Cooperation, conflict and warfare in wild banded mongooses

Submitted by

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SUMMARY

Intergroup conflict can be a strong force in the lives of social species. Conflict can be dramatic, leading to serious injury or death, loss of territory or dominance status, and can impact behaviour, reproductive success and fitness. The impact of intergroup conflict on within-group behaviour is a growing area of research, and evidence for increased affiliation between group members after exposure to intergroup conflict has been found in several species. However, these studies focus on short timescales, the minutes and hours post-conflict, and it is unclear what effect intergroup conflict has on within-group behaviour in the longer term. In this thesis I use the banded mongoose (*Mungos mungo*) as a model system to investigate the effects of intergroup conflict on within-group behaviour in the longer term. I discovered that group level within-group affiliation was only affected in the hour after exposure to conflict, but individual social relationships were affected into the longer term, up to two days after exposure. Unlike other studied populations, banded mongooses reduced within-group affiliation and aggression, and these changes differed between males and females, and between younger and older mongooses. I found only tentative evidence that intergroup conflict affected group movement or home range use, however, the risk of intergroup conflict affected leadership, with evidence that females lead more successfully in areas of high risk at the edge of the territory, which may indirectly affect movements in the longer term. This thesis gives evidence that intergroup conflict affects behaviour in the longer term, beginning to bridge the gap between evolutionary theory and empirical observations, and highlights that groups do not respond in a heterogeneous way, as different sex and age classes react differently, potentially due to differential costs and benefits.

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Network-level consequences of intergroup conflict in a cooperative mammal society: redirection of grooming and aggression between sexes.

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Chapter 1:

General Introduction

The general introduction encompasses both the theoretical and empirical literature associated with intergroup conflict as a topic. To start the theoretical frameworks of kin, group and multi-level selection are discussed in the context of intergroup conflict. Then the empirical literature surrounding intergroup conflict, including who participates in conflict, when and where these conflicts take place, and what the consequences of intergroup conflict might be are explored. Finally the study system is introduced in the context of this theoretical and empirical background.

Intergroup conflict and multi-level selection

Conflict and cooperation are important forces of natural selection. Evolutionary conflict occurs when individuals interact socially and their individual optima cannot be satisfied simultaneously (Cant, 2012). Cooperation and evolutionary conflict occur across many scales of biological organisation, as organisms compete to survive and reproduce. Within organisms, cells cooperate to form fruiting bodies in slime moulds (Strassmann, Zhu and Queller, 2000), and in a more extreme arrangement, cooperate to form multicellular organisms (Maynard Smith and Szathmary, 1995). In contrast, selfish elements of genes are in conflict with the rest of the genome (Werren, Nur and Wu, 1988), and cancerous cells are in conflict with non-cancerous cells inside organisms (Gil and Rodriguez, 2016). Similarly, conflict also occurs at the individual level over many resources, including food and mates, but cooperation is also common, for example, mutualistic relationships between plants and pollinators. At a group level, conflict also occurs, including intergroup conflicts over territories in many animals (Sherratt and Mesterton-Gibbons, 2013; Rusch and Gavrilets, 2016), or between human groups (Johnson and Toft, 2014). In some situations distinct groups of organisms can even cooperate with one another – e.g. human trade, or polydomous ant colonies – although this is rare in animals (Robinson and Barker, 2017).

Cooperation has posed a long-standing puzzle for evolutionary theory to explain, because natural selection is usually expected to favour traits that boost the fitness of an organism at the expense of other members of the population. Currently, the most dominant theory to explain the evolution of cooperation is Hamilton's theory of inclusive fitness, also known as kin selection (Hamilton, 1964). Hamilton's rule ($rb > c$) provides a framework in which cooperation can be selected for under natural selection, if the lifetime fitness cost of an action (c) is less than the lifetime fitness benefit of the action (b), weighted by the coefficient of relatedness of the individual to the recipient of the benefit (r) (Hamilton, 1964). When individuals are closely related r is larger, increasing the size of rb for the same benefit, which leads to increased cooperation between closely related individuals as outweighing the lifetime fitness cost of the action (c) is easier.

Another theory for the evolution of cooperation is reciprocity (first developed in detail by Trivers (1971)) in which cooperation between individuals can be maintained as it is reciprocated (i.e. given both ways between individuals). Repeated opportunities for cooperation lead to individuals cooperating with those they have cooperated with before, as they know they will benefit again in the future (Trivers, 1971). Reciprocity is important as it allows for cooperation between non-relatives. Reciprocity can be direct, i.e. directly interacting with individuals who will cooperate at a later time; indirect, when individuals cooperate with those who are "good co-operators" or have a good reputation; or via network reciprocity in which co-operators cluster in spatial or social networks (Nowak, 2006). One key issue is that an individual cannot ensure that the other individual will reciprocate rather than cheat, in any given interaction. Reputation and clustering of co-operators are ways to avoid cheaters, but are not completely reliable (Nowak, 2006). Reciprocity is also somewhat controversial because it requires high levels of accurate information about who cooperates with whom, and storing all of this information about multiple individuals is potentially cognitively demanding (Nowak, 2006).

One further theory for the evolution of cooperation, that has fallen in and out of favour historically, is multi-level selection (also known as group selection). This theory suggests that selection acts on multiple levels of biological organisation at the same time, including cells, individuals and groups (Okasha, 2009). Cooperation can be favoured within a group if groups with many co-operators outcompete groups with few co-operators (Okasha, 2009). In this case selection against cooperation occurs within the group as individuals compete for resources or mates, but selection between groups favours cooperation, as cooperative groups are more successful (Okasha, 2009). Many studies of multi-level selection have focused on selection within and between groups (Wilson, 1975; Traulsen and Nowak, 2006), however, it is important to note that these theories do not invoke traditional “group selection” in the sense that the group fitness is not the maximand of natural selection (Gardner and Grafen, 2009). A misunderstanding of what is meant by multi-level selection has arisen from a focus on older ideas suggesting that groups would become adapted and reach group optima instead of individual optima (Goodnight, 2015; Kramer and Meunier, 2016). Individual selection is always important, and group selection can either outweigh this (as is the suggestion for cooperation) or may be aligned with individual selection, in which case group selection may be seen as less relevant in determining the direction of selection acting on individual traits. Multi-level selection simply takes into account interactions between individuals and population structure, as well as individual actions and traits (Goodnight and Stevens, 1997). Multi-level selection may therefore be more important for social traits, like cooperation, and in social, group-living species, in which the interests of individuals within the group do not always align, but may do so in the face of between-group competition.

Kin selection and multi-level selection are argued to be formally equivalent on a general level, despite the two theories often being studied as separate frameworks (Kramer and Meunier, 2016). Kin and multi-level selection are deemed to be equivalent as high relatedness strengthens selection for cooperation (kin selection), and high relatedness within a group also reduces genetic variance compared to between group variance, strengthening between-group selection for cooperation (multi-level selection) (Lehmann *et al.*, 2007; Marshall, 2011; Kramer and Meunier, 2016). Furthermore, the two theories are mathematically equivalent, using either the Price equation or contextual analysis (Marshall, 2011; Kramer and Meunier, 2016; Birch, 2019). However, recent work highlights that although the two theories can be considered mathematically equivalent, there is still good reason to use the two terms, as these address different causalities – cooperation emerging from kin relatedness or group structure (Birch, 2019). There is no strict dichotomy between kin and multi-level selection, and Birch (2019) suggests that a “K-G space” is a more useful framework. High K (kin relatedness) and low G (group structure) represents situations where kin selection is important, low K and high G represents multi-level selection importance, and high K and high G represents a hybrid kin-group selection situation (Birch, 2019). High K values may mean that altruism is stable, whereas high G values may mean that evolutionary transitions in individuality are likely to occur (similar to major evolutionary transitions, with group structure leading to a new “superorganism” or new level at which the individual is defined)(Birch, 2019).

Intergroup conflict immediately lends itself to being studied in the framework of multi-level selection, as group dynamics may be important, but selection still acts on individuals within these groups. Conflict between groups may affect the benefits and costs of cooperative acts, as participating could be very costly and/or provide benefits. Darwin himself suggested in The Descent of Man (1871) that intergroup conflict between early human groups might be an explanation for the widespread cooperation seen in human groups, despite low relatedness between cooperating individuals. He suggested that groups that were more cooperative and self-sacrificing would have an advantage over less cooperative groups in warfare, and would therefore spread in the population (Darwin, 1871). These ideas, although Darwin did not explicitly state this, invoke multi-level selection – on individual humans, and the groups they form.

More modern human evolutionary theorists have suggested that intergroup conflict drives cooperation within human groups more formally (Choi and Bowles, 2007; Bowles and Gintis, 2013). They suggest, like Darwin, that any group that has more members that cooperate with each other preferentially (parochial altruism), will be more successful during intergroup fights, and that individuals from this group will then have an increased fitness due to access to resources, territory or reproductive partners, and cooperation will spread (Choi and Bowles, 2007; Bowles and Gintis, 2013). If cooperative groups can outcompete non-cooperative groups and either reduce their numbers or drive these groups to extinction, then cooperative groups, and therefore cooperative individuals, will increase in the population in the context of intergroup conflict. Bowles and Gintis (2013) also suggest “weak multi-level selection” which occurs when groups with a greater proportion of cooperative members are able to produce more offspring than other groups, and therefore have a numeric advantage over other groups in conflict, or simply outnumber them over time.

Evolutionary biologists without a human focus have also suggested a link between intergroup conflict and within-group cooperation in their theoretical models (Reeve and Hölldobler, 2007; Okasha, 2009; Lehmann, 2011; Gavrilets, 2015; Simon and Pilosov, 2016). And intergroup conflict has also been suggested to help drive major transitions, and move societies along a “superorganism continuum”, by reducing internal conflict in the face of external conflict (Reeve and Hölldobler, 2007). Intergroup conflict may therefore not just be important in human evolution, but in the evolution of many species. This may not always be positive, as it has also been argued that within-group cooperation in the context of intergroup conflict can lead to the escalation of that between-group conflict, at least in humans (Bornstein, 2003).

In order for cooperation (or any other trait) to spread via multi-level selection, between-group selection must outweigh within-group selection. In the social sciences and psychology this is analogous to “realistic conflict theory” a social sciences theory in which there is a similar tug-of-war between intra- and intergroup conflict (Coser, 1956; Tajfel and Turner, 1979; Gould, 1999; Bornstein, 2003). For between-group selection to outrun within-group selection between-group differences must be large (Bowles and Gintis, 2013). Genetic evidence shows that in early human groups between-group differences (at a genetic level) were high (Bowles and Gintis, 2013). Cultural differences might also have increased group differences if cooperation was passed on as a cultural rather than a genetic trait (Henrich, 2004; Bowles and Gintis, 2013). Cultural transmission can also increase the homogeneity of individuals within a group, which increases variance between groups (Henrich, 2004; Bowles and Gintis, 2013). Bowles (2009) modelled intergroup conflict and cooperation with rates of mortality from the Pleistocene and early Holocene and concluded that the level of mortality from intergroup conflict would have had substantial effects and allowed altruistic behaviours to spread, even if they had a high cost. Some argue that multi-level selection is only relevant when individuals' fitness is tightly tied to that of the group in that they cannot survive or reproduce outside of the group. However, whenever between-group selection outweighs within-group selection, multi-level selection is important, and this can be the case when individuals can survive and reproduce either in or out of a group. However, intergroup conflict may not provide strong enough selection on cooperation to outrun individual selection against cooperation, and differences between groups may not be large enough, due to migration and intergroup copulations, to allow multi-level selection to be a strong force in many species.

Multi-level selection for cooperation has also been suggested without the need for direct intergroup conflict. For example, when there is variation between groups and possible migration, when the altruistic trait is the type with the highest per capita fitness (Wilson, 1975), or faster reproducing individuals create larger groups that split and spread more often (Traulsen and Nowak, 2006). However, in this scenario, smaller groups and a larger number of groups favour co-operators; and to maintain cooperation in larger groups direct intergroup conflict may be required. Direct intergroup conflict may also exacerbate the variation between groups, strengthening the force of between group selection. As long as between-group competition is relatively larger than within-group competition – intergroup conflict can overcome within-group competition when group size is large, even when within-group relatedness is low (Reeve and Hölldobler, 2007).

Intergroup conflict is prevalent in both humans, and other species, and its behavioural consequences are not fully known. Within theory, and human literature, the focus has been on within-group cooperation and altruism, and in the social sciences this extends into practical modelling of conflict, and how to mitigate this conflict, from international warfare to managing conflict in the workplace. However, in animal species the focus has been on what occurs during the conflicts themselves, which I explore in the next section.

Intergroup conflict in animals

Many social species that live in relatively stable groups engage in some form of intergroup conflict, and these conflicts are potentially lethal. Intergroup conflict is seen across a wide taxonomic diversity of species, including many primates, such as chimpanzees (*Pan troglodytes*) (Watts and Mitani, 2000; Watts *et al.*, 2006; Boesch *et al.*, 2008), gorillas (*Gorilla beringei*) (Rosenbaum, Vecellio and Stoinski, 2016), baboons (*Papio cynocephalus*) (Markham, Alberts and Altmann, 2012), capuchins (*Cebus capucinus*) (Perry, 1996; Gros-Louis, Perry and Manson, 2003), and other monkey species (*Colobus guereza; Colobus polykomos*) (Korstjens, Nijssen and Noe, 2005; Harris, 2006); social carnivores like wolves (*Canis lupus*) (Cassidy *et al.*, 2015), lions (*Panthera leo*) (McComb, Packer and Pusey, 1994; Heinsohn and Packer, 1995), mongooses and meerkats (*Mungos mungo; Helogale parvula; Suricatta suricatta*) (Cant, Otali and Mwanguhya, 2002; Drewe, Madden and Pearce, 2009; Christensen *et al.*, 2016); cooperatively breeding fish (Bruintjes *et al.*, 2015; Hellmann and Hamilton, 2019); cooperatively breeding birds, including green wood-hoopoes (*Phoeniculus purpureus*) (Radford, 2011), pied babblers (*Turdoides bicolor*) (Golabek, Ridley and Radford, 2012), acorn woodpeckers (*Melanerpes formicivorus*)

(Pardo *et al.*, 2018) and brown jays (*Cyanocorax morio*) (Hale, Williams and Rabenold, 2003); and social insects such as ants (Adams, 1990; Whitehouse and Jaffe, 1996) and termites (Thorne, Breisch and Muscedere, 2003; Johns *et al.*, 2009). Chimpanzees even actively patrol their borders and seek out-group individuals to attack (Muller and Mitani, 2002).

Most of the research relating to intergroup conflict in animals focuses on what happens during intergroup conflicts, particularly which classes of individuals participate; when and where conflicts occur; and factors that affect the outcome of these conflicts. These questions are important in assessing both costs and benefits to individuals that take part in these conflicts; investigating why intergroup conflict occurs; and providing insights into how these conflicts might affect population dynamics via the traits of consistent winner, or loser, groups. Studies have been performed in a variety of taxonomic classes, but focus mainly on primates, and several common trends emerge from these studies.

One of the clearest patterns to emerge from the literature is that larger groups often win. Larger groups were more likely to attack, or respond, compared to smaller groups, in chimpanzees (Wilson, Hauser and Wrangham, 2001; Wilson, Britton and Franks, 2002), capuchins (Gros-Louis, Perry and Manson, 2003; Van Belle, 2015), baboons (Markham, Alberts and Altmann, 2012), vervet monkeys (*Chlorocebus pygerythrus*) (Cheney and Seyfarth, 1987), banded mongooses (Cant, Otali and Mwanguhya, 2002; Furrer *et al.*, 2011), wolves (Harrington and Mech, 1979; Cassidy *et al.*, 2015), lions (McComb, Packer and Pusey, 1994; Mosser and Packer, 2009), Ethiopian wolves (*Canis simensis*) (Sillero-Zubiri and Macdonald, 1998) and ants (Adams, 1990). This may be one of the reasons that many species can “count” or assess the size of another other group (e.g. McComb et al., 1994; Mosser & Packer, 2009). Being in a larger group reduces the individual cost of fighting. The cost to each individual is low in a group that outnumbers the rival group as mortality and injury are less likely in the larger group. In chimpanzees this has been called the “imbalance of power hypothesis” (Manson and Wrangham, 1991). However, groups can also suffer from a collective action problem, with individuals avoiding participation where possible, particularly in larger groups when individual participation is less important in determining the outcome of the conflict (Bonanni, Valsecchi and Natoli, 2010; Crofoot and Gilby, 2012; Koch *et al.*, 2016a). This collective action problem can be overcome in some situations, for example through high relatedness between group members or by-product mutualism (Willems and Van Schaik, 2015).

However, large groups do not always win intergroup conflicts. The relationship between group size and outcome can sometimes be overturned if the smaller group is at the core of their territory and has a “home field advantage”, as seen in Verraux’s sifakas (*Propithecus verreauxi*) (Koch *et al.*, 2016b), greater anis (*Crotophaga major*) (Strong, Sherman and Riehl, 2018), capuchins (Crofoot *et al.*, 2008; Crofoot and Gilby, 2012), green wood-hoopoes (Radford and Du Plessis, 2004) and ants (Adams, 1990). Other groups are simply more likely to fight in their core territories, including black and white colobus monkeys (*Colobus guereza*) (Harris, 2006) and banded mongooses (Furrer *et al.*, 2011), perhaps because this area holds a higher value to the group. It has also been suggested that altruism is particularly important in defence, rather than attack, in human conflicts (Rusch, 2013), suggesting that the location of a conflict is important in both humans and animals. In contrast, free-ranging dogs (*Canis familiaris*) were more likely to cooperate in defence at the edge of the territory (Pal, 2015), and Verraux’s sifakas stayed closer to other group members and were more cohesive at the edge of their territory (Benadi, Fichtel and Kappeler, 2008), suggesting that for some species the edge of the territory is equally important. The edge of the territory may also represent increased risk of conflict, as groups are more likely to encounter rivals in this area, which may influence behaviour. Despite this, location was not always important and in other studies group size was consistently more important in determining the outcome of a conflict (Korstjens, Nijssen and Noe, 2005; Cassidy *et al.*, 2015).

Responses to intergroup encounters also vary according to the identity of the rival group. Many species show differential responses to neighbours versus strangers (see Christensen & Radford (2018) for a review). Some species, including banded mongooses (Müller and Manser, 2007), respond more to neighbours than strangers, because neighbours represent a larger and more constant threat (Gill *et al.*, 2012). However, some species respond more to unfamiliar individuals or groups, for example, capped langurs (*Presbytis pileata*) (Stanford, 1991), Thomas langurs (*Presbytis thomasi*) (Wich and Sterck, 2007), Wied's black-tufted-ear marmosets (*Callithrix kuhli*) (French *et al.*, 1995), badgers (*Meles meles*) (Palphramand and White, 2007) and green wood-hoopoes (Radford, 2005, 2008b). Unfamiliar individuals might represent a different kind of threat (e.g. the displacement of a dominant) than rival neighbours. In contrast, neighbours might slowly erode territory and reduce resources. Resident groups may also have an advantage and win more encounters, (Radford and Du Plessis, 2004; Markham, Alberts and Altmann, 2012; Koch *et al.*, 2016b; Strong, Sherman and Riehl, 2018), or attack more, e.g. female hyenas (Boydston, Morelli and Holekamp, 2001), probably because resident groups face a larger cost to losing the encounter.

Who participates in intergroup conflict?

Generally, males seem to be more involved, and more aggressive, in intergroup conflicts than females in many species. Males participated more in intergroup conflict than females in studies of humans (Van Vugt, 2009; McDonald, Navarrete and Van Vugt, 2012), chimpanzees (Muller and Mitani, 2002; Wilson *et al.*, 2014), Japanese macaques (*Macaca fuscata*) (Saito *et al.*, 1998), capuchins (Perry, 1996; Meunier, Molina-Vila and Perry, 2012), bearded sakis (*Chiropotes sagulatus*) (Shaffer, 2013), Verraux's sifakas (Koch *et al.*, 2016a), black and white colobus (Harris, 2010), snub-nosed monkeys (*Rhinopithecus roxellana*) (Zhao and Tan, 2011) and free-ranging dogs (Pal, 2015). This may be because males experience a greater cost if a conflict is lost, and need to defend mates for reproductive opportunities. Males may also be the most powerful fighters, especially in species with a large sexual dimorphism in size. Large or experienced fighters may be more important than mere numbers, for example, in both wolves and black and white colobus monkeys the presence of older or larger males in the group compared to rival group males increased the likelihood of winning a conflict, even if the relative number of males was lower (Harris, 2010; Cassidy *et al.*, 2015). Males may also engage in conflict more than females as it is less energetically, or reproductively, costly to them, especially because they are often the larger sex and therefore have a smaller cost associated with fighting. For example, meerkat males, particularly heavier males, are more involved in repelling out-group meerkats as they face a smaller cost from weight loss than their lighter female counter-parts (Mares, Young and Clutton-Brock, 2012).

Females are also involved in intergroup encounters in some species, particularly when resource defence is important (Mehlman and Parkhill, 1988; Saito *et al.*, 1998). Female vervet monkeys fought more in order to defend food resources and intensively used areas (Arseneau-Robar *et al.*, 2017), and were more aggressive if they were in a small group (Cheney and Seyfarth, 1987). Females and males may defend different resources, for example female free-raging dogs were more defensive when feeding and close to the den, compared to males which were more defensive during mating scenarios and at the boundaries of the territory (Pal, 2015). Females may also defend against extra-group paternity, either to defend their mate choice, or to avoid potential future infanticide by in-group males, for example, black-tufted-ear marmosets were aggressive to out-group males who attempted to mate with them (Decanini and Macedo, 2008). In some species, females are generally more active and aggressive than males in intergroup conflict, and initiate intergroup conflicts, e.g. spotted hyenas (Boydston, Morelli and Holekamp, 2001).

In many primate species females are not involved in intergroup conflict, and are never seen to participate, but across other species both males and females regularly participate. Males and females may differ in their participation rates, and participate for different reasons, as outlined above. Interestingly, there is also evidence that both male and female individuals direct more aggression at same sex individuals during intergroup encounters (Stanford, 1991; Sillero-Zubiri and Macdonald, 1998; Boydston, Morelli and Holekamp, 2001; Lazaro-Perea, 2001; Radford, 2003; Decanini and Macedo, 2008), perhaps due to reproductive conflict. Preventing extra-group mating could be beneficial to both males and females, and aggression towards same sex individuals could also discourage migration between groups, and therefore reduce the likelihood of additional competition from migrants of the same sex.

