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Fitness incentives to male fighters undermine fighting performance in intergroup contests

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In animal societies, groups engage in intergroup conflicts over resources. Group conflict success depends on member contributions to collective fighting, yet individual fitness incentives could undermine group performance. In banded mongooses, *Mungos mungo*, males contribute most to intergroup fights, while females often initiate fights and can mate with rival group males during the fray. We tested how focal group contest outcomes are related to male motivation to defend within-group paternity, as compared to the motivation of rival group males to avoid fighting and instead gain outgroup paternity. Focal groups were most likely to win when their females were in oestrus. However, groups that won fights conceded more paternity to their rivals than groups that lost, suggesting rival group males focused on mating at the expense of contest success. We also found that younger males may be most likely to forgo intergroup fighting to focus on intergroup mating, as these males gained more paternity from between-group matings than within-group matings. Our results contribute a rare link between contest outcomes and fitness in a nonprimate species and run counter to common models of collective action by suggesting that personal fitness incentives, here, paternity, can undermine collective fighting performance. Such conflicts of interest are likely inherent in group combat and can contribute to variation in the frequency and costliness of intergroup violence.

Conflicts between groups, or ‘intergroup contests’, occur across diverse social-living taxa, from ants (Batchelor & Briffa, 2011) and snapping shrimp (Hultgren et al., 2017) to birds (Radford & Fawcett, 2014; Strong et al., 2018) and primates (Majolo et al., 2020), including humans (Glowacki & McDermott, 2022; Glowacki & Wrangham, 2015; Macfarlan et al., 2018). Across this diversity, intergroup conflict is hypothesized to be a major force in social evolution; for instance, cooperation within groups is thought to coevolve alongside aggression between groups (Choi & Bowles, 2007; Dyble, 2021). A common challenge of intergroup conflicts is that group members need to contribute to the collective good of defeating a rival, despite the fact that each member may have disparate interests and motivation (Olson, 1965). Formal models of intergroup conflict have ‘solved’ this collective action problem by assuming that members from winning groups gain direct reproductive benefits, which motivate member participation (Choi & Bowles, 2007; Lehmann & Feldman, 2008). Observational studies of human societies find support for this assumption: for instance, male warriors from winning groups in societies from East Africa and South America gain fitness benefits in the form of marriages and resulting children (Glowacki & Wrangham, 2015; Macfarlan et al., 2018).

In contrast to the evidence from human societies, there is very little understanding of the direct fitness consequences (i.e. parentage over offspring) of conflict outcomes in nonhuman animals. Instead, most studies quantify changes in fitness proxies, like territory size, that result from winning or losing intergroup contests (Crofoot, 2013; Markham et al., 2012; Radford & Fawcett, 2014). For example, groups of baboons (*Papio cynocephalus*) that lost

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intergroup contests spent less time in the area where the conflict occurred, as compared to groups that won (Markham et al., 2012). When direct fitness consequences like offspring production or survival are measured in nonhuman animals, they tend to be in relation to contest frequency, not outcomes (Braga Goncalves et al., 2022; Braga Goncalves & Radford, 2022; Lemoine et al., 2020; Thompson, Marshall, et al., 2017). For instance, groups of daffodil cichlids, *Neolamprologus pulcher*, that faced high rates of intergroup conflict produced eggs less often, and with less protein, than control groups with no intergroup conflict (although groups facing frequent conflict had similar egg-hatching success; Braga Goncalves & Radford, 2022). Quantifying the fitness consequences of intergroup conflict outcomes in nonhuman animal taxa is essential to understanding what motivates group members to contribute to the collective good of winning the fight (Gavrilets & Fortunato, 2014; Lehmann & Feldman, 2008), informing theories of the evolution of warfare (Choi & Bowles, 2007; Dyble, 2021). Here, we examine how fitness costs and benefits, in the form of paternity over offspring, relate to conflict outcomes in a model wild social mammal species, the banded mongoose, *Mungos mungo*.

Banded mongooses engage in frequent (Green et al., 2022) and violent intergroup contests: they are one of a handful of social mammals (including lions, *Panthera leo*, grey wolves, *Canis lupus*, chimpanzees, *Pan troglodytes*, and humans) in which intergroup conflict accounts for more than 10% of adult deaths of known cause (Johnstone et al., 2020). Our study population in Queen Elizabeth National Park, Uganda is composed of 10–12 social groups, each containing approximately 20 (median = 18, interquartile range (IQR) = 9.25; Cant, 2000) adults as well as juveniles (offspring less than 6 months old; Cant et al., 2013). Group sex ratios are male-biased, with an average of 1.8 males per female (Cant, 2000). All females within a group enter oestrus within 1 week of each other, an event termed ‘group oestrus’ and that lasts an average of 6 days (range 3–10 days; Cant, 2000). Oestrous females are closely mate-guarded by dominant males within their groups who are usually the oldest males in the group (Cant, 2000) and who obtain most within-group paternity, while younger males are mostly excluded from reproduction. On average, the three oldest males in groups sire 85% of juveniles per group breeding attempt (Nichols et al., 2010). Males tend to mate-guard, and mate with, the oldest females in groups first, but a substantial majority of females in groups (83%) conceive (Cant, 2000), and almost all pregnant females give birth, usually on the same day (Cant et al., 2013). Furthermore, group members often remain in and breed within their natal group for their entire lives, rarely emigrating voluntarily. Instead, females, and less often males, leave groups when they are violently evicted by groupmates; these evicted individuals form new groups themselves, or join other groups (Thompson, Cant, et al., 2017; Thompson et al., 2016).

At all times during the reproductive cycle, but especially during group oestrus, groups engage in intergroup contests (Fig. 1; Thompson, Marshall, et al., 2017). Many contests begin because oestrous females lead their group into a rival group's territory (Cant et al., 2002; Johnstone et al., 2020), triggering an intergroup contest during which the females can escape their within-group mate guard and mate with a male from the rival group. Females are thought to initiate intergroup contests and mate with rival group males because rival group males are less closely related to them than are their within-group mate guards (Nichols et al., 2012). Juveniles conceived as a result of outgroup matings are more genetically heterozygous and heavier and more likely to survive to adulthood (1 year) than within-group offspring (Nichols et al., 2015). It is unknown whether females vary (e.g. by age rank) in their likelihood of seeking outgroup matings or initiating intergroup conflicts (Cant et al., 2002; Johnstone et al., 2020). While females appear to initiate contests to gain fitter offspring, males are the main participants in the resulting fights, showing higher levels of aggression (Cant et al., 2002), paying more of the costs of injury and death (Johnstone et al., 2020) and being more important to contest success (Green et al., 2022) as compared to females.

Figure 1. Banded mongooses during an intergroup contest. Although all group members can participate, males contribute more and pay more of the costs of competition. Photo: Mark MacEwen.

Our current understanding of this system suggests that males participate disproportionately in contests and that females, especially when in oestrus, usually start contests but contribute little to them otherwise. Common assumptions of intergroup conflict theory (Choi & Bowles, 2007; Lehmann & Feldman, 2008) and findings in human societies (Glowacki & Wrangham, 2015; Macfarlan et al., 2018) would therefore suggest that male banded mongoose should be motivated to compete to maintain fitness in the form of paternity over their offspring. That is, males in focal groups are motivated to quickly dispel rival males from the site of the contest, thereby reducing the likelihood that these rival males mate with focal group oestrous females and usurp focal male paternity. An alternative hypothesis, inspired more directly by the biology of the banded mongoose system, suggests a disconnect between contest outcomes and fitness outcomes. If rival group males are more motivated to mate with focal group oestrous females than to fight, then focal groups with oestrous females may win contests because rival group males are not participating, but the focal group males may also lose paternity to rival group males.

