Conflict within and between groups

of cooperative banded mongooses

Submitted by

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Summary

Conflict within and between social groups is a conspicuous feature of cooperative animal societies. Theoretical and empirical research aims to understand the role of within- and between-group conflict in the evolution of cooperative behaviour, but these forms of conflict are rarely studied together. Eviction as a means of within-group conflict resolution can have important implications for the individuals involved, and the wider population through effects on dispersal, gene flow, and population structure. Intergroup conflict, although prevalent in many social species, is relatively understudied outside of humans and chimpanzees, but could play an important role in the evolution of cooperative behaviours. However, currently there is a lack of understanding of the causes and consequences of within- and between-group conflict to be able to draw conclusions on theoretical links to their role in social evolution. In this thesis, I use a wild population of banded mongooses, *Mungos mungo*, to investigate the causes and consequences of eviction and intergroup conflict in a highly cooperative species. First, I show that eviction in banded mongooses is triggered by reproductive competition in both sexes (**Chapter 2**). Second, I find that, once the decision to evict has been made, younger females and those older, more closely related females are preferentially evicted (**Chapter 3**). This surprising result is explained by a theoretical model which shows that, where individuals are capable of resisting eviction, the usual prediction of positive kin discrimination can be reversed. Third, I show that eviction has demographic effects, with consequences for group size and recruitment (**Chapter 4**). Finally, I show that intergroup conflict is stimulated by intensified resource competition, and that the consequences of intergroup conflict can have measureable costs to both individuals and groups in the long- and short-term (**Chapter 5**). This work shows that the means of resolving within-group conflict at an individual level can resonate to affect demography and dynamics at higher levels, and that the nature and intensity of intergroup conflict has the potential to influence patterns of cooperation and conflict within groups. I suggest that within- and between-group conflict may often be intimately linked, and that recognising this link could help to advance our conceptual understanding of their role in the evolution of cooperative behaviour.

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Author's declaration

All chapters in this thesis were written by Faye J. Thompson with comments provided by Professor Michael Cant and Dr Andrew Young, who provided guidance throughout. Additional comments on Chapter 2 were provided by co-authors on the publication arising from this chapter. Chapter 3 features a theoretical model developed by Professor Rufus Johnstone at the University of Cambridge, who also provided comments on this chapter.

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Publications

At the time of printing, **Chapter 2** has been published in *Proceedings of the Royal Society B: Biological Sciences* exactly as it appears here:

Reproductive competition triggers mass eviction in cooperative banded mongooses

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At the time of printing, **Chapter 3** is in preparation for submission to *Proceedings of the National Academy of Sciences of the United States of America*. This chapter is presented in the style of this journal:

When should animals discriminate against kin? Forced eviction of relatives in the banded mongoose

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Other publications arising during this thesis

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Chapter 1: General introduction

Cooperation and conflict

Altruistic behaviour, where individuals pay a fitness cost to enhance the reproductive success of other group members, is an evolutionary puzzle that has long fascinated researchers. In fact, Darwin acknowledged that the evolution of this behaviour (in the form of sterile castes of social insects) was potentially a major flaw in his theory of natural selection (Darwin 1859). Natural selection should give rise to the evolution of selfishness but, in fact, cooperation is widespread in nature. For example, behavioural altruism is widespread in cooperatively breeding species, in which group members ('helpers') regularly provide care to young that are not their own genetic offspring (Cant 2012a). These systems raise a fundamental question: how can selection favour individuals who forego reproducing themselves, but often retain the capability to do so? The development of kin selection theory (Hamilton 1963, 1964), and later models of cooperation based on group augmentation (Kokko, Johnstone & Clutton-Brock 2001) and coercion (Gaston 1978; Kokko, Johnstone & Wright 2002) have provided testable theories to explain costly helping behaviour. Cooperative systems offer fertile ground to test these evolutionary theories of cooperation.

As well as themes of cooperation, research on cooperatively breeding species has focussed on evolutionary conflict. Evolutionary conflict arises in any social interaction when the fitness optima of individuals (or individual units of selection) differ and cannot be satisfied simultaneously (Parker 2000; Cant 2012b). In cooperative species, breeders and helpers are likely to have shared, but non-identical, interests and for cooperative behaviour to evolve these conflicts of interest must be resolved. Conflict can arise over reproduction, helping effort, parental care and dispersal, and much theoretical and empirical research has focussed on how individuals resolve these within-group conflicts, despite selection for selfishness (Emlen 1991; Koenig & Dickinson 2004; Cant 2012a). For example, where conflict originates over reproductive roles and shares, reproductive skew theory proposes that dominant individuals who have complete control over reproduction in the group will concede a share of their monopoly as an incentive for subordinates to remain peacefully in the group (Vehrencamp 1979, 1983a; b; Johnstone 2000). Conflict over individual workload can be settled by negotiation, where individuals can sometimes gain from adjusting their

effort to compensate for changes in effort by their social partners (Johnstone & Hinde 2006). Punishment, and threats of punishment, can be effective in encouraging group members to behave cooperatively (Cant 2011; Raihani, Thornton & Bshary 2012). These strategies of conflict resolution all have one common theme: they aim to resolve conflict in a way that allows the cooperative interaction to continue.

Where within-group conflict cannot be resolved by these means, individuals are often forced to terminate their social interaction, for example by leaving or evicting their social partners (Cant & Johnstone 2006). In cooperative breeders, the result of the breakdown of cooperative relations is sometimes the forcible eviction or exclusion of individuals from the group (Johnstone & Cant 1999). In 'viscous' populations, that is, populations where there are constraints on dispersal (Taylor 1992), eviction is often a primary mechanism by which individuals permanently disperse from their natal group, and may be an important source of gene flow between groups (Koenig, Haydock & Stanback 1998; Clutton-Brock & Lukas 2012). Eviction differs from other means of conflict resolution because it has the potential to affect individuals outside of the evicting group. Evicted individuals or cohorts might act as a perturbative force in the population as they attempt to disperse and form a new group. In structured populations where groups form tessellating territories, the presence of dispersing individuals and cohorts is likely to stimulate conflict between groups over necessary resources such as food, territory and mates (Koenig *et al.* 1992; Bonte *et al.* 2012; Travis *et al.* 2012). The effects of eviction are likely to be felt more widely than just the evicting group, and eviction has the potential to influence population structure, demography and intergroup relations (Rousset 2004; Lehmann & Rousset 2010).

In addition to intense conflict within groups, cooperative breeding species often exhibit intense and sometimes violent conflict between groups. Intergroup conflict is another notable feature of animals that live in close-knit family groups. Indeed, we do not need to look further than our own species, *Homo sapiens*, for an example of how prevalent conflict can be between groups in social species (Smith 2007). The coordination of large groups of individuals into a coalitionary force to defend territory and resources against rival groups can be viewed as another form of cooperative behaviour, and the evolutionary significance of intergroup conflict for social evolution

has been explored, both theoretically and empirically (Hölldobler & Wilson 1990; Wilson & Wrangham 2003; Thayer 2004). However, the majority of research that examines patterns of intergroup conflict and within-group cooperation stems from theoretical models developed to explain the evolution of coalitional violence in humans (Durrant 2011; Rusch 2014). Tests of these theories have been conducted on empirical data from wild chimpanzees, *Pan troglodytes*, but investigations of intergroup conflict in other social species are limited.

In this thesis, I examine within- and between-group conflict in a cooperatively breeding species. I investigate the causes and consequences of eviction as a means of within-group conflict resolution, and I examine the patterns and consequences of conflict between groups. Below I provide an overview of the hypotheses to explain eviction, and the patterns of eviction in vertebrate systems. I also summarise the adaptive explanations of intergroup conflict in social vertebrates. I finish by giving a general introduction to my study system, and outlining the aims and structure of this thesis.

Eviction in social vertebrates

Forcible eviction of individuals by others within a social group is relatively rare in wild vertebrate animal societies (Table 1). There are well documented observations of usurpations from groups, where immigrating individuals force out others during group takeovers (e.g. primates: Sugiyama 1967; Butynski 1982; Schaffner & French 1997; Fernandez-Duque 2009; and carnivores: Packer & Pusey 1983; Pusey & Packer 1987), but these types of eviction are not conducted by group conspecifics. An obvious question arises: why is eviction not observed in more social vertebrate species? A reason might be that within-group conflict is successfully resolved by other means, and that eviction is a 'last resort' strategy that is only employed when all other means of resolution have failed. In viscous populations, eviction is likely to be employed as a last resort means of conflict resolution because outside options are poor, dispersal is limited, and subordinates would prefer to stay in the group. Additionally, the use of an effective threat by dominants could be sufficient to resolve conflict without having to carry out the act of eviction itself (Johnstone & Cant 1999; Cant 2011). In fish that form size hierarchies, dominants use the threat of eviction to limit the growth and

competitive ability of subordinates (Wong *et al.* 2007), and subordinates starve themselves to curtail their growth in an attempt to avoid triggering eviction (Wong *et al.* 2008). Eviction is often only observed in these species following the experimental manipulation of the size hierarchy that breaks the social rules that the threat of eviction enforces (Wong *et al.* 2007, 2008; Cant 2011). In fact, this applies to many observations of eviction (Table 1). Some species in which eviction is documented to occur only demonstrate eviction when the system is perturbed through experimental manipulations (for example through the temporary removal of individuals; Taborsky 1985; Mulder & Langmore 1993; Balshine-Earn *et al.* 1998). Eviction, therefore, appears to be a rarely observed natural phenomenon in vertebrate societies, consistent with it being a behavioural response of last resort, when other mechanisms of conflict resolution (e.g. through negotiation or threat) fail.

Hypotheses of eviction

In species that exhibit eviction, it is generally dominant individuals that evict subordinates, sometimes temporarily excluding them from the group but in other cases permanently evicting them and forcing them to disperse. There are currently two main hypotheses to explain the occurrence of eviction in social animals: (i) the 'reproductive competition' hypothesis and the 'coercion of cooperation' hypothesis. The reproductive competition hypothesis proposes that eviction is driven by conflict over reproductive or social status within groups (Johnstone & Cant 1999). Eviction is predicted to occur when there is intense competition for breeding positions or vacancies, typically when there is a high number of same-sex, sexually mature individuals (Young *et al.* 2006; Raihani 2008; Cant *et al.* 2010). Eviction is commonly observed in species with high levels of reproductive skew, where one or a few individuals monopolise breeding (Zahavi 1990; Clutton-Brock *et al.* 1998; Buston 2003a). In these systems, eviction may be employed by dominants to reduce the level of reproductive competition in the current breeding attempt by temporarily or permanently excluding subordinates from the group (Johnstone & Cant 1999; Buston *et al.* 2007). However, eviction may also serve to reduce reproductive competition in subsequent breeding attempts, either because the subordinate is forced to permanently disperse, or because the physiological effects of eviction result in a decreased capacity for the subordinate to successfully reproduce (Young *et al.* 2006).

Table 1. Forcible eviction by within-group individuals in wild vertebrate species. 'RC'=reproductive competition, and 'CC'=coercion of cooperation. Symbols: '*' denotes that eviction is naturally observed or inferred; '†' denotes that eviction is induced experimentally; '♂' denotes eviction in males; '♀' denotes eviction in females.

Taxa	Species	Reference	Hypothesis
Fish	Cichlid fish *Neolamprologus pulcher*	Taborsky 1985; Balshine-Earn *et al.* 1998	CC†
	Clown anemonefish *Amphiprion percula*	Buston 2003	RC*†
	Coral-dwelling goby *Paragobiodon xanthosomus*	Wong *et al.* 2007	RC†
	Dwarf angelfish *Centropyge bicolor*	Ang 2010	RC*
Birds	Arabian babbler *Turdoides squamiceps*	Zahavi 1990	RC*
	Montezuma oropendola *Psarocolius montezuma*	Webster 1994	RC*
	Southern pied babbler *Turdoides bicolor*	Raihani 2008; Ridley *et al.* 2008	RC*
	Superb fairy-wren *Malurus cyaneus*	Mulder & Langmore 1993; Mulder 1995	CC†♂ RC*♀
Mammals	Banded mongoose *Mungos mungo*	Cant *et al.* 2001, 2010; Gilchrist 2006	RC*
	Cotton-top tamarin *Saguinus oedipus*	Savage *et al.* 1997	RC*
	Damaraland mole-rat *Fukyomys damarensis*	Faulkes & Bennett 2001; M. Zöttl, pers. comms.	RC*
	Meerkat *Suricata suricatta*	Clutton-Brock *et al.* 1998; Young *et al.* 2006	RC*
	Redfronted lemur *Eulemur rufifrons*	Kappeler & Fichtel 2012	RC*
	Spotted hyena *Crocuta crocuta*	Mills 1990; Holekamp *et al.* 1993	RC*

A second prominent explanation of the function of eviction comes from the 'pay-to-stay' hypothesis (Gaston 1978). This proposes that subordinate group members can compensate for costs that they inflict on dominant breeders (from increased competition for resources and reproduction) by providing help, such as cooperative care of offspring or territory defence, to stay in the group. According to the coercion of cooperation hypothesis, dominant individuals use eviction (and the threat of eviction) to coerce subordinates to help, and to punish 'lazy' individuals that are not providing a high enough level of helping behaviour. Theory suggests that temporary eviction of individuals should force them to work harder on their return through a process of appeasement (Bowles & Gintis 2004; Quiñones *et al.* 2016). Permanent exclusions of lazy helpers might be effective in establishing a dominant's reputation for punishment and therefore act as a means of inducing cooperation from remaining helpers (dos Santos, Rankin & Wedekind 2011). Under the pay-to-stay hypothesis, eviction is predicted to occur when helpers exhibit low levels of helping effort, or when group productivity is poor (Taborsky 1985; Bergmüller & Taborsky 2005; Fischer *et al.* 2014). Eviction should also be associated with a subsequent increase in helping behaviour from remaining or returning helpers, or an improvement in group productivity (Balshine-Earn *et al.* 1998).

Patterns of eviction in social vertebrates

Many of the observations of eviction in fish occur through experimental manipulation (Table 1). In fish that form size-based hierarchies, dominant individuals use the threat of eviction to deter subordinates from growing large enough to challenge their position (Buston 2003a; Wong *et al.* 2007; Ang 2010). In these species, the largest fish monopolise breeding and so eviction is triggered by competition for the breeding position. In cooperatively breeding cichlids, *Neolamprologus pulcher*, however, experimental evidence provides support for the hypothesis that eviction (and the threat of eviction) is used to coerce subordinates to help. Helpers that are experimentally prevented from helping are subject to elevated aggression from dominants and other group members, and subsequently help more, as predicted if aggression is a signal of impending eviction (Taborsky 1985; Bergmüller & Taborsky 2005; Fischer *et al.* 2014). In addition, helpers that are temporarily removed are often

evicted on their return, and those that are reaccepted work harder thereafter (Balshine-Earn *et al.* 1998).

Among bird species where eviction has been observed, much of the evidence of eviction supports the reproductive competition hypothesis. Only one experimental study of superb fairy-wrens, *Malurus cyaneus*, found evidence that eviction is used to coerce cooperation (Mulder & Langmore 1993). Male subordinate helpers that were temporarily removed subsequently received more aggression from male dominants and some were not allowed to return to the nest (Mulder & Langmore 1993). However, a separate study in this species found that dispersal of female helpers occurs after a period of increased aggression from dominant females, suggesting that eviction of females is driven by reproductive competition (Mulder 1995). Similarly, in the southern pied babbler, *Turdoides bicolor*, eviction occurs between same-sex brood mates (Raihani 2008; Ridley *et al.* 2008) and in the tropical Montezuma oropendola, *Psarocolius montezuma*, dominant males exclude lower ranking males to prevent them from approaching nesting females (Webster 1994). In the Arabian babbler, *Turdoides squamiceps*, eviction occurs between same-sex subordinates as they compete for a vacant breeding position after the death of the dominant breeder (Zahavi 1990). In these species where there is high levels of reproductive skew, and monopolisation of reproduction by a dominant breeding pair, competition for the breeding position appears to be the primary cause of eviction.

In social mammals, eviction is exclusively driven by competition over reproduction. Eviction is associated with high levels of competition among females, and with subsequent negative fitness consequences, in banded mongooses, *Mungos mungo* (Cant *et al.* 2010), redfronted lemurs, *Eulemur rufifrons* (Kappeler & Fichtel 2012) and meerkats, *Suricata suricatta* (Clutton-Brock *et al.* 1998). In meerkats, dominant females evict subordinate females in the latter half of their (own) pregnancy to avoid infanticidal attacks on their pups (Clutton-Brock *et al.* 1998). Females that are pregnant when evicted lose weight and become stressed, and often spontaneously abort their litter before gaining re-admittance to their group, similar to patterns observed in banded mongooses (Young *et al.* 2006; Gilchrist 2006). Evidence of eviction in spotted hyenas, *Crocuta crocuta*, Damaraland mole-rats, *Fukyomys*

damarensis, and cotton-top tamarins, *Saguinus oedipus*, is less well documented. In these species, dispersal of subordinate females is associated with increased levels of aggression from dominant females and so eviction is assumed to be triggered by reproductive competition (Mills 1990; Holekamp *et al.* 1993; Savage *et al.* 1997; Faulkes & Bennett 2001).

In most vertebrate species where eviction is observed, eviction of group members is the primary means by which individuals disperse from their natal group. As such, eviction can have important consequences for gene flow between groups, and for population structure and dynamics. Most of the research on eviction to date has focussed on the causes of eviction but, because eviction is only observed in a handful of species, there is a still a lack of understanding of what triggers eviction. Additionally, it is vital to establish which individuals are targeted for eviction to inform on the possible consequences that eviction can have. Theoretical studies to date have focussed on the short-term fitness payoffs of eviction to individuals (Johnstone & Cant 1999; Johnstone 2000; Hamilton & Taborsky 2005; Buston *et al.* 2007) but eviction is likely to have long-term demographic consequences that extend beyond those experienced by evictors and evictees. However, few studies are able to investigate the causes and consequences of eviction in this way because it requires following groups of animals for extremely long periods, being able to identify individuals and collect comprehensive data on their life history, being able to observe eviction in these groups, and tracking evicted cohorts through the population. These are all issues which are logistically very challenging. As such, the consequences of resolving within-group conflict by eviction and the potential effects of eviction on social evolution are not well understood.

Intergroup conflict in social vertebrates

Much of the research on patterns of conflict in social animals has focussed on that which occurs within groups. However, as suggested previously, conflict between groups is another conspicuous feature of animal societies. Intergroup conflict can take various forms, from aggressive vocalisations and territorial displays (Radford 2003; Bonanni *et al.* 2011; Mares, Young & Clutton-Brock 2012), to physical fighting and

lethal combat (Aureli *et al.* 2006; Wrangham, Wilson & Muller 2006; Batchelor & Briffa 2011). Throughout human history, lethal violence between societies has been well documented (Ferguson 1997; Gat 2006; Smith 2007), and there has been a recent resurgence of interest in a long-held suggestion that warfare in humans can exert selection for cooperative traits (Darwin 1871; Bowles 2006, 2009; Choi & Bowles 2007; Rusch 2014).

Violent conflicts are well documented among humans and non-human primates, particularly chimpanzees (Wilson, Wallauer & Pusey 2004; Wrangham *et al.* 2006; Mitani, Watts & Amsler 2010), but also in a range of other primate species (white-faced capuchin monkeys, *Cebus capucinus*, Gros-Louis, Perry & Manson 2003; spider monkeys, *Ateles geoffroyi yucatanensis*, Aureli *et al.* 2006; black and white colobus monkeys, *Colobus guereza*, Harris 2010; black howler monkeys, *Alouatta pigra*, and tufted capuchin monkeys, *Sapajus nigritus*, Belle & Scarry 2015). Outside of primates, violent interactions between groups are less well observed, but have been examined in other social mammals (gray wolves, *Canis lupus*, Mech 1994; Cassidy *et al.* 2015; spotted hyena, Boydston, Morelli & Holekamp 2001; banded mongooses, Cant, Otali & Mwanguhya 2002; African lions, *Panthera leo*, Mosser & Packer 2009), and cooperatively breeding birds (green woodhoopoes, *Phoeniculus purpureus*, Radford 2011; pied babblers, Golabek, Ridley & Radford 2012). Theoretical research has investigated the evolution of intergroup conflict in humans, and studies of patterns of lethal conflict in chimpanzees have provided empirical support for evolutionary models. However, beyond humans and chimpanzees, the significance of intergroup conflict as a selective force in the evolution of social species is not well understood.

Hypotheses of violent intergroup conflict

Evolutionary theories of violent conflict between groups have mainly focussed on the significance of collective violence in humans, but have been examined in the context of intergroup conflict in other social species (Durrant 2011; Rusch 2014). Most explanations for the evolution of violent intergroup conflict suggest that groups can achieve enhanced reproductive success by winning access to resources, such as food, territory and mates, in intergroup contests (Durrant 2011). Violent conflict can therefore apply a selection force at the group level because groups that are successful

in winning these resources outcompete losing rivals (Hamilton 1975; Bowles & Gintis 2011).

The 'imbalance of power' hypothesis (Wrangham 1999) suggests that individual fitness is increased, both in absolute terms and relative to that of neighbours, when individuals participate to injure or kill conspecifics in neighbouring groups. As such, the group becomes more likely to win future contests. Wrangham (1999) proposes that lethal intergroup aggression is selected for when (1) neighbouring groups are sufficiently hostile, and (2) there exists an asymmetry in strength between groups such that one can attack the other at little cost. Selection for individuals who contribute to group violence increases the competitive ability of groups that contain many of these individuals, meaning that the forces of individual and group selection are aligned. The imbalance of power hypothesis is supported by empirical evidence for lethal intergroup attacks from humans and chimpanzees (Wrangham & Peterson 1996; Wrangham 1999), but has been little investigated among other species.

Other hypotheses suggest that violent intergroup conflict has evolved as a facultative male reproductive strategy (van der Dennen 1995), since males can improve reproductive opportunities through increased access to females. Factors such as the capacity to form coalitions, group territoriality, and the ability to distinguish and favour the in-group over the out-group select for male coalitional violence because of a concomitant increase in reproductive fitness. The 'male warrior' hypothesis (van Vugt 2009) similarly suggests that males benefit in fitness terms from violent intergroup conflict. Thus, selection favours male warriors who engage more in intergroup interactions and exhibit in-group allegiance in times of conflict. Under these hypotheses, increased reproductive prospects and access to mates as a result of engaging in contests with rivals is expected to drive the evolution of intergroup conflict.

A final hypothesis to explain the evolution of intergroup conflict proposes that contributing to collective violence may represent a form of individual altruism. The 'parochial altruism' hypothesis (Choi & Bowles 2007) suggests that individuals that exhibit extreme hostility to out-group members and a high degree of altruistic

behaviour to in-group members ('parochial altruists'; Choi & Bowles 2007) increase the likelihood of their group being successful at attaining resources that improve reproductive success. Therefore, groups that contain more parochial altruists are selected for, relative to groups that do not contain these individuals. In a similar model, Lehmann and Feldman (2008) propose that selection for traits of 'bravery' (which increases a group's success in intergroup contests) and 'belligerence' (which increases a group's propensity to engage in intergroup contests) increases when there are constraints on dispersal, and so intergroup conflict is more likely to evolve in groups with high relatedness, such as those which form viscous societies (Hamilton 1975; Lehmann & Feldman 2008).

Despite its prevalence among social species, the adaptive significance of violent intergroup conflict has been explored mainly in humans and chimpanzees (Wrangham 1999; Bernhard, Fischbacher & Fehr 2006; Bowles 2009; Wrangham & Glowacki 2012). Violent intergroup conflict is a notable feature of cooperatively breeding species where there is potential for intergroup conflict to influence demographic processes, such as migration, colonisation of new territory and population expansion (Lehmann & Feldman 2008), and the evolution of social traits (Lehmann & Rousset 2010; Bowles & Gintis 2011). However, a lack of understanding of the causes and consequences of intergroup conflict in species that exhibit conspicuous levels of cooperation and collective violence means that the role of intergroup conflict in the evolution of social behaviours is not well established. Cooperatively breeding species, for which there are long-term data on ecological conditions, genetic population structure, and individual behaviour, can provide the kind of data needed to advance conceptual understanding of the links between within-group and between-group conflict.

Study system: The banded mongoose

This thesis investigates within- and between-group conflict in a wild population of cooperatively breeding banded mongooses, *Mungos mungo*, in Queen Elizabeth National Park, Uganda. The banded mongoose is a small (ca. 1.5 kg) diurnal carnivore (Figure 1) of the family *Herpestidae* which is distributed widely in savannah, open forest and grassland habitats throughout sub-Saharan Africa (Hoffmann 2008).

Figure 1. A resting group of banded mongooses at the study site.

Reproduction

Individuals live in mixed-sex social groups of approximately 20 adults plus offspring, although groups as large as 75 individuals have been observed (Cant 2000). Groups consist of a core of breeding adults (one to five females, and three to seven males) that reproduce on average four times per year, along with a subset of younger individuals that breed occasionally (Cant *et al.* 2010; Nichols *et al.* 2010, 2012). Reproduction is highly synchronised within, but not between, groups: reproductive females in a group enter oestrus within 7-10 days of giving birth, and mate within a week of each other (Cant 2000). Most females start to breed regularly once they are 1 year old, but males form an age based hierarchy in which the oldest three males monopolise mating, generally achieving paternity at 3 years old (Cant *et al.* 2016). During oestrus, dominant breeding males 'mate-guard' receptive females by closely following and trying to mate with them, and aggressively defending them from attempted matings by pestering males (Cant 2000). Each pregnant female gestates one to four pups for an average of 60 days (Cant 2000) and parturition is highly synchronised, with 64% of females giving birth on exactly the same day (Hodge, Bell & Cant 2011).

Cooperative care of young

Pups are born into a communal litter that is cared for by all members of the group (Cant 2003; Gilchrist & Russell 2007; Hodge 2007). There are two distinct forms of cooperative care, and most group members over 6 months old exhibit one or both of these behaviours (Cant *et al.* 2016). In the weeks after birth, pups are guarded at the den by 'babysitters', usually one to five individuals of both sexes (Cant 2003). The number of babysitters left to guard the litter has a strong effect on litter survival to emergence (Cant 2003; Marshall *et al.* 2016). Once pups emerge, at approximately 4 weeks old, they form a one-to-one relationship with an adult 'escort' who protects them from predators, feeds them, and teaches them how to forage (Gilchrist & Russell 2007; Gilchrist 2008). Being escorted also has large fitness benefits to pups. Pups that are more frequently escorted are more likely to survive to nutritional independence (3 months old), grow faster, and reproduce earlier (Hodge 2005).

Within- and between-group conflict

Banded mongooses, as well as exhibiting high levels of cooperative care, also exhibit conspicuous levels of conflict, both within and between groups. Eviction from groups is common, and each eviction event starts suddenly, lasts several days, and involves intense aggression from males and females directed towards multiple individuals (Cant *et al.* 2001, 2010; Gilchrist 2006). Aggression continues until groups of females, and on occasion groups of males alongside them, are driven away from the group *en masse* (Cant *et al.* 2001). Following eviction, evictees are sometimes allowed to return to their group within a week ('temporary evictions') or they may disperse permanently ('permanent evictions'; Gilchrist 2006). In eviction events where the permanently evicted cohort is mixed-sex, males and females split into single-sex cohorts and disperse separately, most likely to avoid inbreeding (Cant *et al.* 2016).

Banded mongooses also experience high levels of conflict between groups. Intergroup conflict between neighbouring groups involves intense aggressive interactions (Cant *et al.* 2002). On meeting or discovering the smell of a rival group, individuals stand on their hind legs and start making 'screeching calls' that alert the rest of the group. Group members cluster together in preparation of attack, and physical fighting is likely if the groups are evenly matched in size (Cant *et al.* 2002). Contests are ferocious:

individuals often die during, or shortly after, these battles, and newly born pups have been observed to be killed by rival groups (Cant *et al.* 2002; Müller & Bell 2009; Jordan *et al.* 2010; Nichols, Cant & Sanderson 2015). Experimental evidence shows that groups respond more aggressively to stimuli from neighbours that represent a territorial threat (Müller & Manser 2007) compared to stimuli from non-neighbours. Both group size and the location of a group in its territory affect the strength of response to playbacks of rival groups: groups respond more intensely to stimuli presented in the core areas of their territory compared to the periphery; and larger groups are more likely to respond to stimuli than smaller groups (Furrer, Kyabulima & Willems 2011). Observations also suggest that males and females engage in intergroup interactions in order to achieve extra-group matings (Cant *et al.* 2002; Nichols *et al.* 2015).

Study site and methods

All research for this thesis was conducted using a habituated population of banded mongooses that inhabit the Mweya peninsula in Queen Elizabeth National Park in south-west Uganda (0°12'S, 27°54'E; Figure 2). This population was first studied by Jon Rood in the 1970s, subsequently by Daniela de Luca in the 1990s, and the current research project was started in 1995 by Mike Cant and Tim Clutton-Brock.

The Mweya peninsula is a 4.95 km^2 heart-shaped promontory that extends into Lake Edward and is connected to the mainland by a narrow isthmus (Figure 2c). The habitat is mainly medium-height grassland with scattered Euphorbia candelabra trees, *Euphorbia candelabrum*, and thickets of the woolly caper bush, *Capparis tormentosa*, and needle bush, *Azima tetracantha* (Cant 2000; Cant *et al.* 2016). The peninsula is split into upper and lower halves by a 40 m high grassy slope (Figure 2c). The climate is equatorial with little fluctuation in temperature (Marshall *et al.* 2016) but seasonal variation in rainfall, with two dry periods in January-February and June-July (Cant *et al.* 2016; Marshall *et al.* 2016). The peninsula is inhabited by large herbivores including African elephant, *Loxodonta Africana*, hippopotamus, *Hippopotamus amphibious*, Cape buffalo, *Syncerus caffer*, waterbuck, *Kobus ellipsiprymnus*, and warthog, *Phacochoerus africanus*. Large predators including leopard, *Panthera pardus*, African lion and spotted hyena are also frequently observed.
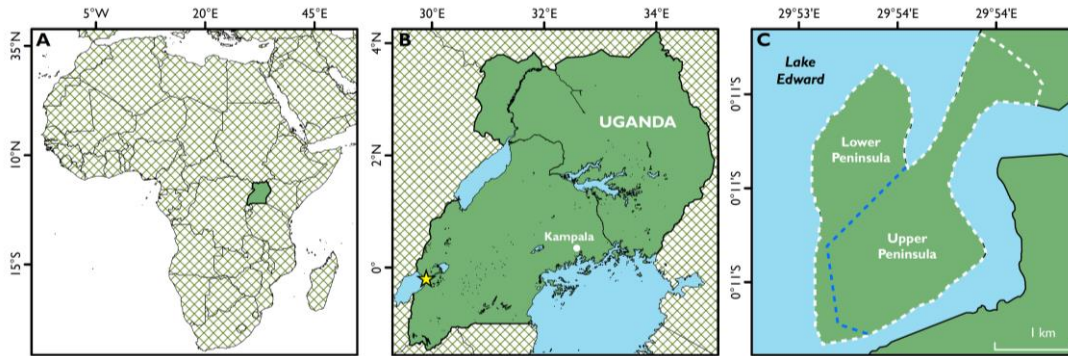
Figure 2. Location of the Banded Mongoose Research Project study site. (a) Location of Uganda on the African continent. **(b)** Location of the Mweya peninsula in Uganda denoted by a gold star. **(c)** Map of the Mweya peninsula; the white dashed line denotes the boundary of the field site, and the blue dashed line denotes the grassy slope that separates the upper and lower peninsula. Maps courtesy of Philip Doherty.

