

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

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23 **Abstract**

24 Competition over access to resources, such as food and mates, is believed to be one
25 of the major costs associated with group living. Two socioecological factors suggested
26 to predict the intensity of competition are group size and the relative abundance of
27 sexually active individuals. However, empirical evidence linking these factors to injuries
28 and survival costs is scarce. Here, we leveraged 10 years of data from free-ranging rhesus
29 macaques where injuries inflicted by conspecifics are associated with a high mortality
30 risk. We tested if group size and adult sex ratio predicted the occurrence of injuries
31 and used data on physical aggression to contextualise these results. We found that
32 males were less likely to be injured when living in larger groups, potentially due to
33 advantages in intergroup encounters. Females, instead, had higher injury risk when

34 living in larger groups but this was not explained by within-group aggression among
35 females. Further, male-biased sex ratios predicted a weak increase in injury risk in
36 females and were positively related to male-female aggression, indicating that male
37 coercion during mating competition may be a cause of injuries in females. Overall, our
38 results provide insights into sex differences in the fitness-related costs of competition
39 and empirical evidence for long-standing predictions on the evolution of group living.

40 Introduction

41 Competition over access to resources is believed to be an important selective pressure for
42 the evolution of group living. By forming groups, animals can gain advantages such as
43 higher success at locating food, more and easily accessible mating opportunities, decreased
44 predation risk and cooperative defence of resources (Jarvis et al., 1998; Ratcliffe and Ter
45 Hofstede, 2005; Silk, 2007; Van Schaik and Van Hooff, 1983). However, life in groups can also
46 be associated with major costs for individuals as a result of competition with conspecifics
47 when valuable resources- such as food and mates- are limited (Terborgh and Janson, 1986;
48 Van Schaik and Van Hooff, 1983; Janson and Goldsmith, 1995). Intense competition in the
49 form of physical aggression can have substantial health costs for individuals because their
50 risk of injury increases (Vogel et al., 2007; Feder et al., 2019). Injuries may indirectly impact
51 reproductive success as animals may need to divert energetic resources to healing (Archie
52 et al., 2014), and can directly impact survival in the case of fatal aggression (Pavez-Fox
53 et al., 2022; Chilvers et al., 2005). Given the fitness costs of injuries, animals are expected
54 to refrain from engaging in physical aggression unless necessary when resources are limited
55 or very valuable (Hammerstein, 1981). Two aspects of a group have been hypothesised to
56 drive the intensity and costs of competition: group size and the operational sex ratio.

57 Group size might determine the intensity of competition within and between groups.
58 Larger groups have more individuals who need access to the food that is available and so
59 usually suffer from higher levels of within-group competition compared to individuals in
60 smaller groups (Heesen et al., 2014; Balasubramaniam et al., 2014; Gillespie and Chapman,
61 2001; Blumstein et al., 1999; Marino, 2010). However, when feeding areas can be monop-
62 olised and are extensive enough to sustain entire groups, larger groups have a numerical
63 advantage, which can be beneficial for the collective defence of such resources (Cheney
64 and Seyfarth, 1987; McComb et al., 1994). For instance, studies in several species have
65 shown that larger groups are more likely to win between-group encounters than smaller
66 groups (Majolo et al., 2020; Balasubramaniam et al., 2014; Willems et al., 2013; Thompson
67 et al., 2017; Dyble et al., 2019). Differences in life history between the sexes mean that
68 the incentive to compete and the costs/benefits of group size may differ between males and
69 females. In mammals, the fitness of females is mainly limited by access to food, while the
70 fitness of males is mainly limited by access to mates (Trivers, 1972). Increased within-group
71 competition over food access in larger groups has been suggested to impact females more
72 than males (Sterck et al., 1997; Koenig, 2002). Males, on the other hand, tend to be more
73 involved in between-group competition (Smith et al., 2022), whereby resident males col-
74 lectively defend females or the resources females feed on or against immigration attempts

75 and where larger groups provide a competitive advantage (Cowlshaw, 1995; Majolo et al.,
76 2020; Scarry, 2013). Thus, how group size influences the costs of competition is likely to be
77 sex-dependent.

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

96 While the drivers of competition in group-living animals have been well established
97 (Van Schaik and Van Hooff, 1983; Clutton-Brock and Huchard, 2013; McComb et al., 1994;
98 Blumstein et al., 1999; Dyble et al., 2019), there is still scarce empirical evidence for how
99 these factors influence the occurrence of physical aggression, with consequences for injuries
100 and fitness. Quantifying the consequences of contest competition and its fitness outcomes
101 has proven difficult in most wild systems where injuries or body damage can be caused
102 by predators and not be the direct result of competition with conspecifics. Obtaining be-
103 havioural information from large wild groups and estimating the operational sex ratio when
104 there are roaming or dispersing males can also be challenging (Kappeler, 2017). Further,
105 given the differences in life history between the sexes, the costs and drivers of competition
106 often are considered separately for males and females, even though there is mounting evi-
107 dence that mating competition can also result in sexual conflict (Davidian et al., 2022; Smit
108 et al., 2022; Baniel et al., 2017).