We tested between these hypotheses by adapting the framework of animal contest theory from its roots in dyadic (one-on-one) contests (Parker, 1974) to the case of intergroup fights (Green, Briffa, et al., 2021). In the contest literature, contest success is defined as the ability of an individual or, in this case, of a group, to dispel its rival from the site of the contest (Briffa et al., 2013). This success depends on two main factors: (1) resource-holding potential (RHP), which is a measure of intrinsic fighting ability, and (2) the motivation to compete, based on the valuation of the contested resource, termed ‘resource value’ or RV (Arnott & Elwood, 2008; 2009; Maynard Smith, 1974; Parker, 1974). In intergroup contests, the RHP/RV framework has been used to test what determines contest outcomes in multiple nonhuman primate species (Majolo et al., 2020), ants (Batchelor & Briffa, 2010; Chapin et al., 2022), lions (Mosser & Packer, 2009), birds (Radford, 2003; Strong et al., 2018) and wolves (Cassidy et al., 2015), among others (reviewed in Green, Briffa, et al., 2021). Most often, intergroup contest RHP is related to overall group size (i.e. number of adults), while RV is related to where on each group's territory a contest occurs (reviewed in Green, Briffa, et al., 2021).

In banded mongoose societies, prior work has shown that group RHP is related to the number of males and the age of the oldest male, which are the primary determinants of group fighting ability and predict a group's success in dispelling its rival from the site of the contest (Green et al., 2022). Both hypotheses we test here predict that RV in banded mongoose contests is related to group oestrus status. That is, whether males from groups with oestrous females are motivated to displace rival males and maintain paternity over their own offspring or rival group males are distracted from fighting by the potential to mate with the focal group's oestrous females; in either case, groups with oestrous females should be likely to win against groups without oestrous females.

We also took advantage of a well-resolved pedigree of the population (Nichols et al., 2012; Wells et al., 2018) to explore links between contest outcomes and fitness outcomes. Specifically, we tested whether or not winning in a behavioural sense (i.e. displacing rival groups) also resulted in winning in a fitness sense. The hypothesis that focal groups win because focal group males are motivated to defend their paternity suggests that success in displacing rival groups should result in a maintenance of or, in scenarios where females in both groups are in oestrus, gain of paternity over juveniles for within-group males. By contrast, if rival group males are distracted from fighting and instead aim to secure outgroup matings, then groups that win while having oestrous females might be expected to lose paternity. Links between contest and fitness outcomes are assumed in theories of the evolution of warfare (Choi & Bowles, 2007; Lehmann & Feldman, 2008) and are supported by observational studies of human societies, where winning intergroup fights comes with fitness benefits to participants (Glowacki & Wrangham, 2015; Macfarlan et al., 2018). However, while studies in nonhuman animal taxa have considered fitness consequences of intergroup conflict ranging from group member death to changes in territory size (reviewed in Braga Goncalves et al., 2022), few, if any, have asked how intergroup conflict outcomes lead to fitness benefits in the form of parentage over offspring.

Finally, we asked how fitness benefits might affect contest participation, specifically testing whether males of different age achieved different fitness benefits by mating instead of fighting during intergroup conflict. Group members may vary in the benefits they receive from participating, or not participating, in intergroup fights. In vervet monkeys, *Chlorocebus pygerythrus*, for example, females motivated to gain food attempt to coerce their male groupmates to fight (Arseneau-Robar et al., 2016), while males, especially those who are wounded and unable to fight well, punish these coercive females to decrease the chance a fight occurs (Arseneau-Robar et al., 2018). In banded mongooses, variation in intergroup conflict participation seems most likely related to the individual fitness benefits that could be gained by mating instead of fighting. Because the oldest males in groups sire the greatest proportion of juveniles per litter (Nichols et al., 2010), younger males may be expected to make up for this fitness detriment by mating instead of contributing to intergroup fighting. Therefore, and irrespective of the drivers of contest outcomes (i.e. the two hypotheses established above), we predicted that younger males in groups would see a disproportionate increase in their mating success when considering offspring sired during intergroup fighting, as compared to offspring sired by within-group mating only.

In summary, we used our long-term data to test alternative hypotheses regarding the link between contest outcomes and reproductive success in banded mongooses. One hypothesis, informed by prior evolutionary theory and studies of human societies, suggests that banded mongoose groups with oestrous females (1) win contests against groups without oestrous females and (2) maintain, or gain, paternity as a result of winning contests. A second hypothesis, modified by our understanding of the banded mongoose system, suggests that groups with oestrous females still (1) win contests against groups without oestrous females but (2a) may lose paternity despite winning contests. Finally, we tested whether (3) younger males in groups gain disproportionate reproductive success when we incorporate outgroup matings.

METHODS

Ethical Note

All research procedures received prior approval from the Uganda Wildlife Authority (reference number COD/96/05), the Uganda National Council for Science and Technology (registration number NS164ES) and the Ethical Review Committee of the University of Exeter. All procedures adhere to the ASAB/ABS Guidelines for animals in behavioural research and teaching.

Study Population and Data Collection

We collected data on naturally occurring contests between banded mongoose groups on and around the Mweya peninsula in Uganda (0°12′S, 29°54′E) from February 2000 until April 2019. Following Thompson, Marshall, et al., 2017, we defined an intergroup contest as occurring when two groups sighted each other and responded by producing collective 'war cry' calls and chasing and/or engaging in physical fighting. We only analysed contests in which a clear winner and loser could be determined; losing groups were those that left the area of the contest, while winning groups remained (often chasing away the losing group). Additionally, because we were interested in how male group members (who disproportionately affect contest success; Green et al., 2022) value resources, we only analysed contests in which each group had at least one male member. Groups without males are rare and almost always short-lived; our filtering removed 51 contests involving three all-female groups. Most (48/51) involved a single all-female group, while two all-female groups accounted for the remaining contests.

For each contest, daily observations of group members allowed us to quantify female oestrous status for each group based mainly on observations of mate guarding: if males were closely mate guarding females on the day of the contest, the group was considered in group oestrus. However, oestrus can be subtle and not involve conspicuous mate guarding; therefore, we added data on group oestrus by back-calculating from birth data. If any females in a group gave birth within 55–70 days of an intergroup contest, we considered the group to be in group oestrus on the date of the contest (55–70 days is a likely time frame between group oestrus and when juveniles are born; Cant, 2000). The main data set contained full data on 261 contests between 16 focal groups and 15 rival groups.

Statistical Analysis

All analyses were completed in R software version 4.4.0 (R Core Team, 2020).

To test the hypothesis that group oestrous status predicted contest outcomes, we first identified 104/261 contests where one group was in oestrus and the other group was not, treating the oestrous group as the 'focal' group. In situations where both groups were in oestrus (15/261 contests) or neither group was (142/261 contests), we randomly selected a focal group. This random selection was based either on the group the field team was following at the time of the contest (followed group being the focal) or by randomly choosing one of the two competing groups to be the focal using the ‘sample’ function in R. We first built a statistical model predicting the probability that the oestrous group, or in cases where neither or both groups were in oestrus, a randomly selected focal group, won from relative oestrous status (both no; one yes, one no; both yes), along with random effects of focal and rival group identity. We fitted the model using a Bradley—Terry model structure (Bradley & Terry, 1952) in the ‘MCMCglmm’ package version 2.34 (Hadfield, 2010). We used the Bradley—Terry structure to account for the fact that, in analyses of the effect of relative (i.e. focal—rival) predictors on contest outcomes when there are repeated observations for each group, focal and rival group identity can be arbitrary and only one observation (win or loss) is recorded for both groups. In these scenarios, a group that consistently wins contests would be expected to win when acting as the (arbitrarily designated) focal group and lead to losses in a focal group when acting as the (arbitrarily designated) rival group. Therefore, in these models the random effect variance of focal and rival group identity should be equal and their correlation equal to −1 (for more justification, see Dyble et al., 2019; Lane et al., 2020; A. J. Wilson, de Boer, et al., 2011; A. J. Wilson, Morrissey, et al., 2011). Following a similar approach as Dyble et al. (2019), each model had uninformative parameter-expanded priors and ran for 1 050 000 iterations, where the first 50 000 iterations were discarded and samples were saved every 250 iterations. We ensured good model fit by inspecting plots of effect sizes across iterations, checking that autocorrelation was low among consecutive thinned observations and fixed effects and by ensuring that Heidelberg and Geweke diagnostic values and plots met expectations for good model fit.

