Socioecological drivers of injuries in female and male rhesus macaques (*Macaca mulatta*)

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Abstract

Competition over access to resources, such as food and mates, is believed to be one of the major costs associated with group living. Two socioecological factors suggested to predict the intensity of competition are group size and the relative abundance of sexually active individuals. However, empirical evidence linking these factors to costs of competition, such as injury risk, is scarce. Here, we leveraged 10 years of data from free-ranging rhesus macaques where injuries are associated with a high mortality risk. We tested if intra-specific variation in group size and adult sex ratio predicted injury risk and physical aggression. We found that males were less likely to be injured when living in larger groups potentially due to advantages in intergroup encounters. Females, instead, had higher injury risk when living in larger groups but this was not explained by within-group competition among females. Further, male-biased sex ratios were positively related to male-female aggression, indicating that male coercion during mating competition may be a cause of injuries in females. Overall, our results provide insights into sex differences in the fitness-related costs of competition and empirical evidence for long-standing predictions on the evolution of group living.

Introduction

Competition over access to resources is believed to be an important selective pressure for the evolution of group living. By forming groups, animals can gain advantages such as higher success at locating food, more and easily accessible mating opportunities, decreased predation risk and cooperative defence of resources (Jarvis et al., 1998; Ratcliffe and Ter Hofstede, 2005; Silk, 2007; Van Schaik and Van Hooff, 1983). However, life in groups can also be associated with major health costs for individuals as a result of competition with conspecifics when valuable resources- such as food and mates- are limited(Terborgh and Janson, 1986; Van Schaik and Van Hooff, 1983; Janson and Goldsmith, 1995). Intense competition in the form of escalated aggression can be costly for individuals because their risk of injury increases (Vogel et al., 2007; Feder et al., 2019; Archie et al., 2014). Injuries may indirectly impact reproductive success as animals may need to divert energetic resources they could otherwise invest in reproduction to healing (Archie et al., 2014), and can directly impact survival in the case of fatal aggression (Pavez-Fox et al., 2022; Chilvers et al., 2005). Given the fitness costs associated with competition, animals are expected to refrain from engaging in escalated aggression unless necessary when resources are limited or very valuable (Hammerstein, 1981). Group size and the operational sex ratio are two aspects of group living that have been hypothesized to drive the intensity and costs of competition within and between groups.

Group size might determine the intensity of competition over food and territories. The number of individuals that a group can sustain is constrained by the abundance of food as more individuals translate into faster depletion of food resources (Wrangham et al., 1993; Chapman and Chapman, 2000). As a result, animals in larger groups usually suffer from higher levels of within-group competition over food access compared to individuals in smaller groups (Heesen et al., 2014; Balasubramaniam et al., 2014; Gillespie and Chapman, 2001; Blumstein et al., 1999; Marino, 2010). However, when feeding areas can be monopolised and are extensive enough to sustain entire groups, larger groups have a numerical advantage, which can be beneficial for the collective defence of such resources (Cheney and Seyfarth, 1987; McComb et al., 1994). For instance, studies in several species have shown that larger groups are more likely to win intergroup encounters over territories or feeding areas than smaller groups (Majolo et al., 2020; Balasubramaniam et al., 2014; Willems et al., 2013; McComb et al., 1994; Thompson et al., 2017). Differences in life history between the sexes mean that group size might affect the intensity of competition differently for males versus females. For mammalian females, the high energetic costs of gestation and lactation are key constraints, so females usually compete over access to food to sustain reproduction. Males, conversely, derive fitness benefits from siring opportunities and therefore mostly compete over access to fertile females (Trivers, 1972). Increased within-group feeding competition has, therefore, been suggested to impact females more than males (Sterck et al., 1997; Koenig, 2002). Males, on the other hand, tend to be more involved in between-group competition (Smith et al., 2022), whereby resident males collectively defend females- or the resources females feed upon against immigration attempts and during intergroup encounters (Cowlishaw, 1995; Majolo et al., 2020; Scarry, 2013). Therefore, how group size affects the chances of engaging in escalated aggression is likely to be sex-dependent.

Another factor suggested to drive competition is the relative availability of sexually active males and females in a group (the operational sex-ratio). When the operational sex ratio is skewed, theory predicts there will be higher competition amongst the more abundant sex over access to the less abundant sex (Kvarnemo and Ahnesjö, 1996; Clutton-Brock and Parker, 1992; Emlen and Oring, 1977). Empirical work on some mammals has provided evidence for a relationship between the operational sex ratio and competition over mates. For instance, in reindeer (*Rangifer tarandus*), female-female competition for males was higher in a group with a female-skewed operational sex ratio than in a group where the sex ratio was balanced (Driscoll et al., 2022). Similarly, in vervet monkeys (*Chlorocebus pygerythrus*), male-male fights were more frequent in groups with male-skewed operational sex ratios (Hemelrijk et al., 2020). However, when the operational sex ratio is too skewed and the costs associated with escalated aggression are too high, a reduction in intra-sexual competition in the abundant sex might be favoured and other strategies could arise (Weir et al., 2011; Rankin et al., 2011). Given that in mammals, females' damaging potential is usually lower than males - particularly in species with sexual dimorphism (*i.e.*, larger body/canine size in males) - one strategy often adopted by males that might reduce costs associated with retaliation is redirecting the aggression towards females (Clutton-Brock and Parker, 1995; Reale et al., 1996; Smit et al., 2022; Davidian et al., 2022). As a consequence, the operational sex ratio might not only determine intra-sexual but also inter-sexual escalated aggression.