109 To quantify the fitness costs of contest competition, here, we explore the socioecological
110 drivers of injuries in free-ranging female and male rhesus macaques living in Cayo Santiago,
111 Puerto Rico. Rhesus macaques live in multi-female multi-male societies where females are
112 philopatric and males disperse at sexual maturation (Thierry et al., 2004). Females form
113 strict despotic dominance hierarchies where rank is maternally inherited (Chikazawa et al.,
114 1979). Males acquire rank via a queuing system where group tenure determines their so-
115 cial status (Manson, 1995; Kimock et al., 2022). Rhesus macaques have a polygynandrous
116 mating system with high synchrony in females' fertile phases, reducing the monopolisation

117 potential of males (Dubuc et al., 2011). As a consequence, male rhesus often rely more on
118 indirect forms of competition, such as sperm competition, endurance rivalry, sneaky copu-
119 lations and female coercion (Higham et al., 2011; Higham and Maestripieri, 2014; Manson,
120 1994), rather than direct male-male conflict (Kimock et al., 2022). There are no preda-
121 tors of rhesus macaques on the Cayo Santiago island, and injuries are primarily caused by
122 conspecifics. Injuries have been linked to a 3-fold decrease in survival probability in this
123 population for both sexes (Pavez-Fox et al., 2022), providing the opportunity to test the
124 fitness-related costs of competition. Demographic information is collected monthly provid-
125 ing accurate information on group membership and sex ratio. Social groups are naturally
126 formed and vary in size from 26 to nearly 300 adults. Although the population is food pro-
127 visioned, competition over monopolizable food and water stations frequently occurs, where
128 high-ranking macaques spend on average more time feeding and drinking than low-ranking
129 animals (Balasubramaniam et al., 2014).

130 To determine the socioecological drivers of injuries in this population, we tested for sex-
131 specific effects of group size and adult sex ratio (sex ratio henceforth), a proxy of operational
132 sex ratio, on the occurrence of injuries. Because injuries were collected opportunistically, we
133 do not have information on who caused the injury, although due to the lack of predators on
134 the island we can be confident that all injuries were inflicted by conspecifics. Given this, we
135 used long-term behavioural observations of physical aggression, where we have data on the
136 sex of both the victim and aggressor, to contextualise the injury data. Specifically, we looked
137 at how sex ratio and group size predicted intrasexual and intersexual physical aggression
138 to help infer the cause of injuries and therefore the underlying drivers of competition in
139 this system. We predicted that in larger groups the risk of injury (*i.e.*, probability of
140 being injured) would be higher for females and lower for males. We predicted that females
141 would experience higher injury risk in larger groups as a result of higher within-group
142 female-female (FF) feeding competition (Wrangham et al., 1993; Chapman and Chapman,
143 2000), thus we further tested if FF physical aggression (*i.e.*, probability of being physically
144 aggressed) was higher in larger groups. For males, we expected that those living in larger
145 groups would have reduced injury risk because having a numerical advantage translates
146 into better chances of winning between-group encounters (Koenig et al., 2013; Janson and
147 Goldsmith, 1995). Given that the behavioural data included only within-group interactions,
148 we could not test patterns of between-group aggression. Instead, we tested whether male-
149 male (MM) physical aggression was influenced by group size to rule out within-group MM
150 competition as a driver of injuries. For sex ratio, if classic socioecological predictions apply
151 to mating competition in rhesus macaques, we expected that in groups with skewed sex
152 ratios, those individuals of the sex in minority would have higher injury risk due to more
153 intense competition over mates (Kvarnemo and Ahnesjö, 1996). That is, male injury risk
154 and MM physical aggression might increase as the sex ratio becomes more male-biased
155 while female injury risk and FF physical aggression are expected to increase as the sex
156 ratio becomes more female-biased. However, we do not necessarily expect these classic
157 predictions for sex ratio in rhesus macaques, because males often rely on indirect forms of
158 competition (Higham et al., 2011; Higham and Maestripieri, 2014; Kimock et al., 2022) and

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

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

Sex ratio classical: general predictions of socioecological models, Sex ratio rhesus: predictions specific to our study system, group size: number of individuals in the group (4 years and older), sex ratio: number of adult females per male during the mating season, aggression: physical aggression, ‘FF’: female-female, ‘MM’: male-male, ‘MF’: male-female.

159 because females live in philopatric societies where the incentive to compete aggressively over
160 mates against their kin is typically low (Davidian et al., 2022). As such, we have alternative
161 rhesus-specific predictions. We expected that the local availability of mating partners would
162 not determine injury risk in males, because males are not expected to frequently engage in
163 direct MM competition over females and there is therefore no reason to expect an effect of
164 sex ratio on MM physical aggression. Instead, we expected that females would have higher
165 injury risk when females are more scarce (male-biased sex ratio). This is because rhesus
166 macaques are sexually dimorphic and male coercion has been reported (Manson, 1994).
167 This means that male-female (MF) physical aggression would be expected to be higher in
168 groups with a male-biased sex ratio where males direct their aggressive behaviours towards
169 females when competition over females increases. Finally, we predicted that FF physical
170 aggression would not be influenced by sex ratio as female rhesus macaques are not expected
171 to fiercely compete over access to males against their kin. All predictions are laid out in
172 Table 1.

173 **Methods**

174 *Study subjects*

175 Study subjects were free-ranging male and female rhesus macaques living on Cayo Santiago
176 island, Puerto Rico. The island is home to a population of ~ 1800 individuals living in 6 to
177 12 mixed-sex naturally formed social groups. The Cayo Santiago field station is managed
178 by the Caribbean Primate Research Center (CPRC), which monitors the population daily
179 and maintains the long-term (>75 years) demographic database including data on births,

180 deaths and social group membership for all animals (Kessler and Rawlins, 2016). Macaques
181 are individually identified based on tattoos located on their chest and legs. Animals have
182 *ad-libitum* access to food and water, the island is predator-free and there is no regular
183 medical intervention for sick or wounded individuals. Here we included data on male and
184 female macaques that were alive between 2010 and 2020. We focused on individuals aged 4
185 years and above (age range: 4 - 28 years), as animals of both sexes have typically reached
186 sexual maturity at that age (Zehr et al., 2005; Bercovitch and Berard, 1993). We restricted
187 our sample to animals belonging to social groups for which we had data on injury occurrence
188 and agonistic behavioural observations ($n = 6$ social groups). The groups analysed varied
189 in size from 26 to 288 animals and sex ratios (n females/ n males) ranged from 0.5 to 4.5
190 (Fig. S1).