In addition to the analysis described above, we used two post hoc analyses to further contextualize our findings regarding how oestrous status affected intergroup contest outcomes. The first analysis compared the effect of group oestrous status as a metric of RV to other potential metrics of RV (relative number of females, relative number of juveniles), as well as to previously established metrics of RHP in this system (relative number of males, relative age of the oldest male; Green et al., 2022). This type of analysis is useful in contextualizing the effect of a hypothesized metric of RV while controlling for the effect of other known, or hypothesized, determinants of contest outcomes (Harris, 2007). In essence, this first post hoc analysis added further predictor variables to the MCMCglmm analysis described above and assayed whether the effect of oestrous status was still (one of) the strongest predictor(s) affecting contest outcomes. The second analysis asked whether contest outcomes were related to the location of the contest on each group’s territory. Contest location (relative to territorial home range) is often a predictor of contest success in other intergroup conflict systems, as territory can contain valuable resources like food and shelter (e.g. Crofoot et al., 2008; Green, Briffa, et al., 2021; Markham et al., 2012; Radford & Fawcett, 2014). In this analysis, we built a MCMCglmm model to test whether contest outcomes in banded mongooses were predicted by previously established metrics of RHP (see above; also see Green et al., 2022) and the amount of time each group spent in the area of the contest in the 90 days prior to the contest. Due to limitations of location data relative to other types of data, the location analysis used a smaller data set than that tested in our main analysis. Both post hoc analyses are briefly reported in the Results and details are given in the Appendix.

To test the prediction that groups that won contests also maintained or gained paternity over offspring, we used previously constructed paternity data for the population (parentage assignments following methods in Sanderson et al., 2015; Wells et al., 2018; pedigree included with deposited data). These paternity data identified 1720 juveniles in 388 litters sired by 250 males. We identified the group to which each juvenile was born and the group to which each juvenile’s sire belonged at the time of the juvenile’s birth. We then randomly assigned focal and rival group identity to each competing group without considering relative oestrous status. That is, in scenarios where one group was in oestrus and the other was not, we did not assign focal status to the oestrous group but instead randomly selected one group as focal. We then identified juveniles born to either the focal or rival group and born within 55—70 days after a contest (a time frame in which juveniles could likely be sired by members of the rival group; Cant, 2000). We subset these data to include only juveniles born when there was a single contest recorded within the 55—70 day oestrous window and for which we knew which group won that contest. Although it was not possible to observe all contests that groups engaged in, this approach gave the most certainty that any change in paternity was a result of a single contest of interest. For each contest, we noted the oestrous status of each group (both groups in oestrus or only one group in oestrus), which group won and the number of juveniles born to and sired by either competing group**.** Our final data set in this analysis consisted of 197 juveniles born in 42 unique litters, with a total of 69 sires.

We then built a statistical model (binomial generalized linear mixed model, GLMM, ‘lme4’ package version 1.1.30; Bates et al., 2015) in which the outcome variable was the proportion of juveniles in a given litter of which paternity was gained, or retained, by the focal group. That is, ‘successes’ in this binomial model were juveniles for which paternity was gained or retained, while ‘failures’ were juveniles for which paternity was lost to males in the rival group. The predictor variables included focal outcome (win/loss) and relative oestrous status (one yes | one no, both yes), and random effects included contest and group identity (for both the group siring the juveniles and the group into which the juveniles were born). While we initially included an interaction term between focal outcome and relative oestrous status, we removed this interaction term after identifying high variance inflation factors in predictor variables when the interaction was included (Zuur et al., 2010). We further tested for model fit by viewing histograms of model residuals, investigating potential outliers (there were none) and running the model with multiple optimizer approaches. All techniques suggested good model fit. We tested for significant effects of focal group outcome and relative oestrous status using a Wald chi-square test in the ‘Anova’ function in the ‘car’ package version 3.1.0**.**

Finally, to test whether younger males achieved disproportionate fitness benefits by mating during intergroup conflict, we analysed the relationship between male age rank and siring success. We first identified how many juveniles in a given litter were sired by each male. We also calculated each male’s age rank in their own group: we ranked each male in each group according to his age 70 days before a given juvenile was born (i.e. on the earliest date of its conception), with the oldest males in a group holding rank one and males of the same age having the same rank (i.e. ties were allowed). We also categorized whether each juvenile born was sired by an ingroup male, a male residing in the same pack as the juvenile 70 days before the juvenile’s birth, or an outgroup male, a male that was not in the juvenile’s pack 70 days before the juvenile’s birth. We assumed that all juveniles born to outgroup males were conceived during intergroup conflict. This is because, in 25 years of near-daily observation of each group in this population, and in contrast to other social animal systems (e.g. Ben Mocha et al., 2018; Young et al., 2007), we have never observed outgroup mating to take place outside of the context of intergroup contests (F. Mwanguhya & M. A. Cant, personal observations). In the lme4 package, we built a GLMM with a binomial error structure. In this model, the proportion of pups sired in each litter was the response variable, while the age rank of male sires, whether the sire was an ingroup or outgroup male, and the interaction of these terms were fixed effect predictors. We also included random effects of sire group identity, sire identity and litter identity. We ensured good model fit by investigating a histogram of model residuals. We tested for the significance of the interaction between sire age rank and ingroup|outgroup status through a Wald chi-square test using the ‘Anova’ function in the car package.

RESULTS

Our test of the hypothesis that group oestrous status affected contest outcomes found that, when one group was in oestrus and its rival was not, the oestrous group won 62% (64/104) of contests. In other relative oestrous status scenarios, the randomly selected focal group’s contest success averaged 49% (77/157 contests; MCMCglmm mean estimate of oestrous status effect on outcomes = 0.69, 95% credible interval (CrI) = 0.08, 1.13, pMCMC = 0.03; Fig. 2, Table 1).

Our post hoc analysis that tested the combined effects of RHP and RV metrics on outcomes showed that the mean estimate of group oestrus (i.e. our hypothesized metric of RV) was higher than that of a previously established metric of group RHP, the relative age of the oldest male in the group (Appendix, Fig. A1, Table A1). However, due to a relatively low sample size of contests in which groups differed in oestrous status, the credible interval of this effect overlapped zero (Appendix, Table A1, Fig. A2). Converting the estimate from this post hoc model to an odds ratio (Halsey, 2019) revealed that groups with oestrous females increased their chances of contest success by a mean of 2.64 times, with a 95% credible interval ranging from 0.88 times to 8.25 times. Other potential metrics of resource value (number of females, number of juveniles, location of the contest on each group’s territory) had little to no impact on contest outcomes (Appendix, Fig. A1, Tables A1–A2).

In our analysis of how contest outcomes affected paternity, we found that 18% (36/197) of juveniles born after intergroup conflicts were sired by males from rival groups. This outgroup siring was uneven across contests: in 25% of contests (12/48), more than half of the juveniles born in a given litter were sired by males from rival groups (mean ± SD = 61 ± 30%; range 17–100% of juveniles born per litter). In the remaining 75% of contests, all juveniles were sired by ingroup males. Counter to our prediction that winning groups retained or gained paternity, there was no significant effect of winning or losing contests on the proportion of juveniles per litter for which paternity was gained or lost (Table 2). In fact, and surprisingly, there was a nonsignificant tendency ($P = 0.10$) for focal groups that won contests to lose a greater proportion of paternity of juveniles to males from the rival group, as compared to groups that lost contests (Fig. 3). Focal groups that won contests saw a mean loss of paternity of 12.4% of juveniles per litter (SD = 39.9%, maximum proportion lost = 100%, maximum proportion gained = 60%), while focal groups that lost saw a mean gain of paternity of 9.5% of juveniles per litter (SD = 35.8%, maximum proportion lost = 60%, maximum proportion gained = 100%). There was no significant effect of relative oestrous status on paternity gain or loss (Table 2). Summary statistics for changes in paternity are reported in the Appendix (Table A3).

