	
5	O93	2020-04	F4	Y	Yes	M08	M08	0	8.1e+14	8.1e+14	>95%
5	O94	2020-06	F18	Y	Yes	M55	M55	0	1.4e+15	1.4e+15	>95%
5	O95	2020-06	F1	Y	Yes	M08	M08	0	1.8e+15	1.8e+15	>95%
5	O96	2020-07	F37	Y	Yes	M08	M08	0	1.3e+15	1.3e+15	>95%
6W	O97	2020-09	F11	Y	Yes	M21	M21	0	1.1e+15	1.0e+15	>95%
6W	O98	2020-10	F44	Y	Yes	M28	M28	0	1.3e+15	1.3e+15	>95%
6W	O99	2021-01	F38	Y	Yes	M21	M21	0	1.3e+15	1.0e+15	>95%
6W	O100	2021-02	F24	Y	Yes	M28	M28	0	9.0e+14	9.0e+14	>95%
5	O101	2021-02	F2	Y	Yes	M38	M38	0	1.1e+15	1.1e+15	>95%
6I	O102	2021-02	F34	Y	Yes	M04	NA	0	1.6e+15	1.3e+15	>95%
5	O103	2021-03	F46	Y	Yes	M55	M55	0	9.6e+14	9.6e+14	>95%
6W	O104	2021-03	F30	Y	Yes	M28	M28	1	1.1e+15	1.1e+15	>95%
6W	O105	2021-07	F10	Y	Yes	M21	M21	0	1.3e+15	1.2e+15	>95%
5	O106	2021-07	F32		No		M55		NA	NA	
6I	O107	2021-08	F35		No		M04		NA	NA	
5	O108	2021-09	F13	Y	Yes	M08	M08	0	9.8e+14	7.8e+14	>95%
5	O109	2021-10	F1		No		M08		NA	NA	
6W	O110	2021-10	F6		No		M21		NA	NA	

Reproductive skew

We calculated reproductive skew using the Multinomial Skew Index (M index, Ross et al. (2020)).

When we fitted the model by Ross et al. (2020) to our data, we ran into severe convergence issues. We therefore reparameterized the model and adapted the Stan code accordingly. In essence, we changed the parameter that reflected the individual probabilities in the multinomial model from a constrained vector (simplex) to an unconstrained vector that we fit as normally distributed. With this modification, the model ran without convergence issues on our data. In figure A1, we visualize posteriors of M that come from model fits using both model parameterizations using the six data sets on human populations from Ross et al. (2020). This figure shows that our modification seems to be by and large equivalent to the original implementation.

We also subjected our modified model to a simple set of posterior predictive checks. For this we used the 50 posterior draws of the estimated probability vector to predict actual numbers of offspring sired by each male. Figure A2 shows the results of this exercise. Within each male, the bubbles indicate the expectation for how many offspring were sired when predicted from the model. When comparing the model predictions to the observed data, we can see that model makes on average adequate predictions.

In addition to calculating M from the observed data, we also calculated M for two hypothetical boundary scenarios (Nonacs, 2000). To arrive at the first hypothetical M when a male monopolizes all reproduction M_{monopoly}, we created a data set where one male sired all offspring, while the other males sired 0 offspring. Accordingly, M_{equal} comes from a synthetic data set where each male obtained exactly one offspring (i.e. equal share). Both scenarios were adapted for each party (table 1).