In our study population of banded mongooses, there are approximately 250 individuals living in 10 to 12 social groups at any one time (Cant *et al.* 2016). The Banded Mongoose Research Project database contains 20 years of life history and behavioural data on over 3000 individuals. All individuals in the study population are uniquely marked, in the past using plastic, coloured collars but more recently with shave patterns on their back. Individuals are captured as pups within 3 weeks of emergence and then every 3 to 6 months until they die or disperse to maintain these identification markings, and to take tissue and blood samples for genetic and physiological analysis. Individuals are trapped using box traps (67 x 23 x 23 cm; Tomahawk Live Trap Co., Tomahawk, WI, USA) and, following capture, anaesthetised using either ketamine or isoflurane (for further details of the trapping procedure, see Cant 2000; Hodge 2007; Jordan *et al.* 2010). On first capture as a pup, a tail tip tissue sample is taken for genetic analysis (Nichols *et al.* 2010). The DNA extracted from these genetic samples has been used to construct a pedigree using a panel of 43 polymorphic microsatellite markers to allow assignment of parentage and relatedness estimates (for further details, see Sanderson *et al.* 2015).

In each group, one or two individuals are fitted with a VHF radio collar (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., UK) that enables observers to locate groups. All individuals within the study population are habituated to the presence of an observer within 5 m, allowing detailed behavioural data to be collected. Groups are visited every 1 to 3 days to record life history and behavioural data, and daily if females are in oestrus, there are dependent pups, if females are expected to give birth, or if an eviction has recently occurred. Observers locate a group in the morning (before 7 a.m.) as they emerge from their den, and then follow them during their morning foraging session which lasts approximately 4 hours. In the middle of the day groups return to the den to rest, before leaving again to forage in the afternoon. Groups are re-located at around 4 p.m. for observations before they return to their den to sleep. Most individuals in the study population are trained to step onto a small portable weighing scale using a dilute milk solution as a reward in order to collect body mass data each week. Individuals in a group are weighed in the morning before foraging begins, in the evening at the end of the afternoon foraging session, and again the next morning to give an estimate of individual daily weight gain and overnight weight loss. Behavioural data are collected using a combination of *ad libitum*, scan sampling, and focal observations (Martin & Bateson 1993) and recorded on Psion LZ-64 handheld data loggers (Psion Teklogix Inc., Ontario, Canada).

Thesis aims and outline

In this thesis, I use the banded mongoose as a model system to examine within- and between-group conflict in a cooperative species. Specifically, the aims of this thesis are to: (i) investigate the causes of eviction as a means of within-group conflict resolution; (ii) examine which individuals are targeted for eviction, and why; (iii) investigate the consequences of eviction for individuals, groups and the wider population; and (iv) investigate the causes and consequences of intergroup conflict. I explain in more detail below:

Chapter 2 examines the triggers of eviction. I test established hypotheses and introduce a new hypothesis to explain the occurrence of eviction as a means of conflict resolution.

Chapter 3 investigates which individuals are evicted during an eviction event. I find a surprising effect of relatedness that motivated the development of a new theoretical model. I test the predictions of this model using data on eviction and another conspicuous manifestation of within-group conflict, infanticide.

Chapter 4 examines the consequences of eviction for evicted individuals and evicting groups by investigating demographic effects such as dispersal, reproduction, survival and group composition. This chapter also investigates the wider effects of eviction by examining the relationship between eviction and intergroup conflict.

Chapter 5 investigates the environmental and social triggers of intergroup conflict in the population, the fitness costs of intergroup conflict for pups and adults, and the long-term consequences for group size.

Finally, **Chapter 6** provides a synthesis and a general consideration of the findings of this thesis.

Chapter 2: Reproductive competition triggers mass eviction in cooperative banded mongooses

Abstract

In many vertebrate societies, forced eviction of group members is an important determinant of population structure, but little is known about what triggers eviction. Three main explanations are (1) the reproductive competition hypothesis; (2) the coercion of cooperation hypothesis; and (3) the adaptive forced dispersal hypothesis. The last hypothesis proposes that dominant individuals use eviction as an adaptive strategy to propagate copies of their alleles through a highly structured population. We tested these hypotheses as explanations for eviction in cooperatively breeding banded mongooses, *Mungos mungo*, using a 16-year dataset on life history, behaviour and relatedness. In this species, groups of females, or mixed-sex groups, are periodically evicted *en masse*. Our evidence suggests that reproductive competition is the main ultimate trigger for eviction for both sexes. We find little evidence that mass eviction is used to coerce helping, or as a mechanism to force dispersal of relatives into the population. Eviction of females changes the landscape of reproductive competition for remaining males, which may explain why males are evicted alongside females. Our results show that the consequences of resolving within-group conflict resonate through groups and populations to affect population structure, with important implications for social evolution.

Introduction

Individuals living in 'viscous' groups, in which there are severe constraints on dispersal, face numerous conflicts of interest with other group members. In cooperative breeders, conflict can arise over reproduction, helping effort, parental care, and dispersal (Emlen 1991; Koenig & Dickinson 2004; Cant 2012a). Much theoretical and empirical work has focused on how individuals resolve these within-group conflicts. In both insect and vertebrate societies, individuals may use threats, aggression, punishment and various strategies of negotiation to settle conflicts without breaking up the group (Johnstone & Hinde 2006; Cant 2011; Raihani *et al.* 2012). In other cases, however, within-group conflict results in the forcible eviction of one or more group members, typically following intense, targeted aggression (Cant *et al.* 2001; Young *et al.* 2006; Koenig & Walters 2011; Fischer *et al.* 2014). Eviction often leads to the permanent dispersal of individuals, or coalitions of individuals, and may be a major source of gene flow between groups (Koenig *et al.* 1998; Clutton-Brock & Lukas 2012). Determining what triggers eviction is therefore important to understand the factors that shape population genetic structure and demography in viscous populations, and hence social evolution (Rousset 2004; Lehmann & Rousset 2010).

In social vertebrates, eviction often appears to be driven by conflict over reproductive or social status within groups. In some mammal species, dominant individuals maintain their reproductive monopoly by evicting reproductive competitors from the group (Young *et al.* 2006; Cant *et al.* 2010). For example, in meerkats, *Suricata suricatta*, dominant females evict subordinate females in the latter half of their (own) pregnancy, often as a strategic measure to avoid infanticidal attacks on their pups (Clutton-Brock *et al.* 1998). Subordinates that are pregnant when evicted experience a deterioration in condition, elevated stress levels, and often spontaneously abort before gaining re-admittance to their group (Young *et al.* 2006). Consequently, eviction reduces future, as well as current, reproductive competition from the perspective of the dominant by suppressing subordinates' future reproductive success. In fish that form size-based hierarchies, dominant individuals use the threat of eviction to deter subordinates from growing large enough to challenge their position (Buston 2003a; Heg, Bender & Hamilton 2004; Wong *et al.* 2007). As a result, in the coral dwelling goby,

Paragobiodon xanthosomus, subordinates starve themselves to avoid triggering eviction (Wong *et al.* 2008).

Alternative explanations for eviction are based on the idea that dominant individuals can use eviction to coerce their subordinates to help. For example, the 'pay-to-stay' hypothesis (Gaston 1978) suggests that dominant individuals can threaten helpers with eviction unless they behave cooperatively. Additionally, dominant individuals might evict temporarily to coerce helpers to work harder on their return (Bowles & Gintis 2004), or evict permanently to establish a reputation for punishment and thereby induce remaining helpers to cooperate (dos Santos *et al.* 2011). Clear evidence in support of such coercive mechanisms comes from the cooperative cichlid, *Neolamprologus pulcher*. Helpers that are experimentally prevented from helping are subject to elevated aggression from dominants and subsequently help more, as predicted if aggression is a signal of impending eviction (Bergmüller & Taborsky 2005; Fischer *et al.* 2014). In addition, helpers that are temporarily removed are often evicted on their return, and those that are reaccepted work harder thereafter (Balshine-Earn *et al.* 1998). In cooperative birds and mammals, evidence for the pay-to-stay hypothesis is less clear-cut. In superb fairy-wrens, *Malurus cyaneus*, temporary removal of helpers results in increased aggression from dominants (Mulder & Langmore 1993), while in naked mole-rats, *Heterocephalus glaber*, and meerkats there is evidence that uncooperative helpers are subject to aggression from dominant breeders (Reeve 1992; Clutton-Brock *et al.* 2005). In addition, temporarily evicted female meerkats are more likely to allolactate on their return to the group than non-evicted females (MacLeod, Nielsen & Clutton-Brock 2013). By contrast, studies of bell miners, *Manorina melanophrys*, (McDonald *et al.* 2008a; b) and chestnut-crowned babblers, *Pomatostomus ruficep*, (Nomano *et al.* 2015) have failed to find support for mechanisms based on pay-to-stay or punishment.

A third, unexplored hypothesis is that eviction is an adaptive forced dispersal strategy used by breeders to spread copies of their alleles through the wider population. Traditionally, studies of cooperative breeders have used the number of surviving offspring as a measure of fitness. However, groups of cooperative breeders can be thought of as miniature populations embedded within a wider metapopulation (Hanski

1998). In this kind of structured population, what matters is not just the number of offspring that are successfully raised, but how successful these offspring are at dispersing to form or join new groups, and in turn produce dispersing offspring of their own - sometimes referred to as metapopulation fitness (Metz & Gyllenberg 2001; Massol, Calcagno & Massol 2009). Forced dispersal could be a strategy to maximise metapopulation fitness, over and above any immediate benefits evictors might gain by reducing local competition (although more intense local competition should strengthen selection for forced dispersal). If eviction is primarily a strategy to export copies of alleles, one would expect dominants to evict related individuals rather than unrelated individuals, to evict when local competition is high, and to evict when the evictees have the best chance of dispersing successfully to found or usurp new groups.

Banded mongooses, *Mungos mungo*, are a good system to test hypotheses about the causes and function of eviction in cooperative societies because evictions are common and conspicuous. This species lives in mixed-sex groups of around 20 adults, plus offspring. Each eviction event starts suddenly, lasts several days, and involves intense aggression from males and females directed toward multiple individuals. Aggression continues until groups of females, and on occasion groups of males alongside them, are driven away from the group, sometimes limping or bleeding (Cant *et al.* 2001). Up to 26 individuals have been observed to be evicted in a single eviction event (Cant *et al.* 2001). Evictees are sometimes allowed to return to their group within a week ('temporary evictions') or they may disperse permanently ('permanent evictions'; Gilchrist 2006). In mixed-sex, permanent eviction events, males and females form same-sex cohorts and disperse separately, most likely to avoid inbreeding (Cant *et al.* 2016).

In banded mongoose groups there is intense reproductive competition among both males and females (Cant, Vitikainen & Nichols 2013). Among males, a few high-ranking 'mate guarding' males aggressively monopolise access to females during oestrus: on average the oldest three males sire 85% of offspring in each group (Nichols *et al.* 2010). Most females give birth in each breeding attempt, usually on the same day (Hodge *et al.* 2011), and the communal litter is reared by the whole group (Cant 2003; Gilchrist 2004). Pups compete for food and access to helpers, and the *per capita*

reproductive success of females declines as the number of breeding females grows large (Cant *et al.* 2010). There is also conspicuous helping behaviour exhibited by both parents and non-parents. Both males and females 'babysit' offspring at the den in the first month after birth (Cant 2003), and after pups emerge they are guarded and provisioned by adult 'escorts' (Gilchrist & Russell 2007).

In this paper we investigated what triggers eviction events in groups of banded mongooses. We tested three distinct but non-exclusive hypotheses: (1) eviction is a response to reproductive competition; (2) eviction is used to coerce cooperation; (3) eviction is an adaptive forced dispersal strategy. We make the following predictions (Table 1). First, if eviction is a response to reproductive competition we predict that an eviction event is more likely to occur when intrasexual competition is high, and when ecological conditions are unfavourable for successful reproduction. Other things being equal, increasing relatedness should reduce the probability of an eviction event, because dominants should be more tolerant of kin competitors (Higashi & Yamamura 1993), and because kinship should reduce competitive effort within groups (Harris 1981; Reeve, Emlen & Keller 1998). Second, if eviction is used to coerce helpers we predict a higher probability of eviction following breeding attempts where helping performance was poor, where the outside options for helpers are good (Bergmüller, Heg & Taborsky 2005; Cant & Johnstone 2009), and where relatedness is low (Zöttl *et al.* 2013b). In addition, if eviction is used as a mechanism to enforce harder work, we expect eviction events to result in improved helping performance in the subsequent breeding attempt. Third, if eviction is a means by which dominants force copies of their alleles into the wider population we expect eviction events to occur when relatedness in the group is high, when local competition is high, and when ecological conditions are favourable for successful dispersal.

We tested these predictions using a dataset of 496 breeding attempts for which we had information on group composition, reproductive success, helping behaviour, relatedness, ecological conditions, and whether eviction occurred. Note in this paper we explicitly focus on the factors that trigger group eviction events, rather than on what features of individuals determine the risk of being evicted.

Table 1. Predictions of the hypotheses of eviction. Predicted effects of social and environmental variables on the probability of eviction under the three hypotheses described in the text. References provide theoretical or empirical support for the predictions.

Hypothesis	Number of competitors	Quality of ecological conditions	Prior helping performance*	Change in helping performance* following eviction	Mean group relatedness
Reproductive competition	More same-sex competitors → more intrasexual competition → more evictions	Poorer conditions → more intrasexual competition → more evictions	No clear prediction	No clear prediction	Lower relatedness → more intrasexual competition[1,2] → more evictions
Coercion of cooperation	No clear prediction	Better conditions → groups less stable[3], or helpers work less hard[4] → more evictions	Poorer helping performance → more evictions	Positive change → more evictions	Lower relatedness → groups less stable[3], or more coercion required[5] → more evictions
Adaptive forced dispersal	Larger group size → more resource competition → more evictions Or More same-sex competitors → more reproductive competition → more evictions	Better conditions → more successful dispersal → more evictions	No clear prediction	No clear prediction	Higher relatedness → forced dispersal more effective → more evictions

* measured by outcome or helping effort

[1] Harris 1981; [2] Reeve *et al.* 1998; [3] Cant & Johnstone 2009; [4] Bergmüller *et al.* 2005; [5] Zöttl *et al.* 2013b

Methods

Study population and data collection

We studied a population of banded mongooses on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E), between October 1996 and February 2013. Details of habitat are given elsewhere (Cant *et al.* 2013). Daily measurements of temperature and rainfall were recorded by the Uganda Institute of Ecology Meteorological Station and, later, using our own weather station. Over the 16-year study period, we observed 496 breeding attempts in 16 groups. Following Hodge *et al.* (2011), we defined a communal litter as one where all pregnant females gave birth within 30 days of one another. We defined a breeding attempt as the 67 day period prior to the birth of each litter (comprised of a 7 day oestrus and a 60 day gestation; Cant 2000). We defined an eviction event to have occurred in a breeding attempt if one or more individuals left their group for at least one day following a period of intense aggression toward themselves or other group members (Gilchrist 2006; Cant *et al.* 2010). In practice, evictions are conspicuous and noisy events that are easy to recognise. Typically, individuals leave only after being repeatedly attacked, but much aggression occurs in the bushes where we are unable to identify the aggressors or their victims. Instances where individuals left their group without any observed aggression toward any group member were defined as voluntary dispersal events and were not considered in our analysis. Groups were visited every 1 to 3 days to record life history and behavioural data. Most were habituated to human presence, allowing observers to watch and follow them from less than 5 m. One or two individuals in each group were fitted with a VHF radio collar (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., UK) that enabled groups to be located. Individuals were easily identifiable by either colour-coded plastic collars or, more recently, unique shave markings on their back. Individuals were regularly trapped to maintain these identification markings (see Jordan *et al.* 2010 for details). On first capture a 2 mm skin sample was collected from the end of the tail using sterilised scissors for genetic analyses. DNA was extracted and used to assign parentage and estimate relatedness using a panel of 43 polymorphic microsatellite markers (see Sanderson *et al.* 2015b for further details).

Statistical analyses

We used an information-theoretic approach (Burnham & Anderson 2002) in which we compared the explanatory power of models to investigate the factors that predict the probability that:

(i)   an eviction event occurred in a breeding attempt ('female evictions'). Since females are evicted in every eviction event, we focused the analysis on the factors predicted to influence female eviction;

(ii)   when an eviction event occurred, males were evicted alongside females ('male evictions'). Here we focused the analysis on the factors predicted to influence male eviction;

(iii)   when an eviction event occurred, it was temporary rather than permanent ('temporary evictions'). Since temporary evictions could be either female-only or mixed-sex events, we included factors predicted to influence both male and female eviction. An eviction was defined as temporary if more than 50% of the evicted cohort were allowed to return to their group.

For each analysis, we constructed a candidate set of models which together provided a comprehensive test of the predictions of our three hypotheses: reproductive competition, coercion of cooperation, and adaptive forced dispersal. The models incorporated additive combinations of the main terms predicted to influence eviction probability for the hypotheses, together with specific two-way interactions where we considered these biologically relevant.

(i) Models of eviction as a response to reproductive competition

To test whether an eviction event is more likely to occur when reproductive competition is high, we fitted the number of reproductive competitors at the start of the breeding attempt (denoted B), mean monthly rainfall (mm) (E) in the previous 6 months, the interaction between these social and ecological variables ($B{:}E$), and mean group relatedness (R) as fixed effects. Rainfall and insect abundance are correlated (Rood 1975; Cant *et al.* 2013; H. Marshall, unpublished data) so we expect low rainfall to intensify competition for food resources. In the female evictions analysis, reproductive competitors were defined as females 10 months and over (10 months is the age at first conception; Gilchrist, Otali & Mwanguhya 2004; Cant *et al.* 2010). In the

male evictions analysis, reproductive competitors were defined as males 3 years and over (3 years is the first age at which males typically become regular mate guards; Cant *et al.* 2016). In the temporary evictions analysis, male and female reproductive competitors were defined as above and fitted as separate fixed effects.

(ii) Models of eviction as coerced cooperation

The coercion of cooperation hypothesis predicts that eviction should be triggered by poor helper performance, but it is not clear whether animals should respond to the outcome of helping (i.e. reproductive success), or to helping behaviour *per se*. We separately investigated these alternatives by using two indices of helping performance: (i) female reproductive success (C_S); and (ii) helping effort (C_E). We also examined the change in helping performance (ΔC_S or ΔC_E).

(i) Female reproductive success, C_S, was defined as the number of emergent pups in the previous breeding attempt, per female that contributed to the communal litter. To account for differences in C_S that could be explained by differences in the amount of help available, we included the number of helpers available to babysit that litter (H) and the interaction between these terms (C_S:H). The interaction term is necessary to capture the difference between the same reproductive outcome achieved with few helpers versus many helpers. We included mean group relatedness (R) and mean monthly rainfall (E) as main effects. In the female evictions analysis, we defined helpers as females aged 6 months to 3 years, since females younger than 3 years are classed as subordinate and are more likely to participate in helping (Gilchrist & Russell 2007; Cant *et al.* 2014). In the male evictions analysis, helpers were defined as males aged 6 months to 3 years, since males do not become consistent breeders until around 3 years of age and, until then, contribute more to helping (Sanderson *et al.* 2015a; Cant *et al.* 2016). In the temporary evictions analysis, male and female helpers were defined as above and fitted as separate fixed effects.

To investigate if eviction is used to coerce helpers to work harder in the subsequent breeding attempt, we tested whether the change in helping performance from one litter to the next predicted the probability that an eviction event occurred in the interim. We reasoned that if eviction is used as a punishment to improve future

helping performance, an eviction event (and temporary eviction events in particular) should be associated with an increase in helping performance of remaining or returning helpers after eviction. We fitted ΔC_S, ΔH and the interaction between them (ΔC_S:ΔH) as fixed effects, where ΔC_S is the change in female reproductive success (i.e. the number of emergent pups, per female that contributed to the litter), and ΔH is the change in the number of available helpers, across two consecutive breeding attempts (the breeding attempt before the eviction, and the subsequent breeding attempt). Again, we included mean group relatedness (*R*) and mean monthly rainfall (*E*) as fixed effects. Note that ΔC_S and ΔH are likely to be affected by the problem of regression to the mean (Kelly & Price 2005) because extremely high or low values in the first measure of a given variable are more likely to move closer to the mean in a second measure of that variable. We controlled for potential problems with regression to the mean following the methods in Kelly & Price (2005) (see Appendix A).

(ii) Helping effort, C_E, was defined as the contribution by helpers (*H*) to babysitting in the previous breeding attempt (i.e. C_E = number of helpers that babysat per day of babysitting). We repeated the analyses outlined above, replacing C_S with C_E. In the female evictions analysis, C_E was defined as the number of female babysitters aged 6 months to 3 years left per day of babysitting of the previous litter. In the male evictions analysis, C_E was defined as the number of male babysitters aged 6 months to 3 years left per day of babysitting of the previous litter. In the temporary evictions analysis, C_E was defined as in the previous two analyses and fitted as separate fixed effects. In the temporary evictions analysis, the model including both the change in female helpers' babysitting effort and male helpers' babysitting effort was too complex to fit to the reduced sample of data and so these variables were fitted in separate models. Since data on babysitting behaviour was not available for all breeding attempts, analysis using this helping effort measure of helping performance was performed on a reduced sample (see Appendix A Tables A2, A4 and A6).

(iii) Models of eviction as an adaptive forced dispersal strategy

To test whether an eviction event is more likely to occur when relatedness is high, ecological conditions are good and local competition is intense, we fitted mean group relatedness (*R*), mean monthly rainfall (*E*), group size (all individuals over 6 months)

(*G*), the interaction between relatedness and rainfall (*R:E*), and the interaction between relatedness and group size (*R:G*) as fixed effects. We included group size to allow for the possibility that local resource competition contributes to the timing of eviction events. The interaction between relatedness and rainfall is particularly important to test the prediction that high group relatedness in combination with favourable ecological conditions will make an eviction event more likely to occur. The definitions of *R*, *E* and *G* were consistent across our three analyses. An alternative prediction is that the nature of competition under which adaptive forced dispersal operates could be reproductive, rather than resource related. We fitted an identical set of models to those described above, but replaced *G* with the number of reproductive competitors (*B*) in each of the three analyses.

(iv) Comparing model performance

Models, including a null model containing no fixed effects, were estimated using generalised linear mixed models (GLMM). Group identity was included as a random intercept to control for repeated measures across groups. In all analyses we used the maximum sample size for which we had data on all the terms in all the models (Appendix A Tables A1-A6). In all three analyses, the eviction metric was fitted as the binomial response variable using a logit link function in the 'lme4' package in R 3.1.2 (Bates *et al.* 2012; R Development Core Team 2014). We performed subsets selection of the maximal model under each hypothesis using the 'MuMIn' package (Bartón 2015), which examines all possible combinations of terms in each full model. Models were ranked by Akaike's Information Criteria (AIC), or corrected AIC (AICc) in analyses where $N/k < 40$, where *N* is the sample size and *k* is the number of parameters in the maximal model (Burnham & Anderson 2002). We defined a 'top model set' as models ≤ Δ6 AIC (or AICc) units of the best supported model (Richards, Whittingham & Stephens 2011), after excluding any models where a simpler nested version attained stronger support (applying the 'nesting rule' of Richards *et al.* 2011). Full model tables are provided in Appendix A.

Results

Observations of eviction

In total, we observed 47 eviction events in 8 out of 16 groups in our population between October 1996 and February 2013 resulting in the expulsion of 457 individuals. More females than males were evicted; in the 46 events for which we knew the sex and identities of the evictees, evictions resulted in the expulsion of 274 females and 170 males, with the median evicted cohort comprising 24% of the total group (range 3% - 60%). Just 3 eviction events (6%) resulted in the eviction of a single individual. In 25 (53%) of eviction events only females were evicted, with a median of 6 females evicted in a single event (range 1-12). On average, an eviction event resulted in the expulsion of 40% of female group members (range 6% - 79%). In the remaining 22 eviction events (47%) a cohort of males was evicted alongside a cohort of females. In these cases the median number of evictees was 13 individuals (range 6-26); median number of female evictees was 6 (range 2-15) and median number of male evictees was 9 (range 1-17). On average, an eviction event resulted in the expulsion of 35% of male group members (range 3% - 65%). Males were only ever evicted alongside females. In 8 out of 22 mixed-sex evictions (36%), some or all of both sexes dispersed permanently as a consequence of eviction. In all these cases, the evicted cohorts of males and females split into single-sex groups and dispersed separately. In 47% of all eviction events, all evictees were eventually readmitted to their group after persistently attempting to re-join. In 32%, some evicted individuals (both males and females) were allowed to return but others were not. Of temporarily evicted individuals, 69% were readmitted to their group within 1 week, 97% within 1 month, and all individuals within 6 months of eviction.

Testing the hypotheses

(i) Female evictions

Models of the reproductive competition hypothesis were by far the best predictors of the probability of an eviction event occurring during a breeding attempt (Table 2). Specifically it was the model containing the number of breeding females that performed the best out of the candidate model set, with an eviction event more likely

to occur when there were more breeding females (Figure 1). Models of the reproductive competition hypothesis had a cumulative adjusted Akaike's model weight of 100% of retained models from the top model set when helping performance was measured in terms of female reproductive success (C_S) (Table 2), and 95% when helping performance was measured in terms of helping effort (C_E) (Appendix A Table A2).
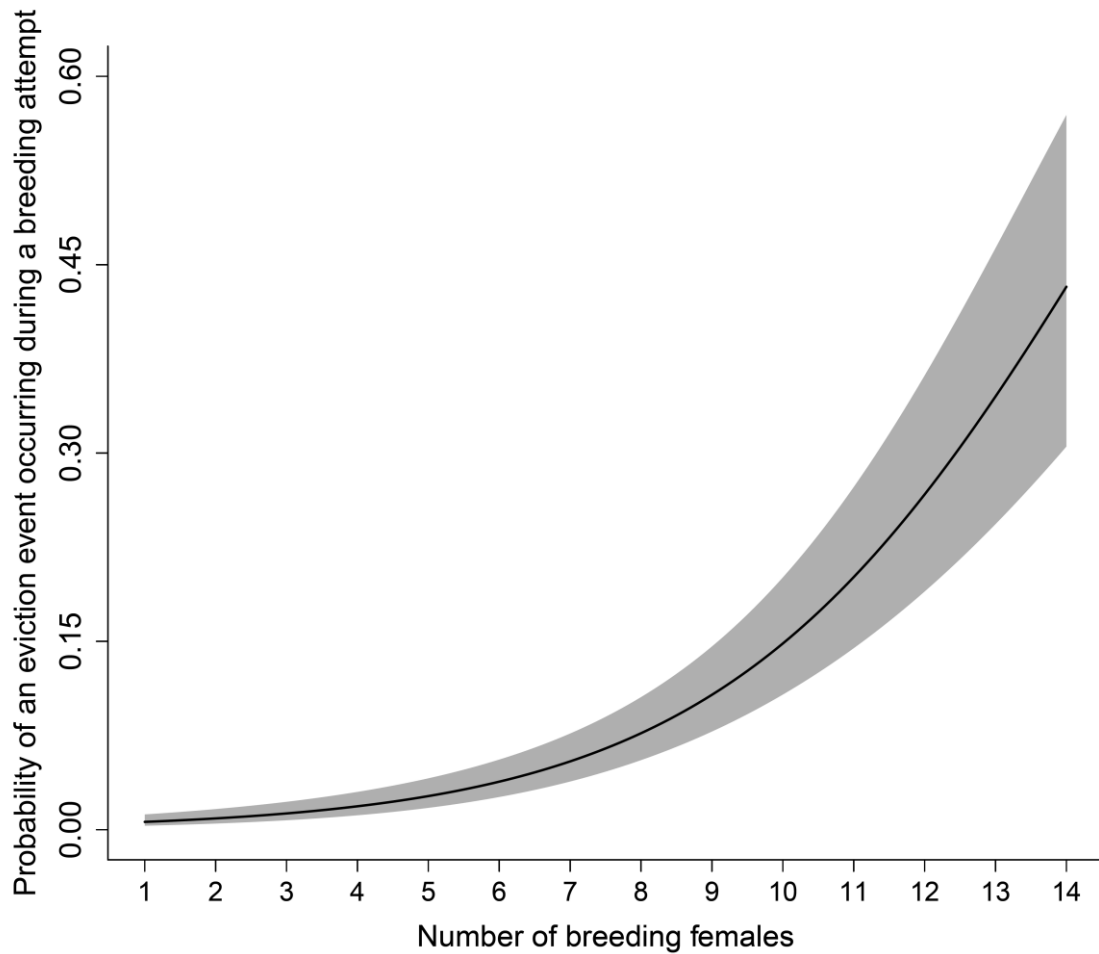
Figure 1. The probability of an eviction event occurring during a breeding attempt (*N*=415 breeding attempts in 15 groups). The line shows model predictions (± standard error).

Table 2. Top models of the analysis of female evictions. Model performance in predicting the probability of an eviction event occurring during a breeding attempt (*N*=415 breeding attempts in 15 groups). Analysis using the female reproductive success (C_S) measure of helping performance under the coercion of cooperation hypothesis. Models comprise the top model set where ΔAIC ≤ 6.