Dominance rank within the group also affects participation in intergroup conflicts. In some cases dominants are more aggressive (Perry, 1996; Koch *et al.*, 2016a). Dominants are more likely to have offspring in the group, and offspring defence may be important, for example dominant male capuchin monkeys and male howler monkeys, that were likely to have fathered offspring that were present, were more likely to participate in intergroup encounters than other males (Van Belle *et al.*, 2014; Arseneau *et al.*, 2015). Higher ranking female vervets, and ring-tailed lemurs (*Lemur catta*) were also more likely to participate than lower ranking females when defending resources and territory (Nunn and Deaner, 2004; Arseneau-Robar *et al.*, 2017). High ranking females may invest in defence for offspring defence, or for defending resources and territory to increase future reproductive success. In other species subdominants are more aggressive – perhaps to defend their right to stay in the group, protect their future reproductive opportunities, or assess opportunities in rival groups (Lazaro-Perea, 2001; Cant, Otali and Mwanguhya, 2002; Hale, Williams and Rabenold, 2003; Radford, 2003). Interestingly free-ranging dogs with more affiliative partners in the group were more likely to participate, but high ranking individuals cooperated only when outnumbered, but not otherwise (Bonanni, Valsecchi and Natoli, 2010).

When and where do intergroup conflicts take place?

There are also trends in when and where intergroup encounters take place, which may give insights into what drives these conflicts. In chimpanzees, and many other species, intergroup encounters were more likely to take place further from the centre of their range (Wilson *et al.*, 2012). This is probably simply because groups are more likely to encounter each other in overlapping and boundary areas.

Mating seasons are a common time for more frequent intergroup encounters and aggression. Meerkat groups scent marked more in the breeding season, particularly when prospecting males were in the area (Jordan, Cherry and Manser, 2007), and wolves and pied babblers responded more to simulated conflict during breeding seasons (Harrington and Mech, 1979; Golabek, Ridley and Radford, 2012). Similarly, in banded mongooses intergroup encounters were seen more frequently when females were in oestrus, and when competition for mates was high (Cant, Otali and Mwanguhya, 2002; Thompson, Marshall, Vitikainen and Cant, 2017). The breeding season can also influence individual behaviour during intergroup conflicts. Male aggression is heightened during the mating season in Bonnet macaques (*Macaca radiata*) (Cooper, Aureli and Singh, 2004), black and white colobus monkeys (Fashing, 2001), and free-ranging domestic dogs (Pal, 2015). Additionally, capuchin monkey males were more likely to contribute during the mating season to increase their reputation, and those that participated more were favoured by females as mates (Arseneau *et al.*, 2015). Male mate defence is also seen directly in some primate species, including chimpanzees (Manson and Wrangham, 1991), capped langurs (Stanford, 1991), Japanese macaques (Saito *et al.*, 1998), Tibetan macaques (*Macaca thibetana*) (Zhao, 1997) and gorillas (Sicotte, 1993; Robbins and Sawyer, 2007). Reproductive conflict and mate defence are probably the causes of this increased frequency of intergroup conflicts, and increased male aggression, in mating seasons.

Intergroup encounters may also provide a way of gaining information about potential mates in other groups, or migration opportunities (Hale, Williams and Rabenold, 2003). Participation in encounters may then help individuals to integrate into a new group, as seen in immigrant females in vervet monkeys, immigrant females that participated in intergroup conflicts were less likely to receive aggression from other group members (Hauser, Cheney and Seyfarth, 1986). This has also been suggested as the reason that common marmoset subdominant females participate in fights, to assess neighbouring groups and potential breeding vacancies (Lazaro-Perea, 2001).

Intergroup conflict may also occur over food resources. Many intergroup conflicts have been linked to the value of food resources available (Mehlman and Parkhill, 1988; Lawes and Henzi, 1995; Saito *et al.*, 1998; Harris, 2006, 2010; Brown, 2014). Sometimes food resources increase the frequency of intergroup encounters, by increasing proximity of neighbouring groups, but not necessarily increasing conflict between those groups, so food resources *per se* may not drive conflict in these species (Robbins and Sawyer, 2007; Wilson *et al.*, 2012). Food conflict could be particularly important in areas of high population density, or times of scarcity for some species, but limited work has been done outside primates to assess why intergroup encounters are occurring.

What are the consequences of intergroup conflict?

Impact on social behaviour and relationships

The consequences of intergroup conflict for behaviour are less well studied than other aspects of intergroup conflict, but might help to reveal the deeper evolutionary causes and effects of intergroup encounters. Building on evolutionary theory in humans – empirical studies in animals have suggested that after intergroup conflicts there should be an increase in social cohesion or cooperation within a group. Theoretical outcomes of post-conflict behaviour within-groups have been extensively reviewed in Radford, Majolo & Aureli (2016), and some empirical studies have also addressed the immediate behavioural consequences of intergroup encounters, most notably work on green wood-hoopoes (see Table 1.1 for a summary of previous studies investigating post intergroup conflict behaviour).

Several experimental and observational studies were performed on green wood-hoopoes, and provided the first experimental evidence that intragroup affiliation, in this case allo-preening, increased following intergroup conflicts (Radford, 2008b). Allo-preening was more frequent in groups which had the highest rates of intergroup conflict, especially after losing (Radford, 2008a), and in response to strangers rather than neighbours (Radford, 2008b). This was caused by an increase in allo-preening from the dominant pair directed at subordinate helpers, which is suggested to help with social cohesion or reward subordinates for participating in these conflicts (Radford, 2008b). Additionally, allo-preening increased in areas where conflicts were more likely to occur (perhaps in preparation for conflict) (Radford, 2011).

Evidence for a similar pattern has also been found in other experimental studies on cooperative fish, (Bruintjes *et al.*, 2015), dwarf mongooses (Morris-Drake *et al.*, 2019), and primate species (Payne, Hallam, Lawes and Henzi, 2003). These studies reveal that in some cases intergroup encounters might lead to increasing intragroup affiliation and social cohesion. This suggests that the multi-level selection theory of cooperation (that cooperation would increase in the context of intergroup encounters) might be occurring in the animal kingdom.

Some studies have also looked at the impact of intergroup conflict on within-group aggression. Here the picture is more mixed: some studies reveal increased aggression within the group (Cooper, Aureli and Singh, 2004; Bruintjes *et al.*, 2015);

and others found no change in aggressive interactions (Nunn and Deaner, 2004; Bruintjes *et al.*, 2015; Morris-Drake *et al.*, 2019). Increased aggression has been interpreted as a release of tension in the group (Polizzi di Sorrentino *et al.*, 2012). Within-group aggression that occured during intergroup encounters, rather than after they have finished, has also been suggested to be a form of punishment of non-participation (Arseneau-Robar *et al.*, 2016). There is not yet any evidence that intergroup conflict leads to reduced aggression, but this could be interpreted as a sign of increased social cohesion, as increased affiliation has been.

The evidence for an impact of intergroup conflict on other social, or collective behaviours, is sparse. However, a steeper dominance hierarchy was detected when capuchin monkeys could see a rival group (Polizzi di Sorrentino *et al.*, 2012), and dwarf mongooses showed increased sentinel behaviour and a smaller nearest neighbour distance after exposure to outgroup faeces and calls, compared to control presentations (Morris-Drake *et al.*, 2019). There may be many more subtle behavioural consequences of intergroup conflict, and these may vary across species.

Table 1.1 – Studies assessing the impact of intergroup encounters on social behaviour, and the timescale on which responses were measured. When behaviour was recorded was coded as “During” the presentation of stimuli/presence of rival group; “Before” the presentation of stimuli/presence of rival group; and “After” the presentation of stimuli/presence of rival group; when behaviours were compared between before and after a (simulated) encounter it was coded as “Before-After”; whereas when behaviour was only recorded afterwards it was coded as “After”. When behaviours were only recorded afterwards they were usually compared to controls. Social behaviours were coded as follows: Aff = affiliation including grooming or allo-preening; Agg = aggression between individuals within the focal group; Def = defensive behaviours including aggression towards the intruders; SM = scent marking; DH = dominance hierarchy; Vig = vigilance behaviour; NN = nearest neighbour distance. + and bold typeface indicates an increase in the behaviour; behaviours in regular typeface are those which were studied but not affected by intergroup exposure. * This is an anecdotal record of grooming increase rather than empirical data

Species (Study)	Observation or experiment?	Captive or wild?	Timescale	When behaviour was recorded	Behaviour
Tufted capuchin monkeys, *Cebus paella* (Polizzi di Sorrentino *et al.*, 2012)	Exp	Captive	10 minutes	During	**Agg+** Aff
			Ad-hoc through study period	During	**Def+** **DH+**
Cichlid fish, *Neolamprologus pulcher* (Bruintjes *et al.*, 2015)	Exp	Captive	10 minutes	Before-After	**Aff+** Agg
			10 minutes	During	**Def+**
Green wood-hoopoe, *Phoeniculus purpureus* (Radford, 2008b)	Exp	Wild	1 hour	Before-After	**Aff+**
Dwarf mongooses, *Helogale parvula* (Morris-Drake *et al.*, 2019)	Exp	Wild	1 hour	After	**NN+** **SB+**
			Until 50% start foraging	After	**Aff+** Agg
Samango monkeys, *Cercopithecus mitis erythrarchus* (Payne, Hallam, Lawes and Henzi, 2003)	Obs	Wild	10 minutes	After	**Aff+**
Bonnet macaques, *Macaca radiata* (Cooper, Aureli and Singh, 2004)	Obs	Wild	Variable	Before-During-After	**Agg+**

Ring-tailed lemurs, *Lemur catta* (Nunn and Deaner, 2004)	Obs	Semi-free-ranging	30 minutes	Before-After	Aff Agg
			Length of encounter	During	**Def+**
Green wood-hoopoe, *Phoeniculus purpureus* (Radford, 2008a)	Obs	Wild	1 hour	Before-After	**Aff+**
Green wood-hoopoe, *Phoeniculus purpureus* (Radford and Fawcett, 2014)	Obs	Wild	1 day	After	**Aff+**
Blue monkeys, *Cercopithecus mitis* (Cords, 2002)	Obs	Wild	-	After	***Aff+**

Individuals’ social relationships may be affected differently by intergroup conflicts according to the individual’s characteristics and traits. Several studies have found that dominants and subordinates react differently to intergroup conflict in terms of their post-conflict behaviour (Radford, 2008a, 2008b, 2011; Bruintjes *et al.*, 2015; Hellmann and Hamilton, 2019). In wood-hoopoes changes to post-conflict affiliation were driven by increased allo-preening of the dominant pair towards their subordinate helpers (Radford, 2008a, 2008b, 2011). In contrast, in cichlid fish, the increase in post-conflict affiliation was driven by increased affiliation by subordinates (Bruintjes *et al.*, 2015). Additionally, aggression between breeding pairs was reduced but subordinate aggression increased in the presence of neighbours (Hellmann and Hamilton, 2019).

Males and females may also respond differently to intergroup encounters. In many cases, there is a clear conflict of interest between the sexes over participation in conflicts. A meta-analysis by Kitchen and Beehner (2007) found that sex differences in participation were explained by food and mate defence, but that within-sex differences were explained by rank and reproductive success, in primates. This may influence individuals’ post-conflict behaviour, for example, male vervet monkeys were aggressive to own-group females during intergroup encounters to stop them instigating fights, and to punish their involvement in fights (Arseneau-Robar *et al.*, 2018). Male vervets with offspring were most likely to do this, especially when wounded (Arseneau-Robar *et al.*, 2018). Female vervets also punished males, but for not participating, and rewarded those who did (Arseneau-Robar *et al.*, 2016). This impacted future male behaviour, with both increasing male participation in future intergroup conflicts (Arseneau-Robar *et al.*, 2016). Bonnet macaques were also aggressive to own group females after intergroup conflicts (Cooper, Aureli and

Singh, 2004), and a meta-analysis of primates showed that increased grooming network density was correlated with increased intensity of intergroup encounters for females, but not for males (Majolo, de Bortoli Vizioli and Lehmann, 2016), suggesting that this relationship may be more widespread.

One major gap in the research surrounding behavioural consequences of intergroup conflict is the impact of these conflicts on behaviour into the longer term. Some recent work has investigated the “longer-term” consequences of intergroup conflicts in green wood-hoopoes, and showed that groups involved in conflicts returned to the zone of conflict to roost in the evening, and were more likely to allo-preen at the roost than if they were not involved in a conflict that morning (Radford and Fawcett, 2014). This study provides evidence that intragroup affiliation increases after conflicts in the longer term, as this appeared to be social rather than stress-relieving preening. However, this study is still very short term, and longer term effects of intergroup conflicts over multiple days, weeks, months and even years, should be explored.

Initial short-term changes in behaviour after intergroup encounters may be caused by physiological mechanisms, including changes in hormone levels. For example, both oxytocin and cortisol levels have been seen to change in wild chimpanzees during intergroup conflict scenarios (Samuni *et al.*, 2017, 2019). Intergroup conflict has also been seen to affect hormone levels in other species, although this work is currently limited to primates (Brockman *et al.*, 1998; Ross, French and Patera, 2004; Ross and French, 2011; Schoof and Jack, 2013; Jaeggi, Trumble and Brown, 2018). These hormonal changes are likely to lead to short-term behavioural changes, as allo-grooming or -preening have often been linked to hormone levels (Dunbar, 2010; Crockford, Deschner and Wittig, 2018), and in meerkats to increased levels of cooperative behaviour (Madden and Clutton-Brock, 2011) but they may also impact behaviour into the longer term. Hormone levels decline, but can persist into the days and weeks after an event, as seen in banded mongoose glucocorticoid levels between breeding events (Sanderson *et al.*, 2014). These hormonal changes could therefore directly mediate change of behaviour into the longer term. Additionally hormonal changes can affect social relationships, via allo-grooming, preening and other affiliative behaviours, and these changes could persist into the longer term through feedback loops of social behaviour (or other adaptive feedback loops (Sih *et al.*, 2015)), perhaps forming or breaking reciprocal relationships that last into the longer term after hormonal (or other physiological) impacts of intergroup encounters have dissipated. However, this is an area of limited research, and the mechanisms of potential behavioural change into the longer term are not yet known.

Impact on movement, home range and leadership

Some studies in primates have found longer term consequences of intergroup encounters in terms of movement behaviour and range use. Baboons were less likely to use areas in the three months after a conflict was lost in that area, than in the three months before (Markham, Alberts and Altmann, 2012). Similarly, Verraux’s sifaka were less likely to use an area in the month after losing an intergroup conflict (Koch *et al.*, 2016b). In the shorter term, capuchin monkeys moved faster, further and had larger displacements on the day that they lost a conflict, and were more likely to change sleeping sites (Crofoot, 2013). In contrast to this, dwarf mongooses moved more slowly and shorter distances after being presented with faeces from a rival group (Christensen *et al.*, 2016). These changes in space use could be important for group dynamics, and may push losing groups into lower quality areas of their territory, or cause energetic costs (Crofoot, 2013). In an extreme case, a chimpanzee group in Uganda expanded their territory into another group's range after a series of lethal intergroup attacks (Mitani, Watts and Amsler, 2009). Combining this type of study looking at movement and range use with detailed behavioural observations before and after intergroup encounters could provide a greater insight into what the consequences of intergroup encounters are for both winning and losing groups.

Theoretical work suggests that leadership is also affected by intergroup conflict. It has been suggested that leadership within a group becomes increasingly despotic, with fewer individuals contributing to leading in times of intergroup conflict (Van Vugt, Hogan and Kaiser, 2008; Smith *et al.*, 2016). This may be because leadership could help to overcome the collective action problem of participating in intergroup conflict (Gavrilets & Fortunato, 2014). Leadership allows individuals to control movement, and therefore potentially engagement in intergroup conflict, which they may use to their own advantage to maximise their fitness, potentially to the cost of other group members (Petit & Bon, 2010). Leadership in the context of intergroup conflict is another gap in our knowledge about animal intergroup conflict. Empirical research has investigated the impact of external conflict on human leadership during warfare (Campbell, Hannah, & Matthews, 2010), and with humans in the lab (Gleibs & Haslam, 2016), but little empirical research has been done in animals, or under natural conditions. Leadership, or lack thereof, in animal intergroup conflict, may have a major impact on the outcome of conflicts, and the behavioural and fitness consequences of these conflicts.

In summary, longer-term studies of post-conflict behaviour, particularly social behaviour are still needed. Longer-term studies will extend the timeframes from minutes and hours post-conflict to weeks, months or even years, helping to bridge the gap from genetic evolutionary models to empirical studies of behaviour. Additionally, disentangling the responses of individuals from their overall group response has not yet been fully explored. Studying individual differences may highlight the costs and benefits of intergroup conflict to different sex or age classes, and the consequences this might have for reproductive success and survival. Here we aim to tackle these questions using an ideally suited cooperatively breeding mammal, the banded mongoose.

Study system: banded mongoose

Banded mongooses (*Mungos mungo*) are a species of small (< 2 kg), diurnal, cooperative mammals in the *Herpestidae* family. They live across sub-Saharan Africa, in savannah, forest and open grassland habitats, but have been extensively studied on the Mweya Peninsula in Uganda (Cant *et al.*, 2016). Banded mongooses are generalists and feed on a variety of invertebrates, reptiles, birds and small mammals, and their foraging is cohesive, but not cooperative (Rood, 1975). Banded mongooses live in stable social groups made up of males and females, of between 10 and 30 individuals, and their offspring (Cant, 2000). These groups are male biased across age classes (Cant, Vitikainen and Nichols, 2013; Cant *et al.*, 2016).

In each breeding attempt multiple male and female banded mongooses breed (Cant, Vitikainen and Nichols, 2013), marking them out from their close relatives the dwarf mongoose and meerkat which generally have a single dominant breeding pair. Females breed from around one year old (Cant *et al.*, 2016), and 83% of females in a group conceive during each breeding attempt (range = 1-12 females (Cant, 2000)). Females synchronise pregnancies, mating within the same week, and giving birth on the same day in 64% of cases (Cant, 2000; Hodge, Bell and Cant, 2011). This synchronisation of births protects females from the infanticide of their litter, as females giving birth before other females in the group often lose their whole litter (Hodge, Bell and Cant, 2011; Cant *et al.*, 2014). Pups born to females giving birth after other females suffer from increased competition, as early, larger pups are more likely to survive and grow, further increasing birth synchrony (Hodge, Bell and Cant, 2011). However, older more dominant females do benefit from subordinate females breeding, as pup survival is higher when the number of females giving birth is higher (Cant, 2000). Male reproductive skew is much higher, with breeding limited to older individuals, 85% of paternity can be attributed to the 3 oldest males in a group (Cant *et al.*, 2016). Males "mate-guard" females during oestrus to defend their paternity from other males (Cant, 2000).

Individuals rarely disperse voluntarily from their social group. Only 12% of females and 13% of males disperse from their natal group, mostly after enforced mass evictions (Cant, Vitikainen and Nichols, 2013; Cant *et al.*, 2016; Thompson *et al.*, 2016; Thompson, Marshall, Vitikainen, Young, *et al.*, 2017). Mongooses that are permanently evicted tend to leave the study area, and it is not known whether they survive, or how far they disperse successfully. Occasionally, evicted individuals form new packs or invade other packs in the study area, but this is rare (Thompson, 2016). Banded mongooses therefore have a highly genetically structured population with large differences between groups (Nichols, Jordan, *et al.*, 2012). Individuals in a group are closely related to one another, and inbred, especially groups formed longer ago (Nichols, Jordan, *et al.*, 2012; Nichols *et al.*, 2014). However, mongooses do attempt to reduce the risks of inbreeding both within the group, and through extra-group mating, according to the current inbreeding risk (Cant, Otali and Mwanguhya, 2002; Nichols, Cant and Sanderson, 2015; Sanderson *et al.*, 2015).

Cooperative breeding

Banded mongooses are cooperative breeders, with pups from multiple females raised as a communal litter. Individuals other than the parents help in two main ways: babysitting litters of pups at the den, defending them from predators and rival groups for the first four weeks after birth; and one-to-one “escorting” of pups by helpers, which includes defending and feeding pups, and social learning of foraging until nutritional independence (Cant *et al.*, 2016). Mongoose pup and escort pairs can recognise each other individually (Müller and Manser, 2008; Cant, Vitikainen and Nichols, 2013), and competition between pups for escorts can be intense (Gilchrist, 2008; Hodge *et al.*, 2009). Research in our study population has shown that escorts have a large influence on the lives of pups, including on their foraging strategies (Müller and Cant, 2010), diet (Sheppard *et al.*, 2018), reproductive success (Hodge, 2005; Vitikainen *et al.*, 2019), and survival (Cant, 2003; Hodge, 2005; Cant *et al.*, 2016). Helping may also be a form of group augmentation to reduce mortality and infanticide risk from intergroup conflict (Kokko, Johnstone and Clutton-Brock, 2001; Cant, Vitikainen and Nichols, 2013).

All age and sex classes contribute to babysitting and escorting (Cant *et al.*, 2016), but young males are most likely to babysit and escort pups, and helping is generally not linked to relatedness between individuals (Cant, Vitikainen and Nichols, 2013; Vitikainen *et al.*, 2017). Helper sex is also more important in pup-escort association than relatedness, with males preferentially escorting male pups, and females escorting female pups (Vitikainen *et al.*, 2017).

Helping behaviour is influenced by the environment, as well as by the sex and age of individual helpers. When food is scarce young females help less than other mongooses, due to the high cost of helping, which can lead to weight loss and reduction in growth that is associated with a reduction in female survival and future reproductive success (Nichols, Amos, *et al.*, 2012). In contrast, adult males can afford to maintain helping behaviour, even when conditions are variable, as their body condition is not associated with reproductive success (Nichols, Amos, *et al.*, 2012; Marshall *et al.*, 2016).

