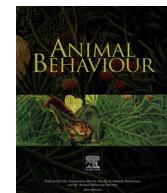




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Causes and consequences of intergroup conflict in cooperative banded mongooses



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Conflict between groups is a notable feature of many animal societies. Recent theoretical models suggest that violent intergroup conflict can shape patterns of within-group cooperation. However, despite its prevalence in social species, the adaptive significance of violent intergroup conflict has been little explored outside of humans and chimpanzees, *Pan troglodytes*. A barrier to current understanding of the role of intergroup conflict in the evolution of social behaviour is a lack of information on the causes and consequences of aggression between groups. Here, we examined the causes and fitness consequences of intergroup conflict in the banded mongoose, *Mungos mungo*, using a 16-year data set of observed intergroup interactions, life history and behaviour. Banded mongooses are cooperative breeders that live in highly territorial groups and engage in frequent, aggressive and violent intergroup interactions. We found that intensified population-wide competition for food and mates increased the probability of intergroup interactions, and that increased intergroup conflict was associated with periods in which groups were growing in size. Intergroup conflict had fitness costs in terms of reduced litter and adult survival but no cost to pregnant females: in fact, females were less likely to abort following an intergroup interaction than when there had been no recent intergroup conflict. Our results suggest that intergroup conflict has measurable costs to both individuals and groups in the long and short term, and that levels of conflict among groups could be high enough to affect patterns of within-group cooperative behaviour. Establishing the consequences of intergroup conflict in cooperative species can shed light on patterns of conflict and cooperation within groups and, in turn, facilitate our understanding of social evolution.

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Cooperatively breeding species have received much attention because the conspicuous helping behaviour they exhibit through the care of young offers an opportunity to test evolutionary theories of cooperation (Cant, 2012; Emlen, 1991; Koenig & Dickinson, 2016). In many social species, individuals also demonstrate high degrees of cooperation and coordination in the form of coalitional aggression, which they employ to defend territories and fight neighbouring conspecifics (Hölldobler & Wilson, 1990; Smith, 2007; Wilson & Wrangham, 2003). Warfare and the coordination of huge armies to invade and battle rival societies have punctuated human history. Recent theoretical models of collective violence in humans suggest that the costs of intergroup conflict can drive the evolution of cooperative behaviour (Bowles, 2006, 2009; Choi & Bowles, 2007; Rusch, 2014), although this remains a subject of

debate (Fry, 2013). Empirical evidence using public-goods and ultimatum games in humans reveals that, in the short term, out-group threats can lead to increased in-group cohesion (Burton-Chellew & West, 2012; Gneezy & Fessler, 2012; Puurtinen & Mappes, 2009).

Violent conflicts (where there is physical or lethal attack) are well documented among nonhuman primates, particularly chimpanzees, *Pan troglodytes* (Mitani, Watts, & Amsler, 2010; Wilson, Wallauer, & Pusey, 2004; Wrangham, Wilson, & Muller, 2006). Aggressive intergroup contests are also observed in a range of other primate species (spider monkeys, *Ateles geoffroyi yucatanensis*, Aureli, Schaffner, Verpoorten, Slater, & Ramos-Fernandez, 2006; Harris, 2010; black howler monkeys, *Alouatta pigra*, and tufted capuchin monkeys, *Sapajus nigritus*, Van Belle & Scarry, 2015; white-faced capuchin monkeys, *Cebus capucinus*, Gros-Louis, Perry, & Manson, 2003). Other than primates, aggressive interactions between groups are also reported in other social mammals (spotted hyaena, *Crocuta crocuta*, Boydston, Morelli, & Holekamp, 2001; grey wolves, *Canis lupus*, Cassidy, MacNulty, Stahler, Smith, & Mech,

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2015; Mech, 1994; African lions, *Panthera leo*, Mosser & Packer, 2009), cooperatively breeding birds (pied babblers, *Turdoides bicolor*, Golabek, Ridley, & Radford, 2012; green woodhoopoes, *Phoeniculus purpureus*, Radford, 2011) and ants (red wood ants, *Formica rufa*, Batchelor & Briffa, 2011; fire ants, *Solenopsis invicta*, Plowes & Adams, 2005; *Formica xerophila*, Tanner, 2006). Intergroup conflict is known to carry large potential costs such as increased mortality and loss of territory (Batchelor & Briffa, 2011; Crofoot, 2013; Jordan, Mwanguhya, Kyabulima, Rüedi, & Cant, 2010; Scarry & Tujague, 2012; Wrangham, Wilson, & Muller, 2006) but, although conspicuous among a variety of animal species, the adaptive significance of intergroup conflict is still much debated.

Explanations for the evolution of collective violence suggest that, by engaging in attacks with rivals, a group can increase access to resources such as territory and food (Wrangham, 1999). Collective violence is selected for because groups that are successful in gaining these resources achieve enhanced reproductive success by outcompeting rivals (Durrant, 2011). Collective violence can therefore evolve by selection acting at the level of the group (Bowles & Gintis, 2011; Hamilton, 1975). Selection at the level of the individual may also favour contributing to collective violence, such that the forces of individual and group selection are aligned. If there are power asymmetries between neighbours then individuals in large groups can attack smaller groups at little personal cost (Wrangham, 1999). By engaging in intergroup encounters, males can improve reproductive opportunities through increased access to females, and so collective violence has been suggested as a facultative male reproductive strategy (van der Dennen, 1995), with selection for successful male 'warriors' (van Vugt, 2009). In other cases, contributing to collective violence may represent a form of individual altruism, which is selected against at the level of the individual, but can spread through benefits to relatives of other local group members (Lehmann & Feldman, 2008). Groups that contain 'parochial altruists' (individuals that cooperate with in-group members at a personal cost and are hostile to out-group members) are more likely to be successful in securing resources important for reproductive success, relative to groups without these individuals (Choi & Bowles, 2007).