While the drivers of competition in group-living animals have been well established (Van Schaik and Van Hooff, 1983; Wrangham et al., 1993; Chapman and Chapman, 2000; Koenig, 2002), there is still scarce empirical evidence for how these factors influence the occurrence of escalated aggression, with consequences for injuries and fitness. Quantifying the consequences of competition and its fitness outcomes has proven difficult in most wild systems where injuries or body damage can be caused by predators and not be the direct result of within- or inter-group competition. Obtaining behavioural information from large wild groups and estimating the operational sex ratio when there are roaming or dispersing males can also be challenging (Kappeler, 2017). Further, given the differences in life history between the sexes, often the costs and drivers of competition are considered separately for males and females, even though there is mounting evidence that mating competition can also result in sexual conflict (Davidian et al., 2022; Smit et al., 2022; Baniel et al., 2017).

Here, we explore the costs of competition by examining the socioecological drivers of injuries in free-ranging female and male rhesus macaques living in the Cayo Santiago island, Puerto Rico. Rhesus macaques live in multi-female multi-male societies where females are philopatric and males disperse at sexual maturation (Thierry et al., 2004). Females form strict despotic dominance hierarchies where rank is maternally inherited (Chikazawa et al., 1979). Males, instead, acquire rank via a queuing system where group tenure determines their social status (Manson, 1995; Kimock et al., 2022). Rhesus macaques have a polygynandrous mating system with high synchrony in females' fertile phases, reducing the monopolisation potential of males (Dubuc et al., 2011). As a consequence, male rhesus often rely more on indirect forms of competition, such as sperm competition, endurance rivalry, sneaky copulations and female coercion (Higham and Maestripieri, 2014; Manson, 1994), rather than direct male-male conflict (Kimock et al., 2022). There are no predators on the island, therefore, injuries are known to be caused by conspecifics. Injuries have been shown to decrease the survival probability in this population for both sexes by 3-fold (Pavez-Fox et al., 2022), providing the opportunity to test the fitness-related costs of competition. Demographic information with monthly updates on male dispersals, allows us to have accurate information on group membership and a good estimate for a group sex-ratio. Social groups are naturally formed and can vary in size from 26 to nearly 300 adults. Long-term behavioural observations have been collected in several of these groups allowing us to pair the injury data with the occurrence of aggressive events to explore sex differences in the identity of the victims/aggressors. Although the population is food provisioned, competition over monopolizable food and water stations frequently occurs, where high-ranking macaques spend on average more time feeding and drinking than low-ranking animals (Balasubramaniam et al., 2014).

To determine the cost of competition in this population, we used long-term demographic and injury records paired with behavioural data on aggression. We tested for sex-specific effects of group size and adult sex ratio (sex ratio henceforth), a proxy of operational sex ratio, on injury risk and the occurrence of physical aggression. For group size, we predicted sex differences in the risk of injuries with females experiencing higher injury risk and males having lower injury risk in larger groups compared to smaller groups. We expected that females would experience higher injury risk in larger groups as a result of higher within-group female-female (FF) competition (Wrangham et al., 1993; Chapman and Chapman, 2000), thus we further tested if FF aggression was higher in larger groups. For males, we expected that those living in larger groups would have reduced injury risk because having a numerical advantage translates into better chances of winning inter-group encounters (Koenig et al., 2013; Janson and Goldsmith, 1995). Given that our behavioural data only included within-group interactions, we could not test the mechanism we expected to be driving injury risk in males, but we could rule out within-group male-male (MM) feeding competition as a driver of injuries by testing if MM aggression was influenced by group size. For sex ratio, we predicted that the local availability of mating partners would not determine injury risk in males but when females are more scarce (male-biased sex ratio), females would have higher injury risk. We expected that males would not engage in direct MM competition over females as male rhesus often rely on indirect forms of competition

Table 1: Predictions for the socioecological drivers of injuries in rhesus macaques.

Sex	**Group size**	**Sex ratio**
Females	↑ injury risk in larger groups	↑ injury risk when male-biased
	↑ FF aggression in larger groups	↑ MF aggression when male-biased, No effect on FF aggression
Males	↓ injury risk in larger groups	No effect on injury risk
	No effect on MM aggression within groups	No effect on MM aggression within groups

sex ratio: number of adult females per male during the mating season, aggression: physical aggression, ‘FF’: female-female, ‘MM’: male-male, ‘MF’: male-female.