Intergroup conflict

Mongoose territories are largely overlapping. On average around 40%, and up to 81%, of the territory is shared with another group (Jordan *et al.*, 2010). Banded mongooses experience violent, and sometimes lethal, intergroup encounters over these territories and resources (Cant, Vitikainen and Nichols, 2013; Cant *et al.*, 2016). Banded mongooses in the study site almost exclusively engage in physically violent inter-group interactions, with very few interactions between groups that are neutral, peaceful, or involve only signalling between groups with no physical interaction, e.g. war dances, or vocal defence. Groups respond to sighting a rival group by standing alert and giving a specific screeching call known as a ‘war cry’ (Cant *et al.*, 2016), after which group members congregate and stand alert. Small groups typically flee from larger groups, with larger groups sometimes giving chase (Cant, Otali and Mwanguhya, 2002; Furrer *et al.*, 2011). If groups are more evenly matched in size then group members bunch together and approach in ‘battle lines’. Fighting can be highly aggressive, involving biting and scratching, and sometimes individuals are held down and attacked by multiple rival group members. Intergroup fights can result in serious injury and sometimes death (Cant, Otali and Mwanguhya, 2002; Nichols, Cant and Sanderson, 2015; Thompson, Marshall, Vitikainen and Cant, 2017).

Conflicts occur frequently (mean encounter rate per group = 0.8 per week (non-oestrus periods) to 2.9 per week (group oestrus); data from 12 groups (Cant, Otali and Mwanguhya, 2002)). The frequency of intergroup conflict is higher when a group is in oestrus, and both males and oestrus females have been seen to instigate fights (Cant, Otali and Mwanguhya, 2002; Cant *et al.*, 2016). Extra-group mating is also seen during intergroup conflicts, in which males may seek to increase paternity and females to avoid the risks of inbreeding (Cant, Otali and Mwanguhya, 2002).

Mongoose groups react more strongly to neighbouring groups (Müller and Manser, 2007), because neighbours are a greater threat than strangers, due to intensive competition for territory, resources, and paternity. Mortality rates during conflict are high (accounting for 20% of all adult deaths for which the cause of death is known (Nichols, Cant and Sanderson, 2015)), and intergroup infanticide is common in this system (Müller and Bell, 2009; Cant, Vitikainen and Nichols, 2013). Mongooses are more likely to enter fights in the core of their territory (Furrer *et al.*, 2011), potentially as this is where dens, and therefore vulnerable pups, are likely to be. Groups of fewer than 10 adults are repeatedly attacked by rival groups, and rarely raise litters, leading to group attrition (Cant *et al.*, 2016).

Study site and methods

Our study population is on the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0^{o}12'S, 29^{o}54'E). The population has been studied continuously from 1995 as part of the Banded Mongoose Research Project, with previous research started in the 1970s (Rood, 1975; Cant *et al.*, 2016). Mweya is a 5 km^2 heart-shaped peninsula, jutting out into Lake Edward, with a narrow isthmus connecting it to the mainland and the rest of Queen Elizabeth National Park. The habitat is grassland, with Euphorbia trees (*Euphorbia candelabrum*) and thickets of scrubby bushes including *Capparis tomentosa* and *Azima tetracantha* (Cant, Vitikainen and Nichols, 2013). In recent years the peninsula has also been invaded by *Dichrostachys cinerea* which has led to the area becoming increasingly scrubby and less open. There is an equatorial climate, with steady temperatures and day length, and rain of between 800-900 mm annually, with two dry seasons in January-February and June-July (Cant, 2000).

The banded mongooses on Mweya are at a relatively high density of 18 individuals per km^2 (Cant, Vitikainen and Nichols, 2013). Mweya also contains a large number of other charismatic mammal species, including African elephants (*Loxodonta africana)*, hippopotamus (*Hippopotamus amphibius*), Uganda kob (*Kobus kob thomasi*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*), warthog (*Phacochoerus africanus*), lion (*Panthera leo*), leopard (*Panthera pardus*), and spotted hyena (*Crocuta crocuta*), as well as many species of bird and reptile. Some mongoose groups remove ticks and other parasites from warthogs – a rare mammal-mammal mutualism (Cant *et al.*, 2016).

Figure 1.1 – Maps 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. Reproduced with permission from (Thompson, 2016).

The Banded Mongoose Research Project has collected detailed life history and behavioural data for over 3000 individuals in the last 25 years. During the study period, the population was made up of around 200 individuals in 10-12 groups. Five of these groups were highly habituated to human presence, and could be approached and followed for behavioural observations. The long term project involves life history, behavioural, and genetic and physiological data collection, and mongooses in the population are captured once every 3-6 months to maintain individual identification marks and take tissue and blood samples for analysis. Individuals are trapped using box traps (67 x 23 x 23 cm; Tomahawk Live Trap Co., Tomahawk, WI, USA). They are then anaesthetised using isoflurane whilst samples and measurements are taken (for further details of the trapping procedure, see (Jordan *et al.*, 2010)). Pedigree analysis of all pups is undertaken using tail tip tissue samples for DNA analysis, to assign parentage and relatedness (further details in (Sanderson *et* *al.*, 2015)). All mongooses in the study population are individually marked using unique hair-shave patterns and are habituated to close observation from 2-4 metres. One to two mongooses in each group are fitted with a radio collar weighing 26-30 g (Sirtrack Ltd, Havelock North, New Zealand) with 20-cm whip antenna (Biotrack Ltd, Dorset, UK) to allow the groups to be located. One to two additional individuals are fitted with a GPS collar weighing 24-41 g (Gipsy4 and Gipsy5, Technosmart, Italy), to allow group movements to be recorded. Groups are located every 1 to 3 days for behavioural and life history observations, which are recorded using computer tablets (via the Mongoose2000 app (Marshall *et al.*, 2018), on Samsung Galaxy Note 10.1 tablets). Mongooses are located using radio collars at their den at around 7am, and followed during their morning foraging session. They rest at a den, or other resting site, in the middle of the day, and are found again at around 4pm and observed until sunset when they return to the den for the night.

Aims and outline of the thesis

This thesis uses the banded mongoose as a model system to investigate the effects of intergroup conflict on animal groups. Specifically, this thesis addresses (1) the behavioural consequences of intergroup conflict; (2) the effect of intergroup conflict on social relationships between banded mongooses; (3) the effect of intergroup conflict on movement patterns and home range use; (4) the impact of risk of intergroup conflict on leadership in banded mongoose groups. I explain more in the following:

In **Chapter 2** I investigate the impacts of simulated intergroup conflicts on group behaviour of banded mongooses. Previous studies have only investigated the minutes and hours after a conflict, so here I extended this to two days after a simulated conflict. I investigate changes in collective alarm calling and scent marking, and social grooming and aggressive interactions within the group before and after exposure to simulated intergroup conflict and control presentations.

In **Chapter 3** I investigate the effect of simulated intergroup conflict on social relationships. Group-level measures ignore differences between individuals, and therefore potentially different responses to conflict. I used social network analysis to investigate post-conflict changes to grooming and aggressive social relationships between males and females of different ages.

In **Chapter 4** I explore the effect of simulated intergroup conflict on the movement patterns and home range use of banded mongooses. Previous studies have found differing responses in movement patterns. Here I investigate the effect of simulated intergroup conflict on movement path characteristics, time spent in core areas, and path characteristics in different areas of the home range.

In **Chapter 5** I use a combination of observations and experiments, to explore where successful leadership takes place, and by which individuals, and to investigate if there is a difference in mongoose groups' responses to leadership bids by males and females, between areas of risk and areas of safety. Leadership is expected to increase, and become more despotic at times, or in places, of risk and differences between the sexes in terms of costs and benefits of intergroup encounters may also influence this.

In **Chapter 6** I provide an overall summary and synthesis of this research.

Chapter 2:

Effects of simulated intergroup conflict on collective behaviour do not persist into the long-term in banded mongooses

Abstract

Intergroup conflict is widespread in nature, and is proposed to have strong impacts on the evolution of social behaviour. Previous work in a number of species has shown that real or simulated intergroup conflict leads to increased intragroup affiliative behaviour, which has been hypothesised to improve future success in conflicts with other groups. However, most studies examine behavioural changes over short time periods (minutes and hours after conflict), and the consequences of intergroup conflict for intragroup dynamics over the longer term is uncertain. We simulated territorial intrusions in a wild population of cooperatively breeding banded mongooses (*Mungos mungo*) and measured social behaviour before, during, and after these intrusions, over a five day period. Banded mongooses responded strongly to simulated intrusions during the presentation of stimuli, and showed lower rates of grooming in the hour afterwards. There was also a short-lived reduction in aggression after stimuli were presented. However, in the subsequent two days the rates of grooming and aggression recovered to the levels observed in the pre-experimental period. There was no evidence that other collective behaviours, scent marking and alarm calling, were affected by simulated intergroup conflicts. Our results suggest that there is only a fleeting impact of simulated encounters on social behaviour, possibly because encounters with other groups are frequent in this system. Behavioural responses to intergroup conflict are complex and dynamic, highlighting the need for new theoretical approaches to explain observed variation in the pattern and intensity of group conflict.

Introduction

Conflict between groups over scarce resources, often referred to as intergroup conflict, can have a strong influence on fitness costs and benefits of social behaviour (Van Belle *et al.*, 2014; Rusch and Gavrilets, 2016; Thompson, Marshall, Vitikainen and Cant, 2017). Conflicts between groups can lead to individual costs in terms of mortality or injury (Manson and Wrangham, 1991; Plowes and Adams, 2005; Rosenbaum, Vecellio and Stoinski, 2016; Thompson, Marshall, Vitikainen and Cant, 2017). Conflicts can also bring individual and group benefits, for example through increased access to resources or mating opportunities (Cant, Otali and Mwanguhya, 2002; Harris, 2010; Arseneau *et al.*, 2015), or via group augmentation effects, because larger groups are often more successful during intergroup fights, and can therefore acquire or defend valuable resources or territories (Cheney and Seyfarth, 1987; Sillero-Zubiri and Macdonald, 1998; Clutton-Brock, Gaynor, *et al.*, 1999; Clutton-Brock, O'Riain, *et al.*, 1999; Gros-Louis, Perry and Manson, 2003; Markham, Alberts and Altmann, 2012; Cassidy *et al.*, 2015). Population genetic models developed to explain human cooperation suggest that high rates of intergroup conflict among ancestral human bands may have favoured the evolution of large-scale human cooperation, even among non-relatives (Henrich, 2004; Bowles, 2006, 2009; Choi and Bowles, 2007; Bowles and Gintis, 2013); but see (Fry, 2013). In these models, groups with a higher frequency of brave, cooperative, warrior-like individuals are more successful at acquiring resources or territory, and hence produce more offspring (Henrich, 2004; Bowles, 2006, 2009; Choi and Bowles, 2007; Bowles and Gintis, 2013; Rusch and Gavrilets, 2016). The fitness benefits to individuals that cooperate in between-group competition can outweigh the individual fitness costs of altruism within groups, allowing alleles for cooperation and intergroup hostility to spread in the population via between-group selection (Choi and Bowles, 2007; Lehmann, 2011).

Intergroup conflicts are widespread, costly, and their causes and consequences vary. Such conflicts are often seen in animal social groups; for example in primates including chimpanzees (*Pan troglodytes*) (Watts and Mitani, 2000; Watts *et al.*, 2006; Boesch *et al.*, 2008), gorillas (*Gorilla beringei*) (Rosenbaum, Vecellio and Stoinski, 2016), baboons (*Papio cynocephalus*) (Markham, Alberts and Altmann, 2012), capuchins (*Cebus capucinus*) (Perry, 1996; Gros-Louis, Perry and Manson, 2003), and other monkey species (*Colobus guereza; Colobus polykomos*) (Korstjens, Nijssen and Noe, 2005; Harris, 2006); in social carnivores like lions (*Panthera leo*) (McComb, Packer and Pusey, 1994; Mosser and Packer, 2009), hyenas (*Crocuta crocuta*) (Boydston, Morelli and Holekamp, 2001), wolves (*Canis lupus*) (Cassidy *et al.*, 2015), and banded mongooses (*Mungos mungo*) (Cant, Otali and Mwanguhya, 2002; Thompson, Marshall, Vitikainen and Cant, 2017); in cooperatively breeding birds, including green wood-hoopoes (*Phoeniculus purpureus*) (Radford, 2011) and pied babblers (*Turdoides bicolor*) (Golabek, Ridley and Radford, 2012); and in social insects such as ants (Adams, 1990; Whitehouse and Jaffe, 1996) and termites (Thorne, Breisch and Muscedere, 2003; Johns *et al.*, 2009). Mortality rates from intergroup conflicts in chimpanzee societies are comparable to those of subsistence human hunter-gatherer and farmer societies (Wrangham, Wilson and Muller, 2006), suggesting that the theoretical models developed to explain human cooperation could apply to some non-human animals (Wrangham, Wilson and Muller, 2006; Cant *et al.*, 2016). Studies of intergroup conflict in animal systems have focused on the outcomes of conflicts (Wilson, Britton and Franks, 2002; Furrer *et al.*, 2011; Markham, Alberts and Altmann, 2012; Koch *et al.*, 2016b); when, where and why these conflicts occur (e.g. Manson and Wrangham, 1991; Cooper, Aureli and Singh, 2004; Harris, 2007; Wilson *et al.*, 2012; Pal, 2015); and how different classes of individuals contribute to conflicts (Boydston, Morelli and Holekamp, 2001; Muller and Mitani, 2002; Kitchen and Beehner, 2007; Mares, Young and Clutton-Brock, 2012; Meunier, Molina-Vila and Perry, 2012; Van Belle *et al.*, 2014; Arseneau *et al.*, 2015; Van Belle and Scarry, 2015). There is also much interest in the behavioural consequences of intergroup conflict (Radford, Majolo and Aureli, 2016). Studies on baboons, capuchins and dwarf mongooses (*Helogale parvula*) have shown changes to movement patterns after intergroup conflicts, including increased border patrolling and territorial expansion (Markham, Alberts and Altmann, 2012; Crofoot, 2013; Christensen *et al.*, 2016). In addition, comparative studies have suggested that grooming systems in different primate species can be explained by different levels of intergroup competition (Cheney, 1992; Majolo, de Bortoli Vizioli and Lehmann, 2016).

A prediction that is usually attributed to theoretical models is that groups that are under attack should pull together and become more cohesive or affiliative (e.g. (Bruintjes *et al.*, 2015)). This prediction has been tested experimentally in green wood-hoopoes (Radford, 2008b, 2008a, 2011), capuchin monkeys (Polizzi di Sorrentino *et al.*, 2012), dwarf mongooses (Morris-Drake *et al.*, 2019) and cichlid fish (*Neolamprologus pulcher*) (Bruintjes *et al.*, 2015). In wood-hoopoes, dwarf mongooses, and cichlids, within-group affiliation increased after simulated encounters with other groups. By contrast, in capuchins, simulated intergroup encounters led to an increase in within-group aggression. Observational studies have also found contrasting evidence of the effect of intergroup conflict on within-group behaviour (grooming or aggression)

(Cords, 2002; Payne, Hallam, Lawes and Henzi, 2003; Cooper, Aureli and Singh, 2004). One challenge when testing theoretical predictions is that existing population genetic models examine the impact of intergroup conflict on the spread of alleles for cooperation on an evolutionary time scale, but do not explicitly predict how groups should respond on a short-term behavioural time scale. With the notable exception of studies of primate ranging behaviour (Markham, Alberts and Altmann, 2012), previous studies have examined only the short-term impacts of intergroup conflict on within-group social behaviour (i.e. in the minutes and hours after an interaction; Table 1.1). It is unknown whether intergroup conflict has longer term impacts on social cohesion and collective behaviour (i.e. over days or weeks). Addressing this gap between theory and data is important to assess the ability of genetic models to predict short-term, plastic behaviours.

Here we test the hypothesis that intergroup conflict has lasting impacts on within-group behaviour using simulated intergroup encounters in wild banded mongooses (*Mungos mungo)*. Banded mongooses are small (< 2 kg) diurnal herpestids that live in stable multi-male, multi-female groups of between 10 and 30 individuals. Multiple females give birth synchronously in each breeding attempt, and offspring are reared cooperatively by the whole group (Hodge, Bell and Cant, 2011). Banded mongooses are ideal for this study because groups are highly territorial and engage in frequent aggressive interactions, with substantial costs to adults and offspring (Thompson, Marshall, Vitikainen and Cant, 2017). Following previous studies in primates and other social vertebrates we use grooming and aggression to measure group social cohesion (Table 1.1), and predict that simulated encounters will lead to increased grooming (affiliative behaviour) and a suppression of within-group aggression, to aid group cohesion. We also measure scent marking and alarm calling, two other potentially affiliative collective behaviours which benefit all group members, which we predict will similarly increase after simulated intrusions. Unlike studies that compare behavioural responses to intruder stimuli versus controls, on the day of presentations, in this experiment we measured within-group social behaviour before, during and in the days after simulated intrusions. Zooming out in this way can shed new light on the function of behavioural responses to intergroup conflict.

Methods

Study Site

Data for this study were collected from wild banded mongooses on the Mweya Peninsula in Queen Elizabeth National Park, Uganda ($0^{o}12'$S, $29^{o}54'$E), between March 2016 and May 2017. This population of banded mongooses is part of a long-term study, and detailed descriptions of the study site can be found in (Rood, 1975; Cant, 2000; Cant, Vitikainen and Nichols, 2013). All mongooses in the study population are individually marked using unique hair-shave patterns and are habituated to close observation from 2-4 m. One to two mongooses in each group are fitted with a radio collar weighing 26-30 g (Sirtrack Ltd, Havelock North, New Zealand) with 20-cm whip antenna (Biotrack Ltd, Dorset, UK) to allow the groups to be located. Five focal groups were used in this study.

Groups are territorial and defend their territories from other groups during frequent, highly aggressive intergroup conflicts (Nichols, Cant and Sanderson, 2015; Thompson, Marshall, Vitikainen and Cant, 2017). Banded mongooses in this study site almost exclusively engage in physically violent inter-group interactions, with very few interactions between groups that are neutral, peaceful, or involve only signalling between groups with no physical interaction, e.g. war dances, or vocal defence. Individuals respond to sighting a rival group by standing alert and giving a specific screeching call known as a ‘war cry’ (Cant *et al.*, 2016), after which group members congregate and stand alert. Small groups typically flee from larger groups, with larger groups sometimes giving chase (Cant, Otali and Mwanguhya, 2002; Furrer *et al.*, 2011). If groups are more evenly matched in size then group members bunch together and approach in ‘battle lines’. Fighting can be highly aggressive, involving biting and scratching, and sometimes individuals are held down and attacked by multiple rival group members. Intergroup fights can result in serious injury and sometimes death (Cant, Otali and Mwanguhya, 2002; Nichols, Cant and Sanderson, 2015; Thompson, Marshall, Vitikainen and Cant, 2017). Intergroup fighting accounts for 20% of all adult deaths for which the cause of death is known (Nichols, Cant and Sanderson, 2015).

Data Collection

Experimental timeline

A single trial of the experiment took place over 5 days. For each trial in each group, we recorded pre-experimental behavioural data on the first and second day. On the third day we presented two stimuli, to simulate an encounter with a rival group (or act as a control) and measured short-term behavioural responses over a period of 1 hour following stimulus presentation. On the fourth and fifth days we collected post-experimental behavioural data for 2 hours each day to test whether there were longer term impacts of the simulated conflict. The experimental timeline is summarised in Figure 2.1.

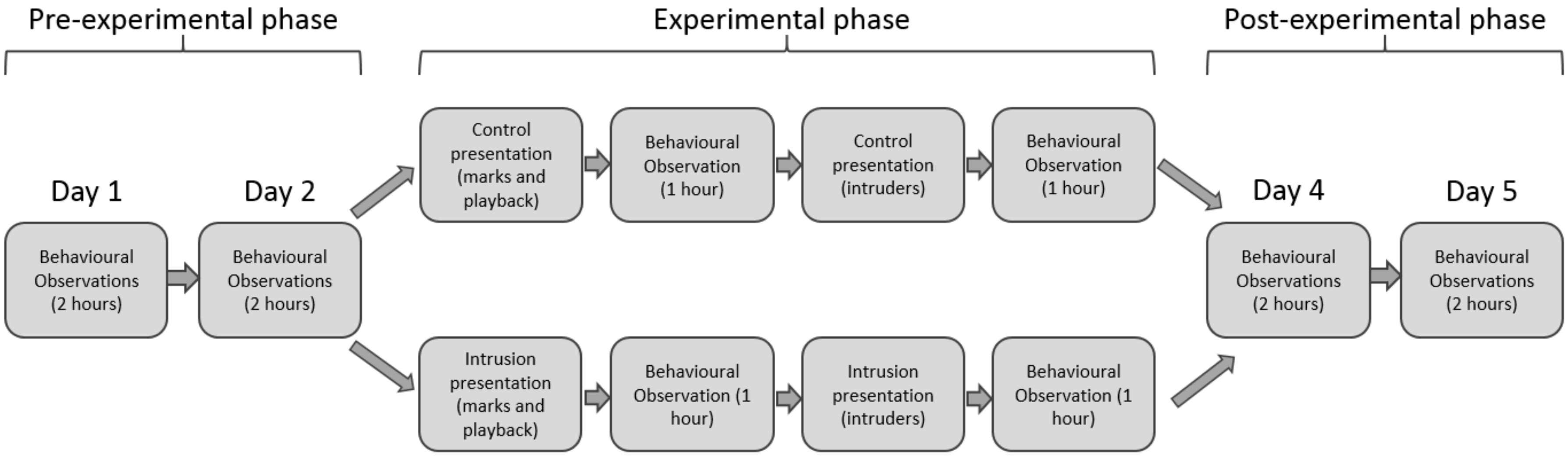

Figure 2.1 – Summary of the experimental timeline – showing when behavioural observations and presentations of various stimuli were performed.