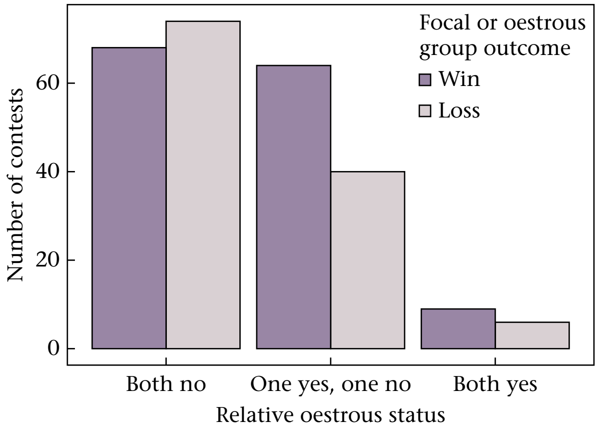

Figure 2. Frequency of contest outcomes grouped by relative oestrous status. Bar plots show the number of contests won or lost by groups according to their group oestrous status and that of the rival group (also see Table 1).

Table 1
Output from MCMCglmm model predicting oestrous group win/loss from relative oestrous status

Predictor	Posterior estimate mean	95% CrI of posterior estimate	pMCMC
Intercept	−0.11	−0.50, 0.30	0.60
One yes, one no	0.69	0.08, 1.33	**0.03**
Both yes	0.61	−0.64, 1.92	0.38
Random effect	Posterior mean	95% CrI of posterior mean	
Oestrous focal ID + oestrous rival ID	0.08	0.00, 0.34	

CrI: credible interval. Estimates for relative oestrous categories are in comparison to the ‘Both no’ category. Significant P values (<0.05) are shown in bold.

Table 2
Output from model predicting the proportion of juveniles per litter for which paternity was retained or gained by the focal group from contest outcome and oestrous status

Fixed effect	Contrast	β	SE	χ^2_1	P
Intercept		11.59	6.69	3.00	0.08
Focal outcome	Loss	0.00	0.00		
	Win	−4.19	2.57	2.66	0.10
Oestrous category	Both yes	0.00	0.00		
	One yes, one no	3.20	3.50	0.84	0.36
Random effect	Variance	SD			
Contest ID	1.65	1.29			
Birth group ID	39.57	6.29			
Sire group ID	38.54	6.21			

Finally, our test of the hypothesis that younger males achieved disproportionate fitness benefits during intergroup conflict showed that, for paternity occurring in nonconflict scenarios (i.e. within-group paternity), older males sired the greatest proportion of juveniles in each litter (Fig. 4; a similar relationship as prior analyses; Nichols et al., 2010). By contrast, and matching our prediction, younger and older males sired an equal proportion of juveniles per litter during intergroup conflicts (GLMM estimate for the interaction term of the effect of sire age rank and paternity category = 0.04, SE = 0.02, $\chi^2_1 = 4.90$, $P = 0.03$; Fig. 4, Table 3). That is, younger males saw a disproportionate increase in their fitness when considering matings during intergroup conflict, as compared to within-group (i.e. nonconflict) matings.

DISCUSSION

Studies of the direct fitness consequences of intergroup fight outcomes are essential to testing theories regarding how and why group members contribute to collective conflict in animal societies (Choi & Bowles, 2007; Lehmann & Feldman, 2008); however, these

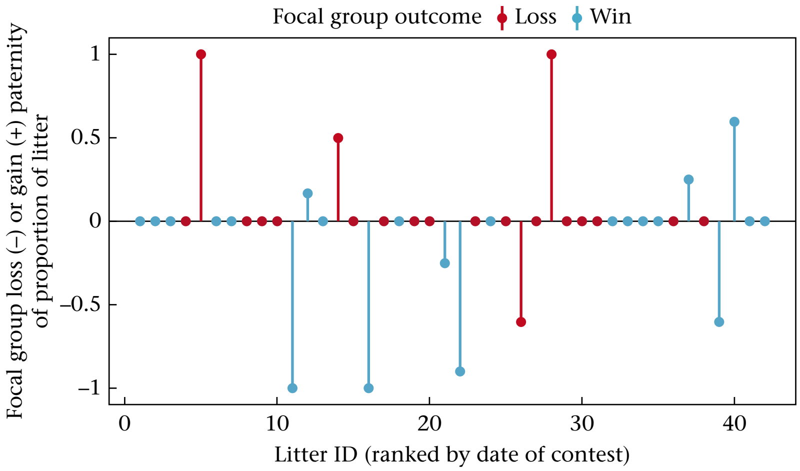

Figure 3. Points with connecting bars show, for each litter born after an intergroup contest (*X* axis), the proportion of juveniles for which paternity was gained (positive *Y* axis values) or lost (negative *Y* axis values) by focal groups (focal group identity was randomly assigned, see Methods; values of zero reflect retention of paternity by the focal group). The *X* axis is ordered based on ranked date of contest (lower contest numbers occurred earlier in data set). Summary statistics are detailed in the Appendix (Table A3).

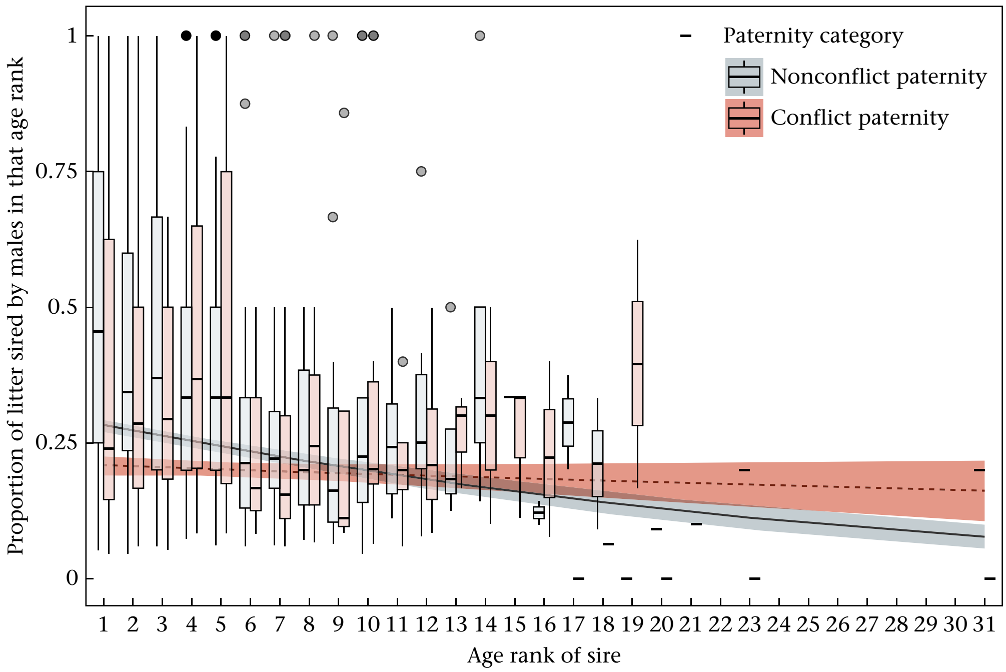

Figure 4. Box plot showing the proportion of juveniles sired by males in each age rank (1 = oldest male in their own group). Lines with error ribbons show predicted values from the interaction term of a binomial GLMM predicting the proportion of litters sired by age rank, nonconflict (solid line with grey ribbon) or conflict (dashed line with orange ribbon) paternity and their interaction.