191 *Observation of Injuries*

192 Since 2010, the CPRC staff have been collecting opportunistic observations on the incidence
193 and recovery from injuries during the daily monitoring of social groups for demographic
194 purposes. Data collection was carried out mainly by the veterinary technician complemented
195 by information from other experienced staff during the working hours of the field station
196 (7:30 to 14:00 from Monday to Friday). If an individual was observed to be wounded or
197 displaying signs of injury (*e.g.*, limping) the staff member recorded the individual ID and
198 if the injury was visible, the type of injury (*e.g.*, puncture, scratch), the area of the body
199 affected, whether the injury was recent or old based on the presence of scars, and if possible,
200 an estimate of the wound size. Records for each individual were updated every time the
201 observers encountered the wounded individuals during the daily census. Here we included
202 all records for visible injuries including bites, scratches, abrasions and cuts along with other
203 more severe injuries such as exposed organs and fractures. We decided to exclude cases
204 where injuries could be inferred but not observed, such as limping or abscesses as these
205 could also be caused by infection unrelated to injury. We excluded injury records from two
206 full years (2015 and 2016), a period for which the veterinary technician was not regularly
207 at the field site, which may have led to biases in the few groups sampled during those years.
208 Our sample consisted of 908 injuries collected from September 2010 to April 2020 on 521
209 unique individuals (n females = 267, n males = 254).

210 *Collection of aggression data*

211 We collected behavioural data using focal samples based on a previously established ethogram
212 (Brent et al., 2014) from twenty different group years (group F 2010-2017, group HH 2014
213 and 2016, group KK 2015 and 2017, group R 2015 and 2016, group S 2011 and 2019, group
214 V 2015-2019). Across the 10 years of study, two external events in 2018 and 2020 - Hur-
215 ricane Maria and the COVID-19 pandemic, respectively - precluded the collection of focal
216 data. These years were excluded from the aggression analyses. In total, this resulted in
217 748 adult individuals (422 females and 326 males) whose ages ranged between 4-28 years
218 old (mean = 10.7). Behavioural data were collected using 10-min (17 group years) or 5-min

219 (3 group years) focal animal samples between 07:30 and 14:00. We stratified sampling to
220 ensure balanced data collection on individuals throughout the day and over the year. Dur-
221 ing focal sampling, dyadic agonistic encounters where the focal animal was involved were
222 recorded, along with the identity of the aggressor and victim. We recorded all agonistic
223 interactions, including submissions, threats, non-contact aggression (*e.g.*, charge, chase),
224 and physical aggression (*e.g.*, bite, hit). Given that the purpose of our study was to use
225 the aggression data to contextualise the occurrence of injuries, we considered only data on
226 physical aggression, which is more likely to lead to an injury. From January 2010 to October
227 2019, we recorded 18880 aggression events including 522 physical aggression.

228 *Quantifying injury risk and aggression rates*

229 The injury dataset included the 521 animals that were recorded injured in addition to
230 1001 uninjured animals (n uninjured females = 525, n uninjured males = 476). Uninjured
231 individuals consisted of all sexually mature individuals who were alive during the period
232 of study, *i.e.*, between 2010 and 2020 excluding 2015 and 2016 to match data on injured
233 animals. Given that the average recovery time for an injury was 43 days and the average
234 time elapsed between consecutive injury records was 42.17 days, the dataset was formatted
235 in a way that each row represented a two-month interval period (*i.e.*, bimonthly interval).
236 By formatting the data this way we could be confident that injury records occurring in
237 different rows were more likely to be independent (for details see SI: Pavez-Fox et al. 2022).
238 An individual's injury status during each bimonthly interval they were alive was coded as
239 a binary variable where 1 = injured and 0 = uninjured.

240 The aggression dataset included the 748 male and female macaques for which focal data
241 were collected. Given that our questions were sex-specific, we split this dataset by the sex
242 of the focal animal resulting in 438 physical aggression events in a total of 422 females and
243 84 physical aggression events in a total of 326 males. We focused specifically on physical
244 aggression received by the focal animal. Each row represented a bimonthly interval to
245 match the format of the injury data. Given that an individual rarely received physical
246 aggression more than once in a given bimonthly interval (Fig. S2), we coded an individual's
247 aggression status as binary, where 1 = physically aggressed and 0 = not physically aggressed.
248 Depending on the question, we split this dataset based on the sex of the victim and the
249 aggressor.