Empirical evidence used to evaluate the hypotheses outlined above comes mainly from humans and chimpanzees (Bernhard, Fischbacher, & Fehr, 2006; Bowles, 2009; Wrangham, 1999; Wrangham & Glowacki, 2012), but there have been few tests of these hypotheses among other species that engage in violent intergroup aggression. This is especially the case for cooperatively breeding species that exhibit levels of intergroup hostility sufficient to influence selection for helping behaviour (Cant, Nichols, Thompson, & Vitikainen, 2016), and where there is potential for intergroup conflict to influence demographic processes, such as migration, colonization of new territory and population expansion (Lehmann & Feldman, 2008). To improve our understanding of the role of intergroup conflict in social evolution it is important to establish the causes and consequences of intergroup conflict in species that feature conspicuous levels of both cooperation and collective violence between groups (Lehmann & Rousset, 2010).

Banded mongooses, *Mungos mungo*, provide an ideal system to investigate the causes and consequences of intergroup conflict because they live in highly cooperative groups that actively defend territories, compete with neighbours for access to food and mates, and regularly engage in aggressive and violent physical contests ('intergroup interactions') with rival groups (Cant et al., 2016; Cant, Vitikainen, & Nichols, 2013). Groups respond more aggressively to experimental stimuli from neighbours that represent a territorial

threat than stimuli from non-neighbours (Müller & Manser, 2007). There is also observational evidence that males and females engage in intergroup interactions in order to achieve extragroup matings (Cant, Otali, & Mwanguhya, 2002; Nichols, Cant, & Sanderson, 2015). As in chimpanzees and humans, fights between groups are costly: individuals are often injured (sometimes fatally) and newly born pups have been observed to be killed by rival groups during these encounters (Jordan et al., 2010; Müller & Bell, 2009; Nichols et al., 2015).

Here we examined the factors that influence the causes of intergroup conflict in banded mongooses, and the fitness consequences of engaging in intergroup interactions for individuals and groups. Specifically, we tested whether (1) the probability of intergroup interactions is influenced by the availability of resources, and the stage of the reproductive cycle; (2) the frequency of intergroup interactions increases as groups grow in number; and (3) intergroup interactions have measurable costs to pup and adult survival, and fertility costs to pregnant females.

METHODS

Study Population and Data Collection

We studied a population of banded mongooses living on the Mweya Peninsula, Queen Elizabeth National Park, Uganda ($0^{\circ}12'S$, $27^{\circ}54'E$). For further details of habitat and climate, see Cant et al. (2013). Typically, our population comprises 10–12 social groups occupying distinct territories (Cant et al., 2016), and over the course of the study period (between November 1999 and January 2016) we studied a total of 43 groups. Groups were visited every 1–3 days to record group composition, life history and behavioural data. We visited groups daily when they were breeding (when females were in oestrus, due to give birth and when pups were newly born). One or two individuals in each group were fitted with a VHF radiocollar (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., Dorset, U.K.) that enabled groups to be located. All individuals were uniquely marked by either colour-coded plastic collars or, more recently, shave patterns on their back and individuals were regularly trapped to maintain these identification markings (see Jordan et al., 2010 for details). Individuals in the population were trained to step onto portable electronic scales to obtain weight measurements. Measurements of daily rainfall were recorded by the Uganda Institute of Ecology Meteorological Station and, later, using our own weather station.

Incidences of intergroup interactions in the population were recorded ad libitum. Intergroup interactions are conspicuous events and occur when neighbouring groups sight each other, with physical fights being particularly likely if the groups are evenly matched in size (Cant et al., 2002). Individuals, on sighting a rival group, stand upright and give a 'screeching call' that alerts the rest of their group and causes them to cluster together in preparation to attack. Where there are large size asymmetries between rival groups the smaller group often flees. Contests between groups are ferocious, with individuals chasing, scratching and biting each other (Cant et al., 2002; Gilchrist & Otali, 2002; Rood, 1975). We defined an intergroup interaction as any occasion that two groups of mongooses sighted each other and responded by screeching, chasing and/or fighting. There is a continuum of intensity of aggression during intergroup interactions, and much between-individual variation in behaviour. We analysed all intergroup interactions because they are always aggressive and hostile, and the density of bushes and cover at our study site means that it is difficult to accurately determine whether there has been physical

contact between groups. Even when there is no observed physical fighting, engaging in intergroup interactions is still likely to involve costs. These include energetic costs, elevated stress levels, changes in ranging behaviour, increased den movements, and disruption to cooperative behaviours such as babysitting and escorting. Interactions between groups most frequently occur between established neighbours (91.6% of intergroup interactions), but occasionally we observed interactions between established groups and known dispersing cohorts (3.5% of intergroup interactions), or cohorts comprising unknown individuals from outside the study population (4.9% of intergroup interactions).

Statistical Analyses

Statistical analyses were performed in R 3.3.0 (R Development Core Team, 2016) using generalized linear mixed-effect models (GLMMs). GLMMs using a binomial error structure with a logit link function were fitted using the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2015), and GLMMs using a negative binomial error structure with a log link function were fitted using the 'glmmADMB' package (Fournier et al., 2012). In each analysis, the maximal model was fitted, including all fixed-effect terms of interest and biologically relevant interactions. We assessed the significance of each fixed effect by comparing the likelihood ratio of the maximal model to that of the model without the fixed effect (Bates et al., 2015). We present the parameter estimates and standard errors from the maximal models, rather than removing nonsignificant fixed effects from the model due to problems associated with stepwise model reduction (Forstmeier & Schielzeth, 2011; Mundry & Nunn, 2009; Whittingham, Stephens, Bradbury, & Freckleton, 2006). We did, however, remove nonsignificant interactions from our maximal model to allow the significance of the main effects to be tested (Engqvist, 2005).