Presentations

We presented two stimulus types as part of each presentation – faeces and calls, and intruders – in order to simulate a strong intergroup encounter. For logistical reasons these were presented at different time points in the day, with faeces and calls presented in the morning, and intruders in the afternoon. Our rationale was to simulate how the mongooses would encounter natural cues from rival groups, culminating in the presentation of multiple intruders, to maximise the impact of the presentation on subsequent behaviour. We carried out repeated simulated intrusion presentations and control presentations on each of five focal groups. Presentations to each focal group were separated by at least two weeks to prevent habituation of the mongooses to the stimuli being presented. It was not possible to standardise the location of each presentation, in terms of the home range (core or periphery), and the location of each presentation was not recorded accurately. In total we performed 22 control presentations, and 22 simulated intrusion presentations (see Table A2.1 for more information). The trials included 435.6 hours of behavioural observations.

Simulated intrusion presentations

Faeces, urine and scent marks from a neighbouring rival group (usually the largest and/or closest neighbouring group) were presented to the focal group on the morning of the presentation day (07:43-10:27 hours). Faeces, urine and scent marks were collected early in the morning from multiple individuals in the rival group, usually as the group emerged from the den or at the first group marking site of the day. Plastic sheets were laid out on the ground to encourage urination and scent marking, and aid collection (these were washed thoroughly with soap and water between presentations). A standardised volume of faeces was used (100 x 137mm ziplock bag). Samples were transferred as quickly as possible to the presentation site, and presented within 2 hours of collection, but generally much faster. The presentation site was placed in the foraging path of the focal group, to ensure that the mongooses encountered the stimulus. The samples were arranged in a semi-circle on open ground, with faeces placed around the sheets of plastic (spaced over 70-100cm) as mongooses often use open patches for territorial marking (Müller and Manser, 2007).

After 3 minutes of exploring the scent marks, or before if the animals began to move away from the area, we played a 30 second playback of 'war cries' from the same rival group. Playbacks were conducted using a portable USB speaker (iHome IHM60) hidden in vegetation. War cries from a whole group, emitted in response to rival mongooses presented in traps, were recorded using an H1 Zoom recorder attached to a Sennheiser directional microphone. Recordings were taken from 2-3 metres away, cut into 30 second sections in which vocalising was occurring, and the amplitude of each clip was standardised using the normalize function in Audacity 2.1.2 to -1dB (http://audacityteam.org). Recordings were collected more than one week before playbacks were used, and never during a period that the focal group was involved in an experimental trial. Each 30 second playback clip was used only once to prevent habituation of the mongooses to particular recordings. The number of calling mongooses was not controlled for, as this represented a realistic representation of the rival group, and we were not investigating the size of the group, but the impact of encountering the focal group's riskiest rival group.

On the afternoon of the same day (16:35-18:18 hours), four adult male individuals from the rival group, were trapped and presented to the focal group, following methods established in previous studies (Cant, Otali and Mwanguhya, 2002). The traps were washed with soap and water to reduce scents from any previous trapping events before the males were captured. Animals in traps were covered with a black cloth to minimise stress at all times except during the 5 minute presentation. During the 5 minute presentations the observers remained close by, and video recorded the behaviour of the group. The rival males in the traps tended to be aggressive back to the focal group, but this behaviour could not be measured systematically. After 5 minutes the males were covered and returned to their own group, usually within 10-20 minutes.

Control presentations

Control presentations used faeces and marks collected from the focal group, early in the morning from multiple individuals, usually as the group emerged from the den or at the first group marking site of the day, and re-presented to them after they had moved away from the area (with a similar gap between sample collection and presentation as intrusion trials). For playbacks, war cries were replaced with close calls (a non-threatening communication call between group members (Müller and Manser, 2008)) from the focal group. The close calls were recorded from the focal group during normal foraging behaviour when there were no threats from rival groups or other sources. Recordings were cut and standardised in the same way as the war cry recordings. Presentations of individuals used 4 adult males from the focal group, which were trapped, covered and removed for half an hour (to a safe, shaded location) before they were presented to the rest of the focal group.

These control presentations were carried out in blocks between experimental trial blocks. This is because control presentations were carried out when one of the two main observers was not present at the study site. The other main observer was joined by one additional observer during control periods, so there was always at least two observers during each trial, and always at least one of the main observers present in each trial. Control trials were performed when only one main observer was present, as these were logistically easier to carry out, requiring visitation of only one pack rather than two on the day of the presentation, and therefore requiring less expertise from the additional observer. Because of these differences between control and experimental trials, a correction factor was applied to one of the variables, grooming, outlined below in the statistical analysis section.

Behavioural Observations

Behavioural observations were carried out for two days preceding either a control or a simulated intrusion presentation (Pre); on the day of the presentation (During); and for two days after the presentation (Post). The focal group was observed for one hour in the morning (starting between 06:56 and 11:32 hours) and for one hour in the afternoon (starting between 15:25 and 18:38 hours) on each of the five days. Behaviours recorded were grooming, aggression, collective scent marking and collective alarm calling, and are defined in Table 2.1. On the day of the presentations these observations were carried out as soon as possible after the presentation ended. In addition we recorded immediate behavioural reactions to the stimuli as they were presented using a video camera. These videos were then analysed to score the behavioural response of the group on a six point ordinal scale (Table 2.2).

Table 2.1 – Description of the behaviours of interest, recorded during behavioural observations.

Behaviour	Description

Grooming (or other affiliative) interaction	One mongoose grooms another mongoose using their mouth, manipulating the fur with the teeth, the head moves in a distinctive backwards and forwards motion; or two mongooses perform “nubbing” behaviour – a mutual genital sniff with raised tails which may also include marking each other and vocalising.
Aggressive interaction	One mongoose is aggressive to another mongoose. This can include lunging, biting, growling or snarling vocalisations, or physical displacement of another individual. Aggressive interactions happen over food resources, during mate-guarding and as part of dominance interactions.
Collective marking event	Three or more individuals mark the ground (or each other) with urine, faeces, or scent marks (rubbing the anal or cheek glands along the surface). One individual marking, or two individuals marking each other were not included as these behaviours are not considered collective.
Collective alarm calling event	Two or more individuals simultaneously “alarm call” by standing in a bipedal stance observing the area with an alert and raised head, this may also be accompanied by alarm vocalisations – shrill, high-pitched cries. This often recruits others to join the alarm calling event.

Due to logistical constraints at the field site the control and intrusion presentations were carried out at different times and by a different main observer, as outlined above. To control for inter-observer differences, the two observers conducted 6 hours of simultaneous behavioural observations on three of the focal groups after all trials had taken place. For grooming behaviour, observer scores were significantly different (paired t-test, t = -4.26, df

= 5, p = 0.008), but highly explained by observer identity ($R^2 = 0.98$), so we applied a correction factor of 14.32 + 1.15x to the number of grooming interactions in the control observations. There was no significant difference in the number of aggressive interactions recorded between observers (Paired t-test, t = -0.61, df = 5, p = 0.57), so no correction factor was applied.

Table 2.2 – Description of the scoring of immediate behavioural reactions.
Scores were recorded from video footage taken during the presentation of intrusion (rival faeces and marks, rival war cries and rival intruders) and control (own faeces and marks, own close calls and own individuals) stimuli.

Score	Description
0	No reaction and no approach towards the stimulus.
1	Approach the stimulus with curiosity, but no alarm.
2	Approach the stimulus with curiosity, and a low level of alarm.
3	Some (< 50%) individuals mark, alarm call, and/or attack.
4	Most (> 50%) individuals mark, alarm call and/or attack.
5	All individuals mark, alarm call and/or attack.

Statistical Analysis

Statistical analysis was performed in R 3.2.2 (R Development Core Team, 2019) using generalised linear mixed models (GLMMs) using the *lme4* package (Bates and Maechler, 2009). Maximal models were fitted including all fixed-effect explanatory variables of interest, and biologically relevant interactions. To assess the significance of each explanatory variable, we compare the likelihood ratio of the maximal model to that of the model without that explanatory variable (Bates *et al.*, 2015). Parameter estimates and standard errors are taken from the maximal models, rather than following a stepwise model reduction procedure, due to problems associated with this method (Whittingham *et al.*, 2006; Mundry and Nunn, 2009; Forstmeier and Schielzeth, 2011). We removed nonsignificant interaction effects from our maximal model prior to testing the main effects (Engqvist, 2005). Post-hoc tests were performed using the *emmeans* package in R, which calculates estimated marginal means from a model and contrasts them (Lenth, 2019).

Immediate behavioural reaction data reaction scores (0-5, Table 2.2) were analysed using a cumulative link mixed model for ordinal regression using the *ordinal* package (Christensen, 2019). Treatment type (control or intrusion) was the explanatory variable of interest, and stimulus type (scent marks and playback or intruders) and an interaction between treatment and stimulus type were also included in the model as explanatory factors. Trial identity was included as a random factor due to the repeated measure of the score between marks/playback and intruder presentations.

Behavioural data were analysed using GLMMs. We analysed the number of grooming events, aggressive events, collective alarm calls, and collective marking events as response variables in four models, each using a Poisson error structure with a log-link function and the same set of fixed and random effects. Most trials had the full 10 hours of observations (mean ± SE = 594 ± 2 minutes), but occasionally observations were cut short by bad weather, external interference or animals returning to the den. For statistical analysis we split observations of behavioural responses to the stimuli into three categories: first 5 minutes after presentation of the stimulus (0-5 minutes), next 55 minutes (5-60 minutes), and the next two days after the presentations (post-experimental). We chose a 5 minute window to measure short-term responses because this mirrored the period for which stimuli were presented (~4 mins for calls/faeces, 5 mins for intruders), and mongooses typically left the presentation site a few minutes after stimuli were removed. To control for variation in observation time between time points (i.e. Pre, 0-5, 5-60, Post), we used an offset function in the model of log(session observation time). Our design allowed us to measure changes in behaviour in the days before, during, and after the presentations, so that each group could act as its own control for a particular trial. For this analysis we treated data from the two presentation types (faeces/playback and intruder) as equivalent, as responses to these stimuli were not significantly different (Table A2.2 – Table A2.5). The models contained treatment (i.e. control vs intrusion), time (Pre, 0-5, 5-60, Post), and the interaction term between treatment and time as explanatory variables. Also included in each of the models were the number of adult individuals present in the group during the observation day (babysitting individuals at the den were not included in this number), the breeding status of the group (oestrus, pregnant, babysitting, escorting, non-breeding), and the mean rainfall from the last 30 days (which is a proxy for food availability). Location could not be included within the model, to account for differences in reactions between the core and periphery of a territory, as this was not recorded accurately. The identity of the trial (due to the repeated measures nature of the experiment) was included as a random effect (Crawley, 2013), and an observation-level random effect was used to address overdispersion (Harrison, 2014). Group identity was also initially included as a random effect, but was removed from the models as it did not explain any variation, and caused issues with singularity and over-fitting of the models.

Results

Immediate reactions

Mongooses approached the stimulus in 100% of the trials, both control and intrusions. Reaction scores were significantly higher during intrusion trials than during control trials (estimate ± SE = 47.55 ± 250.16, $X^2_1 = 42.54$, $p < 0.001$; Table A2.6, Figure 2.2). The animals responded in a very similar way to presentations of faeces/calls and to live intruders; immediate reaction scores were not related to stimulus type (estimate ± SE = 0.09 ± 0.59, $X^2_1 = 0.03$, $p = 0.87$).

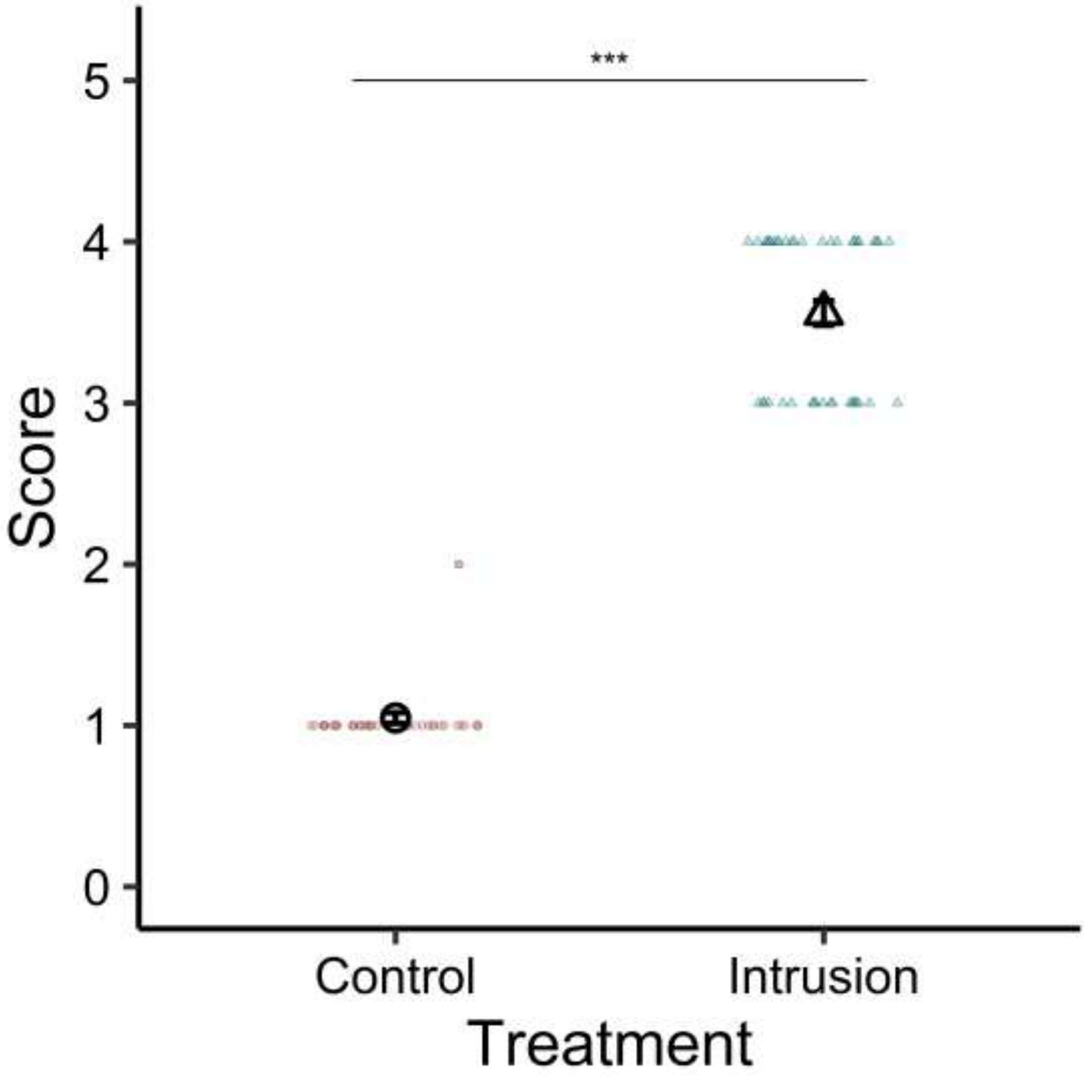

Figure 2.2 – The immediate reaction score of banded mongoose groups to control versus intruder stimuli. Scores ranged from 0 to 5, with 0 indicating no reaction or approach towards the stimuli, and 5 being the strongest reaction to the stimuli. Two types of stimuli were tested: faeces combined with playback (control = own faeces and close calls; intrusion = rival faeces and war cries), or live intruders (control = 4 adult males from the focal group; intrusion = 4 adult males from the rival group). The immediate reaction to these types was almost identical, so combined data are shown. Large black outline points show means from raw data, with standard error error bars. Raw data are shown as small points. Intrusion trials are shown as triangles, and control trials as circles.

Behavioural responses

There was a significant interaction between treatment type and time point in predicting the frequency of grooming (interaction: $X^2_3 = 11.59$, $p = 0.01$, Table A2.7). In intrusion trials, there was no difference between grooming in the pre-experimental phase, and the first 5 minutes after a presentation (post-hoc test (pre – 0-5): $z = -0.42$, $p = 0.98$). However, there was a decrease in grooming in the next 55 minutes compared to the first 5 minutes and the pre-experimental phase (post-hoc test (0-5 – 5-60): $z = 3.34$, $p = 0.004$; post-hoc test (pre – 5-60): $z = 3.34$, $p = 0.005$, Table A2.8; Figure 2.3A). Grooming then started to return to the pre-experimental level during the post-experimental phase (post-hoc test (pre – post): $z = 1.99$, $p = 0.19$). However, grooming levels in the post-experimental phase were not different to those in the 5-60 minute period, suggesting that grooming is starting to return to pre-experimental levels but is at an intermediate level in the two days after an intrusion trial. In control trials there were no significant differences in grooming between time points. From 5 to 60 minutes after the presentation grooming was lower in intrusion than control trials (post-hoc test (control – intrusion): $z = 2.49$, $p = 0.01$). The frequency of grooming was not affected by breeding status (estimate ± SE = 0.01 ± 0.18 (escorting), -0.22 ± 0.18 (non-breeding), -0.19 ± 0.29 (oestrus), 0.32 ± 0.18 (pregnant), $X^2_4 = 9.33$, $p = 0.06$), or past rainfall (estimate ± SE = 0.01 ± 0.08, $X^2_1 = 0.22$, $p = 0.64$), but there was an increase in grooming when more individuals were present in the group (estimate ± SE = 0.05 ± 0.01, $X^2_1 = 4.19$, $p = 0.04$).

There was no interaction between treatment type and time point when predicting aggression ($X^2_3 = 2.63$, $p = 0.45$, Table A2.9). However, rates of aggression were also depressed in the first 5 minutes after presentations, compared to all other time points ($X^2_3 = 22.12$, $p < 0.001$; post-hoc test (pre – 0-5): $z = 3.92$, $p = 0.001$; post-hoc test (0-5 – 5-60): $z = -2.88$, $p = 0.02$; post-hoc test (0-5 – post): $z = -4.26$, $p = 0.0001$, Figure 2.3B, Table A2.9, Table A2.10). Additionally, aggression was more frequent overall in intrusion trials compared to controls (estimate ± SE = 0.79 ± 0.24, $X^2_1 = 9.48$, $p = 0.002$), which may reflect the fact that controls and intrusions were performed in blocks at slightly different times of year. Aggression was higher when more individuals were present (estimate ± SE = 0.07 ± 0.01, $X^2_1 = 23.12$, $p < 0.001$). Other predictors (breeding status, rainfall) had no significant effect (Table A2.9).

There was no change in rates of collective scent marking or alarm calling in either control or intrusion trials. Other predictors (breeding status, rainfall, group size) also had no significant effect (Table A2.11 and Table A2.12).

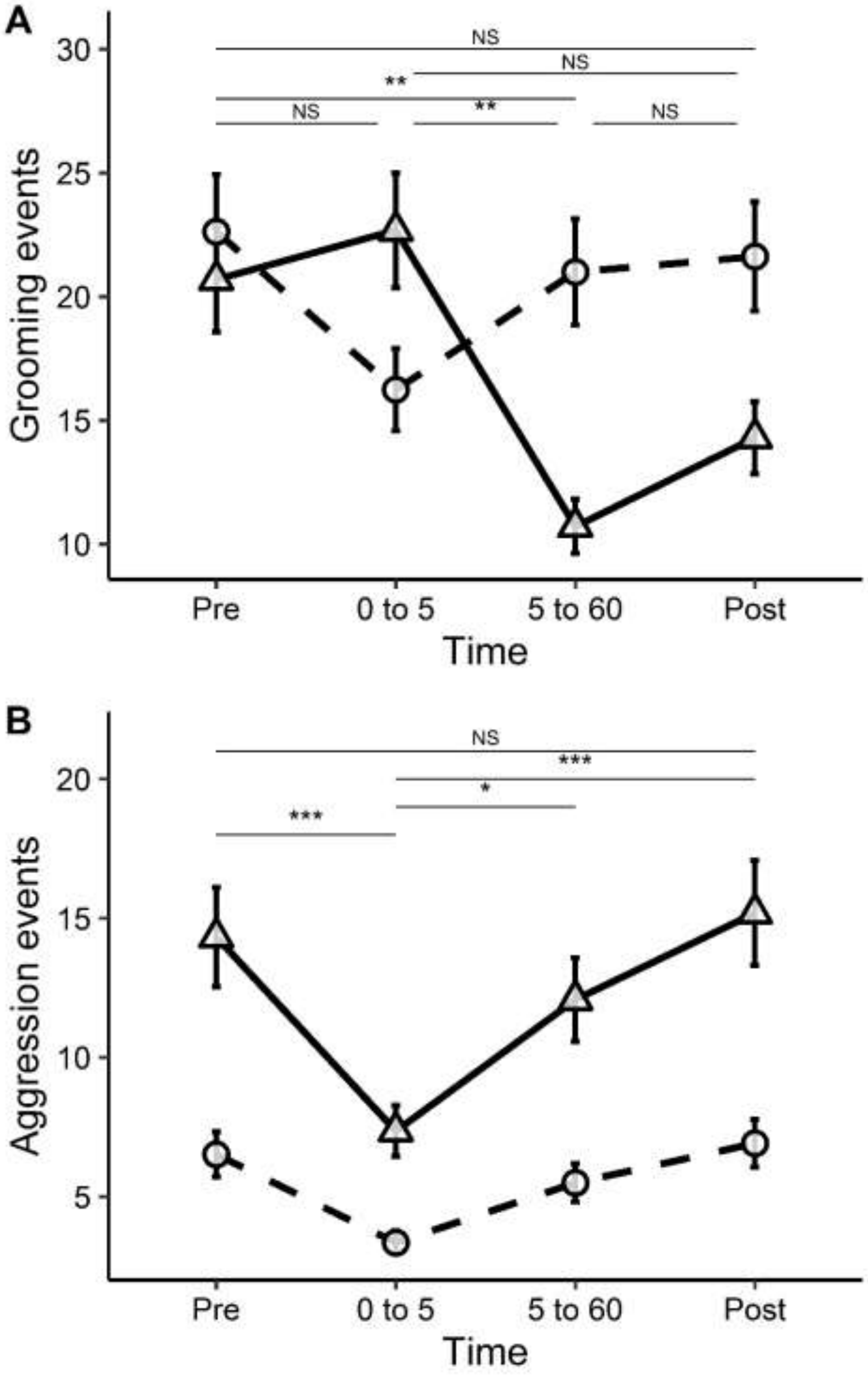

Figure 2.3 – Group-level social behaviour after exposure to simulated intergroup conflict (A) the number of grooming interactions (with the correction factor (14.32 + 1.15x) applied to control trials) and (B) the number of aggressive interactions for intrusion (solid line and triangles) and control (dashed line and circles) presentations, at pre-experimental, during experiment (0-5 minutes and 5-60 minutes) and post-experimental time points. Points show means from the GLMM ± SE. *** P < 0.001, ** P < 0.01, * P < 0.05; asterisks refer to post hoc comparison of means across all four categories within intrusion trials.