Table 3
Output from model predicting the proportion of juveniles in each litter from sire age rank, ingroup|outgroup status and their interaction

Fixed effect		β	SE	χ^2_1	*P*
Intercept		−1.09	0.06		
Sire age rank		−0.19	0.04	17.49	**<0.01**
Ingroup | outgroup	Ingroup	0.00	0.00	8.15	**<0.01**
	Outgroup	−0.28	0.09		
Sire age rank : Ingroup | outgroup		0.15	0.07	4.90	**0.03**

Random effect	Variance	SD
Sire group	0.00	0.06
Sire ID	0.01	0.12
Litter ID	0.06	0.24

Significant *P* values (<0.05) are shown in bold.

data are exceptionally rare outside of humans (Glowacki & Wrangham, 2015; Macfarlan et al., 2018; but see Braga Goncalves et al., 2022). In banded mongooses, oestrous females benefit from their group engaging in intergroup fights because these females gain fitness in the form of outbred offspring that are healthier than offspring sired by more closely related within-group males (Johnstone et al., 2020; Nichols et al., 2015). The analyses we present here suggest contest outcomes may be driven by rival group males avoiding fighting in favour of attempting to gain outgroup matings. Groups with oestrous females were more likely to defeat groups without oestrous females (Fig. 2). However, males from groups that won contests in a behavioural sense, repelling their rivals from the site of the fight, did not see an increase in their fitness; instead, they tended to suffer a net loss of fitness (paternity over juveniles) to males from losing groups (Fig. 3), suggesting males from losing groups were focusing on gaining matings, not on competing. Finally, we found evidence that the youngest males in groups gained disproportionate fitness benefits by mating during intergroup conflict, as compared to the fitness benefits of mating outside of conflict (Fig. 4). Below, we discuss the importance of these results to our understanding of animal conflict and its influence on social evolution.

In both dyadic and intergroup contests, contest outcomes can be determined by either or both of fighting ability (resource-holding potential, RHP) and the motivation to compete, which is driven by resource value (RV; Arnott & Elwood, 2008, 2009; Green, Briffa, et al., 2021). Prior work in banded mongooses showed that the number of males in a group, and the age of its oldest male, comprised RHP (Green et al., 2022). The results presented here show that female oestrous status is a likely metric of resource value in banded mongoose contests. Relative oestrous status had a strong effect on contest outcomes on its own (Fig. 2), and, when tested in a model with other RV and RHP metrics, a stronger effect on outcomes than any other tested RV metric (Appendix, Tables A1−A2). In addition, although our analysis was limited by a small sample size of contests between groups with mismatched oestrous status, the mean estimate value of relative oestrous status was greater than that of a previously established RHP metric, the relative age of the oldest male (Appendix, Table A1; see Green et al., 2022 for further discussion of RHP in banded mongoose contests). Prior studies of resource value effects in nonhuman animal intergroup conflict have generally found that contest outcomes are influenced by, or later affect, territory residency (Crofoot et al., 2008; Markham et al., 2012; Radford & Fawcett, 2014; Strong et al., 2018) and movement patterns (Christensen et al., 2016; Crofoot, 2013). Our results likely stem from specifics of the banded mongoose system, in which groups are relatively highly inbred (Nichols et al., 2012), outgroup mating is an important source of genetic heterozygosity (Nichols et al., 2015) and, from our 25 years of observation, all outgroup matings occur during intergroup conflict (F. Mwanguhya & M. A. Cant, personal observations; Johnstone et al., 2020). However, reproductive resources may affect intergroup conflict outcomes in other systems (Braga Goncalves et al., 2022). For example, just as for banded mongooses, intergroup contests can result in outgroup matings in common marmosets, *Callithrix jacchus* (Lazaro-Perea, 2001), while reproductive individuals are targeted and killed during intergroup conflicts in dampwood termites (Thorne et al., 2003). In these and other systems, however, the gain or loss of reproduction after contests has not been directly connected to the outcomes of contests. More broadly, our results mirror those of other recent studies (Cassidy et al., 2015; Dyble et al., 2019; Green et al., 2022) by showing the importance of looking beyond traditional measures of RHP (e.g. group size) and RV (e.g. territory location) when considering what factors influence the outcomes of intergroup conflict.

While our behavioural results could not directly disassociate whether outcomes were driven by focal group male motivation to defend paternity versus rival group male motivation to gain outgroup paternity, our analysis of paternity data suggested the latter. Groups that won contests (repelling rivals from the site of the contest) did not gain fitness benefits in terms of paternity over offspring. Instead, winning groups tended to lose paternity, as compared to groups that lost contests (Fig. 3). Because we designed our analyses to maximize certainty that any paternity change was a result of a single contest, changes in paternity were rare (12/36 unique contests, 36/197 juveniles) and loss of paternity was not statistically significant after controlling for repeated measures of litter, contest and group identity (Table 2). However, the rate of extra-group paternity we discovered (18% of juveniles sired) is greater than that of most social mammals (mean extra-group paternity rate across 26 species of social mammal = 15.2%; see Isvaran & Clutton-Brock, 2007), showing the relevance of intergroup fighting to outgroup mating in this system. Furthermore, our finding that gaining extragroup offspring does not come as a result of winning intergroup contests runs counter to theory and data on the evolution of warfare in human societies, where victory in intergroup contests is assumed, or found, to bring fitness rewards in terms of enhanced reproductive success (Choi & Bowles, 2007; Lehmann & Feldman, 2008; Lehmann & Rousset, 2010). For example, in Nyangatom societies of Ethiopia and South Sudan, victory in intergroup raids results in material and, correspondingly, fitness benefits to male participants (Glowacki & Wrangham, 2015). By contrast, our findings highlight that contests can result in a disconnect between group success and individual fitness and that the opportunity costs involved in fighting can undermine group cohesion and performance.

Our results may differ from those of other systems for several reasons, suggesting broader work towards understanding links between conflict outcomes and fitness outcomes. For example, in systems like the Nyangatom and other human (Macfarlan et al., 2018) and nonhuman animal systems (e.g. chimpanzees; M. Wilson & Wrangham, 2003), the same individuals both initiate and participate in conflicts. By contrast, in banded mongooses, females are ‘exploitative leaders’, initiating contests while males do most of the fighting, including paying most of the costs (Johnstone et al., 2020). Indeed, it seems likely that male banded mongooses, while participating in fights that their own group’s oestrous females initiate, are distracted from the task of mate guarding females, leaving those females able to find, or be found by, rival group males. More detailed behavioural observations tracking individual movements during contests are needed to confirm this idea. In general, conflicts of interest in contest participation like those we see in banded mongooses also occur in other nonhuman animal systems (Arseneau-Robar et al., 2016, 2018; Smith et al., 2022). Perhaps systems with disconnects between conflict initiation and participation are also more likely to have disconnects between conflict and fitness outcomes, but more data are needed to test this hypothesis.

Further data comparing short-term and long-term fitness consequences of intergroup fights, including in banded mongooses, would also be useful to understanding our results. Our analyses focused on the immediate fitness consequences of contest outcomes; that is, paternity over offspring sired at the time of conflict. However, fitness benefits may not be realized until long after a conflict (Braga Goncalves et al., 2022). In the Waorani of Ecuador, for example, men that participate in intergroup raids together are more likely to marry each other’s kin following cultural ideals (cross-cousin marriages), as compared to men who were not raid partners (Macfarlan et al., 2018). However, these marriages occurred an average of 7 years after the partners' first raid (Macfarlan et al., 2018). Similarly, the link between conflict outcomes and fitness outcomes in Nyangatom warriors (see above) is only realized later in life, not at the time of conflict (Glowacki & Wrangham, 2015). One way that banded mongooses could experience delayed fitness benefits is if certain males participate in conflicts, that is, contribute to collective fighting instead of attempting outgroup mating, in order to signal to within-group females their quality as mates. These males may then receive long-term fitness benefits (i.e. later ingroup matings) that we were unable to quantify here. However, while there is evidence that close inbreeding is avoided within banded mongoose groups (Nichols et al., 2012), our behavioural observations suggest that females show no choice over their male mate guards, and we have no evidence that females select within-group sires based on prior contest participation or fighting ability. In general, models of the evolution of intergroup conflict have not explored variation in the timing or durability of the fitness impacts of victory or loss (Choi & Bowles, 2007; Lehmann & Feldman, 2008; Lehmann & Rousset, 2010), and understanding variation in short- and long-term fitness consequences could be useful to understanding how selection acts on conflict participation in group-living animals.