Hyp.	Int.	*B*	*E*	*R*	*B:E*	*R:B*	*R:E*	k	logLik	AIC	ΔAIC	*w_i*	Retained	Adj. *w_i*
R	-5.44	0.37						3	-108.63	223.26	0.00	0.34	✓	1.00
A	-3.34	0.11		-14.46		1.76		5	-107.25	224.50	1.24	0.18		
A/R	-5.49	0.37		0.42				4	-108.62	225.25	1.99	0.13		
R	-5.45	0.37	0.00					4	-108.63	225.26	2.00	0.13		
A	-3.29	0.11	0.00	-14.52		1.77		6	-107.25	226.50	3.24	0.07		
A/R	-5.51	0.37	0.00	0.43				5	-108.62	227.24	3.99	0.05		
R	-5.37	0.36	0.00		0.00			5	-108.63	227.26	4.00	0.05		
A	-3.34	0.11	0.00	-14.11		1.77	-0.01	7	-107.25	228.49	5.23	0.02		
A	-5.25	0.37	0.00	-1.44			0.03	6	-108.60	229.21	5.95	0.02		
R	-5.42	0.36	0.00	0.44	0.00			6	-108.62	229.24	5.98	0.02		

Hyp. = Hypothesis: A = Adaptive forced dispersal; R = Reproductive competition. Columns 2 to 8 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; *B* = number of breeding females; *E* = mean rainfall in previous 6 months; *R* = mean group relatedness; : = interaction. k = number of estimated parameters including a random intercept for group identity; logLik = log-likelihood; AIC = Akaike's information criterion; ΔAIC = change in AIC value from the best performing model; *w_i* = Akaike's model weight; Retained = ticks indicate that the model was retained after applying the nesting rule of (Richards *et al.* 2011); Adj. *w_i* = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term was absent from that model.

(ii) Male evictions

The probability that males were evicted with females, given that an eviction occurred, was also best explained by the reproductive competition hypothesis (analysis using the female reproductive success (C_S) measure of helping performance). Specifically, the model that performed best contained the number of breeding males (Table 3), with males more likely to be evicted with females as the number of breeding males increased (Figure 2). The only other model to be retained after applying the nesting rule (Richards *et al.* 2011) was the model of adaptive forced dispersal containing group size and mean group relatedness, with males more likely to be evicted alongside females in larger groups and when group relatedness was low, although this model only attained an adjusted weight of 5%. When performing the same analysis but using the helping effort (C_E) measure of helping performance on a reduced sample size, the only model that was retained was the null model which contained an intercept but no fixed effects (Appendix A Table A4).
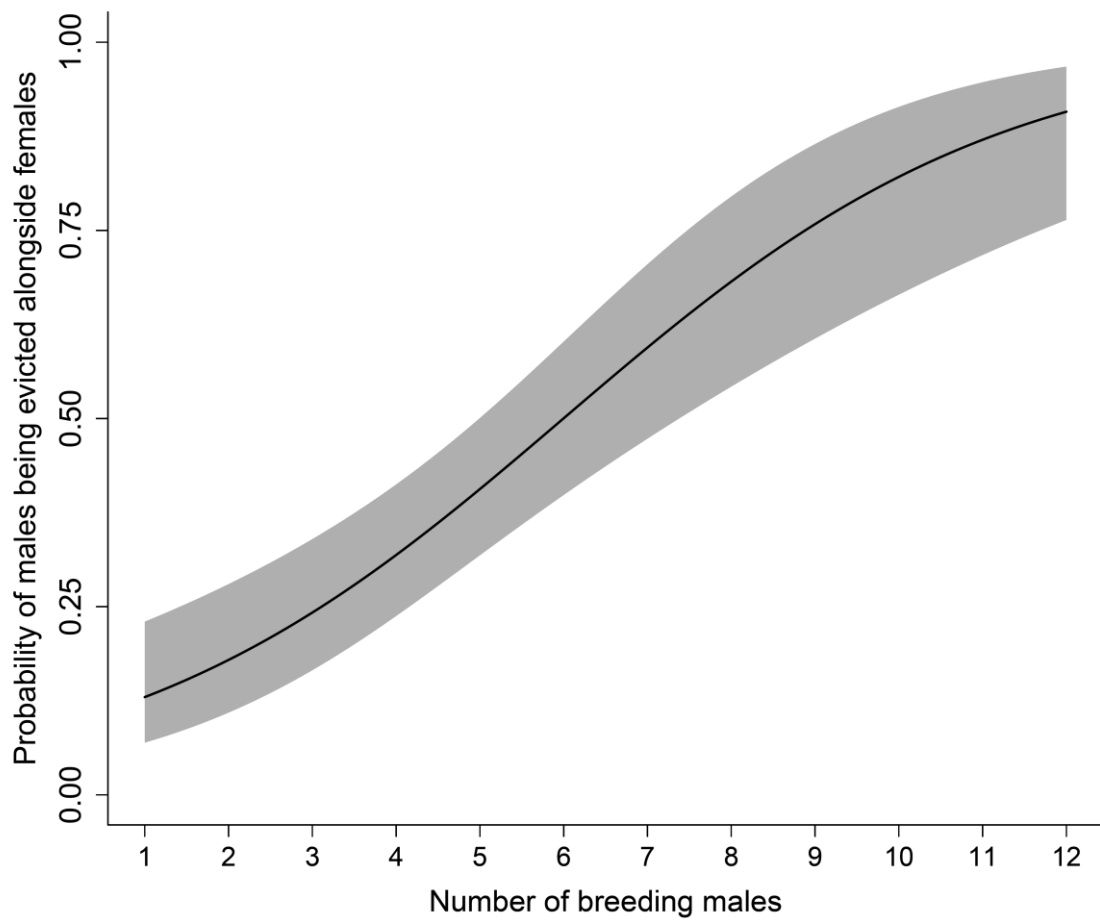
Figure 2. The probability that males are evicted alongside females when an eviction event occurs (*N*=37 eviction events in 7 groups). The line shows model predictions (± standard error).

Table 3. Top models of the analysis of male evictions. Model performance in predicting the probability that males are evicted alongside females when an eviction event occurs (*N*=37 eviction events in 7 groups). Analysis using the female reproductive success (C_S) measure of helping performance under the coercion of cooperation hypothesis. Models comprise the top model set where ΔAICc ≤ 6.

Hyp.	Int.	*B*	*E*	*R*	*B:E*	*R:B*	*G*	k	logLik	AICc	ΔAICc	*w_i*	Retained	Adj. *w_i*
R	-2.28	0.38						3	-20.42	47.57	0.00	0.51	✓	0.95
R	-1.81	0.39	-0.01					4	-20.32	49.88	2.32	0.16		
A/R	-2.16	0.38		-0.68				4	-20.41	50.07	2.51	0.15		
R	-0.30	-0.10	-0.04		0.01			5	-19.78	51.51	3.94	0.07		
A	-0.94	0.11		-9.71		2.02		5	-20.24	52.41	4.85	0.05		
A/R	-1.64	0.39	-0.01	-0.90				5	-20.31	52.55	4.98	0.04		
A	-3.82			-1.58			0.15	4	-22.08	53.41	5.84	0.03	✓	0.05

Hyp. = Hypothesis: A = Adaptive forced dispersal; R = Reproductive competition. Column headings as in Table 2, with the addition of *B* = number of breeding males; *G* = group size; AICc = corrected Akaike's information criterion; ΔAICc = change in AICc value from the best performing model. Ticks indicate that the model was retained after applying the nesting rule of (Richards *et al.* 2011). Blank cells indicate that the term was absent from that model.

(iii) Temporary evictions

None of our hypotheses explained whether eviction events were temporary rather than permanent. The null model performed better than all other models and this result was consistent whether female reproductive success (C_S) or helping effort (C_E) was used as a measure of helping performance (Appendix A Tables A5 and A6).

Discussion

Previous work on eviction in this species highlighted reproductive competition as a driver of female evictions, but did not consider male or temporary evictions, or test alternative hypotheses for eviction behaviour (Cant *et al.* 2001, 2010; Gilchrist 2006). For both female and mixed-sex eviction events, the reproductive competition hypothesis best explained our data. Females were more likely to be evicted when there were many breeding females in the group. These female eviction events are likely to radically alter the landscape of intrasexual competition among remaining males, which may explain why groups of males are commonly evicted alongside females. Males were more likely to be evicted when there were many breeding males in the group, again supporting the hypothesis that high levels of same-sex reproductive competition is a trigger for mass eviction.

Sex differences in the intensity of reproductive competition may explain why evictions of females are almost twice as common as male evictions. Reproductive competition is particularly intense among female banded mongooses because dominants are unable to suppress reproduction by younger females and suffer substantial fitness costs when large numbers of subordinate females breed alongside them (Cant *et al.* 2010, 2014). Dominant males, by contrast, can usually prevent subordinate males from mating, and so are less sensitive to the presence of additional males in the group. However, dominant males are not immune from reproductive competition because they cannot fully control the mating behaviour of females (Cant 2000; Nichols *et al.* 2010). Dominant males might also evict (usually younger) subordinates before these become genuine reproductive competitors, similar to the explanations for eviction in size-based fish hierarchies (Buston 2003a; Heg *et al.* 2004; Wong *et al.* 2007, 2008). At the same time, young male banded mongooses that are excluded from breeding have less to gain from putting up a fight to stay in their natal group compared to females. This potential difference in the level of resistance offered could explain why males sometimes disperse voluntarily, while female dispersal events almost always involve intense aggression.

We found little evidence to support the idea that mass evictions are triggered when it is adaptive for dominants to force subordinates to disperse. We did find weak support for a model that showed that males were more likely to be evicted with females when groups were large, but when mean group relatedness was low. This effect of relatedness is the opposite of that predicted under the adaptive forced dispersal hypothesis. Eviction of either sex was not more likely when mean group relatedness was high, nor when ecological conditions were benign. We cannot rule out adaptive forced dispersal entirely, however, because (1) we currently lack information about the long-term fate of evictees in the wider population; and (2) we currently lack a formal model of the adaptive forced dispersal hypothesis which might provide discriminating predictions beyond those based on our simple verbal arguments. Concerning point (1), eviction did result in the permanent dispersal of 193 individuals, which is 72% of the individuals in our population that left their natal group (Cant *et al.* 2016). Eviction is therefore likely to be a major determinant of gene flow and population structure in this system. Concerning (2), demographic models of kin selection (Johnstone & Cant 2008; Lehmann & Rousset 2010) usually assume that dispersal is under the full control of the offspring themselves, or under full maternal control (e.g. Ronce, Clobert & Massot 1998, but see Uller & Pen 2011). Our observations of eviction, by contrast, suggest that in many real systems, no single party has full control over group membership, and group dynamics are a compromise between the interests of evictors and evictees. A model embedding a conflict resolution mechanism (e.g. similar to Higashi and Yamamura's (1993) insider-outsider conflict model) in a demographic framework could be a useful tool to predict population consequences of reproductive competition.

Finally, we found little evidence to support the coercion of cooperation hypothesis for mass eviction in this system. This contrasts with strong evidence that eviction, and the threat of eviction, is used to coerce helpers to work harder in the cooperative cichlid *N. pulcher* (Balshine-Earn *et al.* 1998; Bergmüller & Taborsky 2005; Heg & Taborsky 2010; Zöttl *et al.* 2013b; Fischer *et al.* 2014). Why should eviction be effective to coerce cooperation in cichlids but not banded mongooses? We suggest two reasons. First, theory suggests that acts and threats of eviction will be much less effective at coercing cooperation when targeted at a group of individuals rather than specific individual

helpers (Cant *et al.* 2010). In a group of helpers, the threat of mass eviction creates a tragedy-of-the-commons over helping effort since the effort of any hard working helper can be readily exploited by the idleness of other potential evictees. Eviction is likely to be much more effective at inducing cooperation when targeted at individual transgressors, for example in dyads and in groups which exhibit a strict rank hierarchy (such as cooperative cichlids; Heg *et al.* 2004; Zöttl *et al.* 2013b; Fischer *et al.* 2014). Second, threats of eviction are predicted to be less effective at inducing pre-emptive cooperation when evictees are often reaccepted into the group, as in banded mongooses (Cant *et al.* 2010; this chapter) and meerkats (Clutton-Brock *et al.* 1998). The best tests of the coercion of cooperation hypothesis require experimental reduction of helper effort (Bergmüller & Taborsky 2005; Fischer *et al.* 2014), or manipulation of the availability of outside options (Heg & Taborsky 2010; Zöttl, Frommen & Taborsky 2013a), which is logistically challenging in birds and mammals. Further innovative experimental tests in a wider range of cooperative vertebrates would help to test the coercion of cooperation hypothesis more rigorously.

To summarise, our results suggest that intrasexual reproductive competition is the trigger for mass eviction of both sexes from groups of banded mongooses. Eviction of females appears to alter the landscape of intrasexual competition among males, leading to the mass eviction of males at the same time as, but separate from, the eviction of females. We did not find evidence to link eviction events to the enforcement of helping or the propagation of alleles through a structured population. Nevertheless, our study highlights that the consequences of resolving within-group reproductive competition can scale up to affect population structure and demography. This link between within-group conflict strategies and population processes has been little studied theoretically or empirically, but may be an important determinant of life history evolution in viscous animal societies.

Chapter 3: When should animals discriminate against kin? Forced eviction of relatives in the banded mongoose

Abstract

Kin selection theory predicts that, where kin discrimination is possible, animals should typically act more favourably towards closer genetic relatives, and direct aggression towards less closely related individuals. Contrary to this prediction, we use game theory to show that selection may, under certain conditions, favour negative kin discrimination in the targeting of aggressive acts, because unrelated targets are selected to invest more in resisting aggression. We tested our model using data from an 18-year study of wild banded mongooses, *Mungos mungo*, in which individuals are targeted for forcible eviction from their group, often suffering severe injury and death as a result. Consistent with our model, negative kin discrimination is restricted to eviction attempts of older females capable of resistance; dominants exhibit no kin discrimination when attempting to evict younger females, nor do they discriminate between more closely or less closely related young when carrying out infanticidal attacks on vulnerable infants who cannot defend themselves. We suggest that in contexts where recipients of selfish acts are capable of resistance, the usual prediction of positive kin discrimination can be reversed. Kin selection theory, as an explanation for social behaviour, can benefit from much greater exploration of sequential social interactions.

Introduction

Kin selection theory aims to understand how selection acts on social traits, such as altruism and selfishness, that affect the fitness of social partners and local group members (Hamilton 1964; Grafen 1984). The theory predicts that where animals can discriminate between more closely and less closely related individuals within their social group, they will preferentially direct altruism towards closer genetic relatives, and aggression towards less closely related targets (Hamilton 1964; Grafen 1984; West & Gardner 2010). Instances of such positive kin discrimination are taxonomically numerous and widespread (Abbot *et al.* 2011), while reported examples of negative kin discrimination are rare (Dunn *et al.* 2014; Foster & Briffa 2014).

Contrary to the predictions of traditional kin selection theory, we found evidence that banded mongooses exercise negative kin discrimination during attempts at eviction; and that this result was not readily explained by inbreeding avoidance. This result motivated us to develop a simple and very general sequential game model of selfish behaviour that takes into account the possibility of active resistance on the part of recipients, and which provides a potential explanation for negative kin discrimination. We first show the results of our initial analysis of patterns of eviction in banded mongooses, and then describe the model. Finally, we test predictions of the model using our data.

Patterns of eviction in banded mongooses

We examine kin discrimination in the context of a conspicuous form of intragroup aggression in cooperatively breeding banded mongooses, *Mungos mungo*: the violent eviction of males and females from the group. Banded mongooses live in highly cooperative groups with limited dispersal and varying levels of relatedness between group members (Cant *et al.* 2016). In our study population in Uganda, groups consist of around 20 adults, plus offspring, and breed on average four times per year (Cant *et al.* 2013). Multiple females give birth synchronously to a communal litter that is cared for by members of both sexes (typically not the parents) (Cant *et al.* 2016). Each group contains a cohort of multiple dominant females (median=4) that are older than the other females, breed more regularly and more successfully, and aggressively evict younger females (Cant *et al.* 2001, 2016; Nichols *et al.* 2010). Older males monopolise mating with oestrus females by mate-guarding them and aggressively driving away younger, subordinate males (Cant 2000; Nichols *et al.* 2010). Previous work shows that both sexes are capable of kin discrimination in the context of mating, supporting the assumption of our model that such discrimination is possible in this system (Sanderson *et al.* 2015b). Evictions are relatively common, involve intense, targeted aggression, and result in the forcible mass exclusion of groups (median=6 individuals) of females (female-only evictions) and, in around half of cases, groups (mean=9 individuals) of males alongside them (mixed-sex evictions; Thompson *et al.* 2016; Chapter 2). These mass evictions are triggered by high levels of intrasexual reproductive competition: females are evicted when there are many breeding females in the group, and males are evicted alongside females when there are many breeding males (Thompson *et al.* 2016; Chapter 2). Evictions are very violent, and evictees are often left with serious injuries as a result of the aggression they receive.

Among adult female banded mongooses, those more closely related to dominant individuals of both sexes (that is, males and females older than 3 years) in the group were more likely to be targeted for eviction (Generalised Linear Mixed Model (GLMM), $\beta \pm SE=9.95 \pm 3.36$, $\chi^2_1=9.51$, $p=0.002$; Figure 1a; Table 1). Younger females were also more likely to be subject to an eviction attempt (GLMM, $\beta \pm SE=-0.003 \pm 0.0005$, $\chi^2_1=39.98$, $p<0.0001$; Table 1), but there was no effect of a female's pregnancy status

or non-pregnant weight on her probability of being targeted for eviction (pregnancy status: GLMM, $\beta \pm$ SE=-0.61 $\pm$ 0.49, χ^2_1=1.63, p=0.20; weight: GLMM, $\beta \pm$ SE=0.002 $\pm$ 0.001, χ^2_1=2.59, p=0.11; Table 1). For a subset of eviction attempts (N=26 eviction attempts) we had data on the identity of 'primary aggressors' (individuals that were recorded as being notably more aggressive than other group members toward potential evictees). Females that were more closely related to primary aggressors were more likely to be targeted for eviction (GLMM, $\beta \pm$ SE=5.47 $\pm$ 2.87, χ^2_1=3.85, p=0.0498; Table 2).
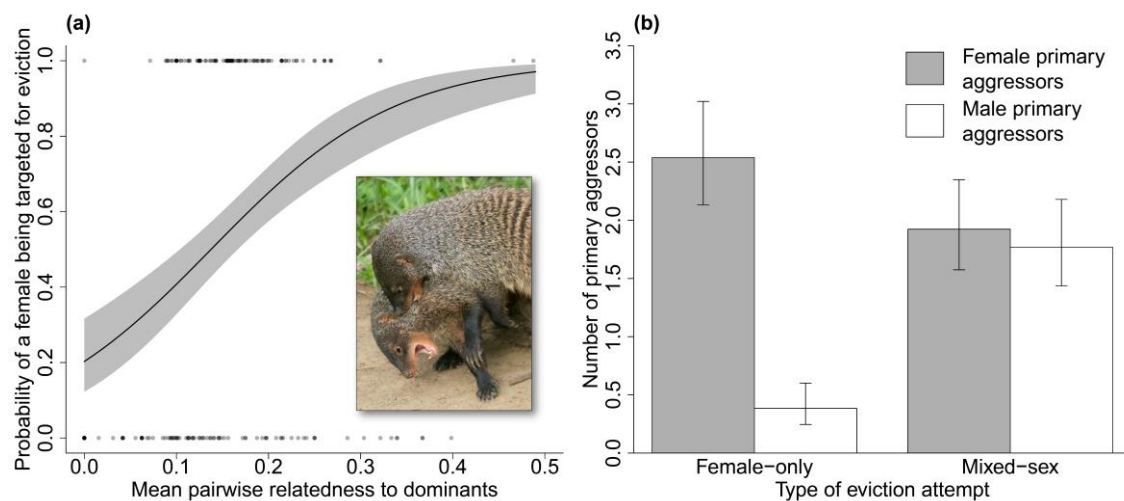
Figure 1. Patterns of eviction and sex-specific aggression in banded mongooses. (a) The effect of mean pairwise relatedness to dominants (males and females older than 3 years) on the probability of a female being targeted for eviction (N=207 females in 29 eviction attempts in 5 groups). The line shows the prediction from the GLMM ($\pm$ standard error). **(Inset)** Eviction attempts are highly aggressive and involve biting, chasing and wrestling (photo courtesy of Dave Seager). **(b)** The number of female (grey bars) and male (open bars) primary aggressors in female-only and mixed-sex eviction attempts (N=26 eviction attempts in 6 groups). The bars show the predictions from the GLMM ($\pm$ standard error).

Table 1. Eviction and relatedness to dominants. Investigating the effect of mean pairwise relatedness to dominants (males and females older than 3 years) on eviction. Models predicting the probability of being targeted for eviction for females (GLMM, N=207 females in 29 eviction attempts in 5 groups) and males (GLMM, N=177 males in 15 eviction attempts in 5 groups). Models were fitted using a binomial error structure and logit link function, and with individual ID, eviction attempt and group as random intercepts. Significant terms are given in bold.

	Response	Fixed effect	β	SE	χ²	*p*
Females	probability of a female being targeted for eviction	intercept	-1.53	1.81		
		relatedness to dominants (males and females>3 years)	**9.95**	**3.36**	**9.51**	**0.002**
		age	**-0.003**	**0.0005**	**39.98**	**<0.0001**
		weight	0.002	0.001	2.59	0.11
		pregnancy status	-0.61	0.49	1.63	0.20
		rainfall	-0.08	0.18	0.21	0.65
		group size	0.02	0.03	0.23	0.63
Males	probability of a male being targeted for eviction in a mixed-sex eviction attempt	intercept	-5.01	2.88		
		relatedness to dominants (males and females>3 years)	0.84	3.08	0.07	0.79
		age	-0.0004	0.0003	2.12	0.15
		weight	0.002	0.002	1.65	0.20
		male breeding status	-0.43	0.49	0.80	0.37
		rainfall	0.16	0.20	0.57	0.45
		group size	0.03	0.04	0.42	0.52

Table 2. Eviction and relatedness to known aggressors. Investigating the effect of mean pairwise relatedness to known primary aggressors on eviction. Models predicting the probability of being targeted for eviction for females (GLMM, *N*=131 females in 19 eviction attempts in 4 groups) and males (GLMM, *N*=130 males in 11 eviction attempts in 4 groups). Models were fitted using a binomial error structure and logit link function, and with individual ID, eviction attempt and group as random intercepts. Significant terms are given in bold.

	Response	Fixed effect	β	SE	χ^2	*p*
Females	probability of a female being targeted for eviction	intercept	2.99	2.87		
		relatedness to primary aggressors	5.47	2.87	3.85	**0.0498**
		age	-0.002	0.0006	12.85	**<0.001**
		weight	-0.0005	0.002	0.06	0.80
		pregnancy status	-1.07	0.68	2.72	0.10
		rainfall	-0.29	0.26	1.28	0.26
		group size	0.03	0.04	0.33	0.57
Males	probability of a male being targeted for eviction in a mixed-sex eviction attempt	intercept	-5.28	1.32		
		relatedness to primary aggressors	2.30	3.24	0.54	0.46
		age	-0.0001	0.0004	0.06	0.80
		weight	0.002	0.002	0.64	0.42
		male breeding status	-0.58	0.64	0.86	0.35
		rainfall	0.21	0.24	0.74	0.39
		group size	0.06	0.05	1.52	0.22

We did not find evidence that this pattern of negative kin discrimination was an attempt to reduce inbreeding between targeted females and dominant males. We tested the effect of relatedness to same-sex and opposite-sex dominants and found that it was relatedness of females to female dominants, not male dominants, that predicted whether they were targeted for eviction. Females were more likely to be targeted if they were more closely related to female dominants (females older than 3 years; GLMM, β ± SE=5.10 ± 2.65, χ^2_1=4.07, *p*=0.044; Table 3), but not if they were more closely related to male dominants (males older than 3 years; GLMM, β ± SE=3.69 ± 2.55, χ^2_1=2.09, *p*=0.15; Table 3). Behavioural data indicate that females are almost entirely responsible for the attempts at eviction of other females: males rarely attacked females in female-only eviction attempts (GLMM, β ± SE=1.80 ± 0.56, χ^2_1=12.48, *p*<0.001; Figure 1b; Table 4). Previous work indicates that eviction attempts

are triggered when the level of reproductive competition in the group is high, not when the potential for inbreeding is high (Thompson *et al.* 2016; Chapter 2); and that both sexes use kin discrimination during mating to avoid inbreeding (Sanderson *et al.* 2015b).

Table 3. Eviction and relatedness to same-sex and opposite-sex dominants. Investigating the effect of mean pairwise relatedness to same-sex and opposite-sex dominants on eviction. Models predicting the probability of being targeted for eviction for females (GLMM, *N*=198 females in 27 eviction attempts in 5 groups) and males (GLMM, *N*=177 males in 15 eviction attempts in 5 groups). Models were fitted using a binomial error structure and logit link function, and with individual ID, eviction attempt and group as random intercepts. Significant terms are given in bold.

	Response	Fixed effect	β	SE	χ²	*p*
Females	probability of a female being targeted for eviction	intercept	0.39	1.72		
		relatedness to male dominants (males>3 years)	3.69	2.55	2.09	0.15
		age	-0.002	0.005	34.49	**<0.0001**
		weight	0.002	0.001	0.66	0.20
		pregnancy status	-0.67	0.50	1.91	0.17
		rainfall	-0.03	0.18	0.021	0.88
		group size	0.002	0.04	0.001	0.98
Females	probability of a female being targeted for eviction	intercept	-0.01	1.78		
		relatedness to female dominants (females>3 years)	5.10	2.65	4.07	**0.044**
		age	-0.002	0.0005	32.58	**<0.0001**
		weight	0.002	0.001	1.80	0.18
		pregnancy status	-0.59	0.51	1.45	0.23
		rainfall	-0.05	0.18	0.06	0.81
		group size	0.0004	0.04	-0.01	1.00
Males	probability of a male being targeted for eviction in a mixed-sex eviction attempt	intercept	-4.90	2.93		
		relatedness to male dominants (males>3 years)	-0.82	2.87	0.08	0.77
		age	-0.0004	0.0003	2.41	0.12
		weight	0.002	0.002	1.70	0.19
		male breeding status	-0.48	0.49	0.97	0.33
		rainfall	0.18	0.20	0.71	0.40
		group size	0.03	0.04	0.48	0.49
Males	probability of a male being targeted for eviction in a mixed-sex eviction attempt	intercept	-5.34	2.84		
		relatedness to female dominants (females>3 years)	2.88	2.50	1.41	0.24
		age	-0.0003	0.0003	1.26	0.26
		weight	0.002	0.002	1.78	0.18
		male breeding status	-0.47	0.50	0.89	0.35
		rainfall	0.11	0.22	0.25	0.62
		group size	0.02	0.04	0.34	0.56

Table 4. Sex-specific aggression during eviction attempts. Model predicting the number of male and female primary aggressors in female-only and mixed-sex eviction attempts (GLMM, *N*=26 eviction attempts in 6 groups). Model was fitted using a Poisson error structure and a log link function, and with eviction attempt and group as random intercepts. Significant terms are given in bold. [a] reference level = males, [b] reference level = mixed-sex eviction attempt.

Fixed effect	β	SE	χ^2	*p*
intercept	0.93	0.17		
sex of primary aggressor [a]	-1.89	0.48		
eviction type [b]	-0.28	0.27		
sex of primary aggressor [a] x eviction type [b]	1.80	0.56	12.48	**<0.001**

Among males, by contrast with females, there was no effect of an individual's mean pairwise relatedness to dominant group members (males and females older than 3 years) on the probability of being subject to an eviction attempt (mixed-sex eviction attempts: GLMM, β ± SE=0.84 ± 3.08, χ^2_1=0.07, *p*=0.79; Table 1). We found no evidence of any discrimination as to which males were targeted for eviction (Table 1). There was also no discrimination of any kind when we restricted our analysis to cases where the identity of primary aggressors was known (Table 2), or when we tested the effect of mean pairwise relatedness to same-sex and opposite-sex dominants (Table 3). Unlike the case for female-only eviction attempts, both males and females were primary aggressors in eviction attempts directed at both sexes (GLMM, β ± SE=1.80 ± 0.56, χ^2_1=12.48, *p*<0.001; Figure 1b; Table 4).

Explaining negative kin discrimination: a model

Consider the interaction between two individuals, the first of whom (Player 1) may perform a selfish act at the other's expense, such as stealing a food item, killing offspring, or, in the case with which we are concerned, evicting the other from the territory or group. We suppose that this act entails some fitness cost to the actor, denoted c_1, but that the cost is outweighed by the benefit to be gained, $b_1 > c_1$. The act, if carried out, also deprives the recipient, Player 2, of a benefit b_2 that it would otherwise enjoy. If the two individuals are related by a coefficient r, then Hamilton's rule tells us that the act will be favoured by selection provided that $b_1 - c_1 - r\,b_2 > 0$. Consequently, selfishness will never be directed toward a closer relative where it would not also be directed toward a more distant one.

Suppose, however, that if Player 1 attempts the selfish act, Player 2 may then choose to resist. Resistance ensures that the act will fail; Player 1 will still suffer the cost c_1 of attempting the act, but will not enjoy the benefit b_1 of success, nor will Player 2 suffer the consequent loss of benefit b_2. At the same time, resistance entails a fitness cost to Player 2 of c_2. This situation may be modelled as a two-step, sequential game, as illustrated in Figure 2.
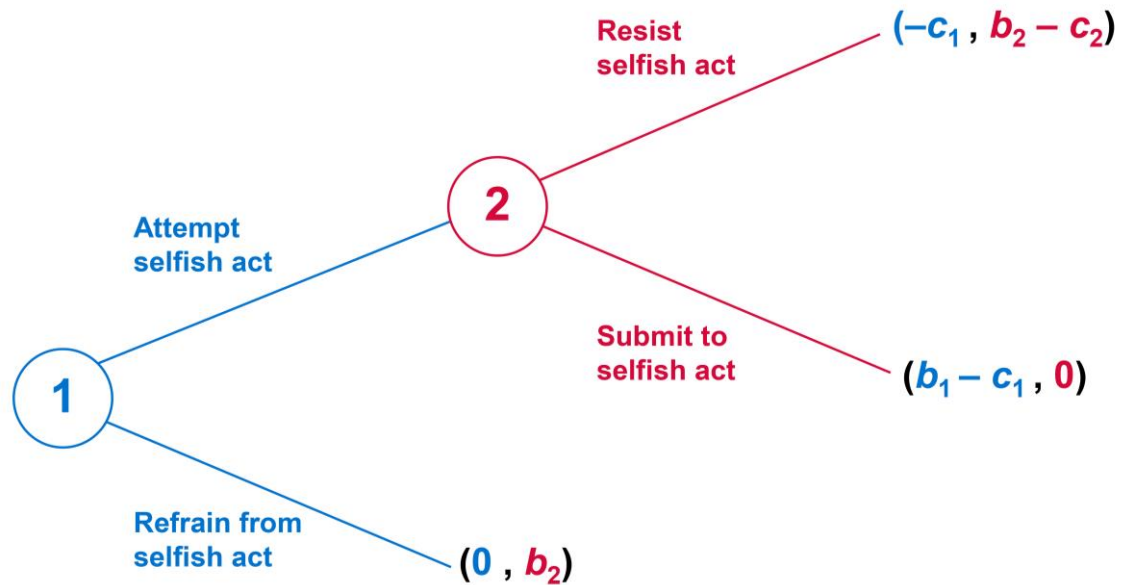
Figure 2. A sequential model of aggression and resistance. Player 1 (blue) first chooses whether or not to attempt a selfish act at the expense of Player 2 (red); in the event of such an attempt, Player 2 then chooses whether or not to resist. Direct fitness payoffs to both players are shown in their respective colours.