250 *Statistical analyses*

251 We ran all the models in a Bayesian framework using the brms R Package (Burkner,
252 2021). Therefore, evidence of an effect was determined based on the degree of overlap between
253 the credible interval (CI) and zero (*i.e.*, 89% non-overlapping reflecting strong evidence of
254 an effect). Given that all the dependent variables were coded as binary, models were fit
255 using a Bernoulli distribution. All continuous predictors were z-scored. In all the models
256 we included random intercepts for individual ID to account for repeated measures and for
257 the specific bimonthly interval within the study period. We assumed normal distributions

258 for priors (mean = 0, SD = 1) and ran 10000 iterations in all the models. Model assump-
259 tions and posterior predictive checks were done using the 'ppcheck' built-in function from
260 the brms package. Marginal effects were calculated using the emmeans R package(Lenth
261 et al., 2018). We reported means as point estimates, standard error (SE) and 89% credible
262 intervals of the posterior distribution. For marginal effects, we reported the median and
263 the 89% highest posterior density interval (HPD).

264 **Group size and sex as drivers of injuries**

265 *Effect of group size on injury risk.* To test whether group size predicted the probability of an
266 individual being injured, we built a model where the dependent variable was an individual's
267 injury status (1/0) and the independent variables included group size, the individual's sex
268 and the reproductive season (1 = mating, 0 = non-mating) in a given bimonthly interval.
269 Because our predictions were sex-specific, we included an interaction term between group
270 size and sex. Using demographic records, we computed group size as the number of adults
271 (4 years and above) that were alive in a subject's group in a given bimonthly interval. We
272 specifically determined a group's size at the middle of the interval (end of the first month),
273 thus if an individual reached 4 years of age or died during the second month, this was
274 only reflected in the following bimonthly interval. We determined the reproductive season
275 following (Hoffman et al., 2008). Briefly, we first computed the mean birth date \pm 2 SD
276 for each year. The start of the birth season was defined as the first birth date and the end
277 as the last birth date. The beginning of the mating season was determined by subtracting
278 the gestation period of rhesus macaques (165 days; Silk et al. 1993) from the start of the
279 birth season, and the end of the mating season was determined by subtracting the gestation
280 period from the end of the birth season. If the middle of the bimonthly interval fell outside
281 the mating season it was considered part of the non-mating period.

282
283 *Effect of group size on female-female aggression.* To test whether FF competition might be
284 a driver of injuries in females living in larger groups, we focused on female-female aggression
285 data. The dependent variable was female aggression status (0/1) and we included the num-
286 ber of females in the group, the reproductive season and an offset term for sampling effort
287 (*i.e.*, hours an individual was focal-followed) as independent variables in the model. We
288 used the number of females in the group rather than group size as a predictor in the model
289 because the former better reflects FF competition and these two metrics were strongly cor-
290 related (Fig. S3A, Pearson's $R = 0.94$, $p < 0.01$). Using the same model specifications, we
291 additionally tested whether group size predicted MF physical aggression (where the victims
292 were females and the aggressors were males) to rule out other drivers of injuries in females
293 related to within-group competition.

294
295 *Effect of group size on male-male aggression.* To test our prediction that within-group MM
296 competition was not a driver of injuries in smaller groups we focused on male-male aggres-
297 sion data. We tested if the number of males in a group, which was positively correlated
298 to group size (Fig. S3B, Pearson's $R = 0.97$, $p < 0.01$), predicted a male's risk of physical

299 aggression from other males in his group. The dependent variable was a male's aggression
300 status (0/1) and the independent variables were the number of males in a group, the re-
301 productive season and an offset term for sampling effort. The occurrence of FM physical
302 aggression was very rare (only 9 cases across the 10 years), thus we disregarded within-group
303 female aggression as a driver of injuries in males.

304

305 **Sex ratio and sex as drivers of injuries**

306

307 *Effect of sex ratio on injury risk.* To test whether the sex ratio predicted the probability of an
308 individual being injured we built a model where the dependent variable was an individual's
309 injury status (0/1) and included sex ratio and sex as independent variables. Given that
310 our predictions were sex-specific, we included an interaction term between the sex ratio and
311 sex. We computed the sex ratio as the number of females (4 years and above) per male
312 in the subject's group in a given bimonthly interval. Therefore, smaller numbers would
313 indicate a male-biased sex ratio while larger numbers would indicate a female-biased sex
314 ratio. For these analyses, we focused on the mating season, to have a better estimate of
315 sexually active individuals and to make sure that the socioecological driver of injuries was
316 competition for mates. As with group size, we determined a group's sex ratio at the middle
317 of the bimonthly interval, thus if an individual reached 4 years of age or died during the
318 second month, this was only reflected in the following interval.

319

320 *Effect of sex ratio on male-female aggression.* To test if MF coercion was a driver of injuries
321 in females we focused on aggression data where the victims were females and the aggressors
322 were males. As a dependent variable, we included a female's aggression status (0/1) and as
323 independent variables, the sex ratio and an offset term for sampling effort. As above, we
324 focused on the mating season for this analysis to make sure that mating competition was
325 the driver of physical aggression.

326

327 *Effect of sex ratio on female-female aggression.* To test whether FF competition over males
328 was a driver of injuries in females we focused on data where the aggressor and the victim
329 were females. As above, we restricted this analysis to the mating season. The dependent
330 variable was a female's aggression status (0/1) and independent variables included sex ratio
331 and an offset term for sampling effort.

332

333 *Effect of sex ratio on male-male aggression.* To test if MM competition over females was
334 a driver of injuries in males we focused on male-male aggression data during the mating
335 season. The dependent variable was a male's aggression status (0/1) and predictors included
336 sex ratio and an offset term for sampling effort. To rule out the possibility that young and
337 old females might not be attractive partners for males to compete over (as we consider all
338 females over 4 years of age), we also tested the effect of the adult sex ratio considering only
339 the number of prime-age females (6-17 years; Lee et al. 2021) per male in the group.