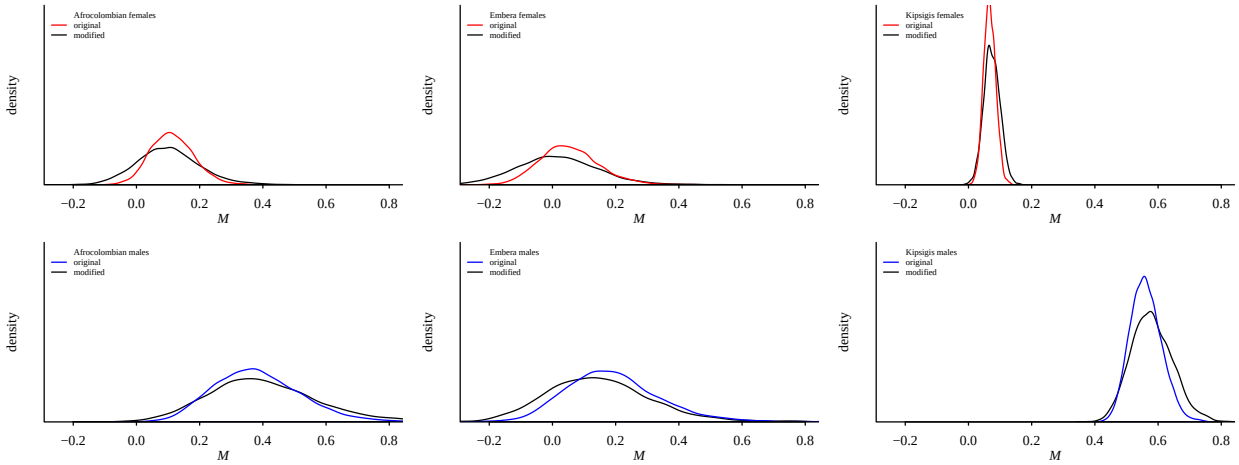

Figure A1: Comparison between the original and modified algorithms to arrive at posterior distributions of the M index (Ross et al 2020). Fits are from six data sets (see figure 2 in Ross et al 2020). In general, there is good agreement between the two algorithms.

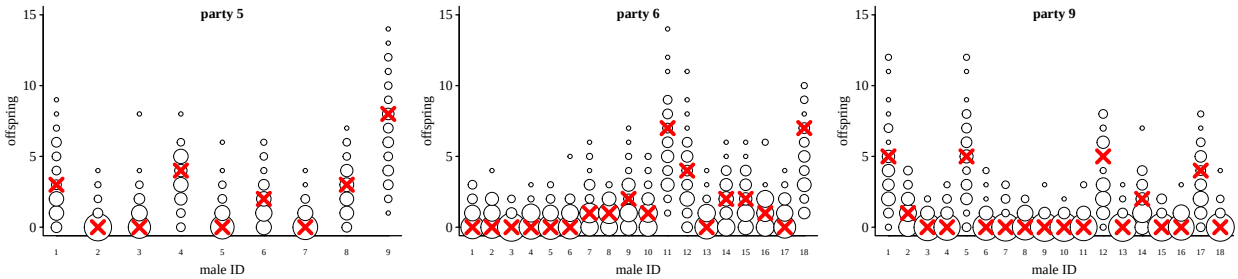

Figure A2: Posterior predictive check for the reproductive skew models. Here we compare predictions from 50 random posterior draws (circles) with respect to the number of offspring a male sired. The observed values are the red crosses. Circle size is proportional to the predicted number of sired offspring.

Modelling reproductive success

This section contains a more detailed model description and some additional model checks and extended results. We fitted our models in Stan 2.33.1 (Stan Development Team, 2023) with the cmdstanr R interface (v. 0.6.1.9000, Gabry et al., 2023) in R 4.2.3 (R Core Team, 2023).

Below we show a detailed specification of our model. For ease of display, we split the description into two parts. The first part describes the modeling of Elo-ratings. The second part describes the actual modeling of the number of females a male had in his unit.

