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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.

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, outgroup 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, Verpooten, 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°12′S, 27°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