How does relatedness affect the outcome of this game? Applying Hamilton's rule once again, if $c_2 > b_2 - r\,b_1$, then the cost of resistance to Player 2 outweighs the benefit of preventing a selfish act. Under these circumstances, Player 2 will submit, and selection once again favours performance of the selfish act provided that $b_1 - c_1 - r\,b_2 > 0$. If, by contrast $c_2 < b_2 - r\,b_1$, then Player 2 will resist, and selection consequently does not favour the selfish act. Since a more closely related recipient of the selfish act may prefer to submit where a more distantly related recipient would resist, it follows that selfishness may be directed toward a closer relative where it would not be directed toward a more distant one. To be precise, if we consider two levels of relatedness, r_{high} and r_{low} ($r_{\text{low}} < r_{\text{high}}$), then provided that

$$\frac{b_1 - c_1}{b_2} > r_{\text{high}} > \frac{b_2 - c_2}{b_1} > r_{\text{low}}$$

then the subgame-perfect equilibrium of the game features targeting of a selfish act towards a recipient related to the actor by r_{high}, but not towards a recipient related by r_{low}. To illustrate, suppose $b_1 = b_2 = 1$, $c_1 = 0.25$ and $c_2 = 0.75$; then the model predicts that a

recipient of low relatedness ($r_{low}<0.25$) would resist a selfish act, and hence should not be targeted, while a recipient of higher relatedness ($0.75>r_{high}>0.25$) will submit, and so should be targeted.

Unrelated recipients are more likely to resist a selfish act, favouring preferential targeting of more closely related victims, when c_2 (the cost of resistance) is small, and b_2 (the benefit to be retained) is large. These effects are illustrated in Figure 3. If c_2 is typically too large, or b_2 too small, even unrelated recipients are unlikely to resist, favouring indiscriminate selfishness; only for smaller values of c_2 or larger values of b_2 is negative kin discrimination predicted.
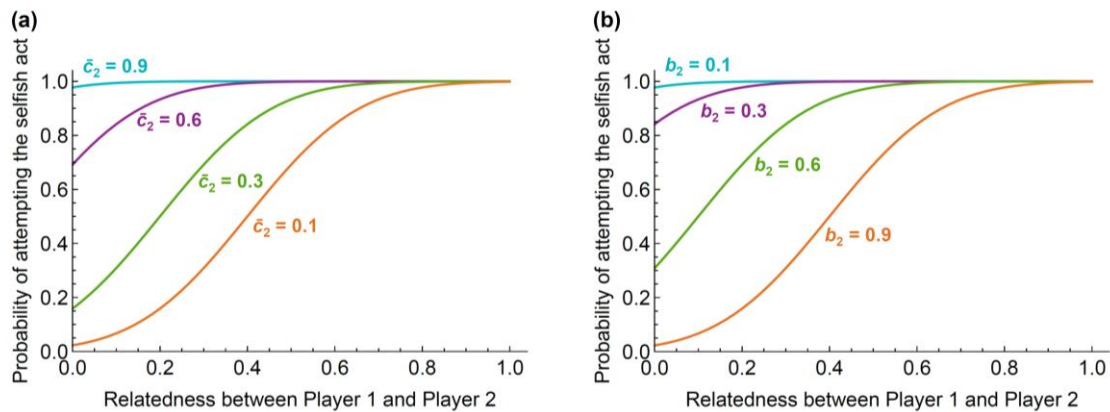
Figure 3. Impact of model parameters on patterns of kin discrimination. Here we focus on a region of parameter space in which Player 1 should carry out the selfish act when unopposed, but in which Player 2 may do best to resist (i.e. $b_1 - c_1 - r b_2 > 0$). We show the probability that, at equilibrium, the actor attempts a selfish act, as a function of relatedness, when c_2 is drawn from a normal distribution with specified mean and standard deviation equal to 0.2. (a) Probability that a selfish act is attempted at equilibrium, assuming that $b_1=1$, $c_1=0.1$, $b_2=0.5$ and mean $\bar{c}_2$ as specified for the plotted curves. (b) Probability that a selfish act is attempted at equilibrium, assuming that $b_1=1$, $c_1=0.1$, $\bar{c}_2=0.5$, and b_2 is as shown in the plot.

Testing model predictions

Two specific predictions of the model are: (1) that selfish acts will be directed preferentially towards closer relatives only when recipients can resist; and (2) that resistance to selfish acts offered by recipients should decrease as their relatedness to the actor increases. After we had developed the model, we tested these predictions. To test the first prediction, we examined how the effect of relatedness varied with the age and weight of potential evictees. We tested the effect of two-way interactions between female relatedness to dominants (males and females older than 3 years) and age, and female relatedness to dominants and weight on a female's probability of being targeted for eviction. Our reasoning was that younger or lighter females should be less able to resist eviction attempts, and that the pattern of negative kin discrimination should therefore be more pronounced when eviction is targeted at older or heavier individuals. We found that older females were indeed more likely to be targeted for eviction when more closely related to dominants, but that no such effect of relatedness was apparent for younger females (interaction between relatedness and age: GLMM, $\beta \pm SE = 0.008 \pm 0.004$, $\chi^2_1 = 5.98$, $p = 0.014$; Figure 4a; Table 5). The strong overall positive relationship between the probability of being targeted for eviction and relatedness was thus driven almost entirely by the pattern in older females. A similar interaction was also found between relatedness and weight (GLMM, $\beta \pm SE = 0.03 \pm 0.02$, $\chi^2_1 = 5.63$, $p = 0.018$; Table 5). Consistent with prediction (1), therefore, negative kin discrimination was restricted to cases in which the targets of eviction were older or heavier, and potentially more capable of offering resistance. As predicted by our model, we found no discrimination on the basis of relatedness for cases where the targets of eviction were younger or lighter, and therefore likely to suffer high costs of resistance (a high value of $\bar{c}_2$; Figure 3a).

In order to investigate whether this model had greater explanatory power than the model in our original analysis, which included main effects only, we performed a model comparison using an information-theoretic approach (Burnham & Anderson 2002). We ranked the two models by corrected AIC (AICc) (since $N/k < 40$, where N is the sample size and k is the number of parameters in the maximal model; Burnham & Anderson 2002). We found that the model including the interactions between

relatedness and age, and relatedness and weight, had greater explanatory power than the model containing only main effects (Table 6). The model including the interaction terms had an Akaike's model weight of over 99% (Table 6). Thus the result that the effect of relatedness on the probability of being targeted for eviction varies significantly with age, displayed in Table 5 and Figure 4a, supersedes the initial motivating result that relatedness has a significant effect independent of age, displayed in Table 1 and Figure 1a. Therefore, negative kin discrimination in banded mongooses in the context of eviction is restricted to older females.
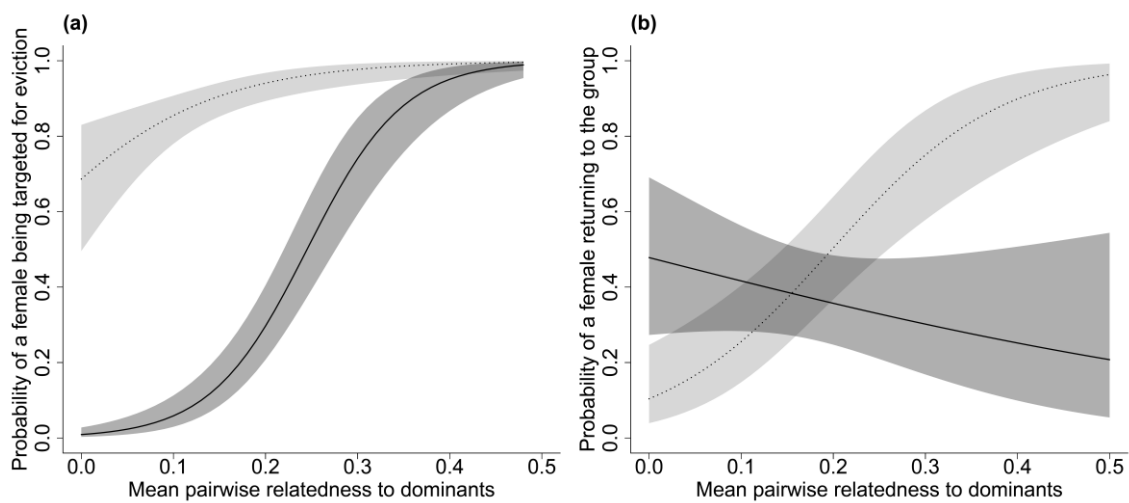
Figure 4. Patterns of kin discrimination towards recipients capable of offering varying levels of resistance. (a) In eviction attempts, dominants (males and females older than 3 years) exhibit negative kin discrimination only towards older females (*N*=207 females in 29 eviction attempts in 5 groups). The lines show the predictions from the GLMM (± standard error) for younger females (dotted line and light grey shaded area, 25th percentile of age=522 days) and older females (solid line and dark grey shaded area, 75th percentile of age=1636 days). **(b)** Following an attempt at eviction, older females who were more related to dominants (males and females older than 3 years) were less successful in regaining entry to the group (*N*=76 females in 14 eviction attempts in 4 groups); this pattern was reversed in younger females. The lines show the predictions from the GLMM (± standard error) for younger females (dotted line and light grey shaded area, 25th percentile of age=446 days) and older females (solid line and dark grey shaded area, 75th percentile of age=922 days).

Table 5. Kin discrimination in eviction and the capacity of recipients to resist. Investigating how the effect of relatedness on eviction varies with age and weight of potential evictees. Model predicting the probability of being targeted for eviction for females (GLMM, *N*=207 females in 29 eviction attempts in 5 groups). Model was fitted using a binomial error structure and logit link function, and with female ID, eviction attempt and group as random intercepts. Significant terms are given in bold.

Fixed effect	β	SE	χ^2	*p*
intercept	5.88	3.31		
relatedness to dominants (males and females>3 years)	-39.36	19.14		
age	-0.005	0.001		
weight	-0.001	0.002		
pregnancy status	-0.60	0.52	1.41	0.24
rainfall	-0.10	0.19	0.20	0.65
group size	-0.0003	0.04	-0.08	1.00
relatedness to dominants (males and females>3 years) x				
age	0.008	0.004	5.98	**0.014**
weight	0.03	0.02	5.63	**0.018**

Table 6. Model comparison of models investigating negative kin discrimination. Models predicting the probability of being targeted for eviction for females (GLMM, *N*=207 females in 29 eviction attempts in 5 groups). Model 1 is the model from the original analysis investigating negative discrimination in banded mongooses (Table 1; Figure 1a). Model 2 is the model from the analysis testing prediction (1) of the theoretical model (Table 5; Figure 4a). Models were fitted using a binomial error structure and logit link function, and with female ID, eviction attempt and group as random intercepts.

	Int.	Rel.	Age	Weight	Preg.	R'fall	G'size	Rel.: Age	Rel.: Weight	k	logLik	AICc	ΔAICc	*wᵢ*
Model 2	5.88	-39.36	-0.005	-0.001	-0.60	-0.10	0.00	0.008	0.031	12	-84.53	194.68	0.00	0.999
Model 1	-1.53	9.95	-0.003	0.002	-0.61	-0.08	0.02			10	-93.44	208.00	13.32	0.001

Columns 2 to 10 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; Rel. = relatedness; Preg. = pregnant; R'fall = rainfall; G'size = group size; : = interaction. k = number of estimated parameters including random intercepts for female, eviction and group identity; logLik = log-likelihood; AICc = corrected Akaike's information criterion; ΔAIC = change in AICc value from the best performing model; w_i = Akaike's model weight. Blank cells indicate that the term was absent from that model.

To test further whether negative kin discrimination depends on the capacity of recipients to resist, we also examined kin discrimination in cases of infanticide of new born pups. Between one and 12 females reproduce in each breeding attempt (Cant *et al.* 2014) and birth is highly synchronised, with pregnant females giving birth on exactly the same morning in 63% of cases (Hodge *et al.* 2011). Experimental and observational evidence suggest that asynchronous litters are often killed by dominant females (Hodge *et al.* 2011; Cant *et al.* 2014). In asynchronous litters, we tested whether a mother's relatedness to dominant females (older than 3 years) predicted the probability that her litter died in the first week after birth (as a proxy for infanticide; Hodge *et al.* 2011; Cant *et al.* 2014). By contrast with the negative kin discrimination described above for eviction of adult females, there was no evidence of kin discrimination in cases of presumed infanticide (GLMM, $\beta \pm SE=-0.64 \pm 2.00$, $\chi^2_1=0.10$, $p=0.75$; Table 7). This is again consistent with our model, which predicts zero or positive kin discrimination where resistance is impossible or prohibitively costly (Figure 2; Figure 3a).

Table 7. Kin discrimination in infanticide. Investigating whether negative kin discrimination depends on the recipient's capacity to resist. Model predicting the probability of a female's litter being killed in an infanticidal attack by dominant females in the first week after birth (GLMM, *N*=57 females giving birth to 52 communal litters in 12 groups). Model was fitted using a binomial error structure and logit link function, and with female ID, litter and group as random intercepts.

Fixed effect	β	SE	χ^2	*p*
intercept	0.39	1.29		
mother's relatedness to female dominants (females>3 years)	-0.64	2.00	0.10	0.75
mother's age	-0.0002	0.0005	0.26	0.61
rainfall	0.29	0.23	2.01	0.16
group size	-0.04	0.04	0.95	0.33

To test the second prediction, that resistance to the selfish act should decrease as the recipient's relatedness to the actor increases, we examined the effects of relatedness to dominants (males and females older than 3 years) and age on the probability of females targeted for eviction overcoming efforts to permanently exclude them from

the group. After being targeted for eviction, some individuals leave the group, splitting into single-sex cohorts and dispersing separately in cases where males and females are evicted together. Other targeted individuals, however, actively resist eviction: they persist in following the rest of the group, despite being aggressively driven away, until efforts to expel them eventually cease (Cant *et al.* 2001). Some attempts at eviction may thus be said to 'fail', largely due to sheer persistence on the part of the potential evictees. We predicted, therefore, that the probability of resisting eviction and regaining entry to the group should decline with relatedness to dominant individuals, particularly among older females who are potentially more capable of resisting eviction. Consistent with this prediction, among older females, individuals that were more closely related to dominants were less likely to regain entry to the group. Among younger females, by contrast, less closely related targets were less likely to regain entry (interaction between relatedness and age: GLMM, $\beta \pm SE$=-0.0. $\pm$ 0.01, χ^2_1=5.96, p=0.015; Figure 4b; Table 8).

Table 8. Resistance to eviction and relatedness. Investigating whether resistance offered by the recipient decreases as relatedness increases. Model predicting the probability of targeted females overcoming efforts to permanently evict them (GLMM, N=76 females in 14 eviction attempts in 4 groups). Model was fitted using a binomial error structure and logit link function, and with female ID, eviction attempt and group as random intercepts. Significant terms are given in bold.

Fixed effect	β	SE	χ^2	*p*
intercept	-4.09	1.95		
relatedness to dominants (males and females>3 years)	23.36	9.76		
age	0.004	0.002		
relatedness to dominants (males and females>3 years) x age	-0.03	0.01	5.96	**0.015**

Discussion

We have shown in very general terms that where recipients can offer resistance, individuals can gain from targeting selfish acts at closer, rather than more distant, relatives. In the particular case of eviction in banded mongooses, this model may therefore explain why dominant females exhibit negative kin discrimination when targeting older females, who are most capable of resistance, for violent attacks and eviction. We found no evidence of kin discrimination when targeting younger females for eviction, or when targeting helpless pups for infanticide. Further tests of the model could adopt an experimental approach to manipulate resistance or the costs and benefits of selfishness, which was not possible in our long-term field study.

While our findings offer qualified support for the predictions of our model, it is important to consider alternative explanations for our results. For example, there has been much recent theoretical interest in the possibility that local competition among kin can erode selection for local helping and instead favour indiscriminate harming behaviour (West, Pen & Griffin 2002; Lehmann & Rousset 2010). A prediction of these models is that, across groups or species, rates of aggression may be independent of relatedness (West *et al.* 2001, 2002). However, these models cannot explain the targeting of closer kin for aggression when less closely related, but otherwise equivalent targets are available (i.e. our result that, among older females, more closely related females are preferentially targeted for eviction when less closely related females are available to target). A second possibility is that relatedness is correlated with some other factor influencing aggression, such as resource holding potential (RHP) or the level of reproductive competition. For example, in sea anemones, higher aggression among closer relatives has been attributed to their greater similarity in RHP (Foster & Briffa 2014). In banded mongooses, there is no evidence that related females are of higher RHP, or represent more of a reproductive threat. In fact, younger females (with lower RHP, and who reproduce less often) are more likely to be targeted for eviction overall, regardless of relatedness (Figure 4a). Moreover, our data show that dominant females do not suffer greater reproductive costs when they co-breed with more closely related subordinates (see Appendix B). Our findings also cannot be explained as a non-adaptive side effect of selection to discriminate between species of

heterospecific competitor, which has been suggested to explain negative kin discrimination in polyembryonic wasps (Dunn *et al.* 2014).

Lastly, it has been suggested that targeting relatives for eviction could be part of an adaptive forced dispersal strategy by breeders to maximise metapopulation fitness in a structured population (Thompson *et al.* 2016; Chapter 2). In a previous study we did not find support for this hypothesis as a predictor of eviction at a group level (Thompson *et al.* 2016; Chapter 2). Moreover, it is difficult to reconcile this idea with our observations of negative kin discrimination among older females within a given eviction attempt. In classic models such as that of Hamilton and May (1977), dispersal entails direct costs for individuals who leave their natal patch, but is nevertheless favoured because it reduces local competition among kin. Because offspring value their own survival more than that of their siblings, while parents value all their offspring equally, offspring favour a lower dispersal rate than do their parents, and selection can therefore favour forced eviction of offspring (Motro 1983; Frank 1986; Taylor 1988). However, eviction by an adult of unrelated offspring offers equal benefits, in terms of reduced local competition, to eviction of related offspring, without inflicting the direct costs of dispersal on a relative. Hence, where adults can choose whom to evict, local kin competition alone cannot explain why they should preferentially target more related, over less related, older females for expulsion. There may be other asymmetries associated with the forced dispersal of kin versus non-kin, deriving, for example, from variation in local competitive ability, or variation in the bet-hedging benefits of dispersal (Hidalgo, de Casas & Muñoz 2016), but the effect of such variation on forced dispersal in heterogeneous groups has been little explored theoretically or empirically (Young 2003; Thompson *et al.* 2016; Chapter 2). In banded mongooses, there is no evidence that closer kin compete more intensely (see Appendix B), or that forced dispersal of kin yields bet-hedging benefits.

Among older females, unrelated females were more likely to regain entry to the group than related females, as we predicted on the basis of the differing inclusive fitness costs of resistance for strong individuals. However, among younger females, closer relatives were more likely to regain entry to the group than older or less closely related females (Figure 4b), which does not fit with our assumption that these females are

weaker and less able to force their way back into the group. This unexpected result suggests that factors other than strength or the costs of resistance may underlie the pattern by which younger females return to the group. For example, following eviction, dominants may voluntarily readmit closely related, younger females, that would otherwise fare very badly outside the group. The negotiation process by which females regain entry to the group may thus be more complex than the simple two-step sequence of eviction and resistance assumed by our model. While our analysis shows that even a two-step game can yield results that diverge from classical predictions, it is likely that many negotiations in family groups may better be modelled as a sequence of three or more steps, something we have not attempted here.

Negative kin discrimination was evident only in eviction attempts of older females: in males we found no relationship between relatedness and the probability of being targeted for eviction. This difference between the sexes could reflect differences in the direct fitness incentive for males and females to retain group membership, which in our model is represented by the parameter b_2 (Figure 1). Females gain greater direct fitness from group membership (i.e. higher b_2) than males because there is little or no reproductive suppression, and most females breed from the age of 10 months (Cant 2000; Gilchrist *et al.* 2004). In males, by contrast, most individuals are excluded from mating by the two or three oldest males within the group (Nichols *et al.* 2010). In our model, low values of b_2 favour little or no kin discrimination (Figure 2b). A relatively low value of b_2 in males compared to females may explain why males sometimes disperse voluntarily as a group, whereas females are invariably forced to leave after being subject to violent attack (Cant *et al.* 2016; Thompson *et al.* 2016; Chapter 2).

More generally, our model shows that incorporating even very simple forms of behavioural anticipation can radically change the predictions of kin selection theory. Where such anticipation is possible, higher relatedness can lead to outcomes that are less favourable on average for all those involved, because the threat of resistance or punishment of selfish behaviour is less credible between relatives than between unrelated individuals. Many empirical studies have shown that animals are in fact capable of adjusting their behaviour according to the anticipated responses of their social partners in a range of contexts. Examples include signalling systems (Tibbetts &

Dale 2004), negotiation over care of offspring (Hinde 2006), restraint in competitive growth (Buston 2003b), and audience effects (Leaver *et al.* 2007). However, few have considered the possibility that this kind of anticipation might lead to less cooperative outcomes among closer kin. An example comes from economic studies of human behaviour in the context of joint-liability group lending, which have found higher rates of loan default when there are more relatives within a group (Sharma & Zeller 1997; Ahlin & Townsend 2007), leading to barring of remaining group members from future borrowing. This pattern has been attributed to the difficulty of group members imposing penalties on relatives to enforce repayment (see Hermes & Lensink 2007; Lamba 2014). Our results suggest that similar patterns might also occur in the behaviour of other species, and that the influence of kinship on aggression and cooperation within animal groups may be considerably more subtle and variable than predicted by classical kin selection theory.

Methods

Study population and data collection

Data were collected from 15 groups of banded mongooses living on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E), between September 1997 and October 2015. For further details of habitat and climate, see (Cant *et al.* 2013). Groups were visited every 1 to 3 days to record group composition, life history and behavioural data. One or two individuals in each group were fitted with a VHF radio collar (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., UK) that enabled groups to be located. Individuals were easily identifiable by either colour-coded plastic collars or, more recently, unique shave markings on their back. Individuals were regularly trapped to maintain these identification markings (see Jordan *et al.* 2010 for details). On first capture a 2 mm skin sample was collected from the end of the tail using sterile scissors for genetic analyses. Individuals were trained to step onto portable electronic scales to obtain weight measurements.

We observed the attempted eviction of 405 individuals from 8 groups in 44 eviction attempts between September 1997 and December 2012. Eviction attempts were conspicuous, violent events and easy to recognise. We defined an eviction attempt to have occurred if one or more individuals left their group for at least one day following a period of intense aggression towards themselves or other group members (Gilchrist 2006; Cant *et al.* 2010; Thompson *et al.* 2016; Chapter 2). Rare instances where individuals left their group without any observed aggression towards any group member were defined as voluntary dispersal events and were not considered in our analyses. Groups were visited every day following an eviction attempt to record the identity of targeted individuals that returned to their group (if any). In 21 out of 44 eviction attempts all targeted individuals re-joined their group; in 14 attempts some targeted individuals returned while others did not; and in 9 eviction attempts all targeted individuals dispersed.

Genetic analyses and calculating relatedness

DNA was extracted from tail-tips and genotyped at up to 43 microsatellite loci isolated from a variety of carnivore species, including the banded mongoose. Genotyping was conducted following (Nichols *et al.* 2010) or (post-2010) using multiplex PCRs (Qiagen® Multiplex PCR Kit, UK) with fluorescent-labelled forward primers and were visualised through fragment size analysis on an ABI 3730 DNA Analyzer. For full details of genotyping methods, see Sanderson *et al.* (2015b). We assigned parentage using MasterBayes 2.51 (Hadfield, Richardson & Burke 2006), implemented in R 3.1.1 (see Sanderson *et al.* 2015b for further details). Estimates of pairwise relatedness were calculated from a 9-generation deep pedigree constructed using a combination of parentage and sibship assignments from MasterBayes 2.51 (Hadfield *et al.* 2006) and COLONY 2.0.5.7 (Jones & Wang 2010). Full details of pedigree construction are given in Sanderson *et al.* (2015b).

Statistical analyses

Statistical analyses were performed in R 3.3.0 (R Development Core Team 2014). We used generalised linear mixed effect models (GLMM) with a binomial error structure using a logit link function, or a Poisson error structure using a log link function, in the 'lme4' package (Bates *et al.* 2012). Models fitted to Poisson data were checked for overdispersion of the response variable (Bolker *et al.* 2008). In all analyses, 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.* 2012). We present the parameter estimates and standard errors from the maximal models, rather than removing non-significant fixed effects from the model due to problems associated with stepwise model reduction (Forstmeier & Schielzeth 2011). We did, however, remove non-significant interactions from our maximal model to allow the significance of the main effects to be tested (Engqvist 2005).

(i) Analysis of patterns of eviction in banded mongooses

Models were fitted to male and female data separately because not all eviction attempts involved males. To examine which females were targeted for eviction we considered adult females over 10 months old, since females younger than 10 months

are unlikely to be regular breeders and are rarely evicted (Cant 2000; Gilchrist *et al.* 2004; Cant *et al.* 2016). We fitted whether or not a female was targeted for eviction during an eviction attempt as the binomial response variable in a GLMM. We included mean pairwise relatedness to dominants in the group, which we defined as males and females over 3 years of age, as a fixed effect. We used age as the criterion for social dominance because, in both males and females, individuals over 3 years of age are more likely to breed, have higher fertility, and appear to be socially dominant (Nichols *et al.* 2010; Cant *et al.* 2014, 2016; Sanderson *et al.* 2015a). For example, in males there is a clear age based dominance hierarchy, evident during oestrus (Nichols *et al.* 2010; Sanderson *et al.* 2015a). In females, experiments show that suppressing reproduction in older females (> 3 years) results in the failure of the communal litter, whereas suppressing reproduction in younger females (< 3 years) does not (Cant *et al.* 2014). Older females also breed more frequently (Cant 2000; Cant *et al.* 2016), and produce larger litters (Inzani *et al.* 2016). Age (days), pregnancy status at the time of the eviction attempt (pregnant or not pregnant), mean non-pregnant weight (grams) in the 60 days before the eviction attempt, mean rainfall (mm) in the 30 days preceding the eviction attempt, and group size (number of individuals over 6 months) were included as additional fixed effects. We controlled for repeated measures of individuals, eviction attempts and groups by including these terms as random intercepts, and fitted the model to data on 207 females in 29 eviction attempts in 5 groups. To examine which males were targeted for eviction we considered adult males over 1 year old, since males under 1 year are unlikely to be regular breeders (Sanderson *et al.* 2015a; Cant *et al.* 2016) and fitted whether or not a male was targeted for eviction during an eviction attempt involving males (mixed-sex evictions) as the binomial response variable in a GLMM. We included the same fixed and random effects as the female model but, instead of pregnancy status, we included the male's breeding status (whether or not the male had been observed mate-guarding or had sired pups in the breeding attempt during which the eviction attempt occurred), and fitted the model to data on 177 males in 15 eviction attempts in 5 groups.

To investigate if the attempted eviction of relatives was in fact the result of inbreeding avoidance, we repeated the analysis of negative kin discrimination outlined above, but instead of including the mean pairwise relatedness to both male and female

dominants in the group, we used the mean pairwise to same-sex dominants aged over 3 years and the mean pairwise relatedness to opposite-sex dominants aged over 3 years as the measure of relatedness in separate models. All other fixed and random effects used in the original male and female analyses remained the same. We fitted the female models to data on 198 females in 27 eviction attempts in 5 groups, and the male models to data on 130 males in 15 eviction attempts in 5 groups.

Aggressive interactions between individuals targeted for eviction and other group members during eviction attempts were numerous, but systematic data on the precise identity of aggressors and their victims was difficult to record. However, since 2000 we have noted *ad libitum* the identity of any individuals that were notably more aggressive than other group members toward potential evictees. Data on the identity and sex of 90 of these 'primary aggressors' were available for 26 eviction attempts. An individual received a single 'count' for each eviction attempt in which it was recorded as a primary aggressor. To investigate if there was a relationship between the sex of recorded primary aggressors and the sex of individuals targeted for eviction we fitted the number of primary aggressors observed in each eviction attempt as the Poisson response variable in a GLMM and included the sex of the primary aggressors, the type of eviction attempt (female-only or mixed-sex), and the interaction between these two variables as fixed effects. We included group identity and eviction attempt as random intercepts to control for repeated measures and fitted the model to 26 eviction attempts in 6 groups.

To investigate the effect of relatedness to known aggressors on the probability of a female (or male) being targeted for eviction, we repeated the first analysis of negative kin discrimination outlined above, but restricted our analysis to eviction attempts where we had data on the identity of primary aggressors. In each of the female and male models we replaced mean pairwise relatedness to dominants in the group with mean pairwise relatedness to primary aggressors. All other fixed and random effects used in the original male and female analyses remained the same. We fitted the female model to data on 131 females in 19 eviction attempts in 4 groups, and the male model to data on 130 males in 11 eviction attempts in 4 groups.