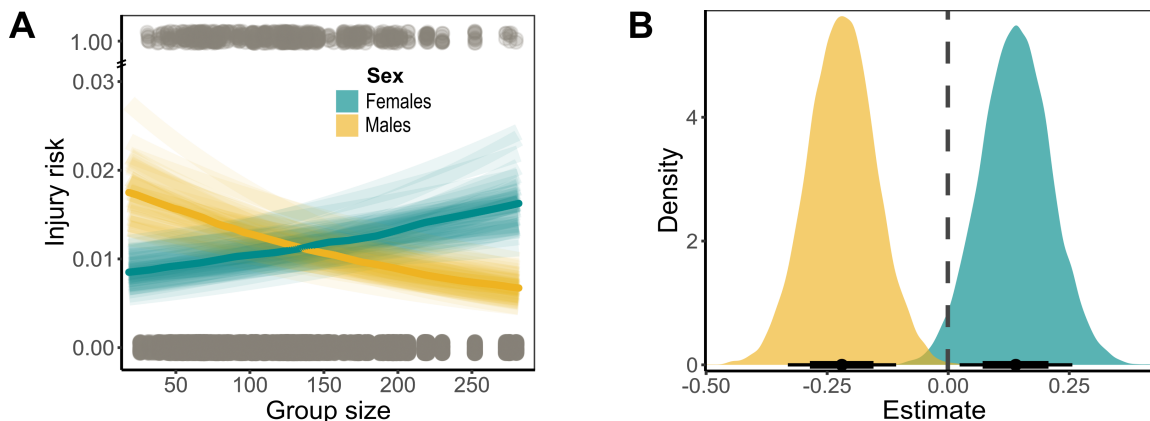


Figure 1: **Sex-dependent effect of group size on injury risk.** **A)** Predicted values of injury risk for females (cyan) and males (yellow) as a function of group size. The darker line indicates the median and the lighter lines show the 89% CI. Raw data are depicted with grey points (top: injured, 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).

340 Results

341 Group size and sex as drivers of injuries

342 *Effect of group size on injury risk.* In support of our predictions, we found a sex-dependent
343 effect of group size on injury risk (Fig. 1A; Log-Odds $\text{group_size} \times \text{sexM} = -0.36$, SE =
344 0.08, 89% CI = -0.49, -0.23; Table S1). Females were 53% more likely to be injured for
345 every one SD (~ 59 individuals) of increase in group size (marginal effect: Log-Odds fe-
346 males = 0.14, 89% HPD = 0.025, 0.26). In the case of males, an increase in one SD
347 in group size was associated with a reduction of 44% in the probability of being in-
348 jured (marginal effect: Log-Odds males = -0.22, 89% HPD = -0.33, -0.11) (Fig. 1B).

349
350 *Effect of group size on female-female aggression.* Contrary to our prediction, females living
351 in groups with more females (*i.e.*, larger groups) were not more likely to be physically ag-
352 gressed by other females in the group (Fig. 2 top panel; Log-Odds fem count = -0.09, SE =
353 0.08, 89% CI = -0.22, 0.03; Table S2). We interpret this to mean that there is no evidence
354 of FF competition driving injuries in larger groups. We could also rule out MF physical
355 aggression with group size, as females were less likely to be physically aggressed by males
356 as group size increased (Fig. 2 middle panel; Log-Odds group size = -0.14, SE = 0.08, 89%
357 CI = -0.26, -0.01; Table S3).

358
359 *Effect of group size on male-male aggression.* As predicted, we did not find evidence of
360 an effect of group size on MM physical aggression within groups. The number of males in
361 a group did not predict the likelihood of a male receiving physical aggression from other
362 resident males (Fig. 2 bottom panel; Log-Odds male_count = -0.06, SE = 0.13, 89% CI =

363 -0.27, 0.15, Table S4).

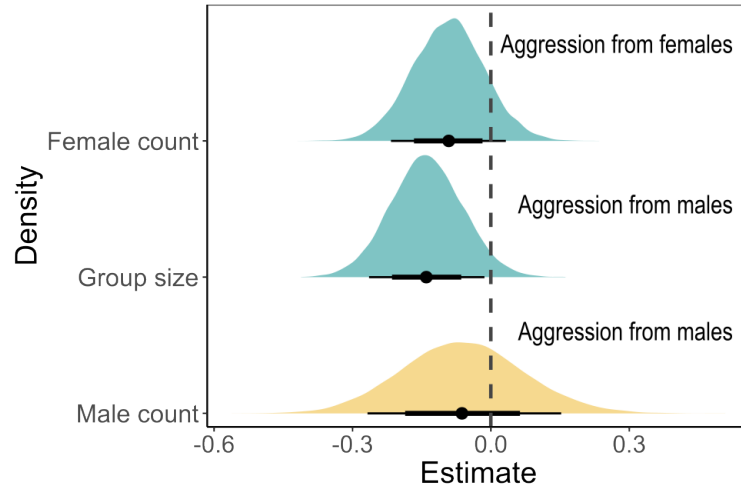


Figure 2: **Sex-specific drivers of injuries with group size.** A) Posterior distributions of estimates from models testing the effect of the number of females in a group on FF physical aggression (top panel), group size on MF physical aggression (middle panel), and the number of males on MM physical aggression (bottom panel). Female victims are depicted with cyan and male victims with yellow. Whisker indicates the median, 89% CI (thinner line) and 66% CI (thicker line).