Our findings highlight the collective action problem (CAP) that is inherent in intergroup conflict and that occurs more generally in both human and nonhuman groups (Crofoot & Gilby, 2012; Lewis et al., 2020; Olson, 1965). Collective action problems arise when individuals contribute to a public good (such as winning an intergroup contest) at personal cost, leading to a temptation to defect or shirk. In heterogeneous groups, weaker group members are predicted to free-ride on the contributions of their stronger groupmates, gaining the benefits of group success while minimizing their own efforts (Green, Briffa, et al., 2021; Olson, 1965). Collective action is further undermined if free-riders can not only avoid the costs of contribution, but also gain a fitness benefit by not contributing, as we found is the case for young adult male banded mongooses (Fig. 4). Older males may make up for their free-riding groupmates by contributing more to the fight; indeed, our results (Appendix, Fig. A1, Table A1) support those of a prior analysis (Green et al., 2022) showing that the oldest males in groups have a disproportionate impact on contest success. A recent theoretical model (Gavrilets & Fortunato, 2014) suggests that stronger (here, older) males may 'solve' the CAP by overcompensating for lack of investment by weaker individuals, ensuring that heterogeneous groups can remain competitive despite free-riders. Our results are consistent with the predictions of this model: when fighting against groups with oestrous females, groups without oestrous females (i.e. those facing a potential CAP) still won 38% of contests (Fig. 2). Although beyond the scope of the present analysis, future analyses should further explore collective action in banded mongooses by accounting for relatedness both within and between competing groups. For example, older males might be more willing to contribute to within-group fighting effort if presumably 'free-riding' younger males in their group are more closely related to them. Similarly, males might fight less hard to defend own-group oestrous females if those males are closely related to rival group males who might attempt outgroup matings.

Much of the recent interest in intergroup conflict stems from its proposed role as a force favouring the evolution of cooperation in group-structured societies. For example, the parochial altruism model suggests that the potential for intergroup conflict can lead to the coevolution of intense hostility (parochialism) towards outgroups and intense favouritism (altruism) towards members of an ingroup (Choi & Bowles, 2007). Banded mongooses have been cited as consistent with this model because of their group structuring (Dyble, 2021; Nichols et al., 2012; Thompson, Marshall, et al., 2017), which is expected to lead to both high levels of hostility and high levels of within-group cooperation. However, the parochial altruism model (and other evolutionary models of human warfare, e.g. Lehmann & Feldman, 2008; Lehmann & Rousset, 2010; Rusch & Gavrilets, 2020) assumes that groups contain *n* identical individuals, such that groups do not face internal conflict over whether to initiate contests or collective action problems over contributions to fighting. The banded mongoose system suggests that within-group heterogeneity can have important effects on the frequency and effectiveness of fighting. The presence of exploitative leaders (females) who take a disproportionate share of the fitness benefits of victory and/or pay disproportionately few costs is predicted to increase the frequency and severity of conflict (Hunt et al., 2024; Johnstone et al., 2020; Sankey et al., 2022). At the same time, our results show that heterogeneity in the costs and benefits of participation, especially the potential gain of fitness by avoiding fighting and instead mating, can also undermine the effectiveness of collective fighting, making victory less likely. Future theory development and testing on tractable systems would help to reveal how these different factors interact to influence intergroup fighting and the evolution of altruism.

In summary, our results show how fitness benefits to individual group members can have the simultaneous effects of motivating participation in intergroup fights for one group while detracting from participation in the other group. In so doing, this study highlights that 'success' in intergroup contests should perhaps be defined more broadly than the common conception of repelling a rival group from the site of a contest. Instead, a greater balance between the individual fitness benefits and group level benefits of intergroup contest outcomes will be useful in efforts to test key theories of the evolution of intergroup conflict in animal societies.

Author Contributions

P.A. Green: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **D.W.E. Sankey:** Methodology, Data curation. **T. Collins:** Formal analysis, Data curation. **F. Mwanguhya:** Project administration, Methodology, Investigation, Conceptualization. **H.J. Nichols:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **M.A. Cant:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **F.J. Thompson:** Writing – review & editing, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Data Availability

The data and code used in this study are available at Figshare, https://doi.org/10.6084/m9.figshare.24302293.

Declaration of Interest

The authors declare no competing interests.

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Appendix

Appendix Analysis Methods and Results

Effect of group oestrus in context

Our results (Fig. 2) showed that group oestrous status impacted conflict outcomes. We further probed this effect by comparing it to the effects of previously established metrics of RHP and other potential metrics of resource value in this system. The previously established metrics of RHP were the relative (focal − rival) number of males in each group and the relative age of the oldest male in each group, two factors shown to predict contest outcomes in a prior study (Green et al., 2022). The other potential metrics of resource value included the relative number of females and the relative number of juveniles in each group. Through data collected via daily observations (see Methods), we calculated the number of males, females and juveniles (group members <6 months old) in each group on the day of the contest. We also calculated the age of the oldest male in each group as the number of days between the date of the contest and the date of birth of the oldest male in each group. We then selected a focal and rival group for each contest; these focal and rival designations were the same as those described in the Methods for the analysis presented in Fig. 3.

We built a statistical model in which the dependent variable was whether the (randomly selected) focal group won or lost the contest (binary: 1 = focal win; 0 = focal loss) and the predictor variables were relative proxies of RHP (relative number of males, relative oldest male age) and RV (relative number of females, relative group oestrous status and relative number of juveniles). This model structure, especially the use of randomly selected focal and rival groups, let us compare the effect of group oestrous status as closely as possible to the effects of previously established RHP metrics, as published in Green et al. (2022).

In most cases, variables were integer variables calculated as focal group value minus rival group value (e.g. if the focal group had 4 females and the rival group had 2 females, relative N females = 2). The group oestrous status variable was similar to that of the model presented in the main text, but instead of testing from the perspective of the group in the group oestrous category (as in the model in the main text), we tested from the perspective of randomly selected focal and rival groups. As a result, relative group oestrous status was a four-level categorical variable with all combinations of focal and rival group oestrous status: focal group in group oestrus and rival group not in group oestrus, focal group not in group oestrus and rival group in oestrus, neither group in group oestrus, both groups in group oestrus. Correlations between integer predictor variables were low (Pearson correlation mean = 0.39, range 0.31–0.61).

Our statistical model had the same Bradley–Terry structure as that presented in the main text, to account for the random selection of focal and rival groups. We also used the same checks of model fit as presented in the main text.

In this model, group oestrous status was the only resource value metric that strongly impacted contest outcomes (Fig. A1). Focal groups had higher contest success rates when they were in group oestrus and their rivals were not. The mean estimate value of this effect was greater than one previously described RHP metric, oldest male age (Fig. A1, Table A1). However, the relative oestrous status estimate had a large credible interval. This large CrI could be a result of either (1) a truly variable effect of relative oestrous status on contest success, or (2) a relatively small sample size of contests in which this relative oestrous status occurred (56/261 total contests). We used a sensitivity analysis of the RHP effects of the relative number of males and the relative age of the oldest male to test whether sample size effects drove this high CrI.