Ecological and social causes of intergroup conflict

Reproduction in banded mongooses is highly synchronized within but not between groups, and so groups in the population can be in different phases of the reproductive cycle at different times. Most females in a group enter a 5–10 day oestrus period within 1 week of each other and, once mated, gestate for between 55 and 60 days (Cant, 2000). Females give birth synchronously to a communal litter which is guarded at the den by 'babysitters' of both sexes for approximately 30 days before they emerge (Cant, 2003). We examined whether the probability of a group being involved in an intergroup interaction depended on their phase of the reproductive cycle or on ecological conditions including rainfall, population density and group size. We fitted whether a group was involved in an intergroup interaction on each day during the study period as the response variable in a GLMM using a binomial error structure. We included the group's reproductive status (which phase of the reproductive cycle they were in on that day) as a fixed effect. A group was defined as being in oestrus when males were observed mate-guarding females, pregnant between the end of oestrus and birth of the communal litter, and babysitting when helpers were left to guard newly born pups at the den. A group was defined as nonbreeding when not in oestrus, pregnant or babysitting. We also included mean rainfall (mm) in the previous 30 days, the density of the study population calculated as the number of individuals in the population aged over 6 months/4.95 km² (the size of the study area; Gilchrist & Otali, 2002; Rood, 1975) and group size (number of individuals aged over 6 months, the age at which group members begin to contribute to both intergroup fighting and helping; Cant et al., 2016, 2002) as fixed effects, along with all two-way interactions between fixed effects. To account for repeated measures of groups we included group ID as a random

intercept. During the breeding attempts of some groups there was an overlap in the phases of the reproductive cycle and, as such, days when a group was classed as being in two or more phases of the reproductive cycle. To determine the effect of the different phases of the reproductive cycle on the probability of a group being involved in an intergroup interaction we first excluded days when a group was classed as being in multiple phases of the reproductive cycle and fitted the model to data on 42 470 study days in 39 groups. We then repeated the analysis including these days when a group was classed as being in multiple phases of the reproductive cycle, but randomly assigning the group a reproductive phase chosen from the multiple phases in which they were classed. For example, if a group was observed as being both in oestrus and babysitting on a particular day, they were randomly assigned to be in oestrus or babysitting. We fitted the model to data on 48 831 study days in 39 groups. We found no qualitative difference in the results of these analyses and so we present the results from the first analysis in which the days on which a group was classed as being in multiple phases of the reproductive cycle were excluded. To determine differences in the probability of a group being involved in an intergroup interaction between all phases of the reproductive cycle, we conducted a post hoc multiple comparison of means using the 'glht' function with Tukey's all-pairwise comparisons in the 'multcomp' package in R (Hothorn, Bretz, & Westfall, 2008; Hothorn et al., 2016).

To further investigate the relationship between group size and the frequency of intergroup conflict we examined whether the change in a group's size influenced the number of intergroup interactions in which they were involved. We predicted that groups that are growing in size should be involved in more intergroup interactions. We fitted the number of intergroup interactions in which a group was involved during a 12-month period as the response variable in a GLMM using a negative binomial error structure (to account for overdispersion of the Poisson response variable). We only included 12-month periods where we observed the group engaging in intergroup interactions. We fitted as fixed effects the group's change in group size (number of individuals aged over 6 months) over this 12-month period (group size at the end of the 12-month period – group size at the start of the 12-month period), group size at the start of the 12-month period and the interaction between change in group size and starting group size. We confirmed that the correlation between change in group size and starting group size was less than levels of correlation known to cause model-fitting issues such as variance inflation in effect estimates ($r = -0.31$; Freckleton, 2011). We also included as fixed effects population density at the start of the 12-month period (calculated as the number of individuals in the population aged over 6 months/4.95 km²), mean monthly rainfall (mm) in the 12-month period, the interaction between starting population density and rainfall, and the number of oestrus events that the group had during the 12 months (as a proxy for reproductive frequency, and because groups are known to engage in intergroup interactions when females are in oestrus; Cant et al., 2002; Nichols et al., 2015). To account for repeated measures of groups we included group ID as a random intercept and fitted the model to data on 113 sample (12-month) periods in 16 groups.

Costs of intergroup conflict to pups and adults

To examine whether intergroup interactions were associated with decreased pup survival we fitted whether or not any pups in a litter survived to emergence (1 = all pups died before emergence, 0 = at least one pup survived to emergence) as the response variable in a GLMM using a binomial error structure. We included whether or not the group was involved in an intergroup interaction in the 30 days after the birth of the litter

(the period in which newly born pups are babysat at the den; Rood, 1974) as the main term of interest and fitted mean rainfall (mm) in the 30 days before the birth of the litter, group size (number of individuals aged over 6 months) at the birth of the litter, and the interaction between rainfall and group size as additional fixed effects. Group size correlates strongly with the number of breeding females in the group (Pearson product-moment correlation: $r = 0.72$, $t_{563} = 24.84$, $P < 0.001$) and also represents the number of available babysitters (since most individuals over 6 months of age contribute to babysitting and pup care; Cant et al., 2016). Therefore group size was included to control for litter survival to emergence being higher when there are more breeding females in the group (Cant, Hodge, Bell, Gilchrist, & Nichols, 2010), and when there are more babysitters left at the den (Marshall et al., 2016). To account for repeated measures of groups we included group ID as a random intercept and fitted the model to data on 515 communal litters born in 19 groups.