(Higham and Maestripieri, 2014; Kimock et al., 2022), thus we rule out this possibility by testing if MM aggression was influenced by sex ratio. Given that the incentive to compete aggressively over reproductive access to males is typically low in female mammals (**?**), particularly in philopatric societies like rhesus macaques where competition is mostly against kin, we expected that female rhesus would not compete aggressively over reproductive access to males. We rule out this by testing whether FF aggression was influenced by sex ratio. Finally, rhesus macaques are sexually dimorphic and male coercion has been reported (Manson, 1994), therefore we expect that male-female (MF) aggression would be higher in groups with a male-biased sex ratio. All predictions are laid out in Table 1.

Methods

Study subjects

Our study subjects were free-ranging male and female rhesus macaques living on Cayo Santiago island, Puerto Rico. The island is home to a population of $\sim$ 1800 individuals living in 6 to 12 mixed-sex naturally formed social groups. The field station is managed by the Caribbean Primate Research Center (CPRC), which monitors the population daily and maintains the long-term (>75 years) demographic database including data on births, deaths and social group membership for all animals (Kessler and Rawlins, 2016). Macaques are individually identified based on tattoos located on their chest and legs. Animals have *ad-libitum* access to food and water, the island is predator-free and there is no regular medical intervention for sick or wounded individuals. Here we included data on sexually mature male and female macaques (age range: 4 - 28 years) that were alive between 2010 and 2020. We restricted our sample to animals belonging to social groups for which we had data on injury occurrence and agonistic behavioural observations (n = 6 social groups). The groups analysed varied in size from 26 to 288 animals and sex ratios (n females/ n males) ranged from 0.5 to 4.5 (Fig. S1).

Observation of Injuries

Since 2010, the CPRC staff have been collecting opportunistic observations on the incidence and recovery from injuries during the daily monitoring of social groups for demographic purposes. Data collection is carried out mainly by the veterinary technician complemented by information from other experienced staff. If an individual was observed to be wounded or displaying signs of injury (*e.g.,* limping) the staff member recorded the individual ID and if the injury was visible, the type of injury (*e.g.*, puncture, scratch), the area of the body affected, whether the injury was recent or old based on the presence of scars, and if possible, an estimate of the wound size. Records for each individual were updated every time the observers encountered the wounded individuals during the daily census. Here we included all records for visible injuries, including bites, scratches, abrasions and cuts along with other more severe injuries such as exposed organs and fractures. We excluded injury records from two full years (2015 and 2016), a period for which the veterinary technician was not regularly at the field site, which may have led to biases in the few groups sampled during those years. Our sample consisted of 908 injuries collected from September 2010 to April 2020 on 521 unique individuals (n females = 267, n males = 254).

Collection of aggression data

We collected behavioural data using focal samples based on a previously established ethogram (Brent et al., 2014). During focal sampling, dyadic agonistic encounters where the focal animal was involved were recorded, along with the identity of the aggressor and victim. We recorded all agonistic interactions, including submissions, threats, non-contact aggression (*e.g.,* charge, chase), and contact (physical) aggression (*e.g.,* bite, hit). Given that the purpose of our study was to match aggression data with the occurrence of injury, we only considered data on physical aggression, which is more likely to lead to an injury. Behavioural data was collected from twenty different group years (group F 2010-2017, group HH 2014 and 2016, group KK 2015 and 2017, group R 2015 and 2016, group S 2011 and 2019, group V 2015-2019), from which seventeen were sampled using 10-min focal sample and three using 5-min focal sample. Across the 10 years of study, two external events in 2018 and 2020 - Hurricane Maria and the COVID-19 pandemic, respectively - precluded the collection of focal data, therefore these years were excluded from the aggression analyses. From January 2010 to October 2019, we recorded 18880 aggression events including 522 physical aggression events (n unique individuals = 748).

Quantifying injury risk and aggression rates

Our injury dataset included the 521 animals that were recorded injured in addition to 1001 uninjured animals (n uninjured females = 525, n uninjured males = 476). Uninjured individuals consisted of all sexually mature individuals that were alive during the period of study, *i.e.,* between 2010 and 2020 excluding 2015 and 2016 to match data on injured animals. Given that the average time elapsed between consecutive records of injury or recovery in the same individual was 41.17 days, the dataset was formatted in a way that each row represented a two-month interval period (*i.e.,* bimonthly interval), therefore injury records occurring in different rows are likely to be independent. An individual's injury status during each interval period they were alive during the study was coded as a binary variable where 1 = injured and 0 = uninjured.

Our aggression dataset included the 748 male and female macaques for which focal data were collected. Given that our questions were sex-specific, we split this dataset by sex resulting in 438 physical aggression events in a total of 422 females and 84 physical aggression events in a total of 326 males. We focused specifically on contact (physical) aggression received by the focal animal. Each row represented a bimonthly interval to match the format of the injury data. Given that an individual rarely received physical aggression more than once in a given bimonthly interval (Fig. S2), we coded an individual's aggression status as binary, where 1 = physically aggressed and 0 = non-physically aggressed. Depending on the question, we split this dataset based on the sex of the victim and of the aggressor.