364 Sex ratio and sex as drivers of injuries

365 *Effect of sex ratio on injury risk.* We found a sex-dependent effect of sex ratio on an indi-
366 vidual's injury risk (Fig. 3A; Log-Odds $\text{sex_ratio} \times \text{sexM} = 0.17$, $\text{SE} = 0.08$, 89% CI = 0.04,
367 0.3; Table S5). Contrary to our rhesus-specific and classical predictions, males who lived
368 in groups with female-biased sex ratios were more likely to be injured. For every increase
369 in one SD of sex ratio (~ 0.5 increase in females relative to males), males experienced a
370 53% increase in their likelihood of being injured (marginal effect: Log-Odds males = 0.12,
371 89% HPD = 0.01, 0.21). Females were more likely to be injured when living in groups with
372 a male-biased sex ratio, but this relationship was weak as the credible interval overlapped
373 with zero (marginal effect: Log-Odds females = -0.05, 89% HPD = -0.16, 0.06) (Fig. 3B).

374
375 *Effect of sex-ratio on male-male aggression.* We did not find evidence for MM competi-
376 tion over females driving injuries, as males were not more likely to receive physical ag-
377 gression by resident males when living in groups with a male-biased operational sex ratio
378 (Fig. 4A top panel; Log-Odds $\text{sex_ratio} = 0.1$, $\text{SE} = 0.17$, 89% CI = -0.19, 0.37, Table
379 S6). This result holds even when only prime-aged females were considered in the computa-
380 tion of sex ratio (Log-Odds $\text{sex_ratio} = 0.04$, $\text{SE} = 0.19$, 89% CI = -0.27, 0.34, Table S7).

381

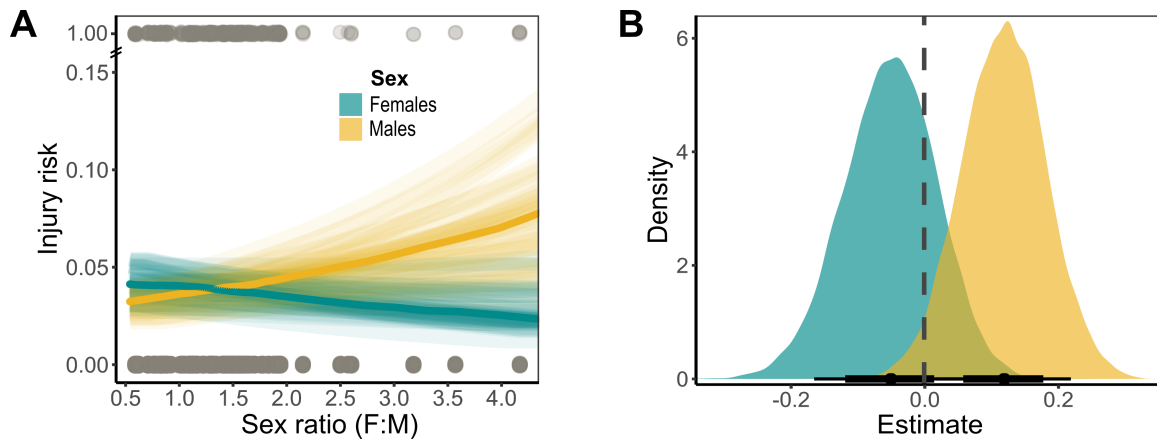


Figure 3: **Sex-dependent effect of adult sex ratio on injury risk.** **A)** Predicted values of injury risk for females (cyan) and males (yellow) as a function of adult sex ratio (*i.e.*, number of females per male during the mating season). The darker line indicates the median and the lighter lines 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).

382 *Effect of sex ratio on male-female aggression.* Consistent with our rhesus-specific prediction,
383 male-to-female physical aggression was negatively associated with the relative availability of
384 females in a group. For every one SD decrease in sex ratio (~ 0.5 decrease in the number of
385 females relative to males), females were 40% more likely to be physically aggressed by males
386 (Fig. 4A middle panel, Fig. 4B; Log-Odds sex_ratio = -0.4, SE = 0.13, 89% CI = -0.62, -0.19,
387 Table S8).

388
389 *Effect of sex ratio on female-female aggression.* We found no evidence of FF competition
390 for males driving injuries. As predicted for rhesus macaques, during the mating season
391 females were not more likely to be physically aggressed by other females in groups when the
392 relative availability of males was low (*i.e.*, female-biased sex ratio) (Fig. 4A bottom panel;
393 Log-Odds sex_ratio = 0.02, SE = 0.15, 89% CI = -0.22, 0.27, Table S9).

394 Discussion

395 In this study, we tested predictions derived from socioecological theory on the sex-specific
396 drivers of injuries. As predicted, we found that living in larger groups may confer a competi-
397 tive advantage to males but a cost to females. Males living in larger groups were less likely
398 to be injured compared to males in smaller groups, whereas females had a higher risk of
399 injury in larger groups. Further, we found that female aggression was not a driver of female
400 injury in this population but instead, our results pointed to the role of male coercion during
401 mating competition. In males, we found no evidence of injuries being driven by within-
402 group aggression, suggesting that injuries were likely caused during inter-group encounters.