Discussion

Banded mongooses showed strong immediate behavioural reactions to simulated intergroup encounters, during the presentation of the stimuli. Moreover, simulated encounters resulted in lower rates of both grooming and aggression in the subsequent hour. However, these behavioural responses to the simulated conflict were relatively short-lived. In the two day period following the encounters, rates of aggression returned to the levels observed prior to the presentation, and rates of grooming began to return to a pre-experimental level. There was no impact of simulated intergroup encounters on two other collective behaviours, scent marking and alarm calling, in either the short-term (up to one hour after the presentations) or the longer-term (2 days after the presentations).

The decrease in grooming after a simulated intergroup encounter contrasts with similar experiments in other social vertebrates. Increases in post-conflict within-group affiliative behaviour have been recorded in both experimental contexts (cichlid fish exposed to single out-group individuals (Bruintjes *et al.*, 2015), allo-preening in green wood-hoopoes (Radford and Du Plessis, 2004), duration of grooming in dwarf mongooses (Morris-Drake *et al.*, 2019), and grooming in marmosets exposed to single female intruders (Schaffner and French, 1997)) and observational studies (allo-grooming in blue monkeys (Cords, 2002), samango monkeys (Payne, Hallam, Lawes and Henzi, 2003), and by female bonnet macaques to males who contributed to conflicts (Cooper, Aureli and Singh, 2004)). These increases in grooming and affiliation between group-members have often been interpreted as representing improved social cohesion, or the strengthening of social relationships. Grooming is assumed to be important to primate relationships, and is even considered to be a currency in biological markets literature (Barrett *et al.*, 1999). The observation that banded mongoose reduce, rather than increase grooming in response to simulated encounters, suggests that grooming may play a reduced role in maintaining social cohesion in this species, at least in the aftermath of an intergroup encounter. Banded mongooses usually engage in grooming during times of rest and play, for example, in between foraging trips or in the evening before entering the den, so a reduction in grooming could reflect a general increase in alertness or activity, and reduced opportunities for relaxed, collective grooming. These considerations highlight that behaviours (such as grooming or affiliative behaviour) that appear quite similar in different species may be manifested in different contexts and serve very different functions, depending on ecology, social structure and sensory abilities.

We found evidence that within-group aggression declined in the first five minutes after presentation of stimuli, but returned to pre-experimental levels in the next 55 minutes, and the two days after the stimuli. This might be taken as an indication that within-group conflict is reduced in response to intergroup encounters, albeit briefly. However, there are two important caveats. First, as with grooming the reduction in aggression may reflect a change in other behaviours, and specifically a shift away from foraging to other behaviours after an encounter. Most aggression in banded mongooses occurs in the context of foraging, but mongooses stopped foraging during exposure to stimuli, and left the site of the presentations shortly afterwards. Second, we observed the same decline in aggression in both intrusion and control trials, which suggests that the effect on aggression may reflect a behavioural response to the experimental apparatus, not to a simulated intergroup encounter *per se*.

In other systems the effect of intergroup conflict on post-conflict aggression is mixed. Elevated post-conflict aggression has been observed in capuchin monkeys (Polizzi di Sorrentino *et al.*, 2012) and bonnet macaques (Cooper, Aureli and Singh, 2004), but not in the cichlid *N. pulcher*, dwarf mongooses (Morris-Drake *et al.*, 2019), or ring-tailed lemurs (Nunn and Deaner, 2004). One potential explanation for the fleeting change in grooming and aggression following intergroup conflicts in our study is that banded mongooses may already show heightened within-group grooming and aggression rates because intergroup encounters are so common. Banded mongooses experience a high level of mortality from intergroup conflicts (Nichols, Cant and Sanderson, 2015), and conflicts occur frequently (mean encounter rate per group = 0.8 per week (non-oestrus periods) to 2.9 per week (group oestrus); data from 12 groups (Cant, Otali and Mwanguhya, 2002)). If pre-experimental grooming and aggression rates are already high, a single simulated intergroup encounter may cause little change in the level of grooming or aggression seen within the group, despite affecting other behaviours. Studying populations of the same species that experience different overall levels of intergroup conflict could help to assess how responses to the same manipulation vary with background levels of conflict. Heightened baseline behaviour may also help to explain why there is no detected change in scent marking or alarm calling behaviour during or after the simulated intrusion.

Alternatively, although we see only a short-term change in the average levels of grooming or aggression within the group, this result may mask more subtle changes in intragroup interactions that arise from within-group heterogeneity. It is well documented that different types of individuals contribute to intergroup conflicts to different degrees (Boydston, Morelli and Holekamp, 2001; Muller and Mitani, 2002; Radford, 2008a; Mares, Young and Clutton-Brock, 2012; Van Belle *et al.*, 2014; Wilson *et al.*, 2014; Arseneau *et al.*, 2015;

Koch *et al.*, 2016a). Males and females often have different costs and benefits associated with participation in intergroup encounters, and therefore behave differently (Boydston, Morelli and Holekamp, 2001; Muller and Mitani, 2002; Mares, Young and Clutton-Brock, 2012; Wilson *et al.*, 2014; Koch *et al.*, 2016a). Dominant and subordinate individuals also experience different costs, which can influence their involvement (Radford, 2008a; Van Belle *et al.*, 2014; Arseneau *et al.*, 2015; Koch *et al.*, 2016a). In green wood-hoopoes, for example, allo-preening by dominant individuals was directed towards subordinates after conflicts (Radford, 2008b). Adult male mongooses suffer higher rates of mortality from intergroup conflicts than females, and females can benefit from intergroup encounters by gaining access to extra-group mating opportunities (Nichols, Cant and Sanderson, 2015). We might therefore expect that changes to intragroup interactions, would differ between males and females, and between different age classes. We use social network analysis to test this hypothesis and investigate the potential for subtle changes in the directionality or network of relationships in response to intergroup encounters in Chapter 3.

Despite the collective, and potentially cooperative, nature of scent marking and alarm calling, neither of these behaviours were affected by simulated intergroup intrusions. Alarm calling and vigilance could be beneficial in avoiding future contests, and mongooses clearly respond to the scent marks, war cries and presence of neighbours, as shown by their strong initial reaction to these stimuli in this experiment. However, this does not seem to have a lasting effect on their behaviour, even during the first five minutes after stimuli are removed. Neither marking, nor vigilance has been studied much in the context of intergroup encounters, but one recent study found increasing levels of sentinel behaviour in dwarf mongooses in response to simulated intergroup encounters (Morris-Drake *et al.*, 2019), and female marmosets increase scent marking when exposed to out-group females (Schaffner and French, 1997).

This study also shows the importance of using a baseline measurement of behaviour, in the pre-experimental or pre-conflict time period. Analysis of the data collected only on the day of the stimulus presentations suggests that not only grooming and aggression are affected by simulated intergroup conflict, but alarm calling too (Table A2.2, Table A2.3, Table A2.5 and Figure A2.1). Comparison of intrusion and control trials suggests that alarm calling is higher after intrusion presentations, however, this effect is not seen when the pre- and post-experimental periods are included. Many previous studies have used this design, of comparing responses to control and intrusion events (Morris-Drake *et al.*, 2019), or comparing to time points not directly before the intergroup conflict (Payne, Hallam, Lawes and Henzi, 2003; Radford, 2008a, 2011). Our results show that this approach may not accurately capture changes in behaviour, particularly if the baseline of a behaviour fluctuates over time.

Although the location of each experimental presentation was not recorded, and could therefore not be included as a factor in the statistical models, this is unlikely to change these conclusions. It is unlikely that there is any systematic bias in location of each trial either on the day of the presentation in control and treatment trials, or in the pre and post trial periods. However, due to the limitations of the experimental design, comparisons between control and intrusion trials should be interpreted with some caution. Each experimental trial contains its own within trial control, the pre-experimental period, which helps to alleviate these concerns, but as control and intrusion trials differed in their observers, and were undertaken in blocks rather than fully randomised, some caution is needed in interpreting these results. Future work should endeavour to include both pre and post experimental periods, as well as balanced control and intrusion trials.

In conclusion, unlike previous studies, banded mongooses showed short-lived reductions in grooming and aggression in response to simulated intergroup encounters, but did not show longer term changes in aggression or collective behaviour. Only grooming was affected into the longer term, and was beginning to return to baseline levels in the two days after an intrusion. The reduction in rates of grooming runs counter to most previous experimental studies of intergroup conflict, and raises questions about the degree to which behaviours assumed to be affiliative are comparable across species. The fleeting nature of behavioural impacts also highlights the disparity between observed individual behavioural responses, which are inherently ephemeral and dynamic, and the static genetic assumptions of population genetic and game theoretic models of intergroup conflict and cooperation. This is an area of research where empirical studies have started to reveal fascinating variation in behaviour which current theory is not well-suited to explain. Further research is needed to bridge this gap between empirical and theoretical studies, and gauge the longer-term consequences of intergroup conflict for social relationships, survival and fitness.

Chapter 3:

Network-level consequences of intergroup conflict in a cooperative mammal society: redirection of grooming and aggression between sexes

Abstract

1) Animal groups are heterogeneous assemblages of individuals with differing fitness interests, which may lead to internal conflict over investment in group territorial defence. Differences between individuals may lead to different behavioural responses to intergroup conflict, particularly between the sexes. These potential impacts have been little studied.

2) We used social network analysis to investigate the impact of simulated intergroup conflicts on social relationships in groups of wild banded mongooses (*Mungos mungo*), in which intergroup fights are more costly for males than females. We predict that social cohesion (specifically male-to-male and female-to-male grooming) will increase after conflict, and aggression will decrease, to minimise conflict between the sexes.

3) Simulated intergroup conflicts were performed by exposing banded mongoose groups to scents, “war cry” playbacks, and live intruders from a rival group. All grooming and aggression interactions between individuals were recorded, and grooming and aggression social networks were created for the two days preceding a simulated intergroup conflict (pre-conflict network) and the two days after (post-conflict network).

4) We found no evidence of an increase in social cohesion, measured as grooming eigenvector centrality. Male-to-male, male-to-female and female-to-male grooming strength decreased compared to female-to-female grooming strength in intrusion trials. However, male-female aggression decreased in intrusion trials compared to other interaction types, consistent with the hypothesis that intergroup encounters reduce the level of intragroup conflict between males and females. Males are more affected socially by intergroup

encounters than females, which may be because they are investing in defence rather than internal relationships.

5) Focusing on individual relationship changes, using social network analysis, can reveal subtle, but important changes in behaviour after intergroup changes in the directionality of behaviour in response to intergroup encounters, and highlight how individual responses to conflict may scale up to affect social networks and, potentially, group performance. This study highlights the importance of studying both group-level behaviours and individual relationships to more fully understand responses to intergroup encounters.

Introduction

Intergroup conflict can be a major force driving evolution in social species (Choi and Bowles, 2007; Rusch and Gavrilets, 2016; Thompson, Marshall, Vitikainen and Cant, 2017). Although intergroup conflict is widespread across social animals (Wilson and Wrangham, 2003; Plowes and Adams, 2005; Golabek, Ridley and Radford, 2012; Cassidy *et al.*, 2015; Thompson, Marshall, Vitikainen and Cant, 2017), the costs and benefits of these conflicts to individual fitness remain poorly understood. Current theory borrows from dyadic animal contest theory, e.g. Hawk-Dove evolutionary game theory (Maynard Smith, 1982) and theory of warfare, e.g. Lanchester’s law of attrition (Lanchester, 1914). These theories often assume that groups act as single entities during conflicts, or that groups are formed of identical individuals (Fearon, 1995; Adams and Mesterton-Gibbons, 2003; Sherratt and Mesterton-Gibbons, 2013; Johnson and Toft, 2014; Rusch and Gavrilets, 2016), although some recent theoretical work recognises heterogeneity of groups (Bornstein, 2003; Gavrilets and Fortunato, 2014; Gavrilets, 2015; Pandit *et al.*, 2016). Empirical work highlights that individuals from the same group respond differently to intergroup conflicts – several studies have shown how different classes of individuals contribute to conflicts, including differences between males and females, differences across dominance rank, and differences between those with offspring in the group and those without (Boydston, Morelli and Holekamp, 2001; Muller and Mitani, 2002; Kitchen and Beehner, 2007; Mares, Young and Clutton-Brock, 2012; Meunier, Molina-Vila and Perry, 2012; Van Belle *et al.*, 2014; Arseneau *et al.*, 2015; Van Belle and Scarry, 2015). As groups are often heterogeneous there can be internal conflict over investment in group territorial defence. Group members may invest differently in territorial defence according to the threat type, the resources at risk, or other factors that affect the costs and benefits associated with territory defence, including social coercion or punishment of non-participation.

Conflicts of interest regularly occur between the sexes. Males and females often differ in their behaviour as their strategies of maximising fitness are different. A clear example is investment in territorial defence, which has different fitness benefits and costs for males versus females (Arseneau-Robar *et al.*, 2017; Thompson, Marshall, Vitikainen and Cant, 2017). Each sex may defend territories in different ways, or at different times (through the reproductive cycle, or according to food availability), according to the value the territory holds for them. In many intergroup conflicts males participate more than females (Muller and Mitani, 2002; Mares, Young and Clutton-Brock, 2012; Wilson *et al.*, 2014; Koch *et al.*, 2016a), suggesting that defence of mates, or territory to support those mates, is an important incentive to fight. The importance of mate defence is supported by observations that male aggression to out-group individuals in intergroup conflicts increases when females are receptive to mating (Manson and Wrangham, 1991; Cooper, Aureli and Singh, 2004; Arseneau *et al.*, 2015; Pal, 2015). There is also evidence that both male and female individuals direct more aggression at same-sex out-group individuals during intergroup encounters (Boydston, Morelli and Holekamp, 2001; Radford, 2003), perhaps due to reproductive conflict. Females are also affected by intergroup conflicts and have been seen to increase grooming towards individuals in their own group who participate in conflicts (Arseneau-Robar *et al.*, 2016), and to integrate into a new social group more successfully (receiving less aggression from their own group) if they participate in intergroup conflicts (Hauser, Cheney and Seyfarth, 1986). Therefore, there may be internal conflict between the sexes within a group over participation in intergroup encounters, that should be suppressed to ensure overall group social cohesion.

Social network analysis can provide detailed information about both direct relationships (between individuals) and indirect relationships across a wider group, which can be used to reveal the underlying social structure of groups, highlight key individuals in networks, or differences between groups, and facilitate understanding of the spread of behaviours or disease between individuals (Krause, Croft and James, 2007; Krause, Lusseau and James, 2009; Kurvers *et al.*, 2014). Social network analysis could be a useful tool to test whether social cohesion or individual social relationships change after intergroup conflicts, and whether this is affected by individual traits such as age or sex. Previous work has used social network analysis to investigate the impact of disturbance on social relationships (Wilson *et al.*, 2015; Formica *et al.*, 2016) (although not in the context of intergroup conflict), and social network traits have also been correlated to participation in group defence in female white-faced capuchins (*Cebus capucinus*) (Crofoot *et al.*, 2011). However, the impact of intergroup conflict on animal social networks has not yet been investigated.

In this study we quantify how individuals differ in their response to intergroup conflicts, and how these individual differences scale up to influence group behaviour. Specifically, we test how banded mongoose (*Mungos mungo*) individuals differ in their social response to simulated intergroup encounters. As banded mongoose groups are heterogeneous, being made up of multiple males and females of different ages, we anticipate that there are differences in how males and females respond to intergroup conflict that lead to changes to grooming and aggressive social relationships, which may not be clear when measuring these behaviours at the group level. We also believe that age may be an important factor, as age correlates with dominance in this study system, however the empirical evidence for whether dominant and subordinate individuals react differently to intergroup conflict is mixed (Payne, Hallam, Lawes and Henzi, 2003; Nunn and Deaner, 2004; Radford, 2008a, 2008b; Polizzi di Sorrentino *et al.*, 2012; Bruintjes *et al.*, 2015; Hellmann and Hamilton, 2019; Morris-Drake *et al.*, 2019), so we do not have concrete predictions surrounding age.

On the basis of previous studies, we predict that intergroup conflict will be associated with increased social cohesion, represented by within-group affiliative behaviour (Schaffner and French, 1997; Radford and Du Plessis, 2004; Radford, 2008a, 2008b, 2011; Bruintjes *et al.*, 2015). Theory suggests that within-group aggression should also be suppressed (Reeve and Hölldobler, 2007), however previous studies have only recorded no change in within-group aggression (Nunn and Deaner, 2004; Bruintjes *et al.*, 2015; Morris-Drake *et al.*, 2019), or an increased rate of within-group aggression following intergroup conflict (Schaffner and French, 1997; Cooper, Aureli and Singh, 2004; Polizzi di Sorrentino *et al.*, 2012; Bruintjes *et al.*, 2015), rather than any decrease. We also predict that there will be differences in responses to intergroup conflicts between males and females, because males experience higher mortality costs from intergroup encounters (Thompson, F.J. *unpublished data*), whereas females can benefit from extra-group paternity (Nichols, Cant and Sanderson, 2015).

We make the following predictions:

1. Social cohesion will increase in response to intergroup conflict. Specifically we predict that grooming eigenvector centrality (a proxy for cohesion) will increase after simulated encounters with rival mongooses.
2. Male-to-male grooming and female-to-male grooming will increase after simulated encounters, as a reward for male participation or as a form of group cohesion. Specifically we predict that male-to-male and female-to-male grooming strength will increase.
3. Aggression will on average decrease after simulated encounters (following theory (Reeve and Hölldobler, 2007)), and this decline will be particularly marked for aggression between males and females.

Materials and Methods

Study Site

Data were collected for this study from wild banded mongooses on the Mweya Peninsula in Queen Elizabeth National Park, Uganda (0º12’S, 29º54’E) between March 2016 and May 2017. The study was performed on banded mongooses that are part of a long-term study population, detailed descriptions of which can be found in (Rood, 1975; Cant, 2000; Cant *et al.*, 2016).

Banded mongooses live in stable multi-male, multi-female groups of between 10 and 30 individuals, and are territorial, defending their territories from other groups during frequent, and sometimes lethal, intergroup conflicts (Nichols, Cant and Sanderson, 2015; Thompson, Marshall, Vitikainen and Cant, 2017). Banded mongooses in the study site almost exclusively engage in physically violent inter-group interactions, with very few interactions between groups that are neutral, peaceful, or involve only signalling between groups with no physical interaction, e.g. war dances, or vocal defence. Mongooses respond to sighting a rival group by standing alert and calling to other members of their group, they often congregate and stand alert looking for the rival mongooses (Cant *et al.*, 2016). Small groups often flee from larger groups, with larger groups sometimes giving chase. If groups are more evenly matched in size then the individuals may bunch together and approach in “battle lines” (Cant, Otali and Mwanguhya, 2002; Cant *et al.*, 2016). Fighting is often highly aggressive involving biting and scratching, and sometimes individuals are held down and attacked by multiple rival mongooses.

All mongooses in the study population are individually marked using unique hair-shave patterns, and are habituated to close observation from 2-4 m. One to two mongooses in each group are fitted with a radio collar weighing 26-30 g (Sirtrack Ltd, Havelock North, New Zealand) with a 20-cm whip antenna (Biotrack Ltd, Dorset, UK) to allow the groups to be located. Five focal groups (which are habituated to being followed) were used in this study.

Data Collection

Experimental timeline

Trials took place over five days (see schematic in Figure 3.1). On the first and second day, we recorded baseline social interaction data that was used to build pre-conflict social networks. On the third day we carried out simulated intrusions or control presentations. On the fourth and fifth days we recorded social interaction data again, to build post-conflict social networks, representing social responses to intergroup conflict.

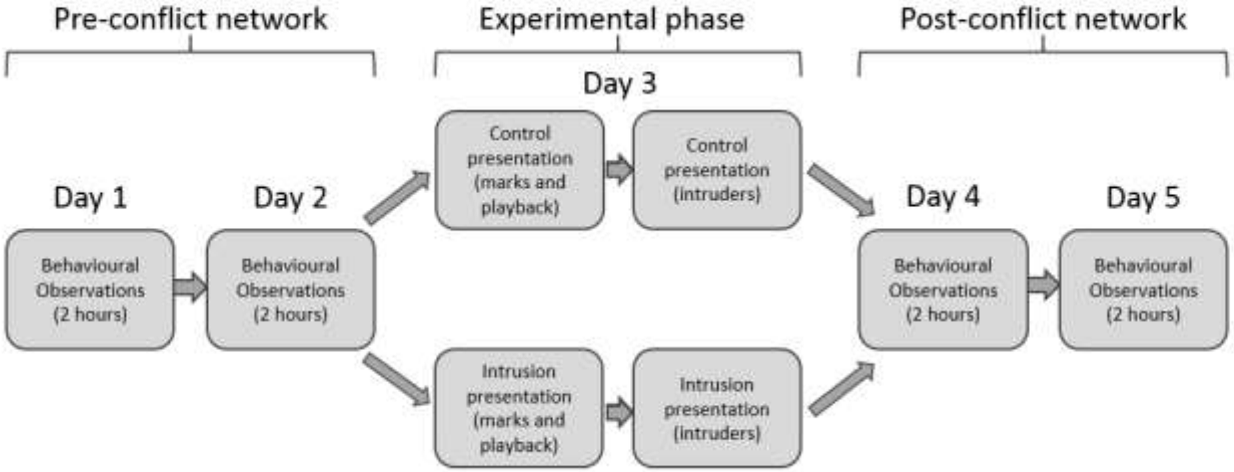

Figure 3.1 – A schematic diagram of the timeline of each trial,showing the process in both control (bottom row) and intrusion (top row) trials.

Presentations

We carried out simulated intrusion presentations and control presentations on each of five focal groups. These presentations were designed to simulate an intergroup conflict with escalating cues, following a natural progression from sensing rivals indirectly, to direct contact. It was not possible to standardise the location of each presentation, in terms of the home range (core or periphery), and the location of each presentation was not recorded accurately. In total we carried out 22 control presentations and 22 simulated intrusion presentations. Presentations to each focal group were separated by at least two weeks to prevent habituation of the mongooses to the stimuli being presented.