We first used our full data set of 261 contests to build a MCMCglmm model predicting the likelihood of a focal win from the two RHP predictors: the relative number of males and the relative age of the oldest male in the contest. This ‘full data set model’ established the estimate and 95% CrI value of both previously established RHP predictors on the full data set. Next, we randomly sampled (without replacement) 56 contests from the overall ($N = 261$ contest) data set and built a MCMCglmm model of the same structure used on the full data set. This ‘downsampled data set model’ established an estimate and 95% CrI for both these predictors on a data set equal in sample size to that for the number of contests in which the focal Y | rival N oestrous category occurred. We extracted the mean and 95% CrI estimate values from the downsampled data set model, then repeated this permutation procedure for a total of 1000 estimate values. We removed models with poor fit, as evidenced by visual inspection of representative ‘caterpillar plots’ and using diagnostics described in the main text. Our final data sets included 902 estimates for relative number of males and 915 estimates for relative age of the oldest male.

We plotted these estimates for both the full data set model and each iteration of the downsampled data set model (Fig. A2). In total, 63 of 902 (7.0%) of the 95% CrIs of the relative number of males effect overlapped zero, while 584 of 915 (63.8%) of the 95% CrIs of the relative age of the oldest male effect overlapped zero. Because these previously established (Green et al., 2022), strong predictors of RHP also showed high levels of variability, including 95% CrI overlap with zero, in many iterations, it suggests that the large CrI of the effect of focal Y | rival N oestrous status on contest outcomes is a product of a relatively small sample size of contests in which this relative oestrous status occurred, not that the effect of relative oestrous status is inherently more variable than that of other effects.

Location effects

In many animal societies, the relative location of the contest on each group’s territory impacts contest success (Christensen et al., 2016; Crofoot et al., 2008; Markham et al., 2012). While we aimed to test for territory location alongside other metrics of resource value, location data were only available for 99 contests sampled across 12 years, compared to the 261 contests and nearly 20 years of sampling for the full data set. When using this limited location data set and building a model with the full set of predictor variables (i.e. those in Fig. A1), we were unable to achieve good model fit. Therefore, in addition to the statistical model described in the main text, we also built a model analysing the effect of previously described metrics of RHP (Green et al., 2022) (relative number of males and relative age of the oldest male) along with the relative location of the contest on each group’s territory. This analysis explicitly tests for the effect of contest location on outcomes, in as similar a way as possible to our analysis above, but while accounting for data set limitations.

Our data set with contest location data (hereafter, the ‘location’ data set) was a subset of the main data set that included 99 contests between eight focal groups and nine rival groups. Location data consisted of GPS location fixes of each group, collected by two methods. Between 2006 and 2014, location data were collected at the start and end of every group observation session using handheld Psion II data loggers (model LZ) and GPS units (Garmin eTrex). These data were called ‘hand’ data. Between 2014 and 2019, GPS fixes were collected every 30 min (between 0700 and 1900 hours, with a break between 1200 and 1500 hours, corresponding to when groups rest during the heat of the day) using GPS collars (Gipsy4 and Gipsy5, Technosmart, Italy) fitted to a maximum of two individuals in each group. These data were called ‘collar’ data. The GPS collar data were filtered for accuracy following methods in (Green, Preston, et al., 2021). In addition to collecting location data throughout each day, the location of each contest was collected (either by hand or collar) at the time of the contest.

Our filtering process removed several GPS locations prior to analysis. GPS locations were discarded if they fell below four satellite connections or if their ‘horizontal dilution of precision’ values (accounting for heteroscedasticity from satellite reception) exceeded a value above 4 (Fleming et al., 2020). GPS locations were also discounted if they exceeded unrealistic altitudes (<800 m or >1100 m) (Preston et al., 2021). All GPS data were clipped using a detailed map of the Mweya Peninsula’s shape, to discount locations that fell in nearby Lake Edward, which is impassable for banded mongooses. GPS collar data often included data collected from two individuals within a group simultaneously. Including these records would constitute a duplicated time stamp and bias home ranges (Seaman & Powell, 1996). Instead, we kept only records for the mongoose that registered the greatest number of GPS locations. We did not average, or try to keep both of, the duplicated GPS trajectories because other days had only one collar measuring group location, and therefore this method is consistent with these nonduplicated days. Finally, we removed GPS locations where individuals wearing collars were guarding juveniles at the den, as any such data would not be reflecting group movement for that time period. In banded mongooses, groups only split when some individuals are left at the den with juveniles (Cant et al., 2013; Rood, 1974). Whether individuals left at the den were also wearing a GPS collar was assessed via field observations.

Our measure of the location of a contest on each group’s territory involved calculating how much time each group spent at the contest location before the contest occurred. Using default parameters in the ‘ctmm’ package (Calabrese et al., 2016), we first built utilization distributions (UDs) for the GPS location data of each group involved in the contest for the 90 days preceding the date of the contest (a time frame representing a full reproductive period; Cant, 2000). These UDs, which accurately account for autocorrelation in the telemetry data, represent a ‘familiarity index’ of each grid cell (average grid cell size was 5 × 5 m). The familiarity index describes how often the group was found in each grid cell, given the observed 90-day locations data. From these UDs, we then used the ‘raster’ function in ‘ctmm’ to generate a rasterized cumulative distribution function (CDF) of the location data. For each group (focal and rival), we calculated the rasterized CDF value of the location of the contest and subtracted this CDF value from 1. This created a metric in which a value of 1 represented a grid of the group’s UD that had been the group’s most occupied grid cell for the 90 days preceding the contest, while a value of 0 represented an unoccupied area of the group’s UD in the same time frame. We subtracted the rival group’s value from the focal group’s value to create a relativized metric that we called ‘relative familiarity’. If relative familiarity for a given contest was greater than 0, it meant the focal group spent more time at the location of the contest in the preceding 90 days than the rival group. Alternatively, if relative familiarity was less than 0, it meant the rival group spent more time at the contest location in the preceding 90 days as compared to the focal group.

With the location data set, we built a statistical model predicting the probability that the focal group won the contest from the relative (focal − rival) number of males, the relative age of oldest male (in days) and relative familiarity. We built this model in the ‘MCMCglmm’ package following the same methods, including the same checks of model fit, as those described for the model presented in Fig. A1.

The analysis of location data showed that relative familiarity did not influence contest outcomes (Table A2). Additionally, compared to the data sets used in Green et al. (2022, their Table S4) and in our analysis of the main data set (Fig. A1, Table A1), this model had lower estimates for the effects of both number of males and oldest male age on contest outcomes (Table A2). We found no differences in the distributions of raw data on the number of males or the oldest male age among the data sets (data set used in main text, location data set and data set from Green et al., 2022; pairwise *t* tests comparing number of males data among data sets: all $P > 0.30$; comparing oldest male age data: all $P > 0.18$). Instead, this discrepancy may be a result of decreased date ranges sampled in the location data set. The data set used in the main text sampled 19.7 years (7205 days), the data set used in Green et al. (2022) sampled 15.4 years (5622 days), and the location data set sampled only 12.3 years (4493 days).

Overall, we found no evidence that the location of the contest on each group’s territory influenced contest outcomes (Table A3).

Table A1

Output from MCMCglmm model predicting focal win/loss from RHP and RV predictors

Predictor	Posterior estimate mean	95% CrI of posterior estimate	pMCMC
Intercept	−0.08	−0.63, 0.50	0.78
Number of males	1.79	1.11, 2.47	**<0.01**
Oldest male age	0.69	0.18, 1.19	**0.01**
Number of females	0.08	−0.61, 0.72	0.79
Number of juveniles	−0.03	−0.46, 0.47	0.89
Focal N | Rival Y oestrus	−0.22	−1.44, 0.87	0.71
Focal Y | Rival N oestrus	0.97	−0.13, 2.11	0.09
Focal Y | Rival Y oestrus	0.56	−1.31, 2.35	0.56
Random effect	Posterior mean	95% CrI of posterior mean	
Oestrous focal ID + oestrous rival ID	2.45	0.00, 6.94	

CrI: credible interval; Y: yes; N: no. Estimates for relative oestrous categories are in comparison to the ‘Focal N | Rival N’ oestrous category. Significant *P* values (<0.05) are shown in bold.