Elo-ratings

We started with declaring a $j+1$ by s matrix, where j is the number of observed dyadic dominance interactions and s is the number of subjects (males). The first row in this matrix corresponded to the ratings of all individuals before any interactions were observed, i.e., it represents the vector of start ratings.

$$M = \begin{pmatrix} \text{elo}_{\text{start,subject[1]}} & \dots & \text{elo}_{\text{start,subject[s]}} \\ \text{elo}_{1,\text{subject[1]}} & \dots & \text{elo}_{1,\text{subject[s]}} \\ \dots & \dots & \dots \\ \text{elo}_{j,\text{subject[1]}} & \dots & \text{elo}_{j,\text{subject[s]}} \end{pmatrix} \tag{1}$$

The remaining rows of M were filled iteratively, going through each interaction in turn. We also declared a vector p_{win}, in which we stored the winning probabilities for each interaction.

$$p_{\text{win}} = \begin{pmatrix} p_{\text{win},1} & \dots & p_{\text{win},j} \end{pmatrix} \tag{2}$$

In the first step of the iterative Elo-rating algorithm, ratings were centered among those individuals who were present in the group at the date of the observed interaction j.

Second, we calculated the expected winning probability $p_{\text{win},j}$ of the subject that won the interaction. This step required only the ratings of the winning and the losing subjects *prior* to the interaction ($\text{M}_{j-1,\text{subject[winner[}j\text{]]}}$ and $\text{M}_{j-1,\text{subject[loser[}j\text{]]}}$). In the case of the first interaction in the sequence, these ratings were the start ratings.

$$p_{\text{win},j} = \frac{1}{1 + exp(\text{M}_{j-1,\text{loser[}j\text{]}} - \text{M}_{j-1,\text{winner[}j\text{]}})} \tag{3}$$

With the obtained winning probability, we updated the ratings of the winning and losing individuals in M_j, and keep the ratings of individuals that were not involved in interaction j, like so:

$$M_{j,s} = \begin{cases} M_{j-1,s} + (1 - p_{\text{win},j}) * k & \text{if } s \text{ won the interaction} \\ M_{j-1,s} - (1 - p_{\text{win},j}) * k & \text{if } s \text{ lost the interaction} \\ M_{j-1,s} & \text{otherwise} \end{cases} \tag{4}$$

We then repeated the steps in equations 3 and 4 over all observed interactions, and filled M in this way. Most importantly, we obtained the vector p_{win} (with the expected winning probabilities), which we then used as the probability vector to model the actual observed outcomes as Bernoulli trials (see Goffe et al. (2018)). Up to this point the algorithm is deterministic (for a given combination of start ratings and k).

To estimate the two required quantities (start ratings and k), we then fitted the following model using p_{win} (which in turn depended on the start ratings and k (equations 3 and 4)). The response in this model was simply a vector of length j, filled with 1s. This vector encoded that the winner of an interaction did indeed win the interaction (Goffe et al., 2018). We set priors for the start ratings and k following Goffe et al. (2018).

$$\text{win}_j \sim \text{Bernoulli}(p_{\text{win},j}) \qquad j = \text{interactions } 1...714 \tag{5}$$

$$\text{elo}_{start} \sim \text{Normal}(0, 1) \tag{6}$$

$$k \sim \text{Exponential}(2) \tag{7}$$

Once we estimated the vector of start ratings and k, we obtained the rating of subject s at a given date. This rating represented the predictor value in the subsequent count model. To arrive at such a rating, we ran the deterministic Elo-rating algorithm to obtain M, using the estimated start ratings and k. Since we were interested in ratings at the end of calendar years, we looked up the last row in M where the corresponding interaction date belonged to the year of interest. Note that these ratings were not point estimates, but full posterior distributions (see figure 2). In other words, each rating we used in the count model was a posterior distribution, which incorporated uncertainty in the estimation of a subject's rating at a given time.

In the description of the actual count model, we refer to this step of obtaining the rating for a given observation via the function $F()$.

Note that we treated the five groups/parties separately, i.e., we estimated five k values and five start rating vectors. For simplicity, we illustrated our model design up to this point with one group only.