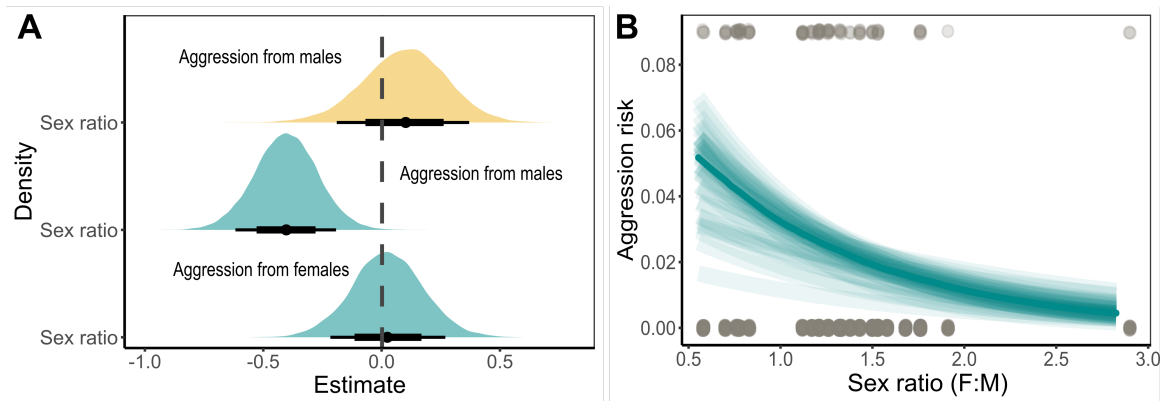


Figure 4: **Sex-specific drivers of injuries with sex ratio.** **A)** Posterior distributions of estimates from models testing the effect of sex ratio (number of females to males) on MM physical aggression (top panel), sex ratio on MF physical aggression (middle panel), and sex ratio on FF physical aggression (bottom panel). Female victims are depicted with cyan and male victims with yellow. Whisker indicates the median, 99% 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 sex ratio. The darker line indicates the median and the lighter lines show the 99% CI. Raw data are depicted with grey points (top: physically aggressed, bottom: not physically aggressed).

403 Taken together these results provide rare evidence of fitness-related costs associated with
404 classic predictors of socioecological models.

405 **How does group size impact injury risk?**

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

409 Females living in larger groups had a higher risk of injury than females in smaller groups.
410 However, contrary to our prediction, we found no evidence that this was driven by within-
411 group FF competition, as females in larger groups did not receive more physical aggression
412 from other female group members. Larger groups are believed to impose major energetic
413 constraints, particularly for females, which require high food intake to fulfil the costs of
414 pregnancy and lactation (Markham and Gesquiere, 2017; Trivers, 1972). As a consequence,
415 females are expected to compete more intensely for food when living in larger groups (Sterck
416 et al., 1997; Koenig, 2002). Yet, our results suggest that this might not be the case in female
417 rhesus macaques at the Cayo Santiago field station. This could be because animals in this
418 population are food-provisioned, thus feeding resources might not be as limited or restricted
419 as in wild populations, reducing the incentive for high-cost physical aggression. However,
420 given that females do engage in conflict over food in this population (Balasubramaniam
421 et al., 2014), a complementary, or possibly even alternative explanation, is that the despotic
422 dominance hierarchy that characterises females of this species mediates access to resources

423 and reduces the need for physical aggression (Thierry et al., 2004; Holekamp and Strauss,
424 2016). In support of the idea that elevated competition in larger groups might be more
425 apparent through non-physical aggression, we found - in a supplementary analysis - that
426 females living in larger groups were more likely to receive non-physical aggression by other
427 females compared to females living in smaller groups (Fig. S4, details in SI).

428 But if not female-female aggression, what is the source of injuries for females living
429 in larger groups? One possible explanation is male aggression. However, we found the
430 opposite pattern as MF physical aggression decreased with group size. Evidence of reduced
431 male aggression toward females in larger groups could be a consequence of the fact that
432 females in larger groups tend to have more kin and therefore more support against males
433 in agonistic encounters. Together these results show that group size could not explain
434 within-group physical aggression patterns that match higher injury risk in females living
435 in larger groups. This, in turn, suggests that injuries for females in these groups might be
436 the result of intergroup aggression. Some studies in primates have shown that females may
437 participate in intergroup coalitionary aggression more than males (Martínez-Íñigo et al.,
438 2021) and that they are also more likely to engage in intergroup conflict when they have
439 more support from male group members Arseneau-Robar et al. (2017). Further investigation
440 is required to determine the incentives for participation in intergroup aggression in female
441 rhesus macaques.

442 Males had a lower injury risk when living in larger groups. Given that the number of
443 males in a group did not predict the risk of physical aggression between resident males, these
444 results suggest that the source of injuries likely comes from intergroup encounters. In line
445 with our predictions and results from previous meta-analyses in mammals where the number
446 of males was associated with the resource-holding potential of a group (Smith et al., 2022;
447 Majolo et al., 2020), our results provide indirect evidence that larger groups might confer
448 a collective competitive advantage to males. Males from many mammal species have been
449 shown to engage more often than females in intergroup encounters, possibly as a strategy
450 to keep other males away from female group members (Jordan et al., 2007; Cooksey et al.,
451 2020), or to defend the feeding resources (Fashing, 2001; Furrer et al., 2011; Scarry, 2013).
452 Whether the cost of living in smaller groups comes from injuries during collective encounters
453 between groups or during male immigration attempts, where more males might be better
454 able to deter immigration without physical aggression remains an open question.

455 **How does sex ratio impact injury risk?**

456 Contrary to classic predictions of theoretical models where skewed sex ratios are proposed
457 to lead to fierce intrasexual mating competition (Kvarnemo and Ahnesjö, 1996), and also to
458 our rhesus-specific predictions (Table 1), we found that males had higher injury risk when
459 the relative availability of females was higher (*i.e.*, female-biased sex ratio). We also found
460 weak evidence for an effect of sex ratio on female injury risk. As above, we discuss these
461 results and the possible socioecological drivers in a sex-specific manner.