To investigate whether intergroup conflict had mortality costs for adults we fitted whether an individual aged over 1 year survived a 3-day period as the response variable in a GLMM using a binomial error structure. Each 3-day period either did or did not immediately follow an intergroup interaction. We used a 3-day period to investigate survival in order to detect the potential immediate effect, in terms of injuries and subsequent death, of intergroup interactions on individuals. For 3-day periods that did not immediately follow an intergroup interaction, the period was randomly selected from the group's lifetime where we knew the group was not involved in an intergroup interaction. We restricted our analyses to 3-day periods where there was no intergroup interaction involving the individual's group recorded in the previous 7 days to allow us to exclude potential effects of any other previous, recent intergroup interactions. Groups were not observed continuously during these 10-day periods, but groups were typically visited by rota and so sampling effort was independent of whether we observed an intergroup interaction or not. We included whether or not the group was involved in an intergroup interaction at the start of the 3-day period as the main term of interest. We fitted sex, age (days), weight (g), group size (number of individuals aged over 6 months) and mean rainfall (mm) in the 30 days before the start of the 3-day period as additional fixed effects. To account for repeated measures of individuals and groups we included individual ID and group ID as random intercepts, and fitted the model to data on 7769 individuals in 628 sample (3-day) periods ($N = 479$ periods that followed an intergroup interaction and $N = 149$ periods that did not) in 17 groups.

To examine whether intergroup conflict has prenatal costs, we fitted whether or not a pregnant female aborted her litter as the response variable in a GLMM using a binomial error structure. Since pregnancy, and thus abortion, is hard to detect accurately in the first 30 days of gestation, we censored the first 30 days of pregnancy (i.e. the 30-day period following the end of oestrus) and only analysed the incidence of abortion after the censored period. We included whether or not the group was involved in an intergroup interaction during gestation after the censored period as the main term of interest and fitted mean rainfall (mm) in the 30 days before the censored period, the number of breeding females (females aged over 10 months; Cant et al., 2010; Gilchrist, Otali, & Mwangi, 2004) in the group, the interaction between rainfall and the number of breeding females, female age (days) and weight (g) at conception as fixed effects. To account for the length of gestation (and therefore the time over which to observe an intergroup

interaction) being shorter for females that aborted than for females that gave birth, we included an offset term of the log_e of the length of gestation (days) following the censored period as an additional fixed effect. We accounted for repeated measures of groups, litters and females by including these terms as random intercepts and fitted the model to data on 931 females giving birth to 274 communal litters in 11 groups.

Ethical Note

All research procedures received prior approval from Uganda Wildlife Authority and Uganda National Council for Science and Technology, and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. All research was approved by the Ethical Review Committee of the University of Exeter.

RESULTS

Ecological and Social Causes of Intergroup Conflict

We observed a total of 570 intergroup interactions in our population over the course of the study period. Groups were involved in 0.73 ± 0.2 intergroup interactions per month (mean \pm SE). Groups were more likely to be involved in an intergroup interaction as population density increased, and this effect was more pronounced when rainfall was low (interaction between rainfall and population density: Fig. 1a, Table A1). The probability of engaging in an intergroup interaction was greater for larger groups (Fig. 1b, Table A1).

The probability of a group being involved in an intergroup interaction varied significantly across different phases of the reproductive cycle (Fig. 2, Table A1). Groups were more likely to be involved in an intergroup interaction when they were in oestrus than during any other phase (Fig. 2, Table A2).

Our analysis of the number of intergroup interactions in which a group was involved over a 12-month period and their growth (or decay) over the same 12-month period revealed that groups that grew in size were involved in more intergroup interactions than groups that shrank (Fig. 3, Table A3). Groups that were larger at the start of the 12-month period were involved in more intergroup interactions over the 12-month period than smaller groups (Table A3), but there was no significant difference in the effect of growth on the number of intergroup interactions for large and small groups (interaction between change in group size and starting group size: Table A3). On removal of an outlier for which change in group size was very large, the interaction between change in group size and starting group size was statistically significant (Table A4). Large groups that grew in size engaged in more intergroup interactions, but there was no effect of change in group size for small groups.

Costs of Intergroup Conflict to Pups and Adults

Pup survival was affected by the occurrence of intergroup conflict during the period in which pups were in the den. A communal litter was significantly more likely to die before emergence if the group was involved in an intergroup interaction during the 30 days after birth (Fig. 4a, Table A5). Similarly, we found that adult survival over a 3-day period was also affected by the occurrence of an intergroup interaction at the start of the period, with individuals more likely to die in a 3-day period immediately following an intergroup interaction than in one that did not follow an intergroup