Count model

$$y_i \sim \text{Poisson}(\lambda_i) \qquad i = \text{observations } 1...190 \tag{8}$$

We used a Poisson likelihood and log-link function, and as predictors we used a male's Elo-rating, age and the interaction between Elo-rating and age.

$$log(\lambda_i) = \mathcal{A}_i + \mathcal{B}_i * \text{elo}_i + \mathcal{C}_i * \text{age}_i + \mathcal{D}_i * \text{elo}_i * \text{age}_i + \epsilon_i \tag{9}$$

As described above, we estimated start ratings and k to arrive at male ratings that corresponded to a given observation.

$$\text{elo}_i = F(\text{elo}_{start}, k, \text{interactions}, \text{year}[i], \text{subject}[i]) \tag{10}$$

To account for overdispersion, we used an observation-level varying intercept (ϵ) (Gelman et al., 2014).

$$\epsilon \sim \text{Normal}(0, \sigma_e) \tag{11}$$

$$\sigma_e \sim \text{Exponential}(5) \tag{12}$$

We fitted varying intercepts and correlated varying slopes for all terms. Specifically, we incorporated varying effects for Elo-rating and age in all grouping variables (subject, group/party, year). For the interaction between age and Elo-rating, we incorporated varying slopes only on the level of group/party and year, but not for males because less than half of the males who were present in the data (20 out of 48) changed age category over the course of the study and only 4 males had at least two data points in each age category.

$$\mathcal{A}_i = \alpha + \alpha_{\text{subject}[i]} + \alpha_{\text{group}[i]} + \alpha_{\text{year}[i]} \qquad \text{intercept} \tag{13}$$
$$\mathcal{B}_i = \beta + \beta_{\text{subject}[i]} + \beta_{\text{group}[i]} + \beta_{\text{year}[i]} \qquad \text{slope for Elo-rating} \tag{14}$$
$$\mathcal{C}_i = \gamma + \gamma_{\text{subject}[i]} + \gamma_{\text{group}[i]} + \gamma_{\text{year}[i]} \qquad \text{slope for age} \tag{15}$$
$$\mathcal{D}_i = \delta + \delta_{\text{group}[i]} + \delta_{\text{year}[i]} \qquad \text{slope for interaction} \tag{16}$$

$$\begin{bmatrix} \alpha_{\text{subject}} \\ \beta_{\text{subject}} \\ \gamma_{\text{subject}} \end{bmatrix} \sim \text{MVNormal}\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, S_{\text{s}} \right) \qquad \text{subject} = 1...48 \tag{17}$$
$$S_{\text{s}} = \begin{pmatrix} \sigma_{sa} & 0 & 0 \\ 0 & \sigma_{sb} & 0 \\ 0 & 0 & \sigma_{sc} \end{pmatrix} R_s \begin{pmatrix} \sigma_{sa} & 0 & 0 \\ 0 & \sigma_{sb} & 0 \\ 0 & 0 & \sigma_{sc} \end{pmatrix} \tag{18}$$
$$\begin{bmatrix} \alpha_{\text{group}} \\ \beta_{\text{group}} \\ \gamma_{\text{group}} \\ \delta_{\text{group}} \end{bmatrix} \sim \text{MVNormal}\left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, S_{\text{g}} \right) \qquad \text{group} = 1...5 \tag{19}$$
$$S_{\text{g}} = \begin{pmatrix} \sigma_{ga} & 0 & 0 & 0 \\ 0 & \sigma_{gb} & 0 & 0 \\ 0 & 0 & \sigma_{gc} & 0 \\ 0 & 0 & 0 & \sigma_{gd} \end{pmatrix} R_g \begin{pmatrix} \sigma_{ga} & 0 & 0 & 0 \\ 0 & \sigma_{gb} & 0 & 0 \\ 0 & 0 & \sigma_{gc} & 0 \\ 0 & 0 & 0 & \sigma_{gd} \end{pmatrix} \tag{20}$$
$$\begin{bmatrix} \alpha_{\text{year}} \\ \beta_{\text{year}} \\ \gamma_{\text{year}} \\ \delta_{\text{year}} \end{bmatrix} \sim \text{MVNormal}\left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, S_{\text{y}} \right) \qquad \text{year} = 1...9 \tag{21}$$
$$S_{\text{y}} = \begin{pmatrix} \sigma_{ya} & 0 & 0 & 0 \\ 0 & \sigma_{yb} & 0 & 0 \\ 0 & 0 & \sigma_{yc} & 0 \\ 0 & 0 & 0 & \sigma_{yd} \end{pmatrix} R_y \begin{pmatrix} \sigma_{ya} & 0 & 0 & 0 \\ 0 & \sigma_{yb} & 0 & 0 \\ 0 & 0 & \sigma_{yc} & 0 \\ 0 & 0 & 0 & \sigma_{yd} \end{pmatrix} \tag{22}$$