Simulated intrusion presentations

Faeces, urine and scent marks on plastic from a neighbouring rival group (considered to be the largest threat to the focal group) were presented to the focal group on the morning of the presentation day (07:43-10:27 hours). Faeces, urine and scent marks from the rival group were collected early in the morning, as the group emerged from the den or from the first group marking site of the day. Plastic sheets were presented to encourage urination and scent marking. These samples were collected from multiple individuals in the group, both males and females from different age classes. Samples were collected within 30 minutes, transferred as quickly as possible to the presentation site, and presented within 2 hours of collection, but generally much faster. The presentation site was placed in the foraging path of the focal group, to ensure that the mongooses encountered the stimulus. The samples were arranged in a semi-circle on open ground, with faeces placed around the sheets of plastic (spaced over 70-100cm) as mongooses often use open patches for territorial marking (Müller and Manser, 2007).

After three minutes of exploring the scent marks, or slightly before if the animals began to move away from the area, a playback of war cries from the same rival group (that the scent marks were collected from) occurred. Playbacks were conducted using a portable USB speaker (iHome IHM60) hidden in vegetation. War cries emitted in response to rival mongooses presented in traps were recorded using an H1 Zoom recorder attached to a Sennheiser directional microphone. Recordings were made when individuals from the rival group were vocalising at rival mongooses that were presented in traps. The recordings were taken from 2–3 metres away from the mongooses, and recorded calls from multiple individuals as the group were calling together. The recordings were cut into 30 second sections in which vocalising was occurring, and the amplitude of each clip was standardised using the normalize function in Audacity 2.1.2 to -1dB (http://audacityteam.org). Each 30 second playback clip was used only once to prevent habituation of the mongooses to particular recordings.

On the afternoon of the same day (16:35-18:18 hours), four adult male individuals from the rival group, were trapped and presented to the focal group. The traps were washed with soap and water to reduce scents from any previous trapping events before the males were captured. Trapped animals were transferred from the rival group to the focal group covered with a black cloth to minimise stress. The traps were placed in the foraging path of the focal group to ensure they encountered the traps, and the cloth was removed. After five minutes the rival males were removed (and the traps re-covered with the cloth) then returned to their own group, to minimise stress levels.

Control presentations

The same procedures were carried out for control presentations. However, faeces and marks were collected from the focal group, and re-presented to them. War cries were replaced with close calls (a non-threatening communication call between group members) from the focal group as the recordings used for the playback. The close calls were recorded from the focal group during normal foraging behaviour when there were no threats from rival groups or other sources. These recordings were cut and standardised in the same way as the war cry recordings. Four adult males were presented in traps, as before, but these were males from the focal group, which were trapped and removed for half an hour (to a safe, shaded location) before they were presented to the rest of the focal group.

These control presentations were carried out in blocks between experimental trial blocks. This is because control presentations were carried out when one of the two main observers was not present at the study site. The other main observer was joined by one additional observer during control periods, so there was always at least two observers during each trial, and always at least one of the main observers present in each trial. Control trials were performed when only one main observer was present, as these were logistically easier to carry out, requiring visitation of only one pack rather than two on the day of the presentation, and therefore requiring less expertise from the additional observer. Because of these differences between control and experimental trials, a correction factor was applied to one of the variables, grooming, outlined below in the statistical analysis section.

Social data collection

Social interaction data were collected during observations of the focal group for one hour in the morning (between 07:00 and 12:00 hours) and for one hour in the afternoon (between 16:00 and 19:30 hours) on each day. Throughout the observation every affiliative and aggressive interaction between individuals was recorded. All affiliative interactions, i.e. grooming and "nubbing" (mutual genital sniffing) were recorded by noting the identity of the individuals involved and the direction of the interaction (see Table 3.1 for detailed descriptions). As most affiliative interactions recorded were grooming interactions, we refer to all affiliative interactions and networks made from these interactions as grooming interactions or grooming networks. All aggressive interactions, including food competition and dominance aggression were also recorded in the same way (see Table 3.1 for detailed descriptions). Interactions that were observed but where individual identity could not be confirmed were not analysed as part of the networks. Social interaction data from two days before the presentation day (total 4 hours of observations) were pooled to create a pre-conflict grooming and a pre-conflict aggressive social network. Social interaction data from two days after the presentation day (total 4 hours of observations) were pooled to create a post-conflict grooming and a post-conflict aggressive social network. Social interaction data were also collected on the day of the presentation, however as behavioural observations were only performed for two hours sampling would not have been even between time periods, so these were not analysed.

Table 3.1 – Description of the interactions of interest, recorded during behavioural observations.

Behaviour	Description
Affiliative interaction (grooming, or "nubbing")	Grooming – one mongoose grooms another mongoose using their mouth, manipulating the fur with the teeth, the head moves in a distinctive backwards and forwards motion. One bout of grooming was defined as active grooming between the same pair of individuals with short breaks of no longer than 30 seconds of rest. If 30 seconds elapsed and the same pair began grooming again this was considered to be a second interaction. Grooming between multiple individuals switching from one partner to the other was recorded as one interaction per actor-recipient pair. Returning to a previous partner was not recorded as a separate interaction, unless 30 seconds of rest (no grooming of any partner) occurred. Nubbing – two mongooses perform "nubbing" behaviour – a mutual genital sniff with raised tails which may also include marking each other and vocalising.
Aggressive interaction	One mongoose is aggressive to another mongoose. This can include lunging, biting, growling or snarling vocalisations, or physical displacement of another individual. Aggressive interactions happen over food resources, during mate-guarding and as part of dominance interactions. One aggressive interaction was defined as aggression between the same pair of individuals with short breaks of no longer than 30 seconds between aggressive behaviours (e.g. lunging, vocalising).

Social network creation and analysis

The pre- and post-conflict social networks for both grooming and aggression were created from the edge lists (lists of observed social interactions, with the identity of each actor and recipient) collected during observations, using the *igraph* package in R (Csardi and Nepusz, 2006). The networks were both directional (included the direction of the interaction) and weighted (i.e. they included the strength of the interaction between individuals – in this case the total number of interactions observed between that pair of individuals during the observation session). In total 10,641 grooming interactions, and 7,435 aggressive interactions, were observed over a total of 348.8 hours of observation across 44 trials and five groups. On average 30.23 ± 1.92 (range = 0-142) grooming interactions, and 21.12 ± 1.44 (range = 0-108) aggressive interactions were observed per hour, and each individual was involved in, on average, 15.6 grooming and 10 aggressive interactions per pre- or post-conflict sampling period. In three pilot control trials pre- and post-conflict grooming and aggression matrices were significantly correlated (Mantel tests: all $p<0.05$) suggesting that the observed social interactions were stable representations of true social preferences over the study period.

The social networks included individual attributes for each node (in this case an individual mongoose), including individual identity, group identity, age and sex. The networks also included an edge (the link between two nodes – here based on social interactions) attribute, which denoted the identity of each edge in terms of the sex of the two individuals it connected, e.g. male-to-male for an interaction from a male towards another male, or female-to-male for an interaction from a female directed to a male.

Prediction 1 – Social cohesion will increase following simulated intergroup encounters

Linear mixed models were used to investigate the change in grooming eigenvector centrality of individuals following simulated intergroup encounter, or control, presentations. The response variable for the model was the change in the grooming eigenvector centrality, i.e. the difference between the pre-conflict and post-conflict grooming eigenvector centrality of each individual present in the networks. Eigenvector centrality is a measure of a node’s connectedness, including indirect connections, i.e. the nodes that the focal node is connected to. High eigenvector centrality indicates a node which is connected to other nodes which are also highly connected in the network (Wasserman and Faust, 1994). Indirect centrality measures have been used to assess social cohesion in a number of studies, and eigenvector centrality is appropriate here as there are no sub-groups (Blumstein, Wey and Tang, 2009; Wiszniewski, Lusseau and Möller, 2010; Kanngiesser *et al.*, 2011; Makagon, McCowan and Mench, 2012; Brent, 2015).

This model contained the change in eigenvector centrality of each individual, in each trial (857 observations from 100 individual mongooses in 5 groups over 44 trials). The maximal model included treatment type (intrusion or control), age of the individual, and sex of the individual, as well as a three-way interaction between these parameters as explanatory variables, as males and females of different ages may react differently to simulated intergroup conflict. Location could not be included within the model, to account for differences in reactions between the core and periphery of a territory, as this was not recorded accurately. Individual identity was included as a random factor. We then used AIC model selection to select the best model, and remove unnecessary interaction effects, whilst retaining biologically relevant two-way interactions. Models within ΔAIC < 2 of the model with the lowest AIC value were considered (Burnham and Anderson, 2002), and the model was selected from these based on biological interest retaining relevant interaction terms, rather than simply choosing the model with the lowest AIC value. The selected model contained treatment type, sex, age, and interactions between treatment type and sex, and treatment type and age.

Prediction 2 – Grooming directed towards males will increase

Linear mixed models were used to investigate the change in grooming strength of individuals after the presentations. Strength, also known as weighted degree, is the sum of all interactions associated with the node. In this study grooming strength directly represents the number of grooming interactions the focal mongoose initiated during observations. Higher grooming strength indicates more grooming performed by the mongoose, and could indicate strengthened social relationships. The response variable for the model was the change in the grooming strength for each edge type. Edge type was defined in terms of the sex of the two individuals it connected: male-to-male interactions (MM), male-to-female interactions (MF), female-to-male interactions (FM) and female-to-female interactions (FF).

This model contained the change for each individual, in each trial. This model contained 1714 observations from 100 individuals from 44 trials. The maximal model included treatment type, age of the individual, edge type, as well as a three-way interaction between these parameters as explanatory variables. Location could not be included within the model, to account for differences in reactions between the core and periphery of a territory, as this was not recorded accurately. Individual identity was included as a random factor. We then used

AIC model selection to select the best model to run, as before. The selected model contained treatment type, edge type, age, and interactions between treatment type and edge type, and treatment type and age.

Prediction 3 – Between-sex aggression strength will decrease following encounters

Linear mixed models were used to investigate the change in aggression strength of individuals after the presentations. In this study aggression strength directly represents the number of aggressive interactions the focal mongoose initiated during observations. Higher aggression strength indicates more aggression performed by the mongoose, and could indicate conflict between group members. The response variable for the model was the change in the aggression strength for each edge type.

All trials were tested at the same time, so this model contained the change for each individual, in each trial. This model contained 2571 observations from 100 individuals from 44 trials. The maximal model included treatment type, age of the individual, edge type, as well as a three-way interaction between these parameters as explanatory variables. Location could not be included within the model, to account for differences in reactions between the core and periphery of a territory, as this was not recorded accurately. Individual identity was included as a random factor. We used AIC model selection to select the best model to run, as before. The selected model contained treatment type, edge type, age, and interactions between treatment type and edge type, treatment type and age, and age and edge type.

Null models and network permutations

Variables calculated from social networks are not independent, so the observed model coefficients were compared to the coefficients from models of randomly shuffled network permutations. As sampling was even within each time period we built null models using node-label permutations (the nodes of each observed network were randomly shuffled). We then applied our models to each of these permuted networks to generate a distribution of potential coefficient values given the non-independence of our data (following the methods of (Croft, James and Krause, 2008; Croft *et al.*, 2011; Farine and Whitehead, 2015). Model coefficients stabilised at 5000 permutations, tested using the method from Bejder, Fletcher and Bräder (1998). We therefore ran 5000 permutations to generate a distribution of random network coefficients. Observed model coefficients were compared to permuted model coefficients, and p-values were calculated as the proportion of randomised model coefficients that were larger/smaller than the observed model coefficient. Here we used α = 0.025 because of the two-tailed nature of the proportions.

Further "post-hoc" tests to determine differences between sex and treatment interactions, where these were found, were performed by splitting the data into each level of each variable (i.e. males and females, FF, FM, MF and MM edges, and controls and intrusions). Simple models of the variables of interest were then run, e.g. change in eigenvector centrality ~ treatment using data from females, to investigate whether change in eigenvector centrality in females differed between treatment types. Node label permutations were performed as described above in order to extract randomised model coefficients used to calculate p-values for these post-hoc tests. These p-values were calculated in the same way as the models using the full data, but a Bonferroni correction was applied to account for multiple testing (grooming eigenvector centrality: 4 post-hoc tests, α=0.006; grooming and aggression strength: 6 post-hoc tests, α=0.004). We also performed post-hoc tests to ascertain whether changes in network measures were significantly different from 0, in cases where control and intrusion trials differed significantly. In this case, the simplified post-hoc models were run again, but with the intercept stripped from the model, so that each model coefficient represents the predicted mean of the response variable for each level of the categorical fixed effect, rather than the difference of the predicted mean from the intercept category. P-values represent whether these actual coefficients differ significantly from zero. Node label permutations were performed as described above in order to extract randomised model coefficients used to calculate p-values for these post-hoc tests (female grooming eigenvector centrality: 1 post-hoc test, α=0.025; grooming and aggression strength: 3 post-hoc tests, α=0.008). All analyses were run in R 3.6.1 (R Development Core Team, 2019), and all models were run using the *lmer* function in the *lme4* package (Bates and Maechler, 2009).

Results

Prediction 1 – Social cohesion will increase following encounters

There was a significant interaction between treatment type and sex (estimate = -0.123, p = 0.006, Table 3.2). For females, there was a greater increase in grooming eigenvector centrality between the pre-experimental and post-experimental phases in intrusion trials than in control trials (post-hoc test (α = 0.006): female data, control-intrusion estimate = 0.055, p < 0.001, Table A3.1, Figure 3.2). However, the change in grooming eigenvector centrality (between the pre- and post-experimental phases) in females in intrusion trials was not significantly different from zero, suggesting that centrality does not increase in real terms (post-hoc test (α = 0.0125): female data, intrusion estimate = 0.008, p = 0.10, Table A3.2). In contrast, among males there was no significant difference in the change in social cohesion (indicated by grooming eigenvector centrality) between control and intrusion trials (post-hoc test (α = 0.006): male data, control-intrusion estimate = -0.050, p = 0.38, Table A3.1). There was no significant difference in the change in grooming eigenvalue centrality between males and females in either control or intrusion trials (post-hoc tests (α = 0.006): control data, female-male estimate = 0.077, p = 0.02; intrusion data, female-male = -0.028, p = 0.78, Table A3.1). There was no relationship between change in grooming eigenvector centrality and either age, or an interaction between treatment type and age (Table 3.2).

Table 3.2 – Model parameter estimates from the grooming eigenvector centrality model, and p values from network permutations (p-values are calculated as a proportion of randomised model coefficients that are larger/smaller than the observed model coefficient, α = 0.025 as these were two-tailed tests). Model was fitted with individual identity as a random intercept (LMM, N = 857 observations (274 = female, 583 = male) across 100 individuals in 5 groups and 44 trials). The reference category for treatment type was control and for sex was female, the intercept therefore represents the estimate for females in control trials. Significant terms are given in bold.

Variable	Estimate	P-value
Intercept	-0.042	
Treatment	**0.121**	**0.0004**
Age	0.0002	0.447
Sex	**0.076**	**0.025**
Treatment:Sex	**-0.123**	**0.006**
Treatment:Age	-0.015	0.878

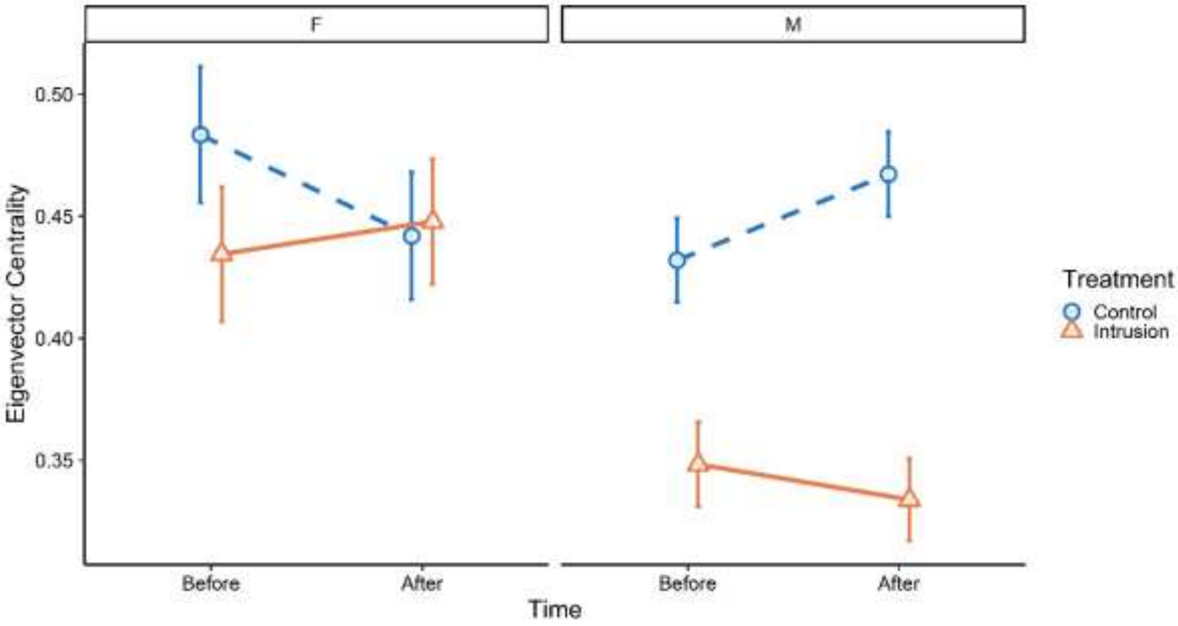

Figure 3.2 – The change in mongoose individual grooming eigenvector centrality from before presentations to after presentations for males and females in intrusion (orange triangles and solid lines) and control (blue circles and dashed lines) trials. The figure shows that for female mongooses intrusion trials led to an increase in grooming eigenvector centrality (although this was not significantly different from zero change), whereas control trials led to a decrease. Points shown are means from the raw data and error bars are standard errors on these means. N = 857 observations (274 = female, 583 = male) across 100 individuals in 5 groups and 44 trials.

Prediction 2 – Grooming directed towards males will increase following encounters

There was a significant interaction between treatment type and edge sex, (intrusion:MM estimate = -0.951, p = 0.006; intrusion:MF estimate = -0.609, p = 0.005; intrusion:MF estimate = -1.152, p = 0.001, Figure 3.3). Grooming strength decreased (which represents a reduction in the number of grooming interactions) in response to intrusion trials in male-to-male (post-hoc test (α = 0.004): MM data control-intrusion estimate = -0.850, p = 0.002, Table A3.3), male-to-female (post-hoc test (α = 0.004): MF data control-intrusion estimate = -0.508, p = 0.0002, Table A3.3) and female-to-male relationships (post-hoc test (α = 0.004): FM data control-intrusion estimate = -1.006, p = 0.0006; Table A3.3, Figure 3.3). Each of these changes in grooming strength was significantly different from zero, suggesting a change in grooming strength in response to simulated intrusion in real terms (post-hoc test (α = 0.008): MM data, intrusion estimate = -0.993, p = 0.00; MF data, intrusion estimate = -0.787, p = 0.00; FM data, intrusion estimate = -1.536, p = 0.00, Table A3.4). Female-to-female grooming strength did not differ between control and intrusion trials (post-hoc test (α = 0.004): FF data control-intrusion estimate = 0.146, p = 0.06; Table A3.3, Figure 3.3). In control trials there was no difference in the response of each edge sex (post-hoc tests (α = 0.004): control data, FF-MM estimate = 0.260, p = 0.09; FF-MF estimate = 0.221, p = 0.12; FF-FM estimate = -0.127, p = 0.53, Table A3.3). In contrast, in intrusion trials both male-to-female and female-to-male grooming decreased compared to female-to-female grooming (post-hoc tests (α = 0.004): intrusion data, FF-MF estimate = -0.530, p = 0.002; FF-FM estimate = -1.279, p = 0.00, Table A3.3). This suggests that female-to-female grooming relationships are not affected by intergroup conflict, but other grooming relationships weaken after intrusion, but not control, trials.

Older individuals reduced their grooming more (negative change in grooming strength) after intrusion trials than younger individuals (Table 3.3, Figure 3.4), and this slope was significantly different from zero (post-hoc test ($\alpha = 0.0125$): intrusion data, age estimate = -0.240, p = 0.00, Table A3.5, Table A3.6). In control experiments there was no change in grooming strength across age classes (post-hoc test ($\alpha = 0.0125$): control data, age estimate = -0.034, p = 0.83, Table A3.5).