Statistical analyses

Group size and sex as drivers of injuries

Effect of group size on injury risk. To test whether group size predicted the probability of an individual being injured we built a model where the dependent variable was an individual's injury status (1/0) and the independent variables included group size, the individual's sex and the reproductive season (1 = mating, 0 = non-mating) in a given bimonthly interval. We also included random intercepts for individual ID to account for repeated measures and the specific bimonthly interval within the study period. Because our predictions were sex-specific, we included an interaction term between group size and sex. Group size was computed as all the individuals aged 4 years and more that were alive in a subject's group in a given bimonthly interval. We determined the reproductive season following (Hoffman et al., 2008). Briefly, we first determined the birth season by computing the mean birth date ± 2 SD for each year, where the start of the birth season was defined as the first birth date and the end, as the last birth date. The mating season was determined by subtracting the gestation period of rhesus macaques (165 days) from the start and the end of the birth season. All the bimonthly intervals falling outside the mating season were considered part of the non-mating period.

Effect of group size on female-female aggression. To confirm that FF feeding competition was a driver of injuries in females living in larger groups we focused only on aggression between females. Group size was strongly correlated with the number of females in the group (Fig. S3A, Pearson's $R = 0.94$, $p < 0.01$). We tested if the number of females in a group, which might better reflect FF competition, predicted the probability of a female receiving physical aggression from another female. The dependent variable was female aggression status and as independent variables, we included the number of females in the group, the reproductive season and an offset term for sampling effort (*i.e.*, hours an individual was subject to focal observations). Random effects for a female's ID and the bimonthly interval were included.

Effect of group size on male-male aggression. To confirm that within-group MM feeding competition was not a driver of injuries in males we focused on male physical aggression data. We tested if the number of males in a group, which was positively correlated to group size (Fig. S3B, Pearson's $R = 0.97$, $p < 0.01$), predicted a male's risk of physical aggression from other males in his group. The dependent variable was a male's aggression status and the independent variables were the number of males in a group, the reproductive season and an offset term for sampling effort. To further investigate if having more males in a group may be advantageous for reducing the chances of injury in intergroup encounters, we tested if the number of males in a group, which was positively correlated to group size predicted reduced risk of injury. The dependent variable was a male's injury status and the independent variables were the number of males in the group and the reproductive season. For both models, we included a male's ID and the bimonthly interval as random effects.

Sex ratio and sex as drivers of injuries

Effect of sex ratio on injury risk. To test whether the sex ratio predicted the probability of an individual being injured we built a model where the dependent variable was an individual's injury status (0/1) and included as independent variables the sex ratio and sex. Given that our predictions were sex-specific, we included an interaction term between the sex ratio and sex. As random effects, we included the individual ID and the bimonthly interval. We computed the sex ratio as the number of females (4 years and above) per male in the subject's group on a given bimonthly interval, therefore smaller sex ratios would indicate male biases while larger sex ratios would indicate female biases. For these analyses, we focused only on the mating season, to have a better estimate of sexually active individuals and to make sure that the socioecological driver was competition for mates.

Effect of sex ratio on male-female aggression. To test if MF coercion was a driver of injuries in females we focused on aggression data where the victims were females and the aggressors were males. As a dependent variable, we included a female's aggression status and as independent variables, the sex ratio and an offset term for sampling effort. As above, we only focused on the mating season for this analysis to make sure that mating competition was the driver of aggression. Random effects for animal ID and bimonthly intervals were also included.

Effect of sex ratio on female-female aggression. To rule out FF mating competition as a driver of injuries in females we focused on data where the aggressor and the victims were females. As above, we restricted this analysis to the mating season. The dependent variable was a female's aggression status and independent variables included sex ratio and an offset term for sampling effort with random effects for animal ID and bimonthly interval.

Effect of sex ratio on male-male aggression. To rule out that MM mating competition was a driver of injuries we focused on male aggression data during the mating season. The dependent variable was a male's aggression status and predictors included the adult sex ratio and an offset term for sampling effort. As random effects, we included a male's ID and the bimonthly interval. To rule out the possibility that young and old females might not be attractive partners for males to compete over (as we consider all females over 4 years of age), we also tested the effect of the adult sex ratio considering only the number of prime-age females (6-17 years; (Lee et al., 2021)) per male in the group.

Bayesian model's specifications

We ran all the models in a Bayesian framework using the brms R Package (Bürkner, 2021), therefore evidence of an effect was determined based on the degree of overlap between the credible interval (CI) and zero (*i.e.*, 89% non-overlapping reflecting strong evidence of an effect). Given that all the dependent variables were coded as binary, models were fit using a Bernoulli distribution. All continuous predictors were z-scored. We assumed normal distributions for priors (mean = 0, SD = 1) and ran 10000 iterations in all the models. Model assumptions and posterior predictive checks were done using the 'ppcheck' in-built function from the brms package. Marginal effects were calculated using the emmeans R package (Lenth et al., 2018). We reported means as point estimates, standard error (SE) and 89% credible intervals of the posterior distribution. For marginal effects, we reported the median and the 89% highest posterior density interval (HPD).