For all parameters, we used fairly vague priors (see figure A3):

$$R_s \sim \text{LKJ}(2) \tag{23}$$
$$\sigma_{sa}, \sigma_{sb}, \sigma_{sc} \sim \text{Exponential}(5) \tag{24}$$
$$R_g \sim \text{LKJ}(2) \tag{25}$$
$$\sigma_{ga}, \sigma_{gb}, \sigma_{gc}, \sigma_{gd} \sim \text{Exponential}(5) \tag{26}$$
$$R_y \sim \text{LKJ}(2) \tag{27}$$
$$\sigma_{ya}, \sigma_{yb}, \sigma_{yc}, \sigma_{yd} \sim \text{Exponential}(5) \tag{28}$$
$$\alpha, \beta, \gamma, \delta \sim \text{Normal}(0, 1) \tag{29}$$

For eight males (representing eleven male-years) that were included in the count model, we had no observed dominance interactions. Those males entered the data set for the count model with ratings based simply on the specified prior for the start ratings (equation 6).

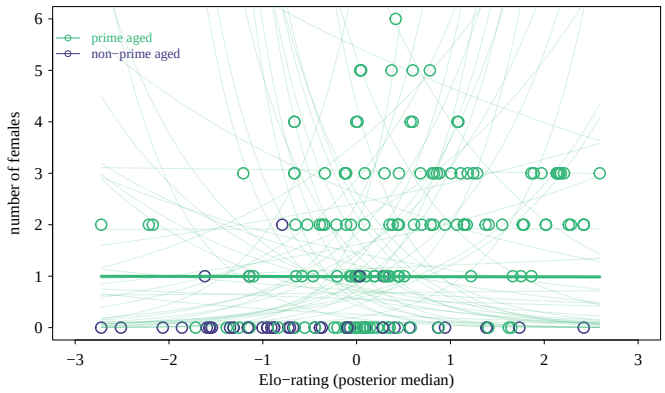

Figure A3: Prior predictive simulation. This plot illustrates the potential range of model estimates for the primary parameter of interest (Elo), given our priors. The lines show 100 individual predictions. On average the priors encode a flat relationship between Elo-rating and number of females (thick line). However, the priors allow negative as well as positive relationships. Note also that our priors lead to a substantial proportion of predictions that are unrealistic, i.e., predicting 10s or 100s of females and therefore could be set tighter (more informative) in future iterations of the model. Note also that for this simulation the parameters related to Elo-rating (k and start rating vectors) were estimated from the data.