(ii) Analysis to test model prediction (1): the selfish act will be directed preferentially towards closer relatives only when recipients can resist

To test the first prediction of the model, we repeated the original analysis investigating negative kin discrimination among females in eviction attempts, but included two-way interactions between female relatedness to dominants (males and females aged over 3 years) and age (days), and female relatedness to dominants and weight (grams). Other fixed and random effects remained the same as in the original analysis. We fitted this model to data on 207 females in 29 eviction attempts in 5 groups. Note that, following the model comparison described in the main text and presented in Table 6, the result of this analysis testing the first prediction of the theoretical model supersedes the result of the original motivating analysis presented in Table 1 and Figure 1a.

To test further model prediction (1), we examined kin discrimination in cases of infanticide of new born pups. Infanticide is known to occur in this system, but is difficult to observe directly as it typically occurs in the den. In asynchronous litters, infanticide appears to be common because early life pup mortality is strongly dependent on the pregnancy status of other females in the group (Hodge *et al.* 2011; Cant *et al.* 2014): pups that are born early in asynchronous litters almost always die in the first few days after birth, whereas pups born last almost always survive (Hodge *et al.* 2011). Between November 1997 and October 2015, we recorded the order in which each pregnant female gave birth in an asynchronous litter (i.e. if she gave birth first, middle or last) and recorded whether any of her pups survived the first week after birth. Following Hodge *et al.* (2011), we used the presence or absence of 'babysitters' (adults left at the den to guard newly born pups) to measure patterns of early life litter mortality. Specifically, to determine the survival of an individual female's pups, we considered only females who gave birth early relative to the rest of the breeding females, and for which the failure of a specific female's litter could be detected using cessation of babysitting (i.e. we did not consider females who gave birth when babysitting of other early birthing females' pups was still ongoing). An individual female's litter was determined to have survived the first week after birth if there were still babysitters being left 7 days after birth, or if she was retrospectively assigned maternity to at least one emergent pup from the communal litter following genetic analysis. We observed 166 females that fitted the criteria outlined above, who gave

birth to 120 asynchronous litters in 15 groups, and recorded whether each female's pups survived the first week after birth. Where none of the female's pups survived, they were assumed to have been subject to an infanticidal attack. To test whether pups are more likely to be targeted for infanticide when mothers are less related to female dominants in the group, we fitted whether or not each female's pups survived the first week after birth (suggesting that they were likely to have been killed in an infanticidal attack) as the binomial response variable in a GLMM (0=no pups survived, 1=at least one pup survived). We included the mother's mean pairwise relatedness to female dominants older than 3 years of age, the mother's age (days), group size (number of individuals over 6 months) and rainfall (mm) in the 30 days before birth as fixed effects. We controlled for repeated measures of mothers, communal litters and groups by including these terms as random intercepts, and fitted the model to data on 59 females giving birth to 52 communal litters in 12 groups.

(iii) Analysis to test model prediction (2): resistance to the selfish act offered by recipients should decrease as their relatedness to the actor increases

To test this prediction we fitted whether or not a female over 10 months old that was targeted for eviction overcame efforts to permanently exclude them from the group as the binomial response variable in a GLMM. We only considered eviction attempts where some evictees were allowed to return and others were not due to problems with fitting a binomial model to outcomes that are exclusively successes or failures. We included mean pairwise relatedness to dominants (males and females over 3 years of age) in the group, female age (days), and the interaction between these two variables as fixed effects. We were unable to include additional fixed effects (such as weight and pregnancy status) in the model due to problems with model convergence using a small sample size. We controlled for repeated measures of individuals, eviction attempts and groups by including these terms as random intercepts, and fitted the model to data on 46 females in 14 eviction attempts in 4 groups.

Chapter 4: Multi-level demographic consequences of eviction in cooperative banded mongooses

Abstract

In animal societies, conflict within groups can result in eviction, where individuals are often permanently expelled from their group. Most theoretical and empirical studies to date have focussed on the short-term fitness payoffs of eviction to individuals, but eviction could have demographic consequences that extend beyond those experienced by evictors and evictees. Here we investigate the consequences of eviction for individuals, groups, and intergroup relations in cooperatively breeding banded mongooses, *Mungos mungo*, using a 16-year dataset on life history and demography. In this species, groups of individuals are periodically evicted *en masse* and eviction is the primary mechanism by which new groups form in the study population. Following eviction, we find significant sex differences in dispersal distance, with females more successful in establishing a new group within the study area. Eviction results in changes in group size and composition, but we do not find subsequent long-term survival or reproductive costs associated with being evicted. We find evidence that permanent eviction increases the *per capita* reproductive success of females in the evicting group, suggesting that eviction can provide fitness benefits by reducing reproductive competition. We find that eviction is not associated with an increase in the intensity of intergroup conflict. Our results show that the demographic consequences of within-group conflict resolution strategies may reach beyond the individuals involved in eviction. These effects may have important implications for the structure and dynamics of groups and populations.

Introduction

Conflict in social groups can be resolved by various means, a conspicuous form of which is eviction or forced expulsion. Eviction, although sometimes temporary, often results in the permanent exclusion of an individual, or cohorts of individuals, from their group (Balshine-Earn *et al.* 1998; Clutton-Brock *et al.* 1998; Buston 2003a; Kappeler & Fichtel 2012; Thompson *et al.* 2016; Chapter 2). The costs, benefits and respective fitness payoffs to evictors in employing eviction as a means of conflict resolution, and to evictees in being expelled, have been the focus of recent theoretical research (Johnstone & Cant 1999; Johnstone 2000; Hamilton & Taborsky 2005; Buston *et al.* 2007; Chapter 3). Empirical studies have focused on the individual consequences of eviction, in particular the short-term fitness costs of eviction to evictors and evictees (Clutton-Brock *et al.* 1998; Young *et al.* 2006; Cant *et al.* 2010; Kappeler & Fichtel 2012; Bell *et al.* 2012). However, the costs and benefits of eviction are not always realised in the period immediately following eviction. In particular, longer term consequences are likely for evicted individuals who are forced to permanently leave their group, for evicting groups who experience considerable changes in group size, and for the wider population into which evicted individuals disperse.

Eviction is likely to impose long-term costs on permanently dispersing individuals who are faced with the challenge of living outside their natal group (Dieckmann, O'Hara & Weisser 1999; Bowler & Benton 2005; Clobert *et al.* 2012). The fitness consequences of eviction for permanently evicted individuals depend on their success in establishing new groups and, where evicted cohorts are composed of same sex individuals, finding opposite sex individuals with whom to form a new group and successfully mate. Potential mates might voluntary leave established groups, or evicted individuals may try to immigrate into other groups, perhaps usurping group members (Pusey & Packer 1987; Braude 2000; Jack & Fedigan 2004). Evicted cohorts and newly forming groups also require territory, mates and access to food resources in order to survive and reproduce. In a saturated population where groups form tessellating territories, establishing a territory may lead to frequent conflicts with other groups, and have perturbative effects on intergroup interactions in the wider population (Koenig *et al.* 1992; Bonte *et al.* 2012; Travis *et al.* 2012). The survival and reproductive success of

evicted individuals is dependent on overcoming these obstacles to establish a new group, but little is known about these consequences of eviction because tracking dispersing cohorts is logistically challenging and the long-term fate of evicted individuals is often unknown.

One obvious consequence of permanent eviction is the step-reduction in group size for the evicting group, and changes in group composition when evicted individuals leave. In cooperatively breeding species, group size is an important determinant of a group's ability to successfully raise offspring, and to defend themselves against neighbouring groups and predators (Courchamp 1999; Courchamp, Clutton-Brock & Grenfell 1999; Kokko *et al.* 2001; Kingma *et al.* 2014). Eviction is therefore likely to affect survival and reproduction in individuals that are allowed to remain in the group following an eviction. These longer term demographic effects of eviction for evictees and natal individuals will be a major determinant of decisions to evict, and decisions to resist eviction. To understand variation in the timing and frequency of eviction, and individual responses to eviction attempts, thus requires studies that can follow individuals over extensive periods, before and after eviction events.

Here we investigate the demographic consequences of eviction in banded mongooses, a highly cooperative species that exhibits conspicuous conflict over reproduction and group membership. In this species, evictions of groups of females, and sometimes groups of males alongside them, are triggered by intense levels of intrasexual reproductive competition (Thompson *et al.* 2016; Chapter 2). Over half (53%) of eviction events result in some or all of evicted individuals permanently dispersing from their group (Thompson *et al.* 2016; Chapter 2). Females that are more closely related to dominants in their group are more likely to be targeted for eviction and, of evicted females, those that are more related to their dominants are more likely to permanently disperse (Chapter 3). Voluntary dispersal is very rarely observed in females, and is also uncommon in males: the vast majority of individuals are born and die in their natal group (Cant *et al.* 2016). Consequently, eviction is the primary mechanism by which new groups form in the population (Cant *et al.* 2016).

In our study population, banded mongooses live in groups of approximately 20 adults, plus offspring, and breed continuously throughout the year. A few older 'mate-guarding' males aggressively monopolise access to females during oestrus (Nichols *et al.* 2010) and most females give birth in each breeding attempt (Cant 2000). Birth is highly synchronised within (but not between) groups (Hodge *et al.* 2011) and the communal litter is cared for by parents and non-parents of both sexes (Cant 2003; Gilchrist & Russell 2007). Individuals in our population have been continuously monitored for over 20 years, therefore we have extensive data on eviction, dispersal, group formation, and individual survival and reproductive success that allows us to examine the long-term demographic consequences of eviction. Here we examine the effects of eviction on (i) the dispersal fate of permanent evictees, (ii) the survival and fertility of evicted and non-evicted individuals, (iii) the size and composition of evicting groups, and (iv) other groups in the study area. In the discussion we evaluate the relevance of our findings for theoretical understanding of the role of demography in social evolution.

Methods

Study population and data collection

We studied a population of banded mongooses in 13 groups living on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E), between December 1996 and December 2012. For further details of habitat and climate, see Cant, Vitikainen & Nichols (2013). Measurements of daily rainfall were recorded by the Uganda Institute of Ecology Meteorological Station and, later, using our own weather station. Groups were visited every 1 to 3 days to record group composition, life history and behavioural data. One or two individuals in each group were fitted with a VHF radio collar (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., UK) 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 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.

Evictions were conspicuous, violent events and easy to recognise. We defined an eviction event to have occurred if one or more individuals left their group for at least one day following a period of intense aggression toward themselves or other group members (Gilchrist 2006; Cant *et al.* 2010; Thompson *et al.* 2016; Chapter 2). Instances where individuals left their group without any observed aggression towards any group member were defined as voluntary dispersal events and were not considered in our analyses. Groups were visited every day following eviction to record the identity of evictees that were allowed to return (if any). We observed 47 eviction events from 8 groups in our population between December 1996 and December 2012 which resulted in the expulsion of 457 individuals (Thompson *et al.* 2016; Chapter 2). Evictions were either temporary (whereby all evictees were re-admitted to the group), permanent (whereby all evictees permanently left the group), or mixed (whereby some individuals re-joined the group but others dispersed).

Statistical analyses

Statistical analyses were performed in R 3.1.2 (R Development Core Team 2014) using generalised linear mixed effect models (GLMM) in the 'lme4' package (Bates *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.* 2012). We present the parameter estimates and standard errors from the maximal models, rather than removing non-significant fixed effects from the model due to problems associated with stepwise model reduction (Whittingham *et al.* 2006; Mundry & Nunn 2009; Forstmeier & Schielzeth 2011). We did, however, remove non-significant interactions from our maximal model to allow the significance of the main effects to be tested (Engqvist 2005). To compare individual, group and population effects before and after eviction we used paired t-tests where data was normally distributed, and paired Wilcoxon signed rank tests where data did not follow a normal distribution.

(i) Consequences of eviction for dispersing evictees

To investigate the consequences of eviction for dispersing cohorts' group size and composition, we compared the size and sex ratio of evicted cohorts, and new groups formed from evicted cohorts, with the evicting groups from which they originated. For each eviction event where at least some of the evictees dispersed permanently, we compared the size of the permanently evicted same sex cohort with the number of same sex individuals aged over 6 months in the group from which they were evicted (*N*=22 evicted female cohorts from 6 evicting groups, and *N*=8 evicted male cohorts from 3 evicting groups). We compared the size and sex ratio (individuals aged over 6 months) of the newly formed group (the female evicted cohort and the males with which they joined in the 6 months after eviction) with that of the group from which they originated (*N*=6 new groups formed from female cohorts evicted from 3 groups).

(ii) Consequences of eviction for survival and fertility

To examine if eviction affected a female's survival we compared the probability of surviving the 12 month period following eviction for females that were not evicted, temporarily evicted or permanently evicted (those that remained on the study

peninsula and for whom we had accurate life history data). We fitted whether or not a female was alive 12 months after eviction as the response variable in a GLMM using a binomial error structure and a logit link function. Eviction category (not evicted, temporarily evicted or permanently evicted) was fitted as the main term of interest, and female age (days), weight (grams) and mean rainfall (mm) in the 30 days before eviction were fitted as additional fixed effects. To account for repeated measures of groups, eviction events and females we included group identity, eviction event and female identity as random intercepts and fitted the model to data on 235 females in 33 eviction events in 5 groups. Note that this analysis could not be performed on male data as no permanently evicted males remained on the study peninsula for longer than 10 months and so we did not have sufficient life history data for these males.

To investigate if eviction affected female reproductive success we compared the number of litters born in the 12 month period following eviction to females that were not evicted, temporarily evicted or permanently evicted (those that remained on the study peninsula and for whom we had accurate life history data). We fitted the number of litters to which a female gave birth in the 12 months after an eviction as the response variable in a GLMM using a Poisson error structure and a log link function. Eviction category (not evicted, temporarily evicted or permanently evicted) was fitted as the main term of interest, and female age (days), weight (grams), and the number of days that she was alive in the 12 months after eviction were fitted as additional fixed effects. To account for repeated measures of groups, eviction events and females we included group identity, eviction event and female identity as random intercepts and fitted the model to data on 296 females in 33 eviction events in 5 groups. We also investigated if eviction affected female lifetime reproductive success by repeating the above analysis but fitting the number of litters born to a female in her remaining lifetime following an eviction as the response variable. We included the same fixed and random effects as the previous analysis but instead of the number of days that the female was alive in the 12 months after eviction, we included the female's remaining lifetime following eviction (in days) as a fixed effect, and we fitted the model to data on 296 females in 33 eviction events in 5 groups.

(iii) Consequences of eviction for the size and composition of evicting groups

To investigate the effect of eviction on the evicting group we compared the size and sex ratio of the group (individuals aged over 6 months) before and after an eviction where at least some of the evicted cohort permanently left the group (*N*=23 permanent evictions in 6 groups). To examine if eviction had an effect on the reproductive success of the evicting group we compared the number of pups that survived to emergence (per female that gave birth) in litters born before and after an eviction event. We restricted our analysis to post-eviction litters born in the same breeding attempt as the eviction event, i.e. litters born within 60 days of an eviction event (the approximate length of gestation; Cant 2000). We compared the number of pups that survived to emergence in a post-eviction litter with the number of pups that survived to emergence in the most recent pre-eviction litter (*N*=18 temporary evictions in 5 groups, and *N*=18 permanent evictions in 6 groups).

(iv) Consequences of eviction for other groups in the study area

To investigate the perturbative effects of eviction on the wider population we examined the frequency of intergroup interactions before and after an eviction. Intergroup interactions occur when neighbouring groups meet, and physical fights are particularly likely if the groups are evenly matched in size (Cant *et al.* 2002). Contests between groups are ferocious and individuals are often injured and die as a result of these fights (Cant *et al.* 2002; Gilchrist & Otali 2002; Jordan *et al.* 2010). We compared the frequency of intergroup interactions in all groups in the population, those involving the evicting group and those involving groups other than the evicting group in the 30 days before and the 30 days after an eviction (*N*=41 eviction events in 8 groups). We also compared the frequency of intergroup interactions in these categories, but excluded any intergroup interaction that involved the evicted cohort to understand the effect that the presence of an evicted had on intergroup conflict in the population. We chose a period of 30 days because, as only 55% of evicted individuals remain on the peninsula longer than 30 days after eviction, any effects of dispersing evicted cohorts on the wider population are likely to be detectable during this period. We used the 'gao' function in the package 'nparcomp' (Gao *et al.* 2008; Konietschke *et al.* 2015) to perform a nonparametric multiple test for many-to-one comparisons. This was because we compared the number of intergroup interactions after eviction (either

including or excluding the evicted cohort) to the number of intergroup interactions before eviction. To be conservative, we present the Bonferroni adjusted p-values.

Results

(i) Consequences of eviction for dispersing evictees

Following a mixed sex eviction (where both males and females were evicted), the permanently evicted group split into single-sex cohorts and dispersed separately, either remaining on the study peninsula or dispersing away from the area. Evicted males always dispersed from the peninsula within 10 months (median time to dispersal from the peninsula=22.5 days, range=0-296 days) and therefore were never successful in joining with a dispersing cohort of females to form a new group in the study area. The majority of evicted females dispersed away from the peninsula within 90 days (median time to dispersal from the peninsula=75 days, range=0-2436 days) but 32% of females that were permanently evicted were successful in forming a new group on the peninsula. A total of 6 new groups were formed by 29 permanently evicted females. They did this either by usurping all females from an established study group (N=1), joining with unknown immigrant males (N=2), joining with dispersing known males (N=1), or joining with dispersing known males and immigrant males (N=1). One cohort of 7 females remained on the peninsula for over 2 years without ever permanently joining with males. Despite this, all females in this cohort were reproductively successful, mating with males from established groups and giving birth to 7 communal litters over the course of their combined lifetime.

Permanently evicted individuals experienced markedly different group environments after leaving their original groups. Males dispersed in cohorts that were on average 42.3% ± 0.04% (mean ± SE) of the size of the male cohort in their natal group (paired Wilcoxon signed rank test, V=36, N=8, p=0.014; Figure 1a). For females this figure was 36.8% ± 0.04% (mean ± SE) (paired Wilcoxon signed rank test, V=253, N=22, p<0.0001; Figure 1a). New groups that were formed on the study peninsula by successfully dispersing female cohorts were significantly smaller than the group from which they originated (paired Wilcoxon signed rank test, V=21, N=6, p=0.031; Figure 1b). However, the sex ratio of these newly formed groups was not significantly different to that of the original group (paired Wilcoxon signed rank test, V=11, N=6, p=0.42).
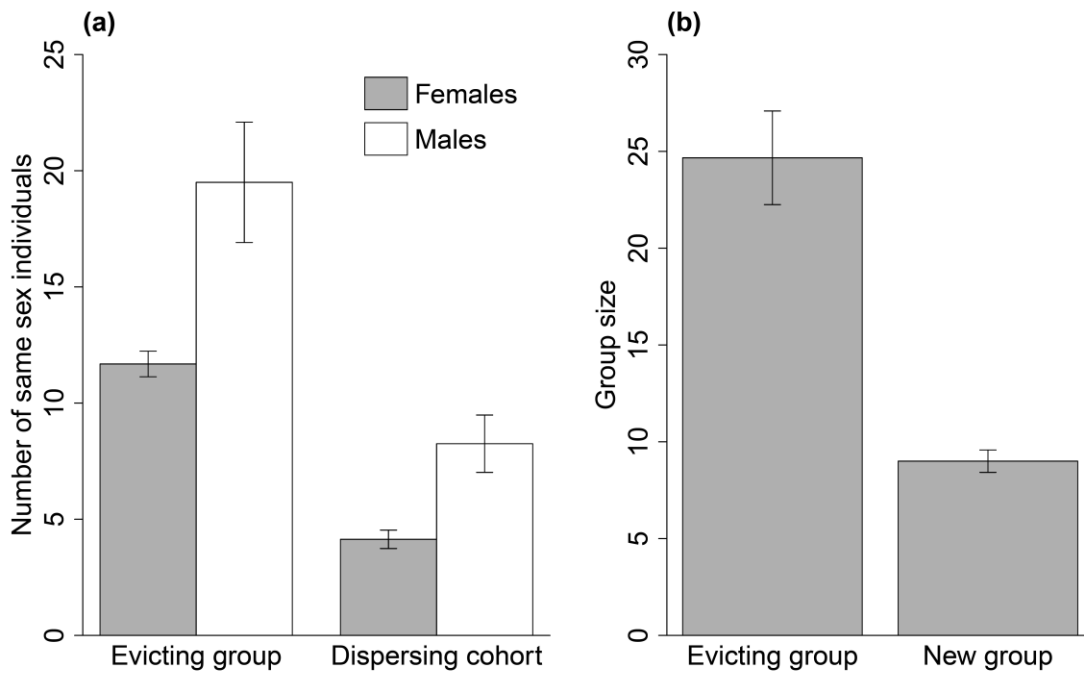
Figure 1. Group size and composition of evicted cohorts and newly formed groups, compared with evicting groups. (a) The size of same-sex dispersing cohorts and the number of same-sex individuals in evicting groups for females (grey bars) and males (open bars) (*N*=22 evicted female cohorts from 6 evicting groups, and *N*=8 evicted male cohorts from 3 evicting groups). The bars show means ± standard error. **(b)** The size of evicting groups and groups newly formed from evicted cohorts (*N*=6 new groups formed from female cohorts evicted from 3 groups). The bars show means ± standard error.

(ii) Consequences of eviction for survival and fertility

We did not find evidence that eviction had adverse effects on female survival or reproduction. For those females that remained on the study peninsula (and for which we could record data on survival and reproductive efforts) there was no significant difference in the probability that they survived the 12 months after eviction compared to temporarily evicted or non-evicted females (GLMM, χ^2_2=3.08, *p*=0.21; Table 1). There was also no significant difference in the number of litters produced in the 12 months following eviction, or in a female's lifetime after eviction, for non-evicted, temporarily evicted or permanently evicted females (reproductive success in 12

months after eviction: GLMM, χ^2_2=0.34, *p*=0.84; Table 2; lifetime reproductive success after eviction: GLMM, χ^2_2=1.23, *p*=0.54; Table 3).

Table 1. Eviction and survival. Model predicting the survival of females in the 12 month period following an eviction event (GLMM, *N*=235 females in 33 eviction events in 5 groups). Model was fitted using a binomial error structure and a logit link function, and with female, eviction event and group identity as random intercepts. Significant terms are given in bold.

Fixed effect		**β**	**SE**	**χ^2**	***p***
intercept		0.52	1.28		
eviction category	not evicted	0.00	0.00	3.08	0.21
	permanently evicted	-0.40	1.05		
	temporarily evicted	-0.98	0.57		
age		-0.002	0.0006	19.68	**<0.0001**
weight		0.003	0.0008	13.78	**<0.001**
rainfall		-0.013	0.017	0.64	0.42

Table 2. Eviction and short-term reproductive success. Model predicting the number of litters born to females in the 12 month period following an eviction event (GLMM, *N*=296 females in 33 eviction events in 5 groups). Model was fitted using a Poisson error structure and a log link function, and with female, eviction event and group identity as random intercepts. Significant terms are given in bold.

Fixed effect		**β**	**SE**	**χ^2**	***p***
intercept		-3.17	0.35		
eviction category	not evicted	0.00	0.00	0.34	0.84
	permanently evicted	0.11	0.20		
	temporarily evicted	0.04	0.12		
age		0.0001	0.00009	2.31	0.13
weight		0.001	0.0002	34.74	**<0.0001**
days alive in 12 month period		0.007	0.0008	95.95	**<0.0001**

Table 3. Eviction and lifetime reproductive success. Model predicting the number of litters born to females in their remaining lifetime following an eviction event (GLMM, *N*=296 females in 33 eviction events in 5 groups). Model was fitted using a Poisson error structure and a log link function, and with female, eviction event and group identity as random intercepts. Significant terms are given in bold.

Fixed effect		β	SE	χ^2	*p*
intercept		-0.44	0.18		
eviction category	not evicted	0.00	0.00	1.23	0.54
	permanently evicted	-0.21	0.19		
	temporarily evicted	-0.06	0.11		
age		0.00007	0.0001	0.44	0.51
weight		0.0004	0.0001	12.69	**<0.001**
days alive after eviction event		0.0009	0.00008	121.82	**<0.0001**

(iii) Consequences of eviction for the size and composition of evicting groups

Following an eviction that resulted in the permanent dispersal of some, or all, of the evicted cohort, there was a significant reduction in the size of the evicting group (paired t-test, t_{22}=6.68, *p*<0.0001; Figure 2a), and a significant increase in the sex ratio of males to females (paired Wilcoxon signed rank test, *V*=67, *N*=23, *p*=0.030; Figure 2b). Temporary evictions (where all evictees were allowed to return to the group) did not affect the reproductive success of the group. In litters born in the 60 days following a temporary eviction, there was no significant difference in the number of pups (per female that gave birth) that survived to emergence (paired Wilcoxon signed rank test, *V*=77, *N*=18, *p*=0.66). However, more pups survived to emergence (per female that gave birth) when there was a step-reduction in group size following a permanent eviction (paired Wilcoxon signed rank test, *V*=24, *N*=18, *p*=0.043; Figure 3).
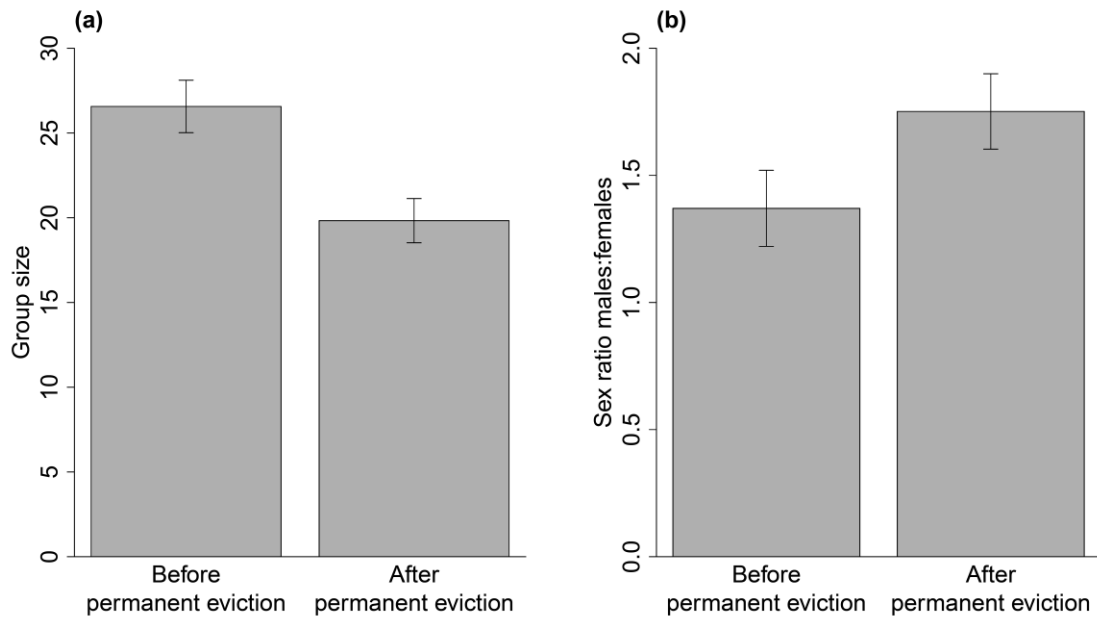
Figure 2. Changes in group size and composition of evicting groups following eviction.
(a) The size of evicting groups before and after a permanent eviction (*N*=23 permanent evictions in 6 groups). The bars show means ± standard error. **(b)** The sex ratio of males to females of evicting groups before and after a permanent eviction (*N*=23 permanent evictions in 6 groups). The bars show means ± standard error.
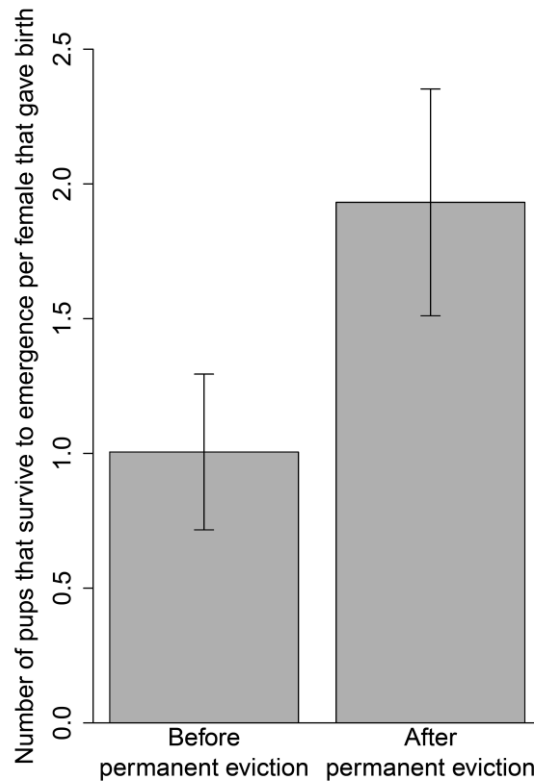
Figure 3. Pup survival following eviction. The number of pups that survive to emergence, per female that gave birth, in the litter born before a permanent eviction and in the first litter born within 60 days after a permanent eviction (*N*=18 permanent evictions in 6 groups). The bars show means ± standard error.

(iv) Consequences of eviction for other groups in the study area

Compared to the 30 days preceding an eviction, in the 30 days after an eviction there was no significant increase in the number of intergroup interactions when considering all groups in the population (estimator=0.10, degrees of freedom=79.5, test statistic=1.64, Bonferroni adjusted p-value=0.21); when considering only those interactions involving the evicting group (estimator=0.09, degrees of freedom=79.9, test statistic=1.53, Bonferroni adjusted p-value=0.26); or when considering only those interactions involving groups other than the evicting group (estimator=0.08, degrees of freedom=79.9, test statistic=1.36, Bonferroni adjusted p-value=0.35). There was also no increase in the number of intergroup interactions following an eviction once the intergroup interactions involving the evicted cohort were excluded (all groups in the population: estimator=0.07, degrees of freedom=79.9, test statistic=1.17, Bonferroni

adjusted p-value=0.48; evicting group: estimator=0.07, degrees of freedom=80, test statistic=1.15, Bonferroni adjusted p-value=0.50; groups other than the evicting group: estimator=0.07, degrees of freedom=80, test statistic=1.09, Bonferroni adjusted p-value=0.55).