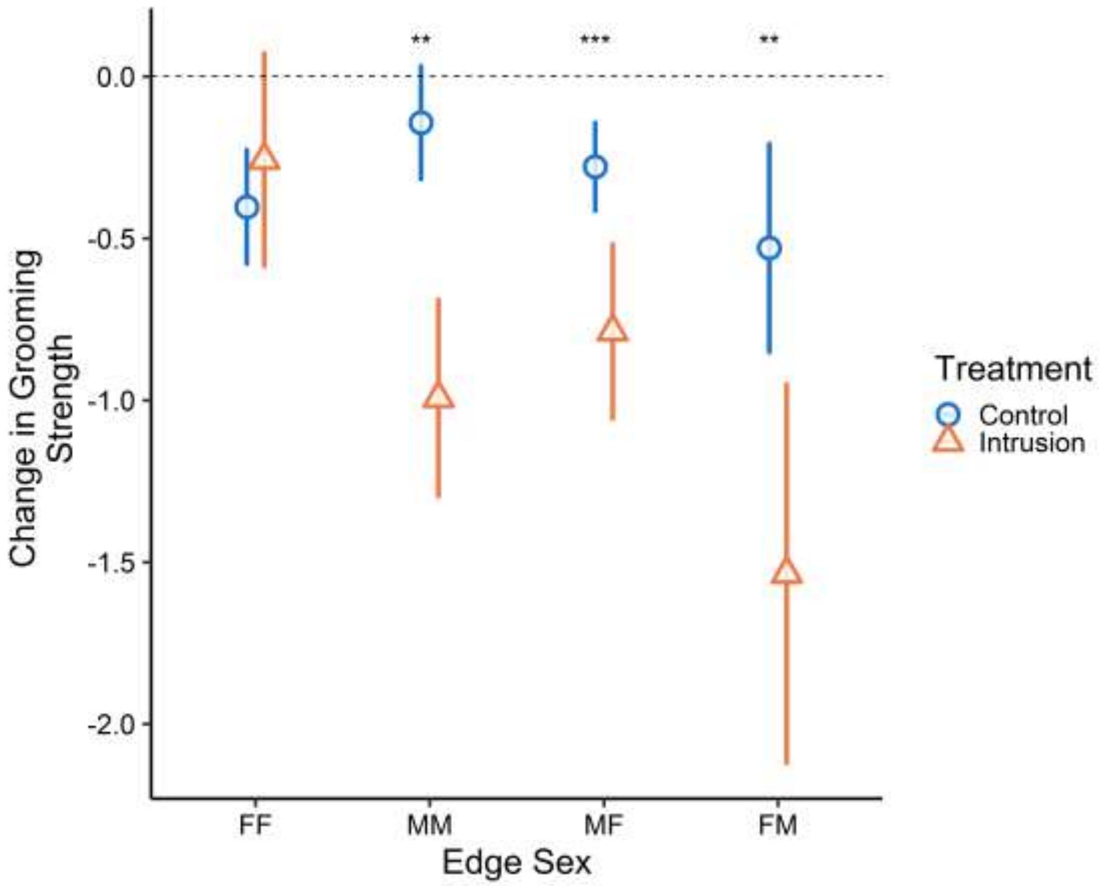

Figure 3.3 – The change in mongoose individual grooming strength from before presentations to after presentations for males and females in intrusion (orange triangles) and control (blue circles) trials. This figure shows that female-to-female grooming is not affected by intergroup conflict, but male-to-male, male-to-female and female-to-male grooming decreases after exposure to simulated conflicts. Points shown are means from the raw data and error bars are standard errors on these means. N = 1714 observations (FF = 274, MM = 583, MF = 583, FM = 274) across 100 individuals from 5 groups in 44 trials.

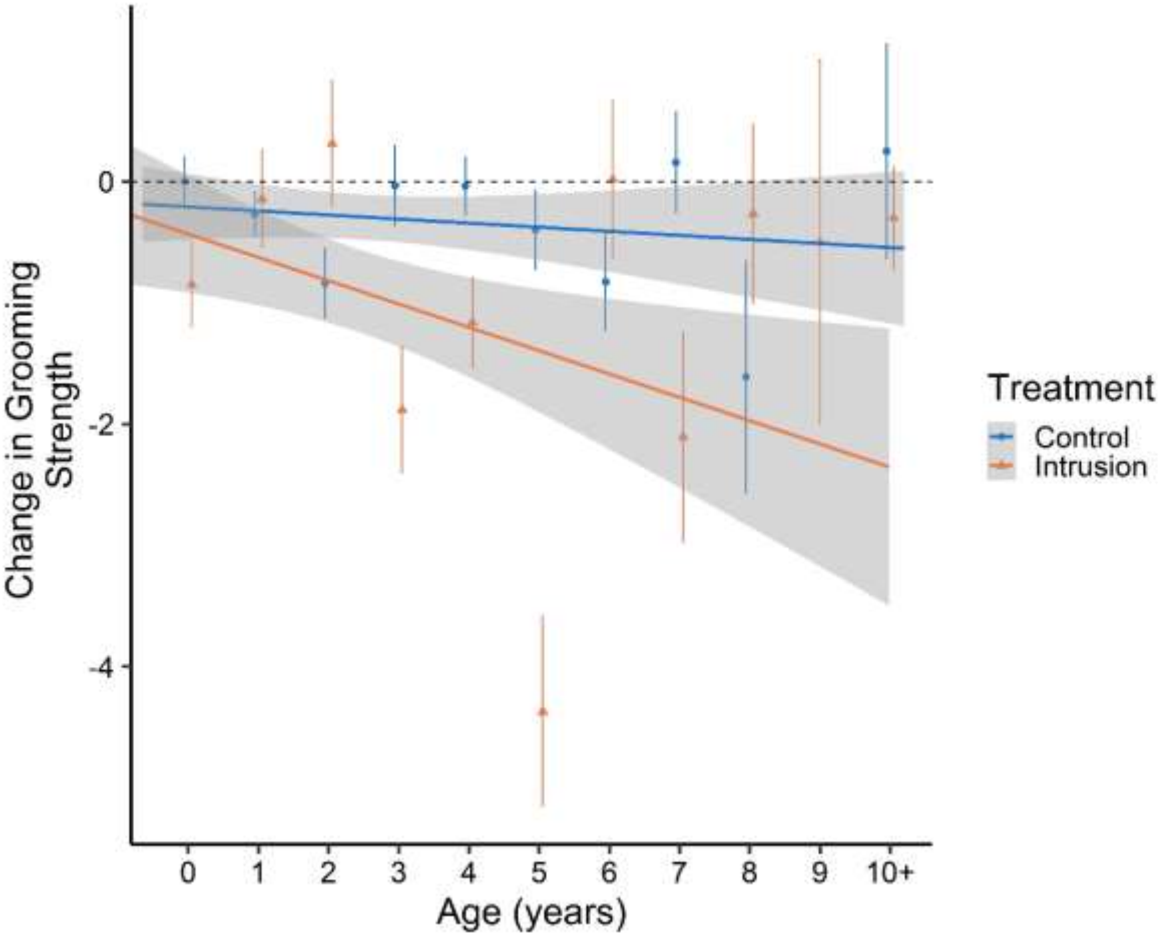

Figure 3.4 – The change in mongoose individual grooming strength from before presentations to after presentations across age classes in intrusion (orange triangles) and control (blue circles) trials. This figure shows that in intrusion trials older individuals reduce their grooming more than younger individuals. Points shown are raw data binned into categories (statistical analysis used a continuous measure) and lines are predictions from the raw data. N = 1714 observations across 100 individuals from 5 groups in 44 trials.

Table 3.3 – Model parameter estimates from the grooming strength model, and p values from network permutations (p-values are calculated as a proportion of randomised model coefficients that are larger/smaller than the observed model coefficient, α = 0.025 as these were two-tailed tests). Model was fitted with individual identity as a random intercept (LMM, N = 1714 observations (FF = 274, MM = 583, MF = 583, FM = 274) across 100 individuals from 5 groups in 44 trials). The reference category for treatment type was control and for edge sex was female-to-female, the intercept therefore represents the estimate for female-to-female grooming strength in control trials. Significant terms are given in bold.

Variable	Estimate	P-value
Intercept	-0.280	
Treatment	**0.631**	**0.004**
Age	-0.040	0.310
MM	0.282	0.080
MF	0.146	0.196
FM	-0.127	0.530
Treatment:MM	**-0.951**	**0.006**
Treatment:MF	**-0.609**	**0.005**
Treatment:FM	**-1.152**	**0.001**
Treatment:Age	**-0.154**	**0.004**

Prediction 3 – Between-sex aggression strength will decrease

Male-to-female aggression decreased significantly more in intrusion trials compared to control trials (estimate = -0.442, p = 0.00, Table 3.4, Figure 3.5; post-hoc test (α = 0.004): MF data control-intrusion estimate = -0.411, p = 0.00; Table A3.7). This decrease in male-to-female aggression in intrusion trials was significantly different from zero, suggesting a decrease in real terms (post-hoc test (α = 0.008): MF data, intrusion estimate = -0.264, p = 0.00, Table A3.8). There was no significant interaction between treatment type and male-to-male aggression (estimate = 0.289, p = 0.03) or female-to-male aggression (estimate = -0.163, p = 0.82), suggesting that changes in these relationships do not differ between trial types (Table 3.4, Figure 3.5).

The effect of both control and intrusion presentations on male-to-female aggression differed depending on the age of the actor (estimate = 0.073, p = 0.002; Table 3.4). Specifically, male-to-female aggression increased in older males following presentations, but not in younger males (Table 3.4, post-hoc test (α = 0.006): MF data, age estimate = 0.079, p = 0.0008, Table A3.9, Table A3.10). The change in aggression between other edge types was not related to age (post-hoc tests (α = 0.006): FF data, age estimate = -0.017, p = 0.95; FM data, age estimate = -0.088, p = 0.88; MM data, age estimate = -0.019, p = 0.74, Table A3.9). This result is of less interest because the effect is very small, and there was no difference in reaction between control and intrusion trials.

Table 3.4 – Model parameter estimates from the aggression strength model, and p values from network permutations (p-values are calculated as a proportion of randomised model coefficients that are larger/smaller than the observed model coefficient, α = 0.025 as these were two-tailed tests). Model was fitted with individual identity as a random intercept (LMM, N = 2571 observations (FF = 857, MM = 857, MF = 583, FM = 274) across 100 individuals in 5 groups for 44 trials). The reference category for treatment type was control and for edge sex was female-to-female, the intercept therefore represents the estimate for female-to-female grooming strength in control trials. Significant terms are given in bold.

Variable	Estimate	P-value
Intercept	0.043	
Treatment	-0.158	0.913
Age	-0.034	0.665
MM	0.008	0.711
MF	-0.075	0.680
FM	0.254	0.230
Treatment:MM	0.289	0.030
Treatment:MF	**-0.442**	**0.000**
Treatment:FM	-0.163	0.824
Treatment:Age	0.057	0.037
Age:MM	0.004	0.425
Age:MF	**0.073**	**0.002**
Age:FM	-0.090	0.876

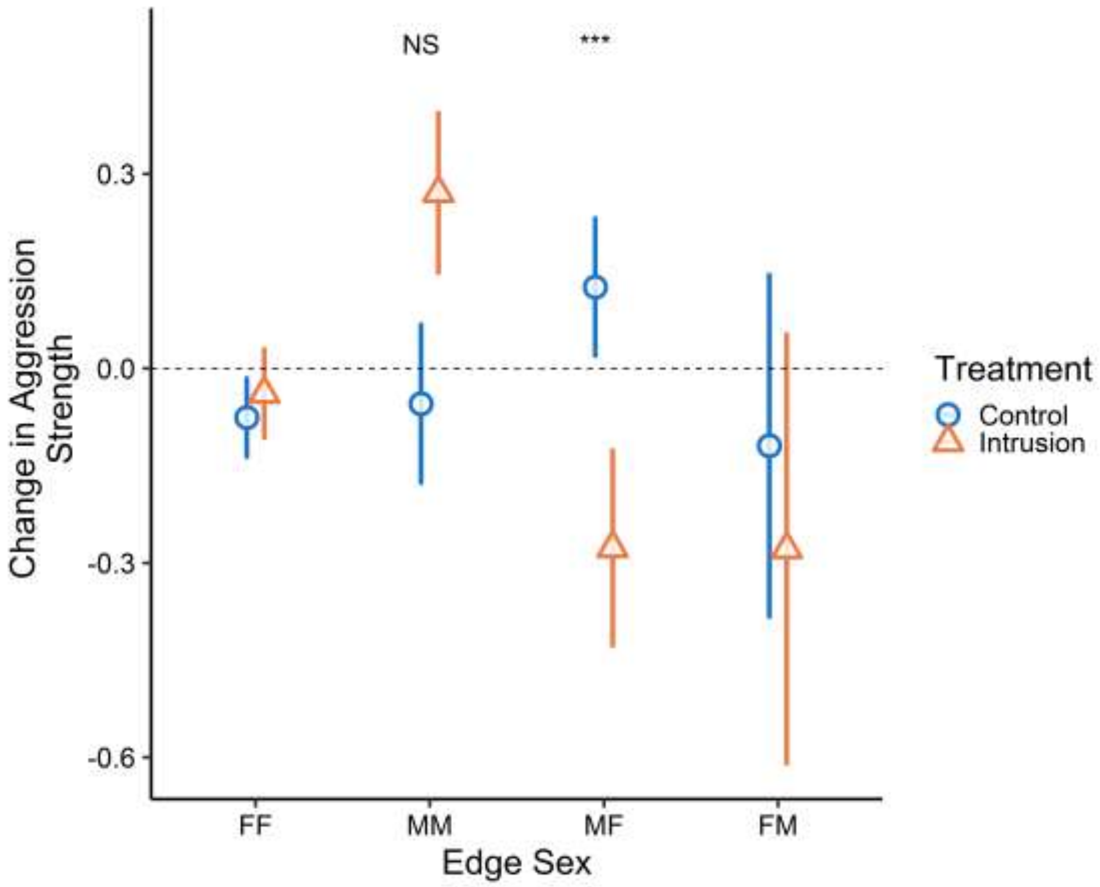

Figure 3.5 – The change in mongoose individual aggression strength from before presentations to after presentations for males and females in intrusion (triangles) and control (circles) trials. This figure shows that male-to-female aggression decreases in intrusion, but not control trials. Points shown are means from the raw data and error bars are standard errors on these means. N = 2571 observations (FF = 857, MM = 857, MF = 583, FM = 274) across 100 individuals in 5 groups for 44 trials.

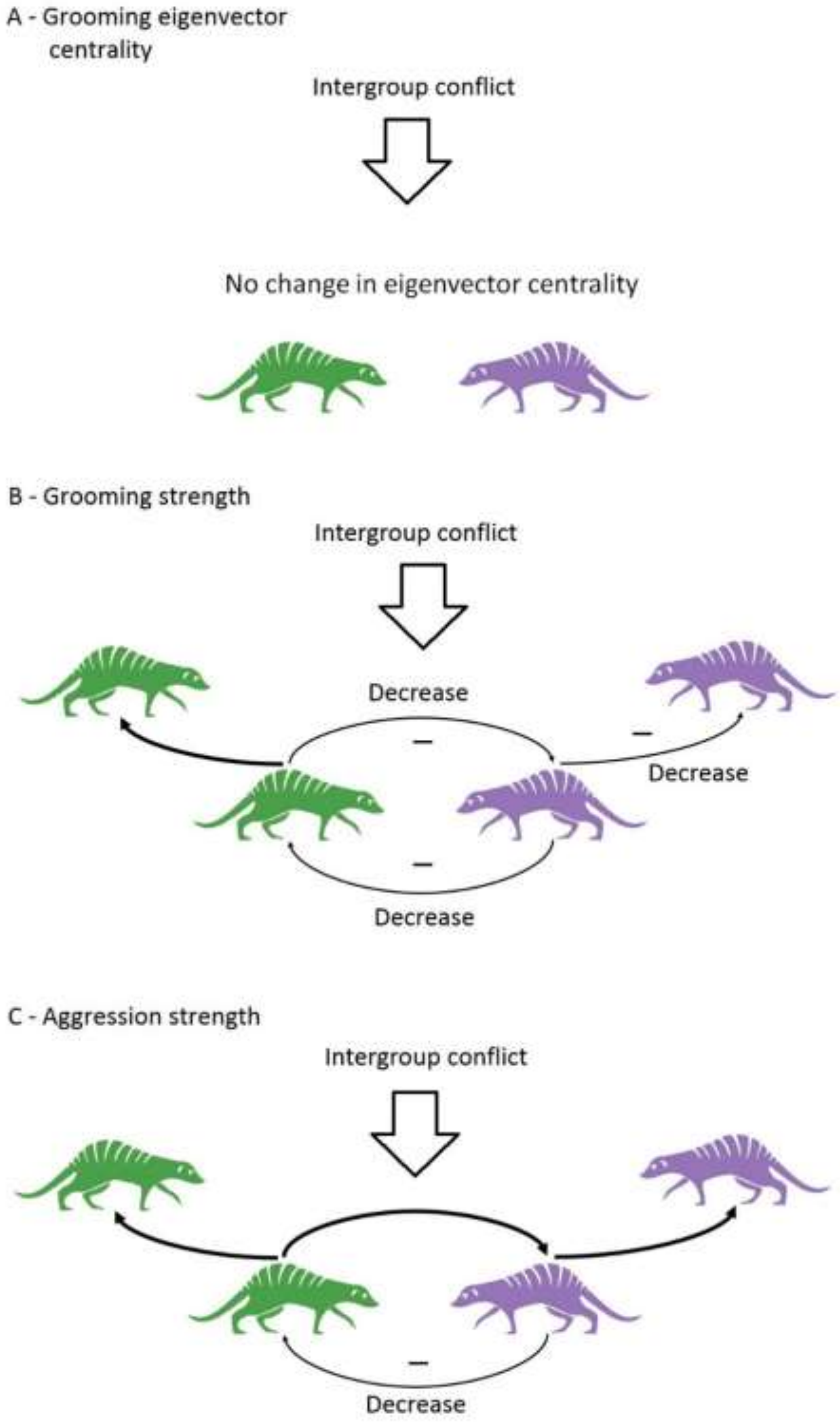

Figure 3.6 – Summary of the effect of intrusion trials on grooming and aggression networks (A) grooming eigenvector centrality does not change; (B) grooming strength decreases in male-to-male, male-to-female and female-to-male relationships; and (C) aggression strength decreases in male-to-female relationships. Female mongooses are shown in green and male mongooses in purple. Thinner lines indicate that grooming or aggression between mongooses decreased, thicker lines indicate that there was no change in the grooming or aggression.

Discussion

Banded mongooses adjusted their grooming and aggressive interactions between group members after simulated intergroup encounters. Following an intergroup encounter, and contrary to our predictions, we found that grooming decreased in male-to-male, male-to-female and female-to-male interactions. We also found that male-to-female aggression was reduced (following our predictions) but female-to-male aggression did not change. Additionally we found that older individuals reduced their grooming more after intrusion trials than younger individuals, and male-to-female aggression was reduced more in older males than younger ones. These results highlight both sex and age differences in the responses of banded mongooses to intergroup encounters.

Prediction 1 – Social cohesion will increase following encounters

Contrary to our simple prediction, we did not find an overall increase in grooming eigenvector centrality in intrusion trials, however, we did find that female eigenvector centrality increased in intrusion trials compared to control trials, but that male eigenvector centrality did not change. However, the increase in female eigenvector centrality in intrusion trials was not significantly different from zero, suggesting that simulated intrusions did not result in a significant change in social cohesion among females. This suggests that, despite differences between control and intrusion trials in female eigenvector centrality, there is no evidence for increased social cohesion after exposure to simulated intergroup conflict. This has not yet been tested for other species, but as affiliation at a group-level decreases rather than increases (as seen in Chapter 2) this might explain why eigenvector centrality did not increase.

Prediction 2 – Grooming directed towards males will increase following encounters

In contrast to our prediction, we found that male-to-male, male-to-female and female-to-male grooming declined after intrusion presentations. Unlike in primates, there seems to be no “reward” given to males from females in the form of grooming (Cooper, Aureli and Singh, 2004; Arseneau-Robar *et al.*, 2016). Male investment in grooming relationships may not be as important after conflicts, but equally males may be investing more time than females in other behaviours, like searching or patrolling, or alarm calling and scent marking, and not engaging in grooming. As yet there is no direct evidence for this, as male contribution to alarm calling, scent marking and movement patterns has not been measured. However, as males face a greater risk from rival groups than females, they may direct more time and energy into combating these external threats through such behaviours, rather than to internal relationships. Females may then reciprocate grooming less, as males are not grooming them, leading to a by-product reduction in female-to-male grooming. A meta-analysis of grooming relationships and intergroup conflict in primates found that increased female grooming was linked to high levels of intergroup conflict, but male grooming was not (Majolo, de Bortoli Vizioli and Lehmann, 2016). This meta-analysis suggests that this sex difference in affiliative behaviour linked to intergroup conflict might be widespread, although here we find the opposite result, with males grooming less. Grooming after a conflict may present itself as a trade-off, in which males reduce investment in internal relationships and increase defensive behaviours. An example of a similar trade-off has been observed in meerkats (*Suricata suricatta*). Males chased intruders more than females as they suffer a greater threat from the intruders, and reduced pup care when intruders were present (Mares, Young and Clutton-Brock, 2012). Our results also provide evidence that males are affected more by intergroup encounters than females, as all grooming strength changes involving males were negative, and female-to-female grooming was not affected by treatment type.

Grooming interactions initiated by older individuals also declined after intrusion presentations. Older individuals are more likely to be dominant and have genetic offspring in the group. They may therefore devote more time to territory defence as a form of offspring defence, rather than invest in affiliative social relationships, as seen in other species (Van Belle *et al.*, 2014; Arseneau *et al.*, 2015).

Prediction 3 – Between-sex aggression strength will decrease

Male banded mongooses reduced aggressive interactions towards the opposite sex after simulated intergroup encounters. This is consistent with the hypothesis that groups respond to an external conspecific threat by suppressing internal conflict to maintain social cohesion, as we predicted. In contrast, previous studies that measured post-conflict aggression found either an increase (Schaffner and French, 1997; Cooper, Aureli and Singh, 2004; Polizzi di Sorrentino *et al.*, 2012), or no change (Nunn and Deaner, 2004; Bruintjes *et al.*, 2015; Morris-Drake *et al.*, 2019), rather than any suppression of conflict. Although, one study exposing groups of cichlid fish to a neighbour group over an extended period of time (rather than a short-lived intrusions into the territory) did find a reduction in conflict between mating pairs (Hellmann and Hamilton, 2019). However, there was no evidence that males became more aggressive to other males in their group, as we predicted, or that males increased aggression directed towards females to discourage emigration or extra-group mating, as seen in previous primate studies (Cooper, Aureli and Singh, 2004). Male banded mongooses suffer higher rates of mortality from intergroup violence than females (Thompson, F.J. *unpublished data*), and females can even benefit from extra-group mating opportunities (Nichols, Cant and Sanderson, 2015). This could create conflict between males and females over engagement in intergroup encounters, which may not be paralleled in previous studies investigating the impact of intergroup conflict on within-group behaviour. A similar inter-sex conflict over engagement is seen in vervet monkeys (*Chlorocebus pygerythrus*), however, studies have shown that both males and females aggress other individuals during intergroup conflicts as a form of punishment or coercion (Arseneau-Robar *et al.*, 2016, 2018), which contrasts with the results of this study. Suppressing conflict between the sexes in banded mongooses may help promote social cohesion when there is risk of another encounter.