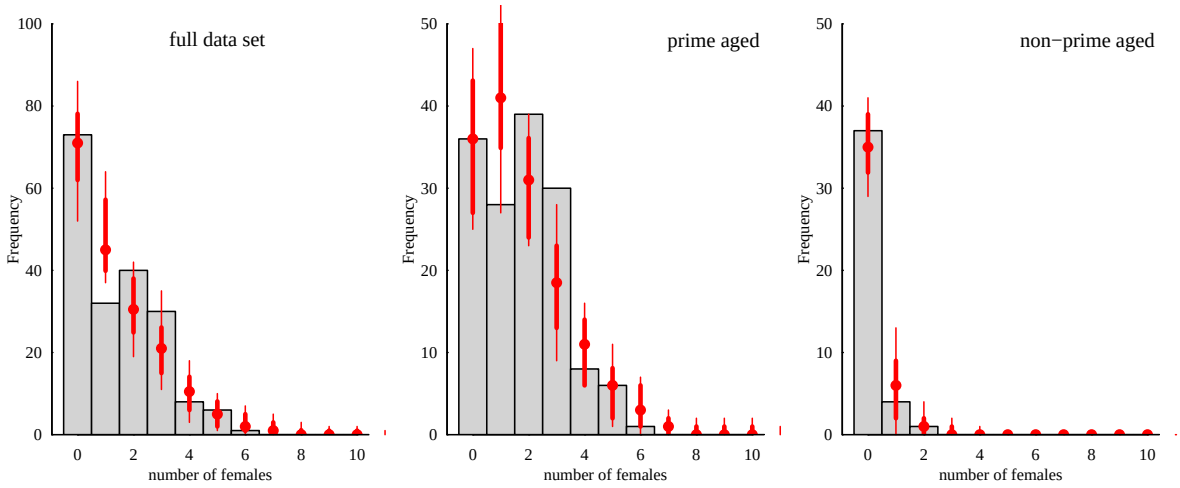

Figure A4: Posterior predictive checks. The histogram shows the observed distribution of number of females. The circles represent the median of 50 randomly selected random draws. The thick lines represent 80% quantiles and the thin lines represent the range across the 50 draws. The figure shows that our model overestimates the occurrences of males having one female compared to what we observed, and underestimates the occurrences of males having 3 females. The two remaining plots show the same approach, but separated by the two age categories.

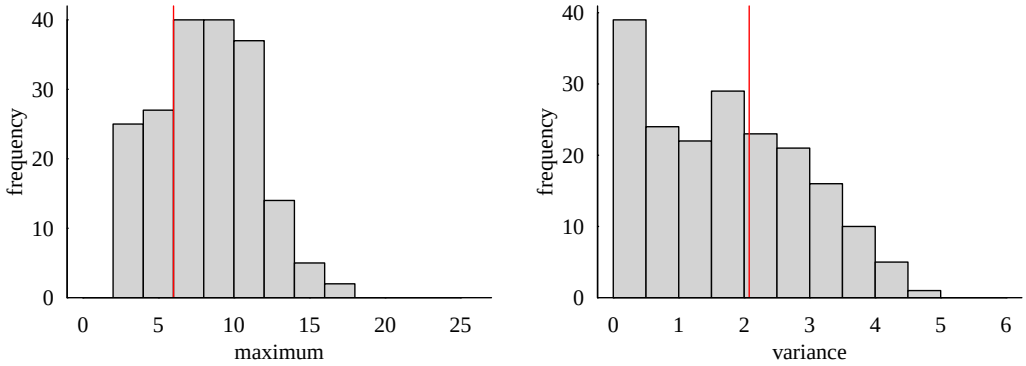

Figure A5: Additional posterior predictive checks. The histograms show the posterior distributions of two summary statistics applied to all posterior samples: maximum value of females and variance in the number of females. The red vertical lines show the corresponding values from the observed data. This plot shows that our model performs well with respect to predicting these two aspects of our observed data.