Discussion

Eviction in banded mongooses had consequences for dispersal, survival, and reproduction in the population, with effects on both evicted individuals and evicting group members. When eviction resulted in permanent dispersal, groups of evicted females occasionally formed new groups in the study area, whereas evicted groups of males did not. Groups that formed from an evicted cohort were significantly smaller than the evicting group from which they originated, and evicting groups also suffered substantial changes in size and composition. Surprisingly, we did not detect survival or long-term reproductive costs to evictees following eviction, in the sample of females that were successful in establishing a new group in the study site. For evicting groups, pup survival improved after a permanent eviction, suggesting that mass eviction is an effective method of reducing reproductive competition. However, eviction was not associated with an increase in intergroup interactions in our population. Our results suggest that eviction can have consequences on demography in cooperative species, and that these effects can occur at an individual, group and population level.

Eviction is the main mechanism by which individuals leave their natal group and is, therefore, the primary means by which new groups form in our population (Cant *et al.* 2016). We found that evicted females tend to remain on the study peninsula for longer following eviction, and are more likely to be successful in establishing a new group in the study area than males. Whether this means that females are more successful dispersers overall, or that males simply travel longer distances before forming groups, requires further study, which may become possible with next generation Global Positioning System (GPS) technology. In other mammals, females that leave their natal group are often unable to join established groups without usurping female group members, and so the formation of new groups occurs on part of their natal group's range (Ethiopian wolves, *Canis simensis*, Sillero-Zubiri & Macdonald 1998; meerkats, *Suricata suricatta*, Clutton-Brock *et al.* 2006; African lions, *Panthera leo*, VanderWaal, Mosser & Packer 2009; yellow-bellied marmots, *Marmota flaviventris*, Armitage *et al.* 2011). Theory suggests that sex differences in dispersal can affect selection for helping and harming behaviours in structured populations (Johnstone & Cant 2008), due to effects on local competition and the genetic structure of the population (Gardner

2010). In general, these models predict that selection will favour helping among members of the more philopatric sex, and harming among members of the dispersing sex (Johnstone & Cant 2008). However, these models assume individuals disperse independently. Eviction of cohorts of same-sex individuals, as occurs in banded mongooses and other cooperative vertebrates (Koenig & Dickinson 2016), may influence selection for helping and harming in ways that have yet to be explored theoretically. For example, simple haploid, asexual models suggest that dispersal of groups of relatives (budding dispersal; Gardner & West 2006) may promote altruism within groups (Gardner & West 2006), but these effects have not been investigated in sexual systems.

We found that eviction resulted in significant changes in the size and composition of groups to which individuals belonged. Permanently evicted females formed smaller groups following dispersal than the group from which they originated, although with a similar sex ratio. Group size is highly important for survival and reproductive success in cooperative species (Courchamp 1999; Courchamp *et al.* 1999; Kokko *et al.* 2001). We might expect, therefore, that eviction would have a major impact on the fitness of individuals in evicting groups and evictees in newly formed groups. However, we found no difference in survival or the number of litters to which a female gave birth following eviction for females that were evicted and permanently dispersed, females that were evicted and allowed to return to their group, or females that were not evicted. Previous studies in this species have shown that dominant females do experience reduced fitness in the form of decreased pup weight and reduced pup survival to independence when they evict individuals during their pregnancy (Bell *et al.* 2012), and evicted pregnant females often abort their litter (Cant *et al.* 2010). Our results indicate that survival and female reproductive success is not affected by eviction beyond short-term negative effects on the subsequent litter.

Previous work in this species has shown that eviction is a mechanism employed to reduce levels of intrasexual reproductive competition in both males and females (Cant *et al.* 2010; Thompson *et al.* 2016; Chapter 2). In banded mongooses, *per capita* female reproductive success is negatively affected as the number of breeding females grows large and competition between pups born in large communal litters intensifies (Cant *et*

al. 2010). Our results suggest that permanent eviction, which resulted in a significant reduction in group size, is successful in alleviating the level of competition among pups: pup survival to emergence was higher following a permanent eviction compared to the most recent pre-eviction litter. Permanent eviction, thus, appears to reduce reproductive competition among females in the subsequent litter, and most likely in several subsequent litters thereafter. In contrast to this pattern in females, permanent eviction increased the ratio of males to females, suggesting that eviction intensifies male-male competition for mates. Consequently, we might expect sexual conflict over eviction of females: dominant females gain from evicting subordinate females, but breeding males stand to lose potential mating partners. This may explain why males are rarely active evictors in female-only evictions, but are frequently active in mixed-sex evictions (Chapter 3). Given such sexual conflict, males might even be predicted to intervene to help subordinate females to resist eviction by dominant females. Future detailed behavioural data on the dynamics of eviction would help to reveal how potential sexual conflict over eviction is resolved.

In conclusion, where within-group conflict resolution strategies result in the dispersal of individuals or cohorts, these processes are likely to have consequences beyond the reduction of conflict for individuals within the group. Both empirical studies of cooperative breeders and theoretical studies of social evolution in structured populations would benefit by broadening the scope of research to examine how these multi-level consequences of within-group conflict resolution affect the long-term demography and dynamics of groups and populations in viscous animal societies.

Chapter 5: Causes and consequences of intergroup conflict in cooperative banded mongooses

Abstract

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, *Homo sapiens,* and chimpanzees, *Pan troglodytes*. A barrier to current understanding of the role of intergroup conflict in the evolution of social behaviours is a lack of information on the causes and consequences of aggression between groups. Here we examine the causes and fitness consequences of intergroup conflict in the banded mongoose, *Mungos mungo*, a highly cooperative species that engages in frequent violent contests between groups. We find that intensified competition for food and mates increases the frequency of aggressive intergroup interactions, but with no resulting costs to adult survival or fertility. Intergroup conflict did have fitness costs in terms of reduced litter survival, and groups were less able to recruit and grow in size when they engaged in more intergroup interactions. 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.

Introduction

Cooperatively breeding species have received much attention because the conspicuous helping behaviour they exhibit through the cooperative care of young offers an opportunity to test evolutionary theories of cooperation (Emlen 1991; Cant 2012a; 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; Wilson & Wrangham 2003; Smith 2007). In humans, *Homo sapiens*, warfare and the coordination of huge armies to invade and battle rival societies has 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), and that out-group threats can lead to increased in-group cohesion (Puurtinen & Mappes 2009; Gneezy & Fessler 2012; Burton-Chellew & West 2012).

Violent conflicts are well documented among non-human primates, particularly chimpanzees, *Pan troglodytes* (Wilson *et al.* 2004; Wrangham *et al.* 2006; Mitani *et al.* 2010), but also in a range of other primate species (Gros-Louis *et al.* 2003; Aureli *et al.* 2006; Harris 2010; Belle & Scarry 2015). Other than primates, aggressive interactions between groups are also reported in other social mammals (Mech 1994; Boydston *et al.* 2001; Mosser & Packer 2009; Cassidy *et al.* 2015), cooperatively breeding birds (Radford 2011; Golabek *et al.* 2012), and ants (Plowes & Adams 2005; Tanner 2006; Batchelor & Briffa 2011). Intergroup conflict is known to carry large potential costs (Wrangham *et al.* 2006; Jordan *et al.* 2010; Batchelor & Briffa 2011; Crofoot 2013) 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. 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 (Hamilton 1975; Bowles & Gintis 2011). If there exist power asymmetries between neighbours then large groups can attack smaller groups at little cost, and so outcompete rivals (Wrangham 1999). 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. 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. 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 that has been used to evaluate these hypotheses comes mainly from humans and chimpanzees (Wrangham 1999; Bernhard *et al.* 2006; Bowles 2009; Wrangham & Glowacki 2012), but has been little investigated among other species in which violent intergroup aggression exists. This is especially the case for cooperatively breeding species that exhibit levels of intergroup hostility sufficient to influence selection for helping behaviour (Cant *et al.* 2016), and where there is potential for intergroup conflict to influence demographic processes, such as migration, colonisation of new territory and population expansion (Lehmann & Feldman 2008). To improve 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 violent physical contests ('intergroup interactions') with

rival groups (Cant *et al.* 2013, 2016). Groups respond more aggressively to experimental stimuli from neighbours that represent a territorial threat (Müller & Manser 2007) compared to stimuli from non-neighbours. There is also observational evidence that males and females engage in intergroup interactions in order to achieve extra-group matings (Cant *et al.* 2002; Nichols *et al.* 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 (Müller & Bell 2009; Jordan *et al.* 2010; Nichols *et al.* 2015).

Here we examine the factors that influence the frequency of intergroup conflict in groups of banded mongooses, and the fitness consequences of engaging in intergroup interactions for individuals and groups. Specifically, we investigate (i) the potential ecological and social triggers of intergroup interactions, and (ii) the survival costs to pups and adults, and fertility costs to pregnant females.

Methods

Study population and data collection

We studied a population of banded mongooses in a total of 38 groups living on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E), between November 1999 and January 2016. For further details of habitat and climate, see Cant, Vitikainen & Nichols (2013). Measurements of daily rainfall were recorded by the Uganda Institute of Ecology Meteorological Station and, later, using our own weather station. Groups were visited every 1 to 3 days to record group composition, life history and behavioural data. One or two individuals in each group were fitted with a VHF radio collar (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., UK) 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.

Incidences of intergroup interactions in the population were recorded *ad libitum.* Intergroup interactions occur when neighbouring groups meet, and physical fights are particularly likely if the groups are evenly matched in size (Cant *et al.* 2002). Individuals, on sighting or discovering the smell of 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 (Rood 1975; Cant *et al.* 2002; Gilchrist & Otali 2002).

Statistical analyses

Statistical analyses were performed in R 3.1.2 (R Development Core Team 2014) using linear mixed effect models (LMM) or generalised linear mixed effect models (GLMM) in the 'lme4' package (Bates *et al.* 2012). LMMs were fitted using a normal error structure with an identity link function, and residuals were checked to ensure they

were normally distributed with constant variance. GLMMs were fitted using a Poisson or binomial error structure with log and logit link functions, respectively. Models fitted to Poisson data were checked for overdispersion of the response variable (Bolker *et al.* 2008; Hilbe 2011). 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.* 2012). We present the parameter estimates and standard errors from the maximal models, rather than removing non-significant fixed effects from the model due to problems associated with stepwise model reduction (Whittingham *et al.* 2006; Mundry & Nunn 2009; Forstmeier & Schielzeth 2011). We did, however, remove non-significant interactions from our maximal model to allow the significance of the main effects to be tested (Engqvist 2005).

(i) Ecological and social causes of intergroup conflict

Reproduction in banded mongooses is highly synchronised 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 5-10 day oestrus period within one 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 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 non-breeding 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 km^2 (the size of the study area; Rood 1975; Gilchrist & Otali 2002), and group size (number of individuals aged over 6 months) 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. In order to be able 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 42470 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 both as being 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 48831 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 if 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 level of correlation between change in group size and starting group size was less than levels suggested by Freckleton (2011) to cause model fitting issues such as inflated variance of effect estimates (correlation between change in group size and starting group size=-0.31). Additionally, we confirmed that the variance inflation factors (VIF) of the change in group size and starting group size variables were less than 2 (the conservative level suggested by Zuur, Ieno & Elphick (2010) to show problematic degrees of collinearity; VIF change in group size=1.24, VIF starting group size=1.50). 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 km^2), 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 has during the 12 month (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.

(ii) Costs of intergroup conflict to pups and adults

To examine whether intergroup interactions resulted in decreased pup survival we fitted whether or not any pups in a litter survived to emergence (1=some pups survived to emergence, 0=all pups died before 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 in the 30 days before the birth of the litter, group size, and the interaction between rainfall and group size as additional fixed effects. To account for repeated measures of groups we included group identity as a random intercept and fitted the model to data on 516 communal litters born in 19 groups.

To investigate if intergroup conflict had mortality costs for adults we split the analysis by sex and fitted a separate model for males and females, since the inclusion of sex as an explanatory variable in the full analysis caused model fitting problems. We fitted whether or not an individual aged over 1 year old survived a 30 day period as the response variable in a GLMM using a binomial error structure. We used a 30 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. We restricted our analyses to 30 day periods where there was no intergroup interaction involving the group recorded in the 30 days prior. This allowed us to exclude potential effects of any other previous, recent intergroup interactions. In both models we included whether or not the group was involved in an intergroup interaction at the start of the 30 day period as the main term of interest. We fitted individual age, weight, group size, mean rainfall in the 30 days before the start of the 30 day period, and the interaction between group size and rainfall as additional fixed effects. We accounted for repeated measures of groups and individuals by including these terms as random intercepts and fitted the female model to data on 1373 females in 17 groups, and the male model to data on 2179 males in 15 groups.

To examine if intergroup conflict has pre-natal costs, we fitted whether or not a pregnant female aborted her litter 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 during gestation as the main term of interest, and fitted mean rainfall in the 30 days before pregnancy, the number of breeding females (females aged over 10 months; Gilchrist, Otali & Mwanguhya 2004; Cant *et al.* 2010) in the group, the interaction between rainfall and the number of breeding females, female age and weight as fixed effects. We accounted for repeated measures of groups, litters and females by including these terms as random intercepts and fitted the model to data on 502 females giving birth to 139 communal litters in 7 groups.

Results

(i) 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 ± 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: GLMM, β ± SE=-0.02 ± 0.005, χ^2_1=7.79, *p*=0.0053; Figure 1a; Table 1). The probability of engaging in an intergroup interaction was greater for larger groups than smaller groups (GLMM: β ± SE=-0.03 ± 0.006, χ^2_1=23.71, *p*<0.0001; Figure 1b; Table 1).

(a)

(b)
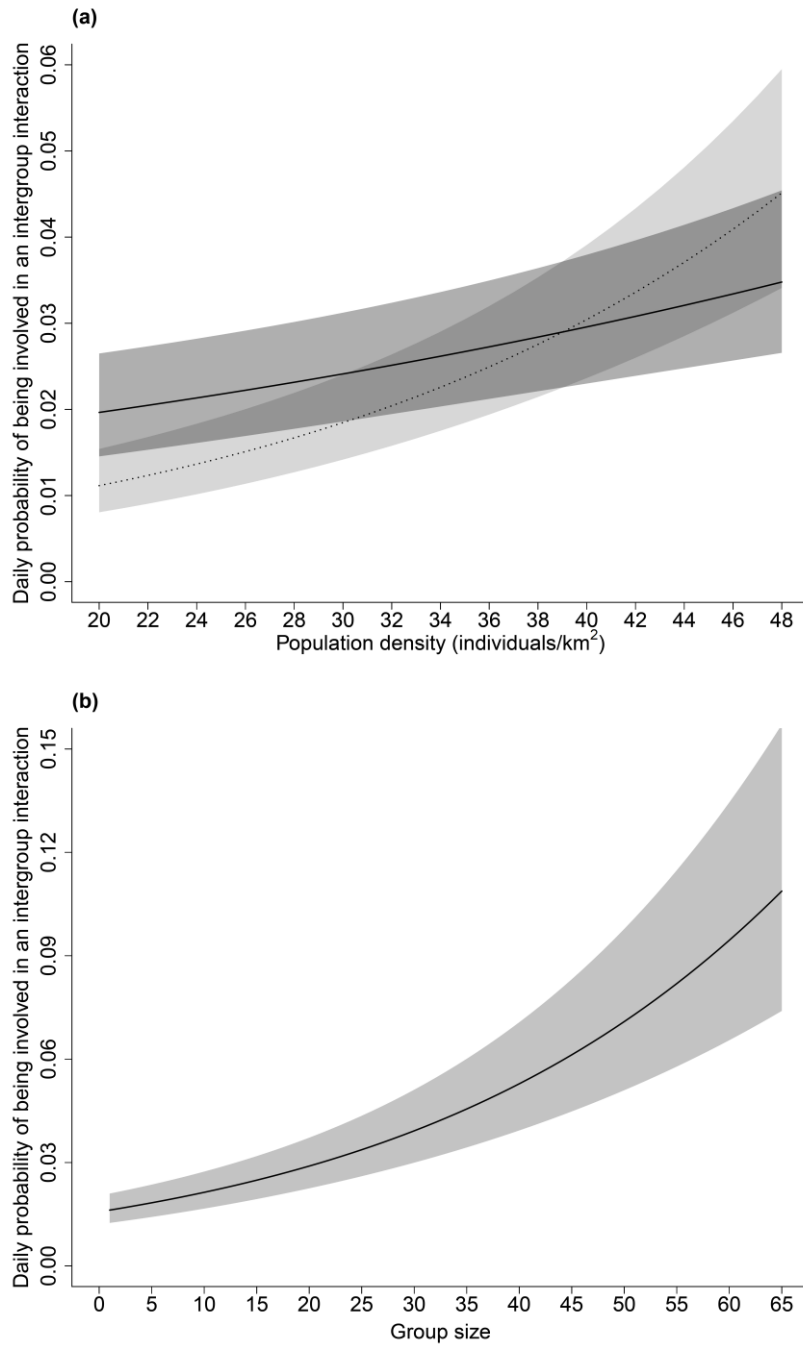
Figure 1. Causes of intergroup conflict. (a) The effect of population density on the probability of a group being involved in an intergroup interaction on a given day. The lines show predictions from the GLMM ± standard error when rainfall is low (dotted line and light grey shaded area, 25th percentile 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*=42470 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 lines show predictions from the GLMM ± standard error (*N*=42470 study days in 39 groups).

Table 1. Ecological and social causes of intergroup conflict. Model predicting the daily probability of a group being involved in an intergroup interaction (GLMM, *N*=42470 study days in 39 groups). Model was fitted using a binomial error structure and a logit link function, and with group ID as a random intercept. Significant terms are given in bold.

Fixed effect		β	SE	χ^2	*p*
intercept		-7.29	0.63		
phase of reproductive cycle	babysitting	0.00	0.00	21.40	**<0.0001**
	oestrus	0.70	0.18		
	pregnant	-0.0009	0.11		
	non-breeding	-0.18	0.14		
rainfall		0.60	0.20		
population density		0.07	0.02		
group size		0.03	0.006	23.71	**<0.0001**
phase of reproductive cycle x	babysitting	0.00	0.00		
	oestrus	0.15	0.13		
	pregnant	-0.04	0.07		
	non-breeding	0.02	0.09		
rainfall				3.43	0.33
phase of reproductive cycle x	babysitting	0.00	0.00		
	oestrus	0.01	0.04		
	pregnant	0.02	0.02		
	non-breeding	0.009	0.03		
population density				1.22	0.75
phase of reproductive cycle x	babysitting	0.00	0.00		
	oestrus	-0.02	0.02		
	pregnant	-0.02	0.01		
	non-breeding	-0.03	0.01		
group size				4.41	0.22
rainfall x					
population density		-0.02	0.005	7.79	**0.005**
rainfall x					
group size		0.0008	0.003	0.09	0.76
population density x					
group size		0.0007	0.0009	0.75	0.39

The probability of a group being involved in an intergroup interaction varied significantly across different phases of the reproductive cycle (GLMM: χ^2_3=21.40, *p*<0.0001; Figure 2; Table 1). Groups were more likely to be involved in an intergroup interaction when they were in oestrus than during any other phase (GLMM with post-hoc Tukey's all-pairwise comparison of means: oestrus versus non-breeding: β ± SE=0.88 ± 0.18, *z*=5.01, *p*<0.001; oestrus versus pregnant: β ± SE=-0.70 ± 0.16, *z*=4.36,

p<0.001; oestrus versus babysitting: β ± SE=0.70 ± 0.18, *z*=3.82, *p*<0.001; Figure 2; Table 2).
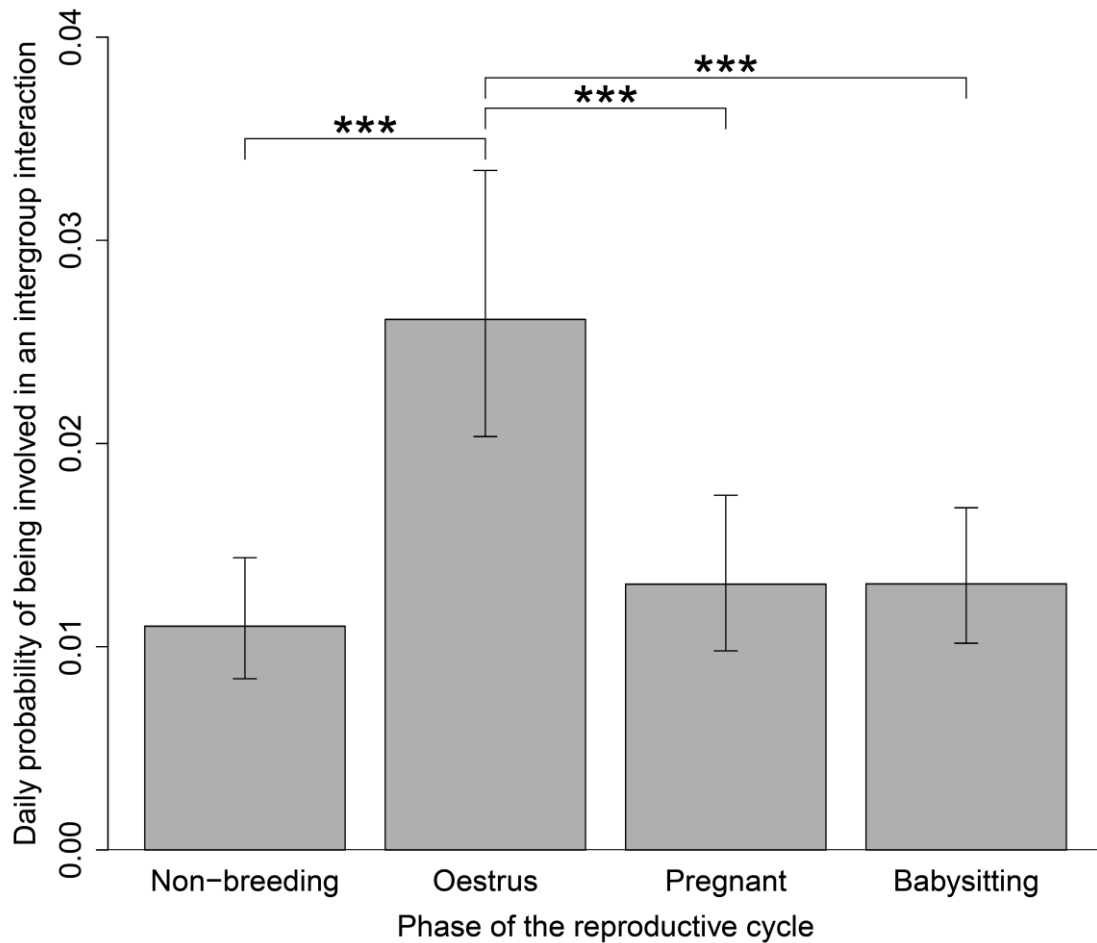
Figure 2. The probability of an intergroup interaction during the reproductive cycle.
The probability of a group being involved in an intergroup interaction on a given day against the phase of the reproductive cycle they are in on that day (*N*=42470 study days in 39 groups). The bars show means from the GLMM ± standard error. Symbol: *** *p*<0.001; asterisks refer to post-hoc Tukey's all-pairwise comparison of means across all four categories.

Table 2. Intergroup conflict during the reproductive cycle. Post-hoc multiple comparison of means with Tukey's all-pairwise comparisons to determine differences in the daily probability of engaging in an intergroup interaction on different phases of the reproductive cycle (GLMM, *N*=42470 study days in 39 groups). Original model was fitted using a binomial error structure and a logit link function, and with group ID as a random intercept. Significant post-hoc comparisons are given in bold.

	β	SE	*z*	*p*
oestrus vs non-breeding	0.88	0.18	5.01	**<0.001**
pregnant vs oestrus	-0.70	0.16	-4.36	**<0.001**
oestrus vs babysitting	0.70	0.18	3.82	**<0.001**
non-breeding vs babysitting	-0.18	0.14	-1.30	0.55
pregnant vs babysitting	-0.0009	0.11	-0.008	1.00
pregnant vs non-breeding	0.17	0.10	1.69	0.32

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 shrunk in size (GLMM: β ± SE=0.03 ± 0.009, χ^2_1=10.96, *p*=0.0009; Figure 3; Table 3). 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 (GLMM: β ± SE=0.03 ± 0.01, χ^2_1=12.09, *p*=0.0005; Table 3), 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: GLMM, β ± SE=-0.0001 ± 0.0007; χ^2_1=0.03, *p*=0.87; Table 3).
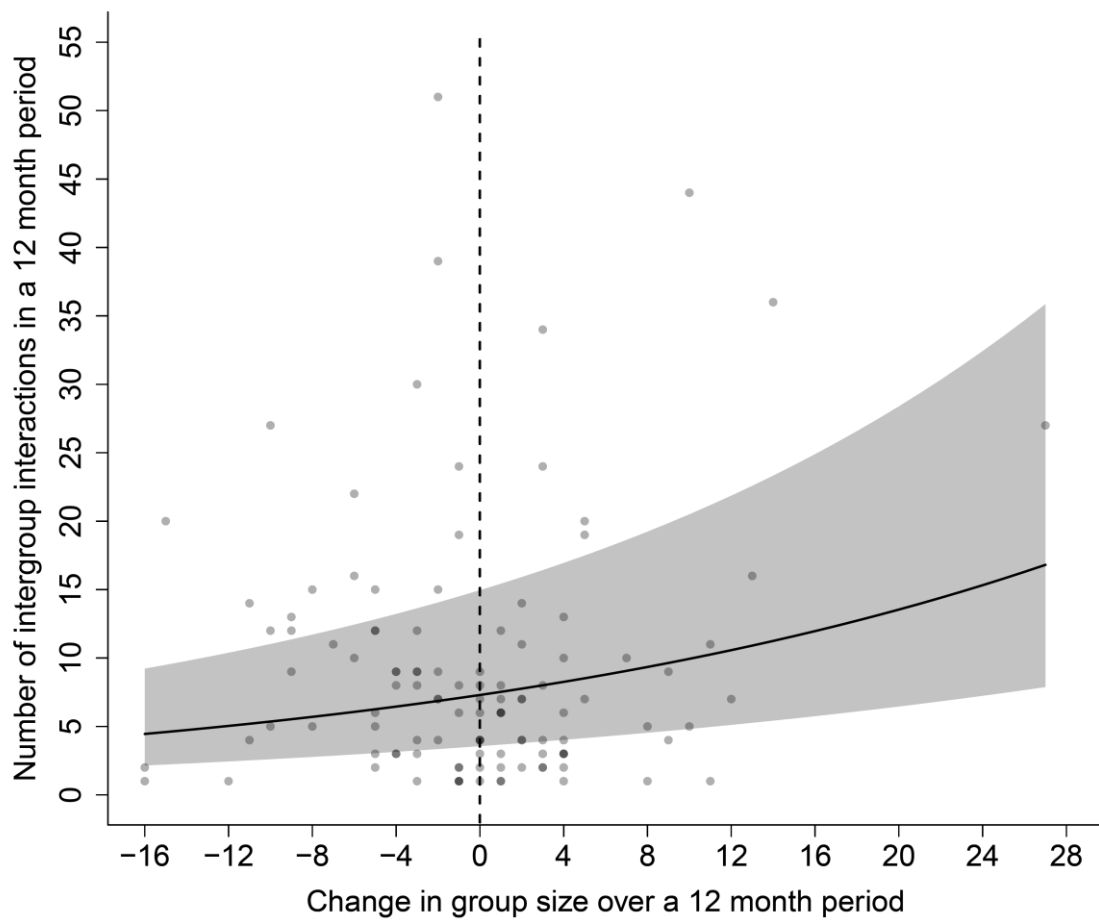
Figure 3. Changes in group size and intergroup interactions. The number of intergroup interactions in which a group is involved over a 12 month period against the group's change in group size over the 12 month period (*N*=113 sample (12 month) periods in 16 groups). The vertical dashed line shows no change in group size. The line shows prediction from the GLMM ± standard error.

Table 3. Changes in group size and intergroup conflict. Model predicting the number of intergroup interactions in which a group is involved over a 12 month period against the group's change in group size over the 12 month period (*N*=113 sample (12 month) periods in 16 groups). Model was fitted using a negative binomial error structure and a log link function, and with group ID as a random intercept. Significant terms are given in bold.

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	0.008	0.004	3.66	0.056
number of oestrus periods	-0.004	0.02	0.03	0.85
change in group size x starting group size	-0.0001	0.0007	0.03	0.87
rainfall x population density	-0.002	0.001	3.32	0.07

(ii) 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 less likely to survive to emergence if the group was involved in an intergroup interaction during the 30 days after birth (GLMM, β ± SE=-0.45 ± 0.20, χ^2_1=5.01, *p*=0.025; Figure 4; Table 4). The occurrence of an intergroup interaction involving their group did not significantly affect male or female survival in a 30 day period. Neither males nor females were significantly more likely to die in a 30 day period following an intergroup interaction than in a 30 day period where there was no intergroup interaction (males: GLMM, β ± SE=0.05 ± 0.48, χ^2_1=0.01, *p*=0.92; females: GLMM, β ± SE=-0.55 ± 0.0007, χ^2_1=1.50, *p*=0.22; Table 5). Pregnant females did not suffer pre-natal costs if their group was involved in an intergroup interaction during their gestation. In fact, a pregnant female was significantly less likely to abort her litter if her group engaged in an intergroup interaction during the period for which she was pregnant (GLMM, β ± SE=-1.29 ± 0.51, χ^2_1=9.12, *p*=0.003; Figure 5; Table 6).
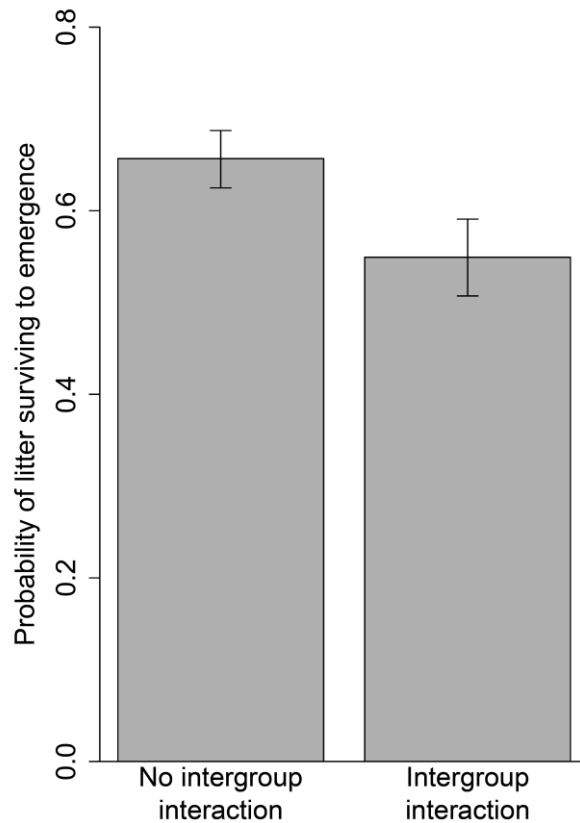
Figure 4. Litter survival following an intergroup interaction. The probability of a litter surviving to emergence against whether or not the group was involved in an intergroup interaction in the 30 days after the birth of the communal litter (*N*=516 communal litters born in 19 groups). The bars show means from the GLMM ± standard error.