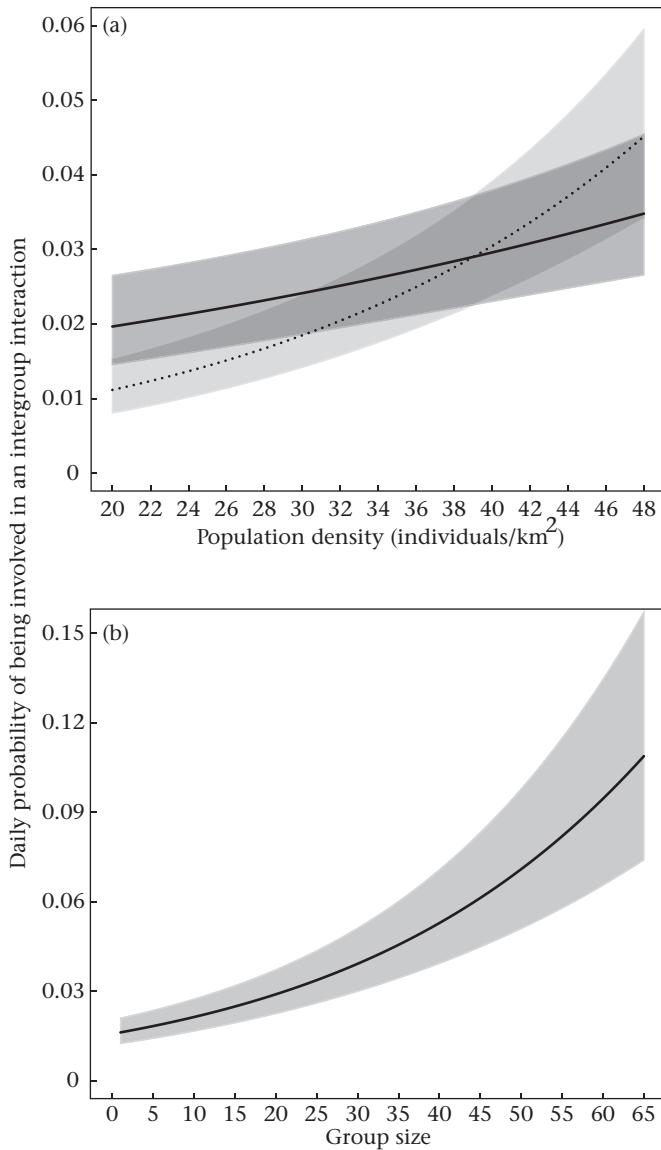


Figure 1. Causes of intergroup conflict. (a) The effect of population density on the probability of a group being involved in an intergroup interaction on a given day. The lines show predictions from the GLMM \pm SE when rainfall is low (dotted line and light grey shaded area, 25th percentile of mean rainfall in the previous 30 days = 0.93 mm) and when rainfall is high (solid line and dark grey shaded area, 75th percentile of mean rainfall in the previous 30 days = 2.91 mm) ($N = 42\,470$ study days in 39 groups). (b) The effect of group size on the probability of a group being involved in an intergroup interaction on a given day. The line shows the prediction from the GLMM \pm SE ($N = 42\,470$ study days in 39 groups).

interaction (Fig. 4b, Table A6). However, we found that pregnant females did not suffer prenatal costs if their group was involved in an intergroup interaction during later gestation (from 30 days after the end of oestrus until birth). In fact, a female was significantly less likely to abort her litter if her group engaged in an intergroup interaction during this period for which she was pregnant (Fig. 5, Table A7).

DISCUSSION

Intergroup conflict in banded mongooses, observed as aggressive and violent interactions between neighbouring groups, was widespread in our population and groups were regularly involved

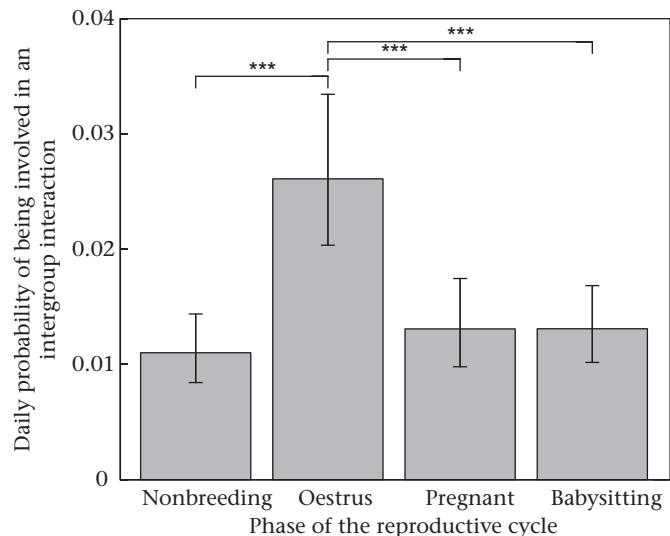


Figure 2. The probability of a group being involved in an intergroup interaction on a given day against the phase of the reproductive cycle they are in on that day ($N = 42\,470$ study days in 39 groups). The bars show means from the GLMM \pm SE. *** $P < 0.001$; asterisks refer to post hoc Tukey's all-pairwise comparison of means across all four categories.

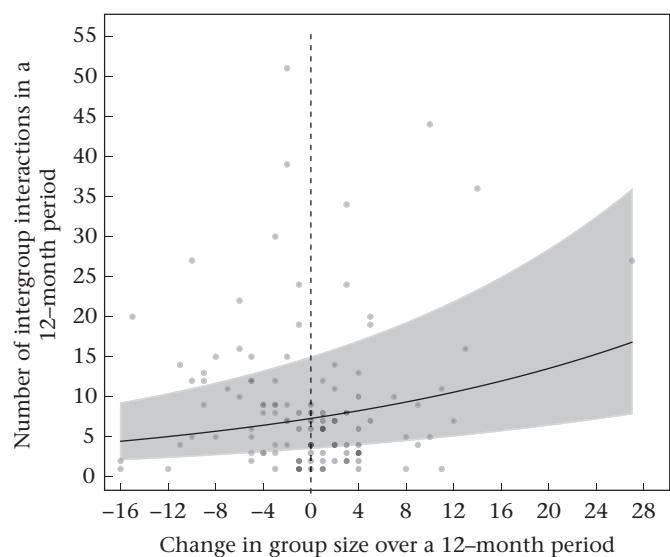


Figure 3. The number of intergroup interactions in which a group was involved over a 12-month period against the group's change in group size over that period ($N = 113$ sample (12-month) periods in 16 groups). The vertical dashed line shows no change in group size. The line shows prediction from the GLMM \pm SE.

in contests with one another. The probability of a group being involved in an intergroup interaction on a given day increased when population density was high and rainfall was low: two factors that increase ecological competition for limited resources. Larger groups were more likely to be involved in intergroup conflict than smaller groups, and groups were involved in more intergroup interactions during periods when they grew in size. The probability of a group being involved in an intergroup interaction on a given day also depended on the phase of the reproductive cycle that they were in, with groups most likely to be involved in an intergroup interaction when their females were in oestrus. Intergroup conflict resulted in fitness costs, through reduced litter and adult survival, but did not have negative effects on female fertility. These results