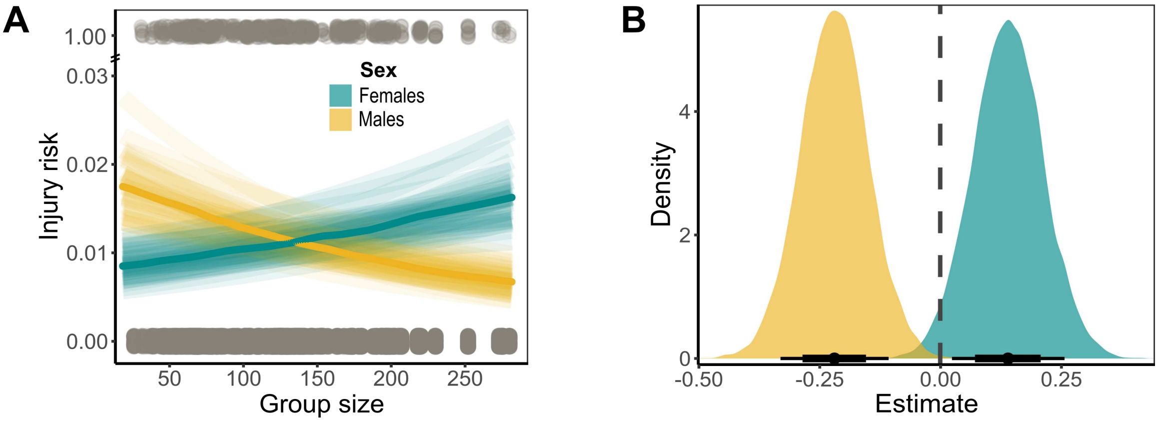

Figure 1: **Sex-dependent effect of group size on injury risk**. **A)** Predicted values of injury risk for females (cyan) and males (yellow) as a function of group size. The darker line indicates the median and the lighter lines show the 89% CI. Raw data are depicted with grey points (top: injured, bottom: uninjured). **B)** Posterior distributions for marginal effects of group size on male and female injury risk. Whiskers indicate the median, 89% CI (thinner line) and 66% CI (thicker line).

Results

Group size and sex as drivers of injuries

Effect of group size on injury risk. In support of our predictions, we found a sex-dependent effect of group size on injury risk (Fig. 1A; Log-Odds group_size*sexM = -0.36, SE = 0.08, 89% CI = -0.49, -0.23; Table S1). Females were 53% more likely to be injured for every one SD ($\sim$ 59 individuals) of increase in group size (marginal effect: Log-Odds females = 0.14, 89% HPD = 0.025, 0.26). In the case of males, an increase in one SD in group size was associated with a reduction of 44% in the probability of being injured (marginal effect: Log-Odds males = -0.22, 89% HPD = -0.33, -0.11) (Fig. 1B).

Effect of group size on female-female aggression. We did not find evidence of FF competition driving injury risk. Contrary to our prediction, females living in groups with more females (*i.e.,* larger groups) were not more likely to be physically aggressed by other females in the group (Fig. 2A top panel; Log-Odds fem_count = -0.09, SE = 0.08, 89% CI = -0.22, 0.03; Table S2).
Effect of group size on male-male aggression. As predicted, we did not find evidence of MM aggression within groups. The number of males in a group did not predict the likelihood of a male being physically aggressed by other resident males (Fig. 2A middle panel; Log-Odds male_count = -0.06, SE = 0.13, 89% CI = -0.27, 0.15, Table S3). We also found that males living in groups with more males (*i.e.,* larger groups) had lower injury risk than males living in smaller groups (Fig. 2A bottom panel, Fig. 2B; Log-Odds male_count = -0.24, SE = 0.08, 89% CI = -0.37, -0.12, Table S4). Similar to our results for group size and injury risk, for every one SD increase in the number of males in a group ($\sim$ 36 males) a male had a 44% reduction in the probability of being injured.

Sex ratio and sex as drivers of injuries

Effect of sex ratio on injury risk. We found a sex-dependent effect of sex ratio on an individual's injury risk (Fig. 3A; Log-Odds sex_ratio*sexM = 0.17, SE = 0.08, 89% CI = 0.04, 0.3; Table S5). Contrary to our predictions, males who lived in groups where females outnumbered males were more likely to be injured. For every increase in one SD of sex ratio ($\sim$ 0.5 increase in females relative to males), males experienced a 53% increase in their likelihood of being injured (marginal effect: Log-Odds males = 0.12, 89% HPD = 0.01, 0.21). Females were more likely to be injured when living in groups with a male-biased sex ratio, but this relationship was weak as the credible interval overlapped with zero (marginal effect: Log-Odds females = -0.05, 89% HPD = -0.16, 0.06) (Fig. 3B).