Table 4. Intergroup conflict and litter survival. Model predicting the probability of a litter surviving to emergence (GLMM, *N*=516 communal litters born in 19 groups). Model was fitted using a binomial error structure and a logit link function, and with group identity as a random intercept. Significant terms are given in bold.

Fixed effect	β	SE	χ^2	*p*
intercept	-0.25	0.29		
intergroup interaction	-0.45	0.20	5.01	**0.025**
rainfall	0.18	0.07	7.51	**0.006**
group size	0.02	0.01	3.66	0.055
rainfall x group size	0.002	0.008	0.06	0.81

Table 5. Intergroup conflict and survival. Models predicting the probability of a surviving a 30 day period for females (GLMM, *N*=1373 females in 17 groups) and males (GLMM, *N*=2179 males in 15 groups). Models were fitted using a binomial error structure and logit link function, and with individual and group identity as random intercepts. Significant terms are given in bold.

	Response	Fixed effect	β	SE	χ^2	*p*
Females	probability of surviving a 30 day period	intercept	1.01	0.0007		
		intergroup interaction	-0.55	0.0007	1.50	0.22
		age	-0.003	0.0004	35.23	**<0.0001**
		weight	-0.0003	0.0006	-0.64	1.00
		group size	0.09	0.0007	1.61	0.20
		rainfall	0.19	0.0007	1.98	0.16
		group size x rainfall	0.03	0.02	1.29	0.26
Males	probability of surviving a 30 day period	intercept	0.38	5.22		
		intergroup interaction	0.05	0.48	0.01	0.92
		age	-0.007	0.003	49.88	**<0.0001**
		weight	-0.003	0.003	1.56	0.21
		group size	-0.27	0.08	22.46	**<0.0001**
		rainfall	0.01	0.15	0.009	0.92
		group size x rainfall	-0.03	0.02	-0.72	1.00
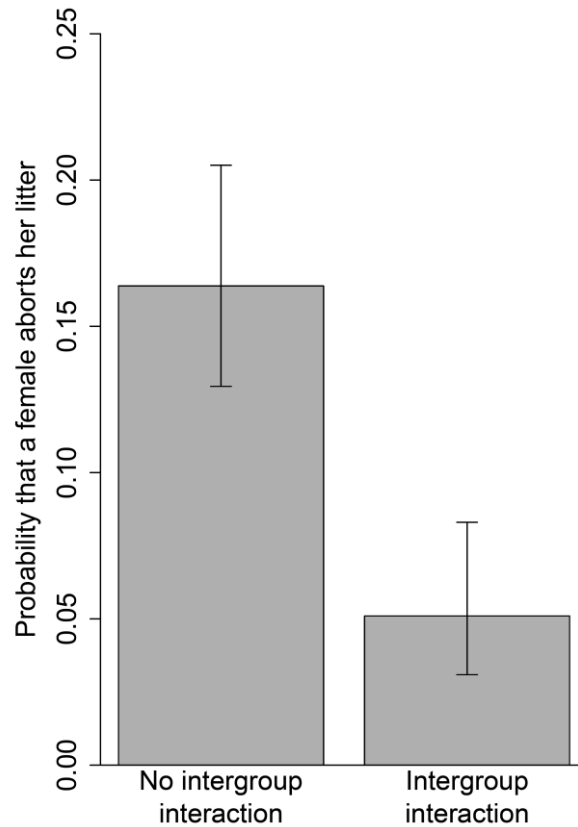
Figure 5. Female abortion following an intergroup interaction. The probability of a female aborting her litter against whether or not her group was involved in an intergroup interaction during gestation (*N*=502 females giving birth to 139 communal litters in 7 groups). The bars show means from the GLMM ± standard error.

Table 6. Intergroup conflict and abortion. Model predicting the probability of a pregnant female aborting her litter (GLMM, *N*=502 females giving birth to 139 communal litters in 7 groups). Model was fitted using a binomial error structure and a logit link function, and with female, litter and group identity as a random intercept. Significant terms are given in bold.

Fixed effect	β	SE	χ^2	*p*
intercept	3.28	1.47		
intergroup interaction	-1.29	0.51	9.12	**0.003**
rainfall	-0.27	0.16	2.92	0.09
number of breeding females	-0.007	0.09	0.005	0.94
age	-0.0004	0.0003	2.87	0.09
weight	-0.003	0.001	7.58	**0.006**
rainfall x				
number of breeding females	0.02	0.07	0.14	0.71

Discussion

Intergroup conflict in banded mongooses, manifested in violent interactions between neighbouring groups, was widespread in our population and groups were regularly involved 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 our results suggest that 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 survival, but did not affect adult fertility or survival. These results show that intergroup conflict has measurable costs to both offspring 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 insect abundance; Marshall *et al.*, in preparation) 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 (Harrison 1983; Isbell 1991; Mech 1994; Harris 2010), and in an attempt to expand territories (Wilson & Wrangham 2003; Mosser & Packer 2009; Mitani *et al.* 2010). In our population, larger groups were more likely to be involved in an intergroup interaction than smaller groups, and our results suggest that 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 greater area, which may inevitably bring them into conflict with their neighbours. In addition,

larger 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. To disentangle these possibilities requires more detailed information on which individuals seek and initiate conflicts. In the future we will have this information from lightweight Global Positioning System (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 (Wrangham 1999; Wilson & Wrangham 2003). In our population, groups engaged more frequently 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 (Lazaro-Perea 2001; Cant *et al.* 2002; Nichols *et al.* 2015). Detailed data on the distribution and movement of groups 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. The development of lightweight Global Positioning System (GPS) collars deployed in our population will allow us to conduct these tests in the near future.

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 (Wrangham 1999; Wilson & Wrangham 2003). 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 (Lazaro-Perea 2001; Cant *et al.* 2002; Nichols *et al.* 2015). Detailed data on the distribution and movement of groups 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 in the near future.

Intergroup conflict, because it frequently results in participants' injury and death, can have important effects on group size and recruitment. Although we did not detect short-term effects on adult mortality, we did find that litters were less likely to survive to emergence 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.* 2002, 2016; Müller & Bell 2009). A previous study in banded mongooses has shown that intergroup interactions contribute to 20% of known pup deaths (Nichols *et al.* 2015). Cases of observed infanticide during intergroup encounters are also common in chimpanzees (Watts, Mitani & Sherrow 2002; Wilson & Wrangham 2003; Wilson *et al.* 2004). This significant cost of intergroup conflict might be a means by which members of rival groups can ensure their own success by reducing the size of neighbouring competitors which, in turn, is likely to give them a greater competitive advantage in future disputes (Wrangham 1999; Mosser & Packer 2009; Batchelor & Briffa 2011; Wrangham & Glowacki 2012; Cassidy *et al.* 2015). In cooperatively breeding species, the maintenance of a critical group size is vital to avoid extinction (Courchamp 1999; Courchamp *et al.* 1999). Intergroup conflict could, therefore, have important consequences for the dynamics and success of groups through group augmentation (Kokko *et al.* 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 pregnant 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; Chapter 2). However, we found that pregnant 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 non-human animal species, but increases in affiliative behaviour following intergroup conflict have been demonstrated in green woodhoopoes, *Phoeniculus purpureus* (Radford 2008, 2011), and the cooperatively breeding cichlid fish, *Neolamprologus pulcher* (Bruintjes *et al.* 2015). Further experimental manipulations of levels of intergroup conflict through simulated territorial intrusions could illuminate how the nature and intensity of intergroup conflict affects patterns of cooperation and conflict within the group in banded mongooses, and other cooperative species.

In conclusion, our results suggest that intergroup conflict is driven by competition for resources and matings in banded mongooses. Groups engaged in intergroup interactions during periods of high competition for resources, and also when females were in oestrus, indicating that individuals fight to attain food, territory and reproductive opportunities that are important for survival and reproductive success. Intergroup conflict also had consequences for litter survival, suggesting that intergroup conflict 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 (Wrangham *et al.* 2006; Nichols *et al.* 2015). 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 which 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.

Chapter 6: General discussion

Overview

Conflict within and between social groups is a conspicuous feature of cooperative animal societies. Eviction, because it results in the break-up of the social group, can have important implications for the individuals involved and the wider population through effects on dispersal, gene flow, and population structure. The logistical difficulties of observing a population for a period long enough to obtain sufficient data to examine these effects means that the causes and consequences of eviction are not well understood. Similarly, intergroup conflict is a notable occurrence in many social species but is relatively understudied outside of humans, *Homo sapiens,* and chimpanzees, *Pan troglodytes*. Violent intergroup conflict could play an important role in the evolution of cooperative behaviours, but there is currently a lack of understanding of the causes and consequences of intergroup conflict to be able to draw conclusions on these theoretical links. It is therefore important to utilise those cooperative species in which within- and between-group conflict is exhibited to a high degree in order to address these shortfalls in our knowledge.

To that end, in this thesis I have examined the causes and consequences of eviction and intergroup conflict in a highly cooperative species, the banded mongoose, *Mungos mungo*. I have found that eviction is driven by competition over reproduction in both sexes. The pattern of eviction among individuals motivated the development of a new theoretical model, which predicted that negative kin discrimination should be restricted to individuals that are more capable of resistance. Our data provided qualified support for this model, and suggested that where individuals are capable of resisting eviction, the usual prediction of positive kin discrimination can be reversed. I have investigated the long-term consequences of eviction beyond those for the evictees and evictors, and found evidence that eviction can have demographic effects on the evicting group and on the wider population. Finally, I have investigated the causes and consequences of intergroup conflict in our population and found that intergroup conflict has measureable costs to both individuals and groups in the long- and short-term. Below, I discuss the key findings of this thesis, the implications for our understanding of within- and between-group conflict in the evolution of cooperative species and, where appropriate, suggest future research objectives.

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Eviction and social evolution

Eviction as a means of within-group conflict resolution is rarely naturally observed in social vertebrates (**Chapter 1**). Where it does occur, it is important to determine what triggers eviction in order to understand how it might influence population genetic structure and demography in structured populations, and hence social evolution (Rousset 2004; Lehmann & Rousset 2010). In **Chapter 2**, I investigated established hypotheses, as well as introducing a new hypothesis to explain patterns of eviction. I employed a model comparison approach to compare competing hypotheses: that eviction is driven by reproductive competition; that eviction is used to coerce cooperation; or that eviction is an adaptive forced dispersal strategy used by dominants to force copies of their genes into the wider population. I found clear evidence that eviction in banded mongooses is driven by competition over reproduction in both sexes. There was little evidence to suggest that eviction is used by dominants to force subordinate helpers to work harder, which is consistent with generally weak evidence for the pay-to-stay hypothesis in cooperative birds and mammals (McDonald *et al.* 2008a; Cant 2012a; Santema & Clutton-Brock 2012; Nomano *et al.* 2015). This hypothesis assumes relatively complex strategies of negotiation and punishment, behaviours that may simply be beyond the capabilities of many cooperative species (Donaldson *et al.* 2013). Eviction as a response to the intensity of reproductive competition that an individual experiences is a simple, biologically feasible mechanism, and the body of evidence from cooperative birds, mammals and fish supports this assertion (**Chapter 1**; **Chapter 2**). I did not find evidence to show that eviction is an adaptive forced dispersal strategy. However, in **Chapter 3** I did find that, among older females, kin were preferentially evicted, suggesting that once the decision to evict (as a response to intensified reproductive competition) has been made, kinship plays a role in which individuals are targeted for eviction, and potential patterns of resistance. Current models of kin selection assume that one party has full control of group membership but, as our results suggest, conflict resolution is a compromise between the interests of both parties. A formal model of the adaptive forced dispersal hypothesis that integrates a mechanism of conflict resolution over group membership (such as a 'tug-of-war'; Reeve, Emlen & Keller 1998) into a demographic framework would provide discriminating predictions

beyond those of our simple verbal arguments. For example, such a model would help to clarify the conditions where it would be adaptive for subordinates to attempt to remain in groups, and adaptive for dominants to force them to disperse. These conditions remain unclear at present.

As well as understanding the triggers of eviction, it is also important to determine which individuals are targeted for eviction because this can have implications for patterns of dispersal, gene flow and population demography and dynamics (Gardner & West 2006; Johnstone & Cant 2008; Gardner 2010; Clutton-Brock & Lukas 2012). In **Chapter 3**, I investigated which individuals are evicted when an eviction occurs and, in females, found that younger individuals, and those older individuals that were more related to dominants in their group, were more likely to be evicted. This latter result, which seems contrary to the prediction of positive kin discrimination under classical kin selection theory, stimulated the development of a theoretical model with collaborators. The model shows that negative kin discrimination can be explained by selection for unrelated subordinates to invest more effort in resisting eviction. Empirical tests of the model predictions showed some support for this explanation. Together, the theoretical and empirical results of this chapter suggest that the capacity to resist may be a crucial determinant of patterns of conflict among kin and, in contexts where recipients are capable of resistance, the usual prediction of positive kin discrimination can be reversed. There is already evidence that animals adjust their behaviour according to the anticipated responses of their social partners (Buston 2003b; Raihani, Grutter & Bshary 2004; Tibbetts & Dale 2004; Wong *et al.* 2007). However, most theoretical models of these interactions examine the evolution of 'sealed-bid' strategies, where players are not permitted to adjust their behaviour depending on the expected response of their social partner. It is unrealistic to assume that theoretical models can reflect the real world in every sense, but in the study of social evolution there appears to be a disconnect between theoretical models and observed behaviour. Our results suggest that the influence of relatedness on within-group conflict and cooperation may be considerably more variable than predicted by classical kin selection theory.

The long-term consequences of eviction are exceptionally understudied because of the logistical difficulties in tracking populations and evicted cohorts over periods long enough to generate sufficient data. The Banded Mongoose Research Project is in a unique position to be able to address these shortfalls in our understanding because we have studied the same population of banded mongooses for over 20 years. In **Chapter 4** I took advantage of this to investigate the long-term demographic consequences of eviction for individuals, groups, and intergroup relations. I found that eviction resulted in changes in group size and composition for evicting groups, but did not translate to long-term survival or reproductive costs for evicted individuals. There was evidence that eviction was successful in reducing reproductive competition among females by increasing *per capita* reproductive success. However, eviction also resulted in a more male-biased sex ratio within evicting groups. These findings suggest that the long-term consequences of within-group conflict resolution strategies reach beyond the individuals involved in eviction, with potential effects on population demography and dynamics. This highlights a current limitation of many theoretical models of within-group conflict resolution, and of many models of social evolution more broadly. At present, most models focus on the drivers of cooperative behaviour and conflict at an individual level, but fail to incorporate the potential effects of population-level consequences of individual decisions (Cant *et al.* 2016). As such, we lack a clear understanding of how individual-level behaviour and population-level processes link up. Long-term empirical studies of cooperative breeders can provide unique insight into how the effects of individual-level behaviour can resonate through groups and populations, and can inform theoretical models with an aim to synthesise these currently disparate themes of research.

Intergroup conflict and social evolution

Violent intergroup conflict is a notable feature of cooperatively breeding species. Theory suggests there is potential for intergroup conflict to influence demographic processes, such as migration, colonisation of new territory and population expansion (Lehmann & Feldman 2008), and the evolution of social and cooperative traits (Choi & Bowles 2007; Lehmann & Rousset 2010; Bowles & Gintis 2011). However, a lack of understanding of the causes and consequences of intergroup conflict in species that

exhibit conspicuous levels of cooperation and collective violence means that the role of intergroup conflict in the evolution of social behaviours is not well established. In **Chapter 5,** I investigated the ecological and social causes, and the fitness consequences, of intergroup conflict in our population. I found that intensified competition for food, territory and mates increased the frequency of intergroup interactions but this did not translate into costs to adult survival or fertility. There is now a need to investigate the more fine-scale interactions of intergroup conflict to gain a better understanding of which individuals instigate contests between groups. Detailed data on the spatial distribution and movement of groups in response to the availability of resources would allow us to test in more detail how resource competition affects patterns of intergroup conflict, and how groups respond to conflict in terms of the expansion or contraction of territory boundaries. The development of lightweight Global Positioning System (GPS) collars deployed in our population will allow us to conduct these tests in the near future. This will shed light on the motivations of individuals to participate in potentially lethal conflict, and will enable tests of the hypotheses of the adaptive function of intergroup conflict.

In **Chapter 5**, I also found that intergroup conflict had fitness costs in the form of reduced litter survival. This result suggests that intergroup conflict has measurable costs to both individuals and groups in the long- and short-term, with important implications for fitness and survival. In banded mongooses, rates of mortality are likely to be high enough to influence patterns of within-group cooperation, as proposed by theoretical models (Choi & Bowles 2007; Lehmann & Feldman 2008). In this chapter, I found that pregnant females were less likely to abort their litter following an intergroup interaction which, although speculative, could suggest that intergroup conflict promotes the suppression of within-group conflict. Further investigation of individual contributions to helping and fighting would clarify whether there are tradeoffs between these forms of cooperation, and stimulate both new theory and new tests of theoretical models. Experimental manipulations of levels of intergroup conflict through simulated territorial intrusions could illuminate how the nature and intensity of intergroup conflict affects cooperation and, in turn, facilitate our understanding of the role of intergroup conflict in social evolution.

Summary

Eviction in banded mongooses is triggered by high levels of reproductive competition in both males and females. When an eviction occurs, younger females, and those older females that are more related to dominants in their group, are targeted for eviction. As predicted by our theoretical model that incorporates the resistance of targets to selfish acts, older, more closely related females that are potentially more capable of resistance are preferentially targeted for eviction, and are less likely to return to their group following eviction. Eviction, as well as having effects on the evicted cohort, has important consequences for litter survival, group size and recruitment in the evicting group. Intergroup conflict in banded mongooses is stimulated by intensified competition for resources and mates, and has measurable fitness costs to individuals and groups in the long- and short-term. This thesis demonstrates that the means of resolving conflict within groups can have effects at an individual, group and population level, and that, conversely, conflict between groups has the potential to influence patterns of cooperation and conflict between groups. Within- and between-group conflict are likely to be closely linked, and recognising this link could help to advance our conceptual understanding of the role of conflict in the evolution of cooperative behaviour.

Concluding remarks

Much of the research into within-group conflict and cooperation has focussed on the drivers of these behaviours within the group, without acknowledging the potential influence of external forces. Similarly, patterns of intergroup conflict are usually considered independently of within-group pressures. In this thesis I have argued that within- and between-group conflict may often be intimately linked, and that recognising this link in the formulation of hypotheses and models could help to illuminate the causes of individual behaviour and population patterns. We aim to pursue this avenue for future research by using simulated territorial intrusions in our population to examine the effect of increased intergroup conflict on the cooperative and social behaviour within groups. We also plan to investigate how social groups

respond spatially to each other using lightweight GPS collars to capture group home range, space use and movement. Social groups in a viscous population are unlikely to behave as discrete units that are insensitive to the external pressures exerted upon them by neighbours. Instead, we hope to determine the behavioural and spatial response of groups to the behaviour of their neighbours, and to discover how the nature and intensity of within-group cooperation and conflict can, in turn, affect the nature and intensity of conflict between groups.

The study of within- and between-group conflict in cooperative species can provide crucial insight into how conflict is resolved and cooperative behaviour maintained in animal societies. There is now a need to unify the study of these forms of conflict by developing integrated theoretical models of individual behaviour and population processes. Cooperatively breeding species are particularly powerful systems to stimulate the development of such models, and to test them, using long-term studies of individuals and populations, across multiple generations and in varying environments. This will certainly enable a huge advance in our conceptual understanding of the links between within-group and between-group conflict, and their role in the evolution of cooperative behaviour.

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Appendices

Appendix A

Controlling for regression to the mean

To account for potential problems with regression to the mean, we calculated ΔC_S, ΔC_E and ΔH as an adjusted change using the formulae from Kelly & Price (2005):

$$\Delta X = (X_2 - \bar{X}_2) - \hat{p}(X_1 - \bar{X}_1)$$

and

$$\hat{p} = \frac{2rs_1 s_2}{s_1{}^2 + s_2{}^2}$$

where X_1 and s_1 are the observation and standard deviation of the observation in the breeding attempt before eviction, and X_2 and s_2 are the observation and standard deviation of the observation in the breeding attempt of the eviction, and r is the correlation between the observations in the two consecutive breeding attempts.

Table A1. Female evictions. Model performance in predicting the probability of an eviction event occurring during a breeding attempt (*N*=415 breeding attempts in 15 groups). Analysis using the female reproductive success (C_S) measure of helping performance under the coercion of cooperation hypothesis. Models above the line comprise the top model set where ΔAIC ≤ 6.

Hyp.	Int.	C_S	H	C_S:H	R	E	ΔC_S	ΔH	ΔC_S:ΔH	B	B:E	R:E	G	R:G	R:B	k	logLik	AIC	ΔAIC	w_i	Retained	Adj. w_i
R	-5.44									0.37						3	-108.63	223.26	0.00	0.34	✓	1.00
A	-3.34				-14.46					0.11					1.76	5	-107.25	224.50	1.24	0.18		
A/R	-5.49				0.42					0.37						4	-108.62	225.25	1.99	0.13		
R	-5.45					0.00				0.37						4	-108.63	225.26	2.00	0.13		
A	-3.29				-14.52	0.00				0.11					1.77	6	-107.25	226.50	3.24	0.07		
A/R	-5.51				0.43	0.00				0.37						5	-108.62	227.24	3.99	0.05		
R	-5.37					0.00				0.36	0.00					5	-108.63	227.26	4.00	0.05		
A	-3.34				-14.11	0.00				0.11		-0.01			1.77	7	-107.25	228.49	5.23	0.02		
A	-5.25				-1.44	0.00				0.37		0.03				6	-108.60	229.21	5.95	0.02		
R	-5.42				0.44	0.00				0.36	0.00					6	-108.62	229.24	5.98	0.02		
C	-4.99	0.47	0.40	-0.07												5	-111.65	233.30	10.04	0.00		
C	-5.07	0.47	0.40	-0.07	0.57											6	-111.63	235.27	12.01	0.00		
C	-4.97	0.47	0.40	-0.07		0.00										6	-111.65	235.30	12.04	0.00		
C	-5.05	0.46	0.40	-0.07	0.57	0.00										7	-111.63	237.27	14.01	0.00		
A	-2.75				-11.13								0.01	0.56		5	-115.16	240.31	17.05	0.00		
A	-4.32				1.65								0.07			4	-116.75	241.50	18.24	0.00		
A	-2.98				-10.94	0.00							0.01	0.56		6	-115.10	242.21	18.95	0.00		
A	-4.60				1.76	0.00							0.07			5	-116.66	243.33	20.07	0.00		
A	-2.65				-13.35	0.00						0.04	0.01	0.56		7	-115.07	244.14	20.88	0.00		
A	-4.19				-1.11	0.00						0.05	0.07			6	-116.62	245.25	21.99	0.00		
C	-2.86						0.37	0.11	0.01							5	-118.19	246.37	23.11	0.00		
Null	-2.87															2	-121.28	246.57	23.31	0.00		
C	-3.37					0.01	0.38	0.11	0.01							6	-117.86	247.71	24.45	0.00		
C	-3.19				2.03		0.38	0.11	0.01							6	-117.98	247.96	24.70	0.00		
Any	-3.15				1.69											3	-121.14	248.28	25.02	0.00		
C	-3.80				2.32	0.01	0.39	0.11	0.01							7	-117.59	249.19	25.93	0.00		
Any	-3.62				1.93	0.01										4	-120.90	249.81	26.55	0.00		
A	-3.00				-2.86	0.00							0.08			5	-120.79	251.57	28.31	0.00		

Hyp. = Hypothesis: A = Adaptive forced dispersal; C = Coercion of cooperation; R = Reproductive competition; Any = Any of the three hypotheses; Null = null model.

Columns 2 to 16 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; C_S = number of emergent pups per female that contributed to the

previous litter; *H* = number of female helpers in the previous breeding attempt; *R* = mean group relatedness; *E* = mean rainfall in previous 6 months; ΔC_s = change in the number of emergent pups per female that contributed to the litter in the breeding attempts before and of the eviction; ΔH = change in the number of female helpers in the breeding attempts before and of the eviction; *B* = number of breeding females; *G* = group size; : = interaction. k = number of estimated parameters including a random intercept for group identity; logLik = log-likelihood; AIC = Akaike's information criterion; ΔAIC = change in AIC value from the best performing model; w_i = Akaike's model weight; Retained = tick indicates that the model was retained after applying the nesting rule of Richards, Whittingham & Stephens (2011); Adj. w_i = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term was absent from that model.

Table A2. Female evictions. Model performance in predicting the probability of an eviction event occurring during a breeding attempt (*N*=270 breeding attempts in 14 groups). Analysis using the helping effort (C_E) measure of helping performance under the coercion of cooperation hypothesis. Models above the line comprise the top model set where ΔAICc ≤ 6.

Hyp.	Int.	C_E	H	C_E:H	R	E	ΔC_E	ΔH	ΔC_E:ΔH	B	B:E	R:E	G	R:G	R:B	k	logLik	AICc	ΔAICc	w_i	Retained	Adj. w_i
R	1.28					-0.11				-0.67	0.02					5	-62.26	134.76	0.00	0.27	✓	0.49
R	1.66				-3.95	-0.11				-0.62	0.02					6	-61.82	135.96	1.20	0.15		
R	-7.65					0.03				0.43						4	-64.04	136.22	1.47	0.13	✓	0.24
R	-5.73									0.44						3	-65.16	136.41	1.65	0.12	✓	0.22
A/R	-6.95				-4.25	0.03				0.45						5	-63.50	137.23	2.48	0.08		
A/R	-5.10				-4.46					0.46						4	-64.55	137.24	2.49	0.08		
A	-6.67				4.71					0.66					-1.13	5	-64.36	138.95	4.20	0.03		
A	-8.49				4.67	0.03				0.64					-1.10	6	-63.33	138.99	4.23	0.03		
A	-8.18				3.23	0.05				0.45		-0.12				6	-63.43	139.17	4.42	0.03		
C	-5.30	-5.16	0.17	0.79		0.03										6	-64.13	140.58	5.83	0.01	✓	0.03
C	-3.44	-5.13	0.18	0.79												5	-65.18	140.60	5.84	0.01	✓	0.02
A	-9.65				11.65	0.05				0.64		-0.11			-1.07	7	-63.27	140.96	6.21	0.01		
C	-3.02	-5.04	0.18	0.79	-2.66											6	-64.95	142.21	7.46	0.01		
C	-4.86	-5.11	0.17	0.79	-2.45	0.03										7	-63.94	142.30	7.55	0.01		
A	-4.97				-1.57								0.13			4	-67.35	142.85	8.10	0.00		
A	-6.56				-1.51	0.03							0.13			5	-66.51	143.24	8.48	0.00		
A	-4.45				-4.97								0.11	0.15		5	-67.33	144.88	10.12	0.00		
A	-7.75				5.59	0.05						-0.11	0.12			6	-66.44	145.20	10.44	0.00		
A	-5.84				-6.40	0.03							0.09	0.22		6	-66.45	145.22	10.47	0.00		
A	-7.02				0.63	0.05						-0.12	0.09	0.24		7	-66.37	147.18	12.42	0.00		
Null	-2.61															2	-75.89	155.83	21.07	0.00		
Any	-5.13				-0.03	0.04										4	-74.03	156.21	21.46	0.00		
C	-5.09					0.04	0.26	-0.54	0.19							6	-72.56	157.45	22.69	0.00		
Any	-2.63				0.15											3	-75.89	157.87	23.12	0.00		
A	-6.61				9.04	0.06						-0.14				5	-73.91	158.05	23.30	0.00		
C	-2.58						0.25	-0.49	0.11							5	-74.37	158.98	24.22	0.00		
C	-5.04				-0.23	0.04	0.26	-0.53	0.19							7	-72.56	159.55	24.80	0.00		
C	-2.53				-0.24		0.25	-0.49	0.11							6	-74.37	161.07	26.31	0.00		

Hyp. = Hypothesis: A = Adaptive forced dispersal; C = Coercion of cooperation; R = Reproductive competition; Any = Any of the three hypotheses; Null = null model.

Columns 2 to 16 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; C_E = number of female helpers left per day of babysitting of the

previous litter; *H* = number of female helpers in the previous breeding attempt; *R* = mean group relatedness; *E* = mean rainfall in previous 6 months; ΔC_E = change in the number of female helpers left per day of babysitting in the breeding attempts before and of the eviction; ΔH = change in the number of female helpers in the breeding attempts before and of the eviction; *B* = number of breeding females; *G* = group size; : = interaction. k = number of estimated parameters including a random intercept for group identity; logLik = log-likelihood; AICc = corrected Akaike's information criterion; ΔAICc = change in AICc value from the best performing model; w_i = Akaike's model weight; Retained = tick indicates that the model was retained after applying the nesting rule of Richards, Whittingham & Stephens (2011); Adj. w_i = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term was absent from that model.

Table A3. Male evictions. Model performance in predicting the probability that males are evicted alongside females when an eviction event occurs (*N*=37 eviction events in 7 groups). Analysis using the female reproductive success (C_S) measure of helping performance under the coercion of cooperation hypothesis. Models above the line comprise the top model set where ΔAICc ≤ 6.