Table A2

Output of MCMCglmm model predicting contest outcomes from resource-holding potential (RHP) variables and relative familiarity (representing contest location)

Predictor	Posterior mode	95% CrI	pMCMC
Number of males	0.88	0.76, 1.84	**0.046**
Oldest male age	0.35	−0.39, 1.12	0.335
Relative familiarity	−0.12	−1.05, 0.57	0.541

CrI: credible interval. Significant *P* values (<0.05) are shown in bold.

Table A3

Summary statistics for paternity of juveniles as a result of focal group outcomes and relative oestrous category

Focal loss or win	Oestrous category	Paternity gained	Paternity lost	Net paternity (gain − loss)	Paternity retained	Number of unique			
						Contests	Litters	Focal groups	Rival groups
Loss	Both yes	4	0	4	4	4	5	4	3
	One yes, one no	2	6	−4	14	15	15	9	4
Win	Both yes	1	6	−5	4	3	5	3	2
	One yes, one no	5	12	−7	16	17	17	6	8

For each win/loss and oestrous category, the table lists the number of juveniles for which paternity was gained or lost by the focal group, the net difference (gain − loss) and the number of juveniles for which paternity was retained. Other columns list the number of unique contests, litters and focal and rival groups for each category.

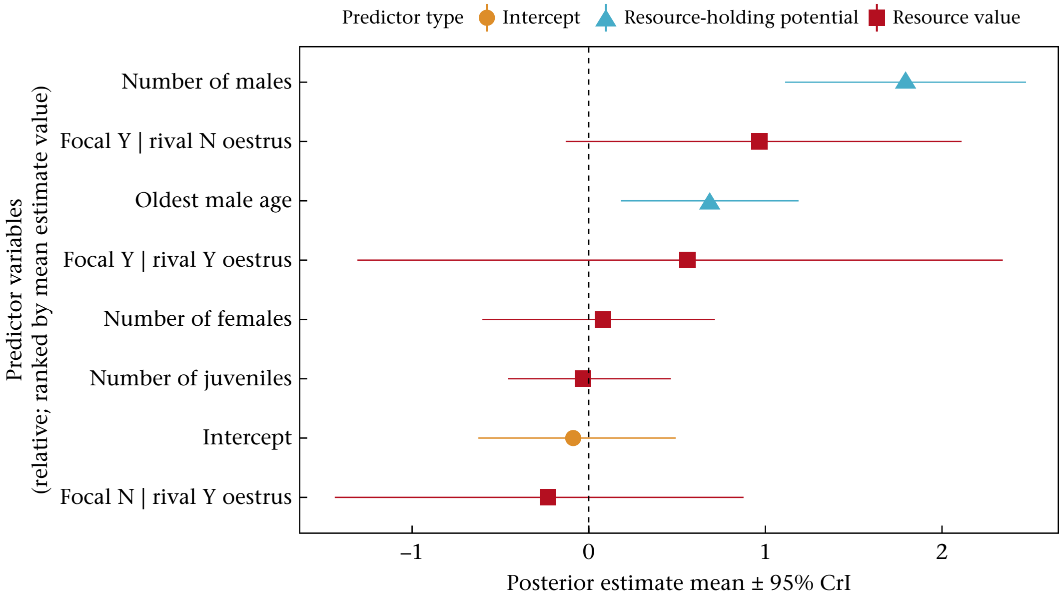

Figure A1. Posterior estimates from a MCMCglmm model testing how resource-holding potential and resource value metrics affected contest outcomes. On the *X* axis, points represent estimate means, lines represent 95% credible intervals (CrIs). Predictor variables (*Y* axis) are arranged in decreasing order of estimate mean (also see Table A1, Fig. A2).

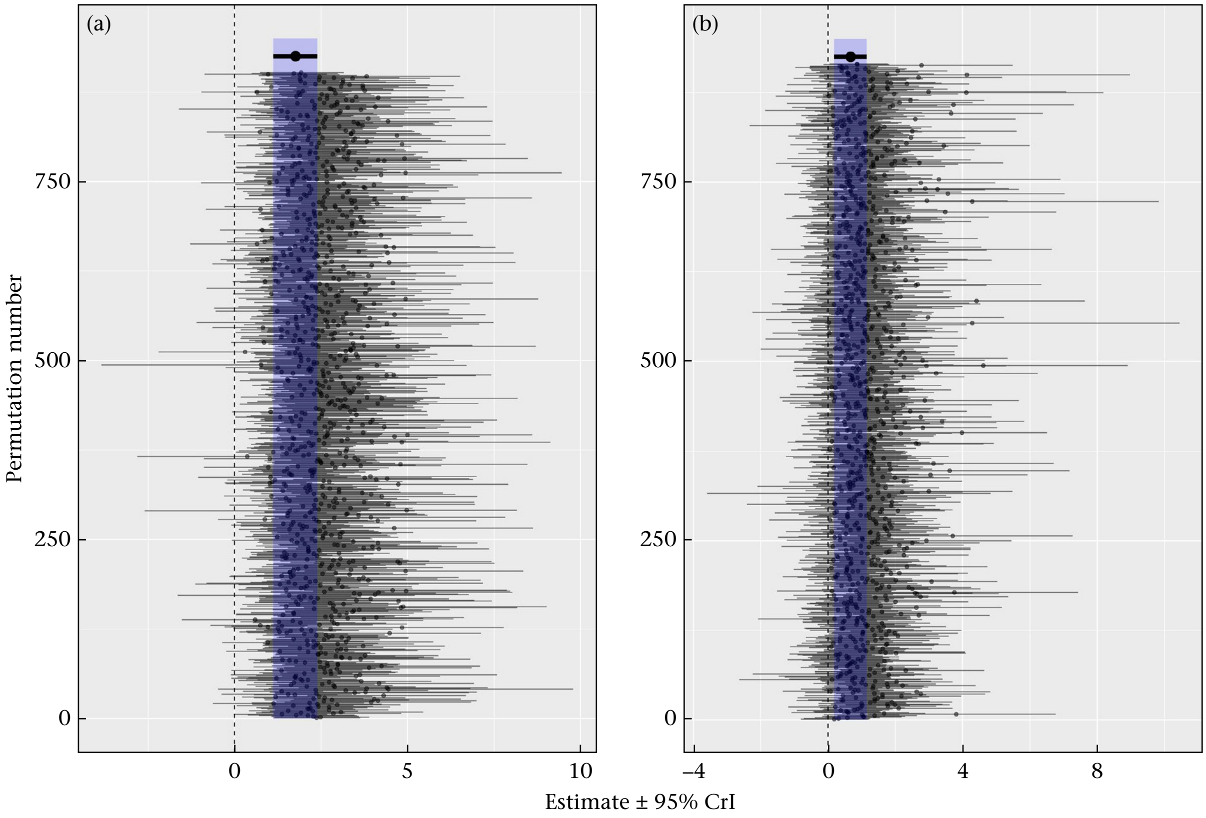

Figure A2. Plot showing estimates and 95% credible intervals (CrIs) for permutation analyses of the effect of (a) relative number of males and (b) relative age of the oldest male on contest success. At top of each figure, the estimate (point) and 95% CrI (lines) for the effect of relative number of males and oldest male age is shown from the full data set ($N = 261$). Blue shaded region shows the 95% CrI of this full-data set analysis throughout the plot. Small points and bars show estimate and 95% CrI (*X* axis) for each of ~1000 MCMCglmm models predicting contest success from both relative number of males and relative oldest male age, in which the sample size of contests was made equal to that of the focal Y | rival N relative oestrous category in the model presented in Fig. A1 (56 contests). Dashed vertical line shows estimate value of 0; small bars crossing this line represent models in which the pMCMC of each effect would be greater than 0.05.