Effect of sex-ratio on male-male aggression. We did not find evidence for males being more likely to be physically aggressed by resident males when living in groups with a male-biased operational sex ratio (Fig. 4A top panel; Log-Odds sex_ratio = 0.1, SE = 0.17, 89% CI =

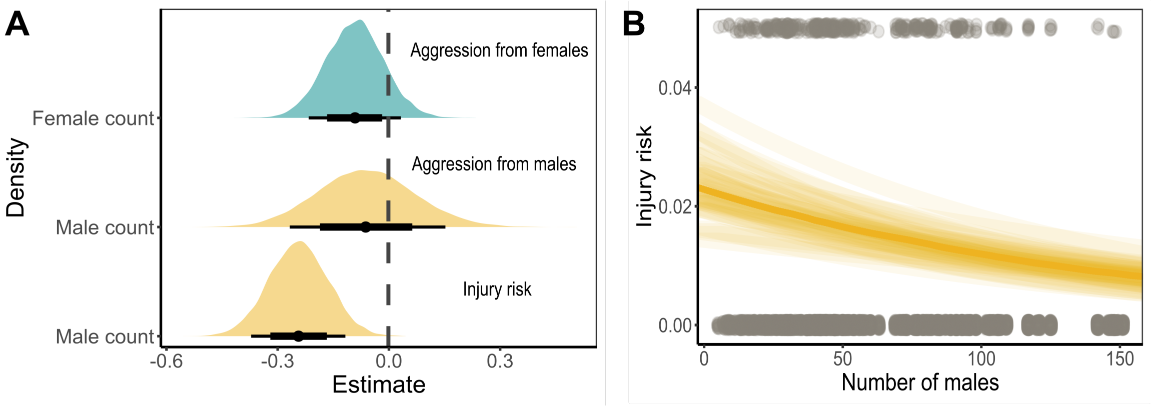

Figure 2: **Sex-specific drivers of injuries with group size**. **A)** Posterior distributions of estimates from models testing the effect of the number of females in a group on FF physical aggression (top panel), the number of males in a group on MM physical aggression (middle panel), and the number of males in a group on injury risk (bottom panel). Whisker indicates the median, 89% CI (thinner line) and 66% CI (thicker line). **B)** Predicted values for injury risk as a function of the number of males in a group. The darker line indicates the median and the lighter lines show the 89% CI. Raw data are depicted with grey points (top: physically aggressed, bottom: non-physically aggressed).

-0.19, 0.37, Table S6). This result holds even when only prime-aged females were considered in the computation of sex ratio (Log-Odds sex_ratio = 0.04, SE = 0.19, 89% CI = -0.27, 0.34, Table S7).

Effect of sex ratio on male-female aggression. Male-to-female aggression was negatively associated with the relative availability of females in a group. For every one SD decrease in sex ratio ($\sim$ 0.5 decrease in the number of females relative to males), females were 40% more likely to be physically aggressed by males (Fig. 4A middle panel, Fig. 4B; Log-Odds sex_ratio = -0.4, SE = 0.13, 89% CI = -0.62, -0.19, Table S8).

Effect of sex ratio on female-female aggression. We found no effect of sex ratio on FF aggression. As predicted, during the mating season females were not more likely to be physically aggressed by other females in groups when the relative availability of males was low (*i.e.,* female-biased sex ratio) (Fig. 4A bottom panel; Log-Odds sex ratio = 0.02, SE = 0.15, 89% CI = -0.22, 0.27, Table S9).

Discussion

In this study, we tested predictions derived from socioecological theory on the sex-specific drivers of competition. As predicted, we found that larger groups may confer a competitive advantage to males but not to females. Males living in larger groups were less likely to be

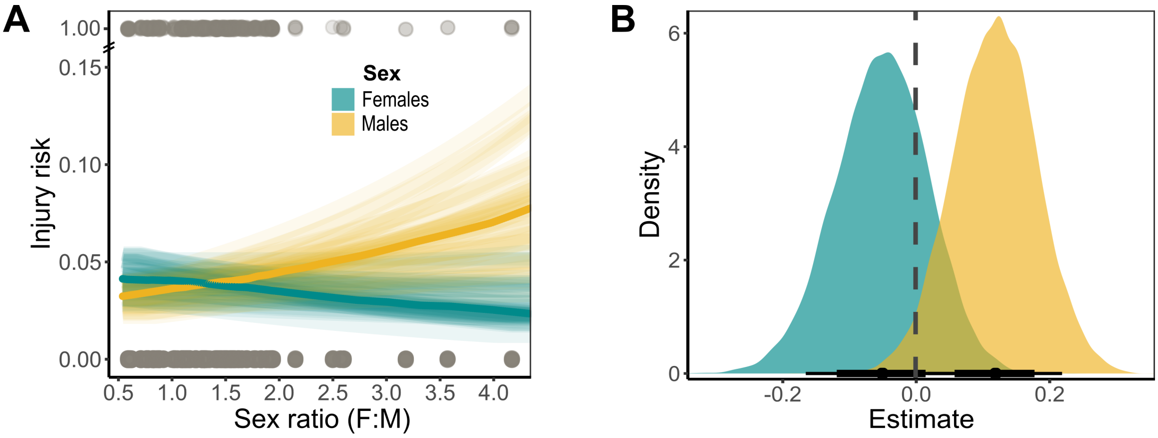

Figure 3: **Sex-dependent effect of adult sex ratio on injury risk**. **A)**Predicted values of injury risk for females (cyan) and males (yellow) as a function of adult sex ratio (*i.e.,* number of females per male during the mating season). The darker line indicates the median and the lighter lines show the 89% CI. Raw data are depicted with grey points (top: injured, bottom: uninjured). **B)** Posterior distributions for the estimates of adult sex ratio on male and female injury risk. Whiskers indicate the median, 89% CI (thinner line) and 66% CI (thicker line).

injured compared to males in smaller groups, whereas females had a higher risk of injury in larger groups. Our results suggest that female-female competition for food was not a driver of female injury in this population but instead pointed to the role of male coercion during mating competition. In males, we found no evidence of injuries being driven by within-group mating or feeding competition, suggesting that injuries were likely caused during inter-group encounters. Taken together our results provide empirical evidence for fundamental factors driving social organisation.