Hyp.	Int.	C_S	H	C_S:H	R	E	ΔC_S	ΔH	ΔC_S:ΔH	B	B:E	R:E	G	R:G	R:B	k	logLik	AICc	ΔAICc	w_i	Retained	Adj. w_i
R	-2.28									0.38						3	-20.42	47.57	0.00	0.47	✓	0.95
R	-1.81					-0.01				0.39						4	-20.32	49.88	2.32	0.15		
A/R	-2.16				-0.68					0.38						4	-20.41	50.07	2.51	0.13		
R	-0.30					-0.04				-0.10	0.01					5	-19.78	51.51	3.94	0.07		
A	-0.94				-9.71					0.11					2.02	5	-20.24	52.41	4.85	0.04		
A/R	-1.64				-0.90	-0.01				0.39						5	-20.31	52.55	4.98	0.04		
A	-3.82				-1.58								0.15			4	-22.08	53.41	5.84	0.03	✓	0.05
Null	-0.38															2	-24.98	54.31	6.75	0.02		
R	-0.25				-0.35	-0.04				-0.10	0.01					6	-19.78	54.37	6.80	0.02		
A	-0.21				-10.96	-0.01				0.09					2.25	6	-20.10	55.00	7.44	0.01		
A	-1.35				-3.19	-0.01				0.39		0.03				6	-20.30	55.40	7.84	0.01		
A	-3.45				-1.54	-0.01							0.16			5	-21.90	55.74	8.18	0.01		
A	-6.12				14.14								0.25	-0.70		5	-21.95	55.84	8.27	0.01		
Any	0.09				-2.97											3	-24.83	56.38	8.82	0.01		
A	0.11				-13.50	-0.01				0.08		0.04			2.26	7	-20.10	58.05	10.49	0.00		
A	-5.84				14.56	-0.01							0.26	-0.71		6	-21.78	58.36	10.80	0.00		
A	-2.14				-11.17	-0.03						0.14	0.16			6	-21.85	58.49	10.93	0.00		
Any	0.18				-3.00	0.00										4	-24.82	58.90	11.33	0.00		
C	-1.61	0.38	0.11	-0.02												5	-24.15	60.24	12.68	0.00		
C	-0.53						0.35	0.01	-0.05							5	-24.21	60.35	12.78	0.00		
A	2.51				-22.06	-0.03							0.28			5	-24.48	60.90	13.34	0.00		
A	-4.48				4.69	-0.03						0.16	0.27	-0.76		7	-21.71	61.28	13.72	0.00		
C	-1.25	0.37	0.12	-0.02	-2.29											6	-24.07	62.95	15.38	0.00		
C	-1.47	0.38	0.11	-0.02		0.00										6	-24.14	63.09	15.52	0.00		
C	-0.25				-1.74		0.33	0.02	-0.05							6	-24.16	63.12	15.55	0.00		
C	-0.81					0.00	0.37	0.01	-0.05							6	-24.17	63.14	15.57	0.00		
C	-1.10	0.37	0.12	-0.02	-2.33	0.00										7	-24.06	65.98	18.42	0.00		
C	-0.52				-1.55	0.00	0.35	0.01	-0.05							7	-24.13	66.12	18.56	0.00		

Hyp. = Hypothesis: A = Adaptive forced dispersal; C = Coercion of cooperation; R = Reproductive competition; Any = Any of the three hypotheses; Null = null model.

Columns 2 to 16 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; C_S = number of emergent pups per female that contributed to the

previous litter; H = number of male helpers in the previous breeding attempt; R = mean group relatedness; E = mean rainfall in previous 6 months; ΔC_S = change in the number of emergent pups per female that contributed to the litter in the breeding attempts before and of the eviction; ΔH = change in the number of male helpers in the breeding attempts before and of the eviction; B = number of breeding males; G = group size; : = interaction. k = number of estimated parameters including a random intercept for group identity; logLik = log-likelihood; AICc = corrected Akaike's information criterion; ΔAICc = change in AICc value from the best performing model; w_i = Akaike's model weight; Retained = tick indicates that the model was retained after applying the nesting rule of Richards, Whittingham & Stephens (2011); Adj. w_i = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term was absent from that model.

Table A4. Male evictions. Model performance in predicting the probability that males are evicted alongside females when an eviction event occurs (*N*=22 eviction events in 6 groups). Analysis using the helping effort (C_E) measure of helping performance under the coercion of cooperation hypothesis. Models above the line comprise the top model set where ΔAICc ≤ 6.

Hyp.	Int.	C_E	H	C_E:H	R	E	ΔC_E	ΔH	ΔC_E:ΔH	B	B:E	R:E	G	R:G	R:B	k	logLik	AICc	ΔAICc	w_i	Retained	Adj. w_i
Null	0.18															2	-15.16	34.95	0.00	0.31	✓	1.00
R	-1.00									0.24						3	-14.24	35.80	0.86	0.20		
A	-3.25				1.65								0.13			4	-13.56	37.47	2.52	0.09		
Any	0.06				0.70											3	-15.15	37.64	2.69	0.08		
R	-2.36					0.02				0.22						4	-14.07	38.50	3.55	0.05		
R	8.86					-0.16				-2.33	0.04					5	-12.42	38.59	3.65	0.05		
A/R	-1.28				1.53					0.24						4	-14.21	38.77	3.82	0.05		
C	-0.07						-0.11	0.52	0.53							5	-12.83	39.41	4.46	0.03		
Any	-1.98				1.23	0.03										4	-14.83	40.01	5.06	0.02		
A	-1.86				-8.18								0.06	0.46		5	-13.50	40.75	5.81	0.02		
A	-2.66				1.49	-0.02							0.14			5	-13.50	40.76	5.81	0.02		
C	-2.04	0.46	0.27	-0.07												5	-13.92	41.59	6.65	0.01		
A/R	-2.75				1.86	0.02				0.23						5	-14.03	41.82	6.87	0.01		
A	-0.63				-2.63					0.08					1.02	5	-14.18	42.11	7.16	0.01		
R	8.82				3.88	-0.17				-2.40	0.04					6	-12.28	42.16	7.21	0.01		
A	-7.27				36.23	0.11						-0.55				5	-14.51	42.77	7.82	0.01		
C	1.11					-0.02	-0.21	0.58	0.66							6	-12.77	43.13	8.18	0.01		
C	-0.35				1.53		-0.10	0.52	0.53							6	-12.81	43.21	8.27	0.01		
A	-6.95				31.77	0.05						-0.47	0.15			6	-13.27	44.14	9.19	0.00		
A	-1.68				-6.27	-0.01							0.09	0.36		6	-13.47	44.55	9.60	0.00		
A	-7.38				32.88	0.10				0.22		-0.48				6	-13.79	45.18	10.23	0.00		
C	-2.74	0.46	0.25	-0.07		0.01										6	-13.87	45.34	10.40	0.00		
C	-1.87	0.50	0.28	-0.08	-1.25											6	-13.91	45.41	10.47	0.00		
A	-1.84				-5.55	0.03				-0.06					1.83	6	-13.96	45.51	10.56	0.00		
C	0.83				1.48	-0.02	-0.20	0.58	0.66							7	-12.74	47.49	12.54	0.00		
A	-7.32				33.14	0.13						-0.98	-0.08	1.48		7	-12.93	47.85	12.91	0.00		
A	-7.20				30.57	0.12				-0.26		-0.63			2.97	7	-13.59	49.18	14.23	0.00		
C	-2.58	0.49	0.26	-0.08	-1.02	0.01										7	-13.86	49.72	14.78	0.00		

Hyp. = Hypothesis: A = Adaptive forced dispersal; C = Coercion of cooperation; R = Reproductive competition; Any = Any of the three hypotheses; Null = null model.

Columns 2 to 16 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; C_E = number of male helpers left per day of babysitting of the

previous litter; *H* = number of male helpers in the previous breeding attempt; *R* = mean group relatedness; *E* = mean rainfall in previous 6 months; ΔC_E = change in the number of male helpers left per day of babysitting in the breeding attempts before and of the eviction; ΔH = change in the number of male helpers in the breeding attempts before and of the eviction; *B* = number of breeding males; *G* = group size; : = interaction. k = number of estimated parameters including a random intercept for group identity; logLik = log-likelihood; AICc = corrected Akaike's information criterion; ΔAICc = change in AICc value from the best performing model; w_i = Akaike's model weight; Retained = tick indicates that the model was retained after applying the nesting rule of Richards, Whittingham & Stephens (2011); Adj. w_i = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term was absent from that model.

Table A5. Temporary evictions. Model performance in predicting the probability that evictees are allowed to return to their group following an eviction event (*N*=37 eviction events in 7 groups). Analysis using the female reproductive success (C_S) measure of helping performance under the coercion of cooperation hypothesis. Models above the line comprise the top model set where ΔAICc ≤ 6.

Hyp.	Int.	C_S	H_F	H_M	$C_S:H_F$	$C_S:H_M$	R	E	ΔC_S	ΔH_F	ΔH_M	$\Delta C_S:\Delta H_F$	$\Delta C_S:\Delta H_M$	B_F	B_M	$B_F:E$	$B_M:E$	R:E	G	R:G	R:B_F	R:B_M	k	logLik	AICc	ΔAICc	w_i	Ret.	Adj. w_i
Null	0.6																						2	-24.0	52.3	0.0	0.2	✓	1.00
R	1.9													-0.1									3	-23.5	53.8	1.5	0.1		
Any	1.4						-4.9																3	-23.6	53.9	1.6	0.1		
R	0.8														0.0								3	-24.0	54.6	2.3	0.1		
C	0.7								0.1	-0.1	-0.5												5	-21.5	54.9	2.6	0.1		
A/R	2.5						-4.5							-0.1									4	-23.2	55.7	3.3	0.0		
Any	2.3						-5.3	0.0															4	-23.3	55.8	3.5	0.0		
R	2.5							0.0						-0.1									4	-23.3	55.9	3.6	0.0		
R	1.9													-0.1	0.0								4	-23.5	56.3	4.0	0.0		
A/R	1.7						-5.2								0.0								4	-23.5	56.3	4.0	0.0		
A	1.3						-4.9												0.0				4	-23.6	56.4	4.1	0.0		
R	1.5							0.0							0.0								4	-23.7	56.6	4.3	0.0		
C	1.7						-5.8		0.1	-0.1	-0.5												6	-21.0	56.7	4.4	0.0		
C	0.7								0.1		0.3		-0.2										5	-22.7	57.4	5.1	0.0		
A	-0.4						13.3							0.2							-2.2		5	-22.8	57.5	5.1	0.0		
C	0.9							0.0	0.1	-0.1	-0.5												6	-21.5	57.7	5.4	0.0		
A	-0.2						15.4	0.0										-0.3					5	-22.9	57.8	5.5	0.0		
A/R	3.2						-4.7	0.0						-0.1									5	-23.0	57.9	5.5	0.0		
C	-0.8	0.8		0.2		-0.1																	5	-23.1	58.2	5.9	0.0		
R	-0.3							0.0						0.2		0.0							5	-23.1	58.2	5.9	0.0		
A/R	2.6						-4.6							-0.1	0.0								5	-23.2	58.3	6.0	0.0		
A	2.0						-5.1	0.0											0.0				5	-23.2	58.4	6.1	0.0		
A/R	2.5						-5.5	0.0							0.0								5	-23.2	58.4	6.1	0.0		
R	2.5							0.0						-0.1	0.0								5	-23.3	58.6	6.3	0.0		
C	0.8								0.0	-0.3	0.3	-0.4	-0.2										7	-20.4	58.7	6.4	0.0		
A	0.8						0.8								0.1							-1.4	5	-23.4	58.7	6.4	0.0		
R	0.5							0.0							0.3		0.0						5	-23.4	58.8	6.5	0.0		
A	1.8						-8.7												0.0	0.2			5	-23.6	59.1	6.7	0.0		
C	1.4	-0.5	-0.1		0.1																		5	-23.6	59.1	6.7	0.0		
C	1.8						-6.4		0.0		0.3		-0.2										6	-22.2	59.2	6.9	0.0		
C	1.6								0.0	0.0	0.3		-0.2										6	-22.4	59.6	7.3	0.0		
C	1.9						-5.9	0.0	0.0	-0.1	-0.5												7	-21.0	59.8	7.5	0.0		
C	0.1	0.8		0.2		-0.1	-5.7																6	-22.6	60.0	7.7	0.0		
A	0.4						11.0	0.0						0.2							-1.9		6	-22.6	60.1	7.8	0.0		

Hyp.	Int.	C_S	H_F	H_M	$C_S{:}H_F$	$C_S{:}H_M$	R	E	ΔC_S	ΔH_F	ΔH_M	$\Delta C_S{:}\Delta H_F$	$\Delta C_S{:}\Delta H_M$	B_F	B_M	$B_F{:}E$	$B_M{:}E$	R:E	G	R:G	R:B_F	R:B_M	k	logLik	AICc	ΔAICc	w_i	Ret.	Adj. w_i
A	-0.7						15.6							0.3	-0.1						-2.5		6	-22.7	60.1	7.8	0.0		
A	-1.2						19.1	0.0										-0.4	0.0				6	-22.8	60.4	8.1	0.0		
C	2.4						-8.8		-0.2	-0.3	0.4	-0.4	-0.2										8	-19.6	60.4	8.1	0.0		
C	2.8	-0.7	-0.1		0.1			0.0															6	-22.8	60.4	8.1	0.0		
A	1.1						10.5	0.0						-0.1				-0.2					6	-22.8	60.4	8.1	0.0		
C	0.0	0.8		0.2		-0.1		0.0															6	-22.9	60.5	8.2	0.0		
R	1.1						-4.1	0.0						0.1		0.0							6	-22.9	60.6	8.3	0.0		
A	-0.1						15.1	0.0							0.0			-0.3					6	-22.9	60.6	8.3	0.0		
A	1.5						4.4	NA						-0.2	0.3							-2.0	6	-23.0	60.7	8.4	0.0		
R	1.5						-5.6	0.0							0.3		0.0						6	-23.0	60.7	8.4	0.0		
A/R	3.3						-4.8	0.0						-0.1	0.0								6	-23.0	60.7	8.4	0.0		
R	1.5							0.0						-0.1	0.3		0.0						6	-23.0	60.8	8.5	0.0		
C	3.5						-8.1	0.0	-0.2		0.4		-0.3										7	-21.6	61.1	8.7	0.0		
R	-0.3							0.0						0.2	0.0	0.0							6	-23.1	61.1	8.8	0.0		
A	1.8						-0.9	0.0							0.1							-1.0	6	-23.2	61.1	8.8	0.0		
A	2.7						-10.0	0.0											0.0	0.2			6	-23.2	61.2	8.9	0.0		
C	2.0	-0.4	-0.1		0.1		-3.8																6	-23.3	61.5	9.2	0.0		
C	1.2							0.0	0.0	-0.3	0.4	-0.4	-0.2										8	-20.4	61.9	9.6	0.0		
C	0.9	0.8		0.2		-0.1	-5.9	0.0															7	-22.3	62.5	10.2	0.0		
C	0.7	-0.1	-0.3	0.2	0.1	-0.1																	7	-22.4	62.6	10.3	0.0		
A	-1.2						22.8	0.0						0.2				-0.2			-1.8		7	-22.5	62.9	10.6	0.0		
A	-1.0						19.8							0.2	0.2						-2.2	-1.5	7	-22.5	62.9	10.6	0.0		
A	0.2						13.2	0.0						0.3	-0.1						-2.2		7	-22.6	63.0	10.7	0.0		
R	2.2						-4.8	0.0						-0.1	0.3		0.0						7	-22.6	63.2	10.9	0.0		
C	3.2	-0.7	-0.1		0.1		-3.1	0.0															7	-22.7	63.2	10.9	0.0		
A	-0.3						12.4	0.0										-0.4	0.0	0.4			7	-22.7	63.3	11.0	0.0		
A	2.3						2.9	0.0						-0.1	0.2							-1.7	7	-22.8	63.5	11.1	0.0		
A	1.1						10.5	0.0						-0.1	0.0			-0.2					7	-22.8	63.5	11.2	0.0		
A	-0.7						19.3	0.0							0.1			-0.3				-1.0	7	-22.9	63.6	11.3	0.0		
R	1.1						-4.2	0.0						0.2	0.0	0.0							7	-22.9	63.6	11.3	0.0		
C	3.2						-9.0	0.0	-0.2	-0.3	0.5	-0.4	-0.2										9	-19.5	63.7	11.4	0.0		
R	0.4							0.0						0.0	0.3	0.0	0.0						7	-23.0	63.8	11.5	0.0		
C	1.9	-0.3	-0.2	0.2	0.2	-0.1		0.0															8	-21.9	64.8	12.5	0.0		
C	1.3	0.1	-0.3	0.3	0.1	-0.1	-4.9																8	-22.1	65.3	13.0	0.0		
A	-0.3						17.3	0.0						0.2	0.1						-2.0	-1.3	8	-22.5	66.1	13.8	0.0		
A	-1.2						22.9	0.0						0.3	0.0			-0.2			-2.0		8	-22.5	66.1	13.8	0.0		
R	2.2						-4.8	0.0						-0.1	0.3	0.0	0.0						8	-22.6	66.4	14.1	0.0		
A	0.5						15.5	0.0						-0.1	0.2			-0.2				-1.5	8	-22.7	66.5	14.2	0.0		
C	2.3	-0.2	-0.2	0.2	0.2	-0.1	-4.2	0.0															9	-21.6	67.9	15.6	0.0		
A	-1.5						25.9	0.0						0.2	0.1			-0.2			-1.9	-1.2	9	-22.4	69.5	17.2	0.0		

Hyp. = Hypothesis: A = Adaptive forced dispersal; C = Coercion of cooperation; R = Reproductive competition; Any = Any of the three hypotheses; Null = null model. Columns 2 to 23 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; C_S = number of emergent pups per female that contributed to the previous litter; H_F = number of female helpers in the previous breeding attempt; H_M = number of male helpers in the previous breeding attempt; R = mean group relatedness; E = mean rainfall in previous 6 months; ΔC_S = change in the number of emergent pups per female that contributed to the litter in the breeding attempts before and of the eviction; ΔH_F = change in the number of female helpers in the breeding attempts before and of the eviction; ΔH_M = change in the number of male helpers in the breeding attempts before and of the eviction; B_F = number of breeding females; B_M = number of breeding males; G = group size; : = interaction. k = number of estimated parameters including a random intercept for group identity; logLik = log-likelihood; AICc = corrected Akaike's information criterion; ΔAICc = change in AICc value from the best performing model; w_i = Akaike's model weight; Ret. = tick indicates that the model was retained after applying the nesting rule of Richards, Whittingham & Stephens (2011); Adj. w_i = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term was absent from that model.

Table A6. Temporary evictions. Model performance in predicting the probability that evictees are allowed to return to their group following an eviction event (*N*=22 eviction events in 6 groups). Analysis using the helping effort (C_E) measure of helping performance under the coercion of cooperation hypothesis. Models above the line comprise the top model set where ΔAICc ≤ 6.

Hyp.	Int.	C_{EF}	H_F	C_{EF}:H_F	C_{EM}	H_M	C_{EM}:H_M	R	E	ΔC_{EF}	ΔH_F	ΔC_{EF}:ΔH_F	ΔC_{EM}	ΔH_M	ΔC_E:ΔH_M	B_F	B_M	B_F:E	B_M:E	R:E	G	R:G	R:B_F	R:B_M	k	logLik	AICc	ΔAICc	w_i	Ret.	Adj. w_i
Null	0.0		✓																						2	-15.2	35.1	0.0	0.3	✓	1.0
R	2.0															-0.2									3	-14.6	36.5	1.4	0.1		
R	0.9																-0.2								3	-14.7	36.8	1.7	0.1		
Any	-0.2							0.9																	3	-15.2	37.8	2.7	0.1		
C	-2.8	32.0	0.3	-4.0																					5	-12.1	38.0	2.9	0.1		
R	3.1															-0.2	-0.2								4	-14.0	38.4	3.2	0.0		
R	2.9								0.0								-0.1								4	-14.4	39.1	4.0	0.0		
R	3.1								0.0							-0.2									4	-14.4	39.2	4.0	0.0		
A/R	1.8							1.6								-0.2									4	-14.5	39.5	4.3	0.0		
Any	2.4							0.3	0.0																4	-14.7	39.8	4.7	0.0		
A/R	0.8							0.3									-0.2								4	-14.7	39.8	4.7	0.0		
A	0.9							0.7														0.0			4	-15.1	40.5	5.3	0.0		
C	0.3									3.5	-0.2	-1.0													5	-13.4	40.5	5.4	0.0		
A	-6.6							67.4	0.1											-1.0					5	-13.7	41.2	6.1	0.0		
A	-3.1							32.9								0.4							-4.1		5	-13.9	41.5	6.3	0.0		
C	-3.9	33.3	0.4	-4.2				4.7																	6	-12.0	41.5	6.4	0.0		
R	3.8								0.0							-0.2	-0.2								5	-13.9	41.6	6.5	0.0		
R	23.3								-0.3							-2.5		0.0							5	-14.0	41.7	6.6	0.0		
A/R	3.0							0.9								-0.2	-0.2								5	-14.0	41.8	6.6	0.0		
C	-2.0	31.4	0.4	-4.0					0.0																6	-12.1	41.8	6.7	0.0		
R	3.4								0.0								-0.2		0.0						5	-14.4	42.5	7.4	0.0		
A/R	3.0							-0.2	0.0								-0.1								5	-14.4	42.5	7.4	0.0		
A/R	2.9							1.0	0.0							-0.2									5	-14.4	42.5	7.4	0.0		
C	3.7								-0.1	3.5	0.0	-1.0													6	-12.7	42.9	7.8	0.0		
A	1.8							-5.9									-0.4							1.5	5	-14.7	43.1	8.0	0.0		
A	2.4							0.3	0.0												0.0				5	-14.7	43.2	8.1	0.0		
A	-3.6							46.5								0.7	-0.3						-5.9		6	-12.9	43.3	8.2	0.0		
C	1.1				-0.3	-0.1	0.1																		5	-14.8	43.4	8.2	0.0		
C	-0.1												-0.3	0.1	0.0										5	-15.0	43.8	8.6	0.0		
A	0.4							4.3													0.0	-0.2			5	-15.0	43.8	8.7	0.0		
A	-7.3							79.6	0.1								-0.2			-1.2					6	-13.1	43.9	8.8	0.0		
C	0.9							-2.9		3.9	-0.2	-1.2													6	-13.3	44.2	9.1	0.0		
A	-5.4							61.8	0.1							-0.1				-0.9					6	-13.5	44.7	9.5	0.0		
A	-2.8							44.3	0.0							0.8							-6.0		6	-13.6	44.7	9.6	0.0		
R	19.0								-0.3							-2.0	-0.1	0.0							6	-13.7	45.0	9.9	0.0		
A	-6.6							67.6	0.1											-1.0	0.0				6	-13.7	45.0	9.9	0.0		
R	24.5							2.7	-0.4							-2.8		0.0							6	-13.9	45.4	10.3	0.0		
C	4.3								-0.1				-0.7	0.3	0.5										6	-13.9	45.5	10.3	0.0		
A/R	3.7							0.5	0.0							-0.2	-0.2								6	-13.9	45.5	10.3	0.0		

Appendix A

Hyp.	Int.	C_{EF}	H_F	$C_{EF}{:}H_F$	C_{EM}	H_M	$C_{EM}{:}H_M$	R	E	ΔC_{EF}	ΔH_F	$\Delta C_{EF}{:}\Delta H_F$	ΔC_{EM}	ΔH_M	$\Delta C_E{:}\Delta H_M$	B_F	B_M	$B_F{:}E$	$B_M{:}E$	R:E	G	R:G	$R{:}B_F$	$R{:}B_M$	k	logLik	AICc	ΔAICc	w_i	Ret.	Adj. w_i
R	3.5								0.0							-0.2	-0.1			0.0					6	-13.9	45.5	10.3	0.0		
A	3.1							-0.1								-0.2	-0.2							0.2	6	-14.0	45.6	10.5	0.0		
C	-3.1	32.9	0.4	-4.1				4.6	0.0																7	-11.9	45.9	10.7	0.0		
C	3.5				-0.3	-0.1	0.1		0.0																6	-14.3	46.1	11.0	0.0		
A	3.4							-3.4	0.0								-0.3							0.8	6	-14.4	46.3	11.2	0.0		
R	3.4							-0.1	0.0								-0.2			0.0					6	-14.4	46.3	11.2	0.0		
A	1.5							7.9	0.0												0.1	-0.4			6	-14.7	47.0	11.8	0.0		
C	0.8				-0.4	-0.2	0.1	2.5																	6	-14.7	47.1	11.9	0.0		
C	4.2							-3.1	-0.1	4.0	-0.1	-1.3													7	-12.6	47.1	12.0	0.0		
A	-2.7							46.6	0.0							0.8	-0.3						-6.1		7	-12.7	47.5	12.3	0.0		
C	-0.2							0.8					-0.3	0.1	0.0										6	-15.0	47.6	12.5	0.0		
A	-3.3							44.5								0.8	-0.5						-6.4	1.5	7	-12.8	47.6	12.5	0.0		
A	-5.9							73.0	0.1							-0.2	-0.2			-1.1					7	-12.9	47.8	12.7	0.0		
A	-6.5							70.8	0.1								-0.6			-1.3				2.6	7	-13.0	48.0	12.9	0.0		
A	-6.6							72.0	0.1							0.5				-0.7			-3.8		7	-13.3	48.5	13.4	0.0		
A	-7.2							70.2	0.2											-1.5	-0.2	1.2			7	-13.5	49.0	13.9	0.0		
R	19.9							1.9	-0.3							-2.2	-0.1	0.0							7	-13.7	49.3	14.2	0.0		
C	-1.5	65.7	0.9	-8.2	-4.7	-0.4	0.3																		8	-11.1	49.3	14.2	0.0		
R	21.0								-0.3							-2.1	-0.3	0.0	0.0						7	-13.7	49.4	14.2	0.0		
C	4.2							0.2	-0.1				-0.7	0.3	0.5										7	-13.9	49.9	14.7	0.0		
R	3.5							0.4	0.0							-0.2	-0.1			0.0					7	-13.9	49.9	14.7	0.0		
A	3.6							0.6	0.0							-0.2	-0.2							0.0	7	-13.9	49.9	14.7	0.0		
C	3.3				-0.4	-0.1	0.1	2.0	0.0																7	-14.2	50.5	15.3	0.0		
A	-6.5							75.3	0.1							0.5	-0.3			-0.7			-4.2		8	-12.4	51.9	16.8	0.0		
A	-2.6							44.9	0.0							0.8	-0.4						-6.3	1.0	8	-12.7	52.5	17.4	0.0		
A	-5.5							67.7	0.1							-0.1	-0.5			-1.1				1.7	8	-12.9	52.8	17.7	0.0		
C	-4.1	103.6	1.6	-13.0	-7.7	-0.8	0.5	10.2																	9	-10.7	54.3	19.2	0.0		
R	23.0							2.3	-0.3							-2.4	-0.4	0.0	0.0						8	-13.6	54.4	19.2	0.0		
C	-3.8	88.7	1.3	-11.1	-6.7	-0.7	0.4		0.0																9	-11.0	54.9	19.8	0.0		
A	-6.4							72.4	0.1							0.5	-0.5			-0.7			-4.4	1.9	9	-12.4	57.8	22.6	0.0		
C	-7.7	135.9	2.1	-17.1	-10.5	-1.1	0.7	11.0	0.1																10	-10.4	60.8	25.7	0.0		

Hyp. = Hypothesis: A = Adaptive forced dispersal; C = Coercion of cooperation; R = Reproductive competition; Any = Any of the three hypotheses; Null = null model.

Columns 2 to 25 show parameter effect sizes from GLMMs on the logit scale: Int. = Intercept; C_{EF} = number of female helpers left per day of babysitting of the previous litter; H_F = number of female helpers in the previous breeding attempt; C_{EM} = number of male helpers left per day of babysitting of the previous litter; H_M = number of male helpers in the previous breeding attempt; R = mean group relatedness; E = mean rainfall in previous 6 months; ΔC_{EF} = change in the number of female helpers left per day of babysitting in the breeding attempts before and of the eviction; ΔH_F = change in the number of female helpers in the breeding attempts before and of the eviction; ΔC_{EM} = change in the number of male helpers left per day of babysitting in the breeding attempts before and of the eviction;

ΔH_M = change in the number of male helpers in the breeding attempts before and of the eviction; B_F = number of breeding females; B_M = number of breeding males; G = group size; : = interaction. k = number of estimated parameters including a random intercept for group identity; logLik = log-likelihood; AICc = corrected Akaike's information criterion; ΔAICc = change in AICc value from the best performing model; w_i = Akaike's model weight; Ret. = tick indicates that the model was retained after applying the nesting rule of Richards, Whittingham & Stephens (2011); Adj. w_i = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term was absent from that model.

Appendix A references

Kelly, C. & Price, T.D. (2005) Correcting for regression to the mean in behavior and ecology. *The American Naturalist*, **166**, 700–707.

Richards, S.A., Whittingham, M.J. & Stephens, P.A. (2011) Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, **65**, 77–89.

Appendix B

Analysis to investigate whether closer relatives represent a reproductive threat

To investigate the possibility that more closely related individuals represent more of a reproductive threat we examined whether dominant females suffered higher reproductive costs when cobreeding with more closely related subordinates. We fitted the number of emergent pups to which each dominant breeding female (females over 3 years of age) was assigned maternity as the Poisson response variable with a log link function in a generalised linear mixed effect model (GLMM). We included each dominant female's mean pairwise relatedness to cobreeding subordinate females (females less than 3 years of age that contributed to the communal litter), the number of cobreeding subordinates, and the interaction between these two variables as fixed effects. We also included the dominant female's age (days), group size (number of individuals over 6 months), and mean rainfall (mm) in the 30 days before birth. We controlled for repeated measures by including dominant female, litter and group ID as random intercepts, and fitted the model to data on 566 dominant females giving birth to 256 litters in 16 groups. This model was checked for overdispersion of the response variable.

We found that there was no difference in the number of emergent pups to which dominant females were assigned maternity when they were more closely related to female subordinate cobreeders (GLMM, $\beta \pm$ SE=-0.002 $\pm$ 0.36, χ^2_1=0.00005, p=0.99; Table B1). Therefore, we did not find evidence that dominant females suffer greater reproductive costs when they cobreed with more closely related subordinate females.

Table B1. Investigating whether closer relatives represent a reproductive threat. Model predicting the number of emergent pups to which each dominant breeding female is assigned maternity (GLMM, *N*=566 dominant females giving birth to 256 litters in 16 groups). Model was fitted using a Poisson error structure and log link function, and with dominant female, litter and group ID as random intercepts.

Fixed effect	β	SE	χ²	*p*
intercept	-1.12	0.35		
relatedness to subordinate cobreeders	-0.002	0.36	0.00005	0.99
number of subordinate cobreeders	0.013	0.050	0.07	0.79
dominant female age (days)	0.0002	0.0001	2.46	0.12
group size	0.006	0.013	0.23	0.63
rainfall (mm)	0.082	0.052	2.48	0.11
relatedness to subordinate cobreeders x number of subordinate cobreeders	0.31	0.25	1.60	0.21