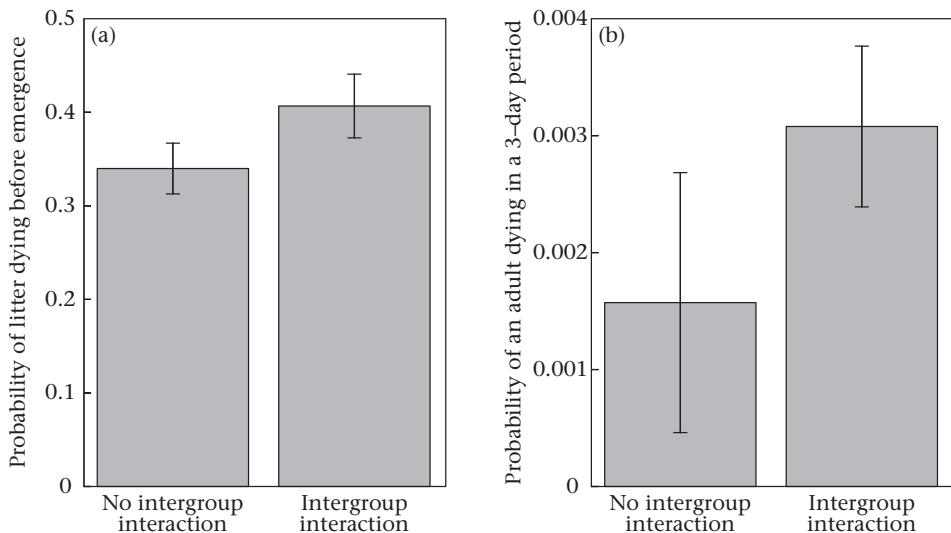


Figure 4. Survival costs of intergroup conflict for pups and adults. (a) The probability of a litter dying before emergence (30 days after birth) against whether or not the group was involved in an intergroup interaction in the 30 days after the birth of the communal litter ($N = 515$ communal litters born in 19 groups). The bars show means from the data \pm SE. (b) The probability of an adult dying in a 3-day period against whether or not the group was involved in an intergroup interaction at the start of that period ($N = 7769$ individuals in 628 sample (3-day) periods in 17 groups). The bars show means from the data \pm SE.

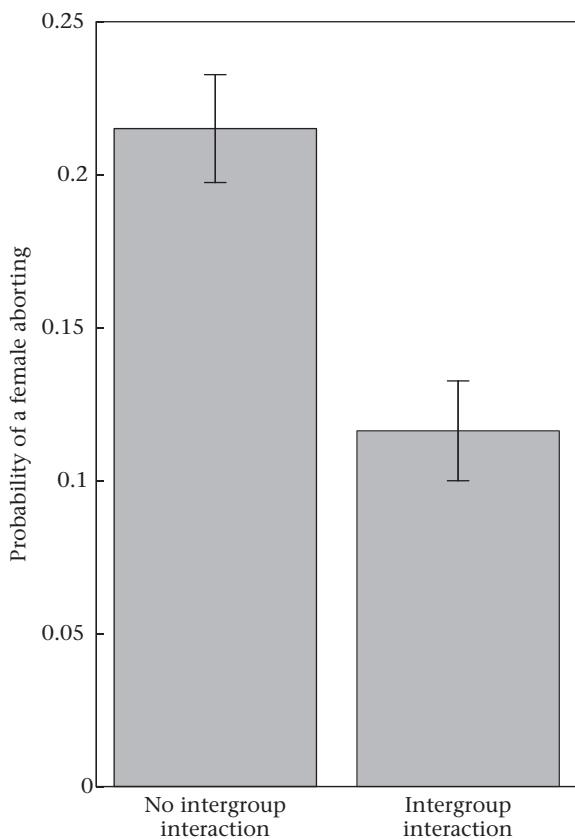


Figure 5. The probability of a pregnant female aborting during the latter half of gestation against whether there was an intergroup interaction involving her group during this period of gestation ($N = 931$ females giving birth to 274 communal litters in 11 groups). The bars show means from the data \pm SE.

show that intergroup conflict has measurable costs to both individual survival and group recruitment, and suggest that the consequences of intergroup conflict can have important effects on individual fitness and group dynamics.

In our population, intensified population-wide resource competition was associated with a greater probability of being involved in aggressive contests with other groups. Low rainfall (known to negatively affect invertebrate abundance, Marshall et al., 2017) and individual condition (Marshall et al., 2016) coupled with increased population density resulted in a greater probability of intergroup interactions, suggesting that competition for food resources exacerbates intergroup conflict. As in other social carnivores and primates, scarcity of resources might force groups to travel further, encroaching more on one another's territories to find sufficient food (Harris, 2010; Harrison, 1983; Isbell, 1991; Mech, 1994; but see Golabek et al., 2012), and in an attempt to expand territories (Mitani et al., 2010; Mosser & Packer, 2009; Wilson & Wrangham, 2003). In our population, large groups were more likely to be involved in an intergroup interaction than small groups, and groups engaged more frequently in intergroup interactions during periods of growth. This pattern could arise because groups that grow in size need to forage in a larger area, which may inevitably bring them into conflict with their neighbours. Large groups probably experience lower per capita costs of intergroup fighting and greater success in such conflicts, so groups that grow in size may actively start to seek out competition with neighbours. In addition, the relative group size of competing groups is likely to play an important role in the decision to engage in intergroup conflict and on the outcome of intergroup interactions. To understand in more detail the dynamics of intergroup conflict requires more detailed information on which individuals seek and initiate conflicts. In the future, we will have this information from lightweight GPS collars that we have recently deployed in our population.