How does group size impact injury risk?

As predicted by socioecological models and life–history traits (Koenig, 2002; Scarry, 2013; Trivers, 1972), we found clear sex differences in how group size predicts injury risk. We discuss these results and the possible socioecological drivers in a sex-specific manner below.

Females living in larger groups had a higher risk of injury than females in smaller groups. However, contrary to our prediction, we found no evidence that this was driven by within-group female feeding competition, as females in larger groups did not receive more aggression from other female group members. Larger groups are believed to impose major energetic constraints, particularly for females, which require high food intake to fulfil the costs of pregnancy and lactation (Markham and Gesquiere, 2017; Trivers, 1972). As a consequence, females are expected to compete more intensely for food when living in larger groups (Sterck et al., 1997; Koenig, 2002). Yet, our results suggest that this might not be the case in female rhesus macaques at the Cayo Santiago field station. This could be because animals in this population are food-provisioned, thus feeding resources might

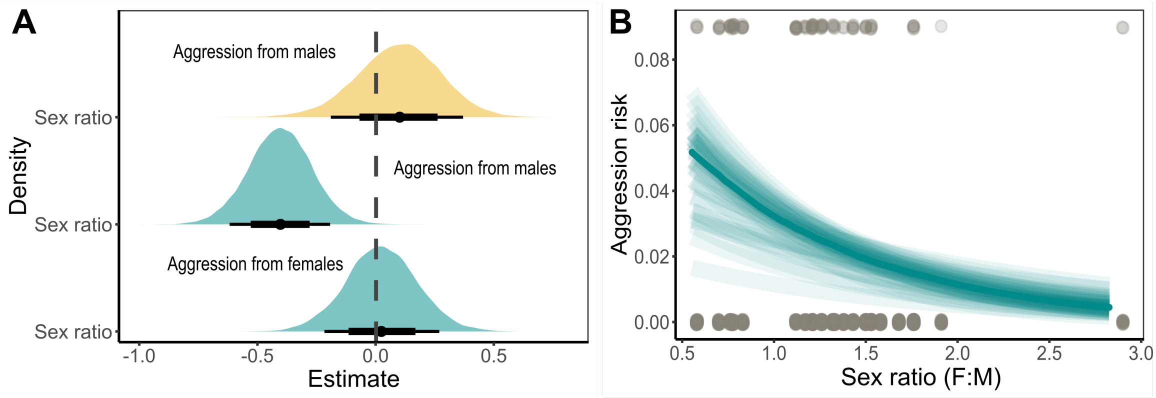

Figure 4: **Sex-specific drivers of injuries with sex ratio**. **A)** Posterior distributions of estimates from models testing the effect of sex ratio (number of females to males) on MM physical aggression (top panel), sex ratio on MF physical aggression (middle panel), and sex ratio on FF physical aggression (bottom panel). Whisker indicates the median, 89% CI (thinner line) and 66% CI (thicker line). **B)** Predicted values for the risk of physical aggression from males to females as a function of the adult sex ratio. The darker line indicates the median and the lighter lines show the 89% CI. Raw data are depicted with grey points (top: physically aggressed, bottom: non-physically aggressed).

not be as limited or restricted as in wild populations, reducing the incentive for high-cost escalated aggression. However, given that females do engage in conflict over food in this population (Balasubramaniam et al., 2014), a complementary or possibly even alternative explanation is the despotic dominance hierarchy that characterises females of this species, where access to resources is highly determined by an individual's dominance rank (Thierry et al., 2004). Such a strict hierarchy might indeed have evolved to reduce costs associated with competition by relying on submissive cues and threats, instead of physical aggression (Holekamp and Strauss, 2016). In support of this, we found - in a supplementary analysis - that females living in larger groups were more likely to be non-physically aggressed by other females compared to females in smaller groups (Fig. S4, details in SI).

But if not female-female aggression, what is the source of injuries for females living in larger groups? One possible explanation is male-female competition for food. However, in a supplementary analysis, we did not find evidence for inter-sexual aggression being related to group size. That is, females living in larger groups did not have a higher risk of physical aggression from resident males when compared to females in smaller groups (Fig. S5, details in SI). Together these results show that group size does not predict within-group aggression towards females, either from males or other females, which suggests that higher injury risk in females living in larger groups might be the result of intergroup aggression. The context when such aggression occurs, however, is not clear. It may be possible that females in larger groups are more likely to engage in intergroup conflict to instigate resident males, knowing their numerical advantage (Koch et al., 2016), but at the risk of being injured by extra-group members while doing so.