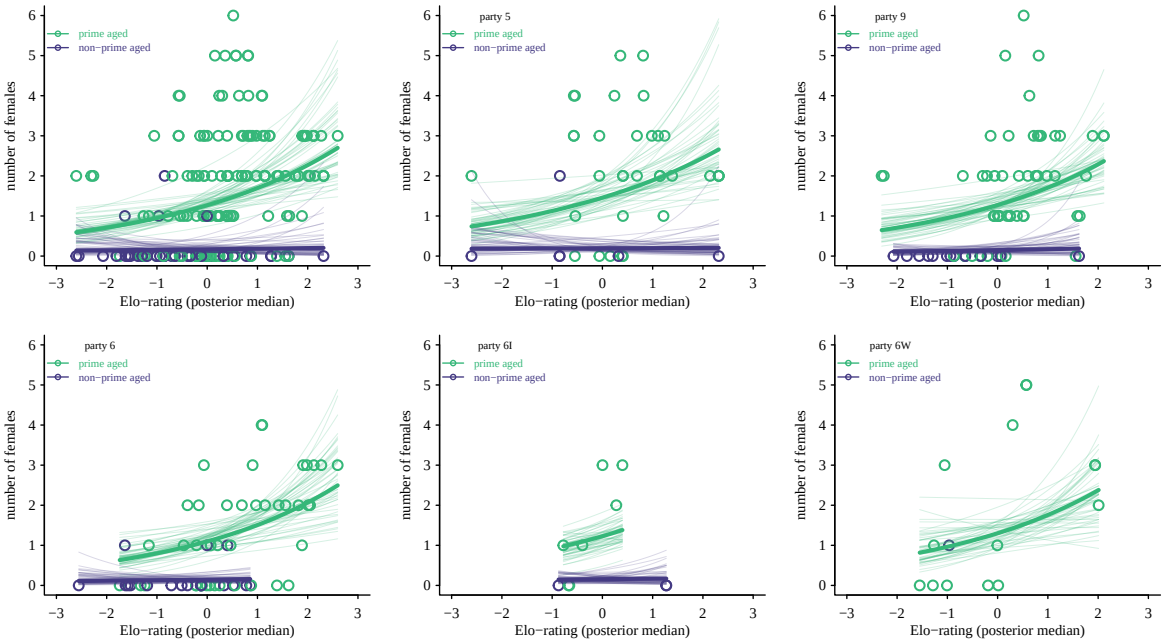

Figure A6: Same as figure 3, but split by party. There was suprisingly little variation across the parties in the estimated relationship between Elo-rating and number of females.

Table A5: Extended results for the reproductive success model.

	mean	median	5.5%	94.5%	$\hat{R}$	ESS_{bulk}	ESS_{tail}
intercept (α)	0.24	0.24	-0.03	0.49	1.00	2068	1934
Elo-rating (β)	0.29	0.29	0.10	0.49	1.00	2335	2365
age (γ)	-2.01	-2.01	-2.72	-1.34	1.00	4352	2928
interaction Elo-rating : age (δ)	-0.21	-0.20	-0.81	0.40	1.00	3125	2676
varying intercepts (SD)							
male ID, σ_{sa}	0.45	0.45	0.29	0.64	1.00	1252	1232
group/party, σ_{ga}	0.18	0.15	0.01	0.43	1.00	1469	2168
year, σ_{ya}	0.07	0.06	0.01	0.19	1.00	2401	1815
varying slopes (Elo-rating) (SD)							
male ID, σ_{sb}	0.10	0.08	0.01	0.26	1.00	1439	1694
group/party, σ_{gb}	0.09	0.07	0.01	0.25	1.00	2283	2088
year, σ_{yb}	0.07	0.05	0.00	0.17	1.00	2253	2122
varying slopes (age) (SD)							
male ID, σ_{sc}	0.21	0.15	0.01	0.62	1.00	2778	1937
group/party, σ_{gc}	0.21	0.14	0.01	0.61	1.00	3200	2205
year, σ_{yc}	0.20	0.14	0.01	0.57	1.00	3627	2340
varying slopes (interaction) (SD)							
group/party, σ_{gd}	0.17	0.12	0.01	0.48	1.00	3119	2089
year, σ_{yd}	0.19	0.14	0.01	0.57	1.00	3360	2323

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