In addition to food, groups compete for access to mates, particularly when there is a high risk of inbreeding within the natal group. In chimpanzees, for example, intergroup aggression is linked to male competition to gain access to females (Wilson & Wrangham, 2003; Wrangham, 1999). In our population, groups were more likely to engage in intergroup interactions during oestrus than during any other phase of the reproductive cycle, suggesting that individuals may be more inclined to engage in intergroup conflict to increase access to mates. Our previous observations (Cant et al., 2002; Nichols et al., 2015) suggest two mechanisms that could

account for this result: (1) males from neighbouring groups might detect when the females of a focal group are in oestrus (for example, through a change in the hormonal composition of faecal or scent marks) and lead their group to an encounter with the focal group to obtain extragroup matings, or (2) oestrus females in a focal group might lead their own group to neighbouring groups in order to obtain matings with neighbouring males (which are unrelated and sire offspring that are less homozygous; Nichols et al., 2015). Detailed data on the distribution and movement of groups, and specifically which individuals lead groups into neighbouring territory, in response to food resources and mating opportunities would allow us to test in more detail how resource competition affects patterns of intergroup conflict and how intergroup fighting can subsequently influence patterns of territory expansion. Again, the development of lightweight GPS collars deployed in our population will allow us to conduct these tests.

Intergroup conflict, because it can result in participants' injury and death, can have important effects on group size and recruitment. We found that adults were more likely to die in a 3-day period immediately after an intergroup interaction than in one that did not follow an intergroup interaction. We also found that litters were less likely to survive when groups were involved in intergroup interactions during the babysitting period, which is suggestive of intergroup infanticide. These data are supported by occasional direct observations of intergroup infanticide (and cannibalism) in this population (Cant et al., 2016, 2002). A previous study in banded mongooses has shown that intergroup interactions contribute to 20% of known pup deaths (Nichols et al., 2015). Cases of infanticide during intergroup encounters are also observed in chimpanzees (Watts, Mitani, & Sherrow, 2002; Wilson et al., 2004; Wilson & Wrangham, 2003). These significant costs of intergroup conflict might be a means by which members of rival groups can ensure their own success by reducing the size of neighbouring groups which, in turn, is likely to give them a greater competitive advantage in future disputes (Batchelor & Briffa, 2011; Cassidy et al., 2015; Mosser & Packer, 2009; Wrangham, 1999; Wrangham & Glowacki, 2012). This is particularly relevant if a group's size relative to that of its rival is an important determinant of the outcome of intergroup interactions, as observed in a broad range of social species (Crofoot, Gilby, Wikelski, & Kays, 2008; Radford & du Plessis, 2004; Tanner, 2006; Wilson & Wrangham, 2003). The loss of adult breeders or of a litter is likely to be especially costly for small groups that are more sensitive to a reduction in group size. In cooperatively breeding species, the maintenance of a critical group size is vital to avoid extinction (Courchamp, 1999; Courchamp, Clutton-Brock, & Grenfell, 1999). Intergroup conflict could, therefore, have important consequences for the dynamics and success of groups through group augmentation (Kokko, Johnstone, & Clutton-Brock, 2001), particularly if the costs of engaging in and losing an intergroup interaction are higher for groups that are already small.

Recent theoretical models have proposed that intergroup conflict and collective violence in humans can influence the evolution of cooperative behaviour within groups through selection for individuals that display high levels of in-group favouritism and out-group hostility (Choi & Bowles, 2007; Lehmann & Feldman, 2008). Although we did not specifically examine the link between intergroup aggression and helping behaviour in groups that were involved in intergroup interactions, we did find an interesting relationship between intergroup conflict and a potential marker of within-group reproductive conflict: spontaneous abortion. Abortion in females is more likely when they have been evicted from their group (Cant et al., 2010), which occurs during intense periods of reproductive competition (Cant et al., 2010; Thompson et al., 2016). However, we found that females were significantly less likely to abort their litter if their group was involved in an

intergroup interaction during their gestation. One hypothesis to explain this otherwise puzzling result is that within-group conflict over reproduction is suppressed during periods of high out-group conflict, perhaps to compensate for higher rates of litter mortality following intergroup fighting. Links between intergroup conflict and within-group cooperation are not well studied in nonhuman animal species, but increases in affiliative behaviour following intergroup conflict have been demonstrated in green woodhoopoes (Radford, 2008, 2011), and the cooperatively breeding cichlid fish *Neolamprologus pulcher* (Bruintjes, Lynton-Jenkins, Jones, & Radford, 2015). Further experimental manipulations of levels of intergroup conflict through simulated territorial intrusions could illuminate how the nature and intensity of intergroup conflict affect patterns of cooperation and conflict within the group in banded mongooses and other cooperative species.

Conclusions

In conclusion, our results suggest that intergroup conflict in banded mongooses is driven by competition for resources and matings. Intergroup conflict also has consequences for litter and adult survival, suggesting that it can have important implications for individual fitness and group recruitment. In banded mongooses, rates of mortality resulting from intergroup conflict are comparable to those experienced by chimpanzees and humans (Nichols et al., 2015; Wrangham et al., 2006). According to recent theoretical work, it is therefore likely that levels of conflict among groups of banded mongooses are sufficient to provide a selective force in the evolution of within-group cooperative behaviour (Choi & Bowles, 2007). Studies of cooperative breeders that exhibit high levels of both intragroup cooperation and intergroup conflict can provide a new lens through which to understand social evolution among competing cooperative groups.

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Data accessibility

The data used in this paper are available on Figshare at <https://doi.org/10.6084/m9.figshare.4649980.v1>.