Males had a lower injury risk when living in larger groups. Given that the number of males in a group did not predict the risk of physical aggression between resident males, but it was associated with reduced injury risk, it is likely that the source of injuries comes from intergroup encounters. These inferences support our predictions and results from previous meta-analyses in mammals where the number of males was associated with the resource-holding potential of a group (Smith et al., 2022; Majolo et al., 2020). Males from many mammal species have been shown to engage more often than females in intergroup encounters, possibly as a strategy to keep other males away from female group members (Jordan et al., 2007; Cooksey et al., 2020), or to defend the feeding resources (Fashing, 2001; Furrer et al., 2011; Scarry, 2013). In rhesus macaques where females are the core of the society, it is also likely that males engage in intergroup encounters due to female instigation, so that females can gain access to feeding areas and/or extra-group copulations (Johnstone et al., 2020; Arseneau-Robar et al., 2016). Whether the cost of living in smaller groups comes from injuries during collective encounters between groups or during male immigration attempts, where more males might be better able to deter immigration without escalated aggression, requires further investigation.

How does sex ratio impact injury risk?

Contrary to classic predictions of theoretical models where skewed sex ratios might lead to fierce mating competition (Kvarnemo and Ahnesjö, 1996), and also to our rhesus-specific predictions (listed in the Introduction), we found that males had higher injury risk when the relative availability of females was higher (*i.e.,* female-biased sex ratio) and no effect of sex ratio on female injury risk. As above, we discuss these results and the possible socioecological drivers in a sex-specific manner.

We found that in groups where males outnumber females, males did not experience higher injury risk or heightened intra-sexual physical aggression. These results support our predictions and previous research suggesting that despite moderate levels of sexual dimorphism, contest competition for mates between resident male rhesus macaques is not common (Higham and Maestripieri, 2014; Kimock et al., 2022). Instead, rhesus macaque males are believed to rely on strategies of indirect competition, such as sperm competition, endurance rivalry (Higham et al., 2011), group tenure (Manson, 1995), sneak copulations (Higham and Maestripieri, 2014), and to a lesser extent, female coercion and mate-guarding (Manson, 1994). However, contrary to our predictions, we found that males were more likely to be injured in groups with a female-biased sex ratio, but this was not driven by heightened aggression from males in the group. It is possible that males in these groups are more likely to suffer injuries if the higher relative abundance of females makes the group more attractive to immigrant and outsider males, especially if there are fewer males to resist immigration attempts (Alberts and Altmann, 1995). Indeed, males in this population usually disperse during the reproductive season (Hoffman et al., 2008) and may incur higher costs of injuries when doing so (Kimock et al. *in prep.*).

We found no evidence that females engage in conflict over mates. We found that sex ratio did not predict intra-sexual physical aggression among females, consistent with our predictions. As highlighted by Davidian et al. (2022), there might be strong selective pressures for reduced intra-sexual mating competition in most female mammals. The incentive to physically compete over males may be low as sharing mating opportunities with other females is not as costly as it is for males (although there might be some cases where female-female mating competition does occur; Baniel et al. (2018)). Female philopatry may favour the use of less costly means of competition to reduce escalated aggression against kin (Young and Bennett, 2013). Further, physical aggression and its consequences may be too costly for females given their higher energetic demand for reproduction (Trivers, 1972). More specifically for rhesus macaques, female extra-group copulation (Manson, 1992) and low risk of infanticide (Camperio Ciani, 1984), might further reduce the need to compete fiercely over mating opportunities with resident males Baniel et al. (2018).

We found some support for male coercion as a possible cause of injuries in females. Females living in groups with a male-biased sex ratio were more likely to be physically aggressed by males (although we did not find evidence for a similar effect on female injury risk). These results together provide partial support for our predictions and previous evidence suggesting that males of this species and others, may rely on coercive strategies when competition for females is intense (Bercovitch, 1997; Bercovitch et al., 1987; Smit et al., 2022; Baniel et al., 2017). One likely explanation for resident rhesus males relying on coercive strategies is to deter female mate choice, as female rhesus macaques prefer to mate with outsider males, potentially due to benefits derived from increasing genetic variability or quality (Manson, 1992). The lack of evidence for an effect of sex ratio on female injury risk might also be attributed to reduced sample size, as unlike the analyses exploring injury risk with group size, we only considered injuries that occurred within the mating season. Although we can not confidently conclude that male physical aggression results in females being injured, our results suggest that aggression from resident males could be the source of injuries in female rhesus macaques.

Conclusion

In this study, we provide rare empirical evidence for long-standing predictions on the costs of competition in group-living mammals. We showed a sex-dependent effect of group size and sex ratio on the occurrence of injuries, which have been shown to have detrimental survival consequences. Males experienced fewer injuries when living in larger groups. Instead of these being mediated by within-group competition, our results suggest that injuries were mostly the consequence of inter-group encounters. We also found that in groups with fewer reproductive females per male (*i.e.,* male-biased sex ratio), females received more physical aggression from resident males, suggesting that male coercion could be a cause of female mortality in this population. While the Cayo Santiago population is food-provisioned and predator-free, which might reduce the need for contest competition over food and mates, the episodes of escalated aggression and injuries we detected here suggest that the fitness costs of competition in wild populations might be even higher. Overall, our study provides one of the first direct tests of classic predictions of socioecological models.

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