462 We found that in groups where males outnumber females, competition among males was
463 not associated with injury risk or heightened physical aggression during the mating season.

464 These results support our rhesus-specific predictions and previous research suggesting that
465 despite moderate levels of sexual dimorphism, contest competition for mates between resi-
466 dent male rhesus macaques is not common (Higham and Maestripieri, 2014; Kimock et al.,
467 2022). Instead, rhesus macaque males are believed to rely on strategies of indirect compe-
468 tition, such as sperm competition, endurance rivalry (Higham et al., 2011), group tenure
469 (Manson, 1995), sneak copulations (Higham and Maestripieri, 2014), and to a lesser extent,
470 female coercion and mate-guarding (Manson, 1994). However, contrary to our predictions,
471 we found that males were more likely to be injured in groups with a female-biased sex ratio.
472 Males in these groups may be more likely to suffer injuries if the higher relative abundance
473 of females makes the group more attractive to immigrant and outsider males, especially if
474 there are fewer males to resist immigration attempts (Alberts and Altmann, 1995). Indeed,
475 males in this population usually disperse during the reproductive season (Hoffman et al.,
476 2008) and may incur higher costs of injuries when doing so (Kimock et al. *in prep.*).

477 We found no evidence that female mating competition might result in injuries. Con-
478 sistent with our rhesus-specific predictions but contrary to classical socioecological theory,
479 we found that sex ratio did not predict physical aggression among females. As highlighted
480 by Davidian et al. (2022), there might be strong selective pressures for reduced intrasexual
481 mating competition in most female mammals. The incentive to physically compete over
482 males may be low as sharing mating opportunities with other females is not as costly as it
483 is for males (although there might be some cases where female-female mating competition
484 does occur; Baniel et al. 2018). Female philopatry may favour the use of less costly means
485 of competition to reduce physical aggression against kin (Young and Bennett, 2013). In line
486 with this, we found in a supplementary analysis that as the group becomes more female-
487 biased, and thus FF mating competition is expected to be higher, non-contact aggression
488 among females increases (Fig. S5, Table S11; details in Supplementary). Further, physical
489 aggression and its consequences may be too costly for females given their higher energetic
490 demand for reproduction (Trivers, 1972). More specifically for rhesus macaques, female
491 extra-group copulation (Manson, 1992) and low risk of infanticide (Camperio, 1984), might
492 further reduce the need to compete fiercely over mating opportunities with resident males
493 (Baniel et al., 2018).

494 We found some support for male coercion as a possible cause of injuries in females.
495 Females living in groups with a male-biased sex ratio were more likely to be physically
496 aggressed by males (although we did not find evidence for a similar effect on female injury
497 risk). These results together provide partial support for our rhesus-specific prediction and
498 previous evidence suggesting that males of this species and others, may rely on coercive
499 strategies when competition for females is intense (Bercovitch, 1997; Bercovitch et al., 1987;
500 Smit et al., 2022; Baniel et al., 2017). One likely explanation for resident rhesus males relying
501 on coercive strategies is to deter female mate choice, as female rhesus macaques prefer
502 to mate with outsider males, potentially due to benefits derived from increasing genetic
503 variability or quality (Manson, 1992). The lack of evidence for an effect of sex ratio on
504 female injury risk might also be attributed to reduced sample size, as our injury results
505 trended in the expected direction but unlike the analyses exploring injury risk with group

506 size, we considered only injuries that occurred within the mating season, which substantially
507 reduced our sample size. Alternatively, it is also possible that males rely on less severe forms
508 of physical aggression when coercing females in their groups (like slaps or hits), which might
509 not lead to injuries. Although we can not confidently conclude that male physical aggression
510 results in females being injured, our results suggest that aggression from resident males could
511 be one source of injuries in female rhesus macaques.

512 **Conclusion**

513 In this study, we showed a sex-dependent effect of group size and sex ratio on the occur-
514 rence of injuries, which have been shown to have detrimental survival consequences. Our
515 group size results demonstrate that within-group intrasexual competition might not lead to
516 injuries in males or females, suggesting instead that intergroup conflict may play a role in
517 individual injury risk and mortality in this population. Moreover, we also found that male
518 coercion might be one source of female injury during mating competition. While the Cayo
519 Santiago population is food-provisioned and predator-free, which might reduce the need for
520 contest competition over food and mates, the episodes of physical aggression and injuries
521 we detected here suggest that the fitness costs of competition in wild populations might
522 be even higher. Overall, our study provides empirical evidence for fitness-related costs of
523 fundamental aspects of social organisation.

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529 **Data and code availability**

530 Data used in the analyses will be made available upon acceptance. R code used for models
531 and plots available at
532 <https://github.com/MPavFox/Socioecological-drivers-of-injuries/>

533 **Author contribution**

534 Conceptualization, M.A.P-F., L.J.N.B. and D.D.; Methodology, M.A.P-F., D.D., E.R.S. and
535 S.E.; Resources, L.J.N.B., J.P.H., N.S-M., and A.R-L; Data Curation, M.A.P-F., C.M.K.,
536 N.R-B., J.E.N-D., and D.P.; Writing – Original Draft, M.A.P-F.; Writing – Review &
537 Editing, M.A.P-F., D.D., E.R.S., L.J.N.B., C.M.K., J.P.H.; Supervision, D.D. and L.J.N.B.

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549 **Conflict of interest**

550 None.

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