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APPENDIX

Table A1

Model predicting the daily probability of a group being involved in an intergroup interaction

Fixed effect	β	SE	χ^2	P
Intercept	-7.29	0.63		
Phase of reproductive cycle	Babysitting Oestrus Pregnant Nonbreeding	0.00 0.70 -0.0009 -0.18	21.40	<0.0001
Rainfall (mm)		0.60		
Population density		0.07		
Group size		0.03	23.71	<0.0001
Phase of reproductive cycle*	Babysitting Oestrus Pregnant Nonbreeding	0.00 0.15 -0.04 0.02		
Rainfall (mm)		0.00	3.43	0.33
Population density		0.01		
Phase of reproductive cycle*	Babysitting Oestrus Pregnant Nonbreeding	0.00 0.02 0.009		
Population density		0.00	1.22	0.75
Phase of reproductive cycle*	Babysitting Oestrus Pregnant Nonbreeding	0.00 -0.02 -0.02 -0.03		
Group size		0.00	4.41	0.22
Rainfall (mm)*				
Population density		-0.02	7.79	0.005
Rainfall (mm)*		0.0008		
Group size		0.0007	0.09	0.76
Population density*		0.0009		
Group size		0.0007	0.75	0.39

Model was fitted using a binomial error structure and a logit link function, and with group ID as a random intercept (GLMM, $N = 42$ 470 study days in 39 groups). Significant terms are given in bold.

Table A2

Post hoc multiple comparison of means to determine differences in the daily probability of engaging in an intergroup interaction at different phases of the reproductive cycle

	β	SE	z	P
Oestrus versus nonbreeding	0.88	0.18	5.01	<0.001
Pregnant versus oestrus	-0.70	0.16	-4.36	<0.001
Oestrus versus babysitting	0.70	0.18	3.82	<0.001
Nonbreeding versus babysitting	-0.18	0.14	-1.30	0.55
Pregnant versus babysitting	-0.0009	0.11	-0.008	1.00
Pregnant versus nonbreeding	0.17	0.10	1.69	0.32

Post hoc multiple comparison of means using Tukey's all-pairwise comparisons. Original model was fitted using a binomial error structure and a logit link function, and with group ID as a random intercept (GLMM, $N = 42\,470$ study days in 39 groups). Significant post hoc comparisons are given in bold.

Table A3

Model predicting the number of intergroup interactions in which a group was involved over a 12-month period

Fixed effect	β	SE	χ^2	P
Intercept	-0.13	0.46		
Change in group size	0.03	0.008	10.96	0.0009
Starting group size	0.03	0.01	12.09	0.0005
Population density	0.03	0.01	4.21	0.04
Rainfall (mm)	0.008	0.004	3.66	0.056
Number of oestrus periods	-0.004	0.02	0.03	0.85
Change in group size*				
Starting group size	-0.0001	0.0007	0.03	0.87
Rainfall (mm)*				
Population density	-0.002	0.001	3.32	0.07

Model was fitted using a negative binomial error structure and a log link function, and with group ID as a random intercept ($N = 113$ sample (12-month) periods in 16 groups). Significant terms are given in bold.

Table A4

Model predicting the number of intergroup interactions in which a group was involved over a 12-month period after removal of an outlier for which change in group size was very large

Fixed effect	β	SE	χ^2	P
Intercept	-4.17	2.23		
Change in group size	-0.04	0.03		
Starting group size	0.04	0.01		
Population density	0.14	0.07		
Rainfall (mm)	0.08	0.04		
Number of oestrus periods	0.01	0.02	0.51	
Change in group size*				
Starting group size	0.002	0.001	4.66	0.031
Rainfall (mm)*				
Population density	-0.002	0.001	3.97	0.046

Model was fitted using a negative binomial error structure and a log link function, and with group ID as a random intercept ($N = 112$ sample (12-month) periods in 16 groups). Significant terms are given in bold.

Table A5

Model predicting the probability of a litter dying before emergence

Fixed effect	β	SE	χ^2	P
Intercept	0.19	0.30		
Intergroup interaction	0.47	0.21	5.43	0.02
Rainfall (mm)	-0.20	0.07	8.47	0.004
Group size	-0.02	0.01	3.13	0.08
Rainfall (mm)*				
Group size	-0.003	0.008	0.14	0.71

Model was fitted using a binomial error structure and a logit link function, and with group ID as a random intercept (GLMM, $N = 515$ communal litters born in 19 groups). Significant terms are given in bold.

Table A6

Model predicting the probability of an adult dying in a 3-day period

Fixed effect	β	SE	χ^2	P
Intercept	-0.17	0.003		
Intergroup interaction	0.24	0.006	10.11	0.001
Sex ^a	-0.50	0.008	-6.48	1.00
Age (days)	0.002	0.0006	19.99	<0.0001
Weight (g)	0.002	0.001	-4.06	1.00
Group size	-0.10	0.002	6.23	0.01
Rainfall (mm)	-0.12	0.005	-4.60	1.00

Model was fitted using a binomial error structure and a logit link function, and with individual ID and group ID as random intercepts (GLMM, $N = 7769$ individuals in 628 sample (3-day) periods in 17 groups). Significant terms are given in bold.

^a Reference level = males.

Table A7

Model predicting the probability of a pregnant female aborting her litter

Fixed effect	β	SE	χ^2	P
Intercept	-1.53	0.0005		
Intergroup interaction	-4.24	0.58	54.23	<0.0001
Rainfall (mm)	-0.59	0.0005	-0.32	1.00
Number of breeding females	0.10	0.0005	-0.82	1.00
Age (days)	-0.001	0.0003	6.05	0.01
Weight (g)	-0.002	0.0003	5.40	0.02
Rainfall (mm)*				
Number of breeding females	-0.002	0.08	-5.26	1.00

Model was fitted using a binomial error structure and a logit link function with the log_e of the length of gestation following the 30 days after the end of oestrus as an offset term, and with individual ID, litter and group ID as random intercepts (GLMM, $N = 931$ females giving birth to 274 communal litters in 11 groups). Significant terms are given in bold.