Despite evidence that male-to-female aggression is suppressed after an intergroup encounter, there seems to be no change in aggression within each sex, or from females to males. No change in within-sex aggression might suggest that within-sex conflicts are not strongly affected by intergroup conflict, and are more heavily influenced by other factors, such as dominance hierarchies (e.g. (Clutton-Brock *et al.*, 2006)) or reproductive conflict (Cant *et al.*, 2010). Alternatively, although not seen in this study (although male to male aggression increases but significantly), suppression of aggression to boost social cohesion may be balanced by intensified aggression within sex classes leading to no overall change in mean group aggression levels. Same-sex aggression may serve to encourage participation in future conflict, or to relieve tension from losing a conflict (Radford, Majolo and Aureli, 2016). A study on capuchins (*Cebus apella*) found an increase in within-group aggression and steeper dominance hierarchies after exposure to a neighbouring group, and suggested that as the conflicts were frequent and unresolved there was increased tension, rather than increased cohesion in the group (Polizzi di Sorrentino *et al.*, 2012). Banded mongooses experience frequent intergroup encounters, and the nature of the simulated intrusions may cause them to be "unresolved" as neither group clearly won, which may similarly cause tension within the group, and particularly within each sex. This may also mean that any changes to social networks are ephemeral and do not persist as intergroup interactions occur so frequently and disrupt social relationships regularly.

Caveats and limitations

Although the location of each experimental presentation was not recorded, and could therefore not be included as a factor in the statistical models, this is unlikely to change these conclusions. It is unlikely that there is any systematic bias in location of each trial either on the day of the presentation in control and treatment trials, or in the pre and post-trial periods. However, due to the limitations of the experimental design, comparisons between control and intrusion trials should be interpreted with some caution. Each experimental trial contains its own within trial control, the pre-experimental period, which helps to alleviate these concerns, but as control and intrusion trials differed in their observers, and were undertaken in blocks rather than fully randomised, some caution is needed in interpreting these results. Future work should endeavour to include both pre and post experimental periods, as well as balanced control and intrusion trials.

Conclusions

In conclusion, focusing on individual relationship changes using social network analysis can reveal important changes in behaviour after intergroup encounters. We found differences between males and females in their response to intergroup encounters, some of which were also affected by age. In banded mongooses, males are more socially affected by intergroup conflicts than females, changing both their grooming and aggressive patterns. This study reveals that suppression of between-sex competition, particularly from males to females, occurs post-conflict, and may be important for overcoming inter-sex conflict over entering into intergroup conflicts. Measuring group-level behaviours can be important in recognising general behavioural change after disturbance, but these measurements ignore the differences between individuals in groups. These individual differences may be more important when assessing changes in relationships, particularly, as in the case of intergroup conflict, when individuals have different costs and benefits associated with interacting with other groups. This study highlights the importance of studying both group-level behaviours and individual relationships to more fully understand responses to intergroup encounters. Social network analysis can reveal changes in within-group social dynamics that are susceptible to being obscured in studies of group level behaviour.

Chapter 4:

The effect of simulated intergroup encounters on movement patterns and home range use in banded mongooses

Abstract

Intergroup conflicts have a wide range of impacts, including affecting movement and ranging patterns. Previous studies found contrasting responses to intergroup conflicts, but no explanation for these differences has been suggested. However, these can be broadly grouped into those following what I call a “conflict avoidance” response: avoiding areas close to the fight; and those following what I call a “defence” strategy: “patrolling” and using the edges of the group’s territory. We simulated intergroup encounters in banded mongoose groups to assess whether mongooses respond to intergroup encounters by avoiding conflict, or investing in defence. We measured movement characteristics; path characteristics in the core or periphery of the home range; and changes to home range use. We found that mongooses spend more time in the core in the hours after presentations, and after presentations groups moved faster when in the periphery, and further when in the core of their territory. However, these effects were similar in both control and experimental trials, raising questions as to how the trials were perceived by the mongooses. Overall our results provide tentative evidence that intergroup conflict affects use of the home range over a few hours, and movement patterns in different areas of the territory over at least seven days, suggesting a longer-term impact of conflict on mongoose behaviour. These longer-term movement responses to stimuli of intergroup conflict may have important effects on survival, reproduction and fitness. These changes may provide one link between short-term behavioural changes and long-term genetic evolutionary models.

Introduction

For social animals, possession of an exclusive group territory is crucial for individual fitness (Harper, 1985; Both and Visser, 2000; Mosser and Packer, 2009; Mumme *et al.*, 2015). Territories can boost fitness by providing resources, and access to mates, or helpers (for cooperative breeders). As territories are beneficial, and differ in their quality and availability, conflicts over territories are widespread – both for individuals holding territories, and for groups that defend a territory together (Adams, 1990; McComb, Packer and Pusey, 1994; Whitehouse and Jaffe, 1996; Watts and Mitani, 2000; Boydston, Morelli and Holekamp, 2001; Cant, Otali and Mwanguhya, 2002; Gros-Louis, Perry and Manson, 2003; Korstjens, Nijssen and Noe, 2005; Harris, 2006; Boesch *et al.*, 2008; Markham, Alberts and Altmann, 2012; Golabek, Ridley and Radford, 2012; Briffa and Hardy, 2013; Kokko, 2013; Cassidy *et al.*, 2015; Rosenbaum, Vecellio and Stoinski, 2016). Conflicts over territories can have consequences including territory expansion or shrinkage; shifting home ranges or concentration of use; or changes to movement patterns, like moving faster or further (Mitani, Watts and Amsler, 2009; Markham, Alberts and Altmann, 2012; Crofoot, 2013; Christensen *et al.*, 2016). These conflicts can have repercussions for fitness via territory changes, as well as behavioural changes of individual animals.

Intergroup conflict can have dramatic, but varied, impacts on a social group's territory and movement behaviour. Groups may be competing directly for territory and the resources inside, or more indirectly for mates and breeding opportunities provided by a territory. Groups' responses to intergroup conflict, can be relatively long term, for example, baboons (*Papio cynocephalus*) were less likely to use areas in the three months after a conflict was lost in that area, than in the three months before (Markham, Alberts and Altmann, 2012). Responses to intergroup conflict are also varied: capuchin monkeys (*Cebus capucinus*) moved faster, further and had larger displacements for the rest of the day after losing a conflict, compared to after winning a conflict (Crofoot, 2013), whereas, dwarf mongooses (*Helogale parvula*) moved more slowly and over shorter distances after being presented with faeces from a rival group (Christensen *et al.*, 2016). These changes in space use and movement patterns could be important for group dynamics, and may push losing groups into lower quality areas of their territory, or be energetically costly (Crofoot, 2013). In an extreme case, a chimpanzee (*Pan troglodytes*) group in Uganda expanded their territory into another group's range after a series of lethal intergroup attacks (Mitani, Watts and Amsler, 2009). These previous studies highlight that groups don't necessarily respond in similar ways to intergroup conflict, but that the impacts can be dramatic and long-lasting.

Broadly it seems that there may be two different types of response to intergroup conflict in terms of movement and home range use. Groups may attempt to avoid conflict – which I call the conflict avoidance hypothesis – which is characterised by avoiding areas where conflict occurs, and moving faster and further away from these areas. Conflict avoidance could be beneficial as groups can avoid further costs associated with intergroup conflict (e.g. mortality, resource/territory loss), and seems to occur when intergroup fights are lost (Markham, Alberts and Altmann, 2012; Crofoot, 2013). In contrast, groups may start to patrol their boundaries, or actively seek out rival groups, in order to try and defend their territory – which I call the defence hypothesis – characterised by moving towards the edges of a territory (where other groups are likely to be encountered) and potentially involving slower more deliberate movements over shorter distances. Investing in defence may be a beneficial strategy for groups engaged in intergroup conflict, as groups which are “prepared for battle” may be more successful during encounters, and at defending their territory. Patrolling behaviour may even reduce the likelihood of conflict, acting as a deterrent to rival groups (Sillero-Zubiri and Macdonald, 1998; Jordan, Cherry and Manser, 2007).

In this study we test these two contrasting hypotheses in banded mongooses (*Mungos mungo*) using simulated territorial intrusions to assess how mongoose group movements are affected by intergroup conflict. Banded mongooses experience frequent and violent encounters, with consequences for their social behaviour (see Chapter 2) and relationships (see Chapter 3). We therefore expect that banded mongoose movements and territorial use will also be affected by intergroup encounters. We hypothesise that banded mongooses will respond to intergroup conflict following the predictions from the conflict avoidance hypothesis, as conflicts are costly (in terms of mortality and potential loss of paternity (for males)), and it is therefore beneficial to flee from areas of conflict. However, frequent and high cost encounters could mean that defensive “patrolling”-type behaviour is beneficial to defend the territory pre-emptively, or to attempt territory expansion. Small groups may “patrol” to reduce the likelihood of intergroup encounters, through early detection of rival groups or indirect defence (e.g. scent marks), as they are at a higher risk of group attrition via adult mortality and reduced pup survival from intergroup attacks, and avoidance of conflict is important (Cant *et al.*, 2016). Large groups may “patrol” for the opposite reasons, to seek out rival groups, and attempt to expand territory and resources.

In this study, we ask three questions, and make specific predictions following the conflict avoidance and defence hypotheses. Firstly, we ask how movement path characteristics (e.g. speed) are affected by exposure to intergroup conflict. We predict that mongooses will move further, faster and more directly if they are avoiding conflict, and more slowly, over shorter and more meandering paths if they are investing in defence by patrolling. Secondly, we ask whether mongooses change their movements in different areas of the territory after exposure to conflict. We predict that mongooses will move further and faster when in peripheral areas compared to core areas of the territory if they are avoiding conflict, and the opposite if they are patrolling. Thirdly, we ask which areas of their territory mongooses use after exposure to intergroup conflict. We predict that mongooses will use areas closer to the core if they are avoiding conflict, and areas further from the core if they are investing in defence.

Methods

Study Site

Data were collected for this study from banded mongooses on the Mweya Peninsula in Queen Elizabeth National Park, Uganda (0^{o}12'S, 29^{o}54'E), between January 2016 and May 2017. The study was performed on individuals that are part of a long-term study population. In depth descriptions of the study site can be found in (Rood, 1975; Cant, 2000; Cant, Vitikainen and Nichols, 2013).

Banded mongooses are small (< 2 kg) diurnal herpestids that live in stable multi-male, multi-female groups of between 10 and 30 individuals. Groups are territorial and defend their territories from other groups during frequent, and sometimes lethal, intergroup conflicts (Nichols, Cant and Sanderson, 2015; Thompson, Marshall, Vitikainen and Cant, 2017). Banded mongooses in the study site almost exclusively engage in physically violent inter-group interactions, with very few interactions between groups that are neutral, peaceful, or involve only signalling between groups with no physical interaction, e.g. war dances, or vocal defence. Mongooses respond to sighting a rival group by standing alert and calling to other group members, after which they often congregate and stand alert looking for the rival group (Cant *et al.*, 2016). Small groups typically flee from larger groups, with larger groups sometimes giving chase (Cant, Otali and Mwanguhya, 2002; Furrer *et al.*, 2011). If groups are more evenly matched in size then mongooses bunch together and approach in “battle lines”. Fighting can be highly aggressive involving biting and scratching, and sometimes individuals are held down and attacked by multiple rival group members (Cant, Otali and Mwanguhya, 2002; Nichols, Cant and Sanderson, 2015; Thompson, Marshall, Vitikainen and Cant, 2017).

All mongooses in the study population are individually marked using unique hair-shave patterns and are habituated to close observation from 2-4 m. One to two mongooses in each group are fitted with a radio collar weighing 26-30 g (Sirtrack Ltd, Havelock North, New Zealand) with a 20-cm whip antenna (Biotrack Ltd, Dorset, UK) to allow the groups to be located. One to two additional individuals are fitted with a GPS collar weighing 24-41g (Gipsy4 and Gipsy5, Technosmart, Italy), to allow group movements to be recorded. Five focal groups (which are habituated to being followed) were used in this study.

Data Collection

Experimental timeline

Experimental trials took place over 15 days, with simulated intrusion or control presentations on the 8th day, and more intensive observation in the five central days (see Figure 4.1). We recorded a group behavioural baseline of movement behaviour during the first seven days (pre-experimental phase). We carried out simulated intrusions or control presentations on the eighth day (experimental phase). During the final seven days of the trial we recorded movement behavioural responses to the presentations (post-experimental phase).

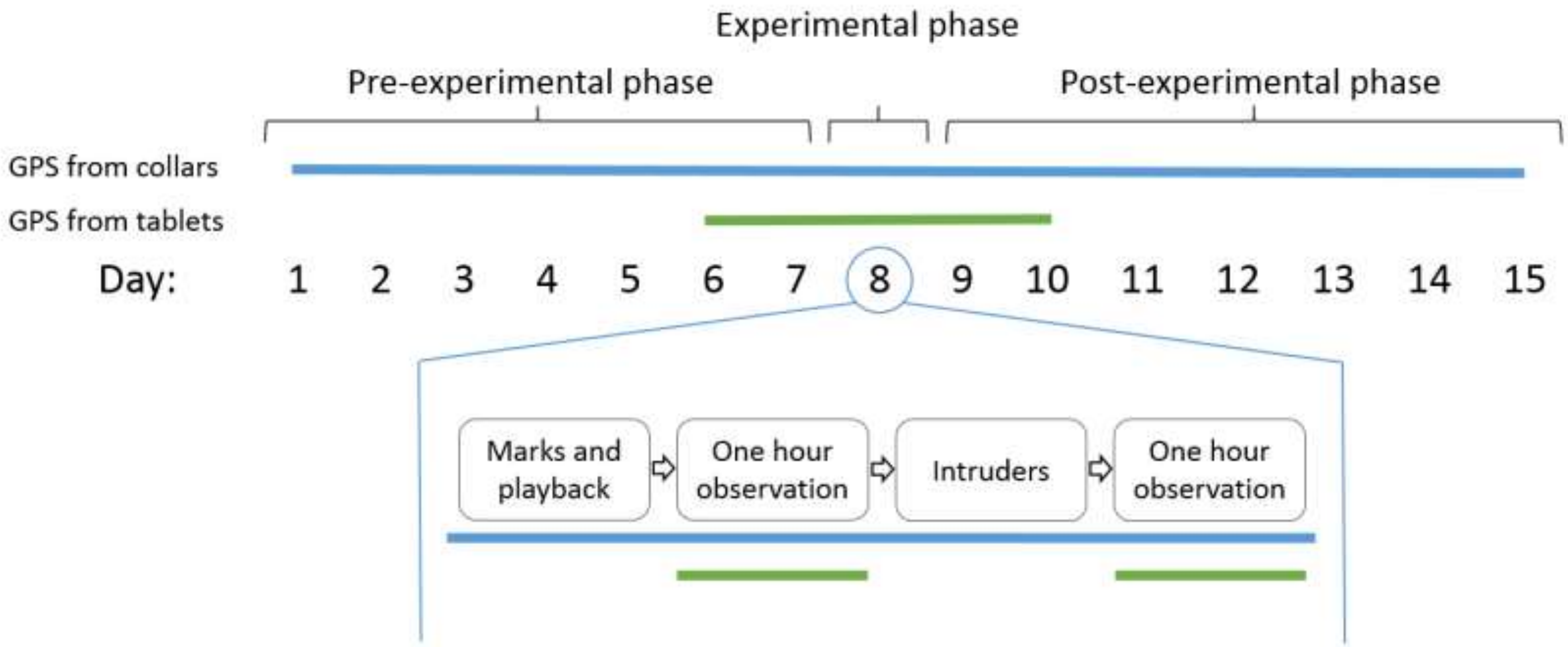

Figure 4.1 – Summary of the experimental timeline. Blue lines show when collar GPS data were collected (30 minute fixes from day 1 to day 15 continuously), and green lines show when tablet GPS data were collected (minute fixes from day 6 to day 10 during behavioural observations for one hour each morning, and one hour each afternoon). The area under the blue arch shows a zoomed in area of the timeline during the experimental phase when presentations were performed. The timeline was the same for both control and intrusion trials.

Presentations

We carried out simulated intrusion presentations and control presentations with five focal groups. Presentations to each focal group were separated by at least two weeks to prevent habituation of the mongooses to the stimuli being presented. It was not possible to standardise the location of each presentation, in terms of the home range (core or periphery), and the location of each presentation was not recorded accurately. In total we carried out 22 control trials, and 22 simulated intrusion trials.

Simulated intrusion presentations

Faeces, urine and scent marks on plastic from a neighbouring rival group (considered to be the largest threat to the focal group) were presented to the focal group on the morning of the presentation day (07:43-10:27 hours). Faeces, urine and scent marks were collected early in the morning from the rival group. These samples were collected from multiple individuals in the group, both males and females from different age classes, and were collected within 30 minutes. These samples were usually collected as the group emerged from the den or from the first group marking site of the day. Plastic sheets were presented to encourage urination and scent marking. These samples were transferred as quickly as possible to the presentation site, and presented within 2 hours of collection. The presentation site was placed in the foraging path of the focal group, to ensure that the mongooses encountered the stimulus. The samples were arranged in a semi-circle on open ground, with faeces placed around the sheets of plastic (spaced over 70-100cm) as mongooses often use open patches for territorial marking (Müller and Manser, 2007).

The mongooses were allowed to explore the scent marks for three minutes, after which a playback of war cries from the same rival group (that the scent marks were collected from) occurred. Playbacks were conducted using a portable USB speaker (iHome IHM60) hidden in vegetation. War cries emitted in response to rival mongooses presented in traps were recorded using an H1 Zoom recorder attached to a Sennheiser directional microphone. Recordings were taken from 2-3 metres away, cut into 30 second sections in which vocalising was occurring, and the amplitude of each clip was standardised using the normalize function in Audacity 2.1.2 to -1dB (http://audacityteam.org). Recordings were collected more than one week before playbacks were used. Each 30 second playback clip was used only once to prevent habituation of the mongooses to particular recordings.

On the afternoon of the same day (16:35-18:18 hours), four adult male individuals from the rival group, were trapped and presented to the focal group. The traps were washed with soap and water to reduce scents from any previous trapping events before the males were captured. Trapped animals were transferred from the rival group to the focal group and were placed in the foraging path of the focal group to ensure they encountered the traps. After five minutes the rival males were removed and returned to their own group, to minimise stress levels. Traps were covered at all times except during the five minute presentation.

Control presentations

The same timeline and procedures were followed for control presentations. However, faeces and marks were collected from the focal group, and re-presented to them after they had moved to a new area. War cries were replaced with close calls (a non-threatening communication call between group members (Müller and Manser, 2008)) from the focal group as the playback recordings. The close calls were recorded from the focal group during normal foraging behaviour when there were no threats from rival groups or other sources. These recordings were cut and standardised in the same way as the war cry recordings. Four adult males were presented in traps, as before, but these were males from the focal group, which were trapped and removed for half an hour (to a safe, shaded location) before they were presented to the rest of the focal group.

These control presentations were carried out in blocks between experimental trial blocks. This is because control presentations were carried out when one of the two main observers was not present at the study site. The other main observer was joined by one additional observer during control periods, so there was always at least two observers during each trial, and always at least one of the main observers present in each trial. Control trials were performed when only one main observer was present, as these were logistically easier to carry out, requiring visitation of only one pack rather than two on the day of the presentation, and therefore requiring less expertise from the additional observer. Because of these differences between control and experimental trials, a correction factor was applied to one of the variables, grooming, outlined below in the statistical analysis section.

Movement data

Movement data were collected in two ways – from GPS collars on individuals in each group (Gipsy4 and Gipsy5 collars, Technosmart, Italy), and from GPS fixes collected by tablet computers (via the Mongoose2000 app (Marshall *et al.*, 2018), on Samsung Galaxy Note 10.1 tablets).

The tablet GPS data were used to analyse fine-scale (locations every minute) but short-term movements. These data were collected for two days preceding either a control or a simulated intrusion presentation; on the day of the presentation; and for two days after the presentation, alongside behavioural observations. Tablets collected GPS fixes every minute, and were used to collect GPS data for one hour in the morning (starting between 06:56 and 11:32 hours) and for one hour in the afternoon (starting between 15:25 and 18:38 hours) on each of the five days. Occasionally collection of tablet GPS data failed, but all trials (n = 44) had more than 8 hours of movement data from an expected 10 hours (mean = 9.6 ± 0.1 hours, total number of GPS fixes = 24,536).

The collar GPS data were used to analyse broader-scale (locations every half an hour) and more mid-term movements (over 15 days). Data were collected between 07:00 and 19:00 at 30 minute intervals, with a gap between 12:00 and 15:00. These times correspond with mongoose activity, mongooses emerge after sunrise, and return to their den at sunset, but activity drops when they rest during the hottest time in the middle of the day. GPS collars took a burst of 10 fixes at each scheduled fix time, and these were then filtered for accuracy. To filter for accuracy all GPS fixes with fewer than 4 satellite connections and fixes with an HDOP (horizontal dilution of precision) value of over 4 were removed. Additionally fixes with unrealistic longitude (< 28.85 or > 29.95), latitude (< -0.21 or > -0.15), or altitude (< 800m or > 1100m) values for the study site were removed. Finally, data were restricted to the Mweya peninsula, using a shape file of the area, to remove fixes that fell in the lake. If multiple fixes were still associated with a scheduled fix time, the final fix in the burst was used to ascertain the likely position of the collar, as the final fix is likely to be the most accurate. These data were collected throughout the study period, and were also used to calculate the home ranges of each group. Four experimental trials were removed from this data set, as data were too patchy to be reliable (experimental trials with no GPS fixes across multiple days). These excluded trials were from four different groups, and included three intrusion trials and one control trial. All included trials (n = 40) had at least 12 days of data, from an expected 15 days (mean = 14.4 ± 0.2 days, mean number of fixes per trial = 176.6 ± 0.3 (range = 93 – 221), total number of fixes = 5,690).

Home range calculation

Home ranges were calculated for the three months preceding the day of each presentation, using the collar GPS data. Three months represents approximately one breeding cycle of the group (from oestrus to oestrus), and should therefore account for any differential use of the home range across the breeding cycle.

Each home range was calculated using the *ctmm* package in R, which uses autocorrelated kernel density estimation (Fleming and Calabrese, 2019). Rasters were created for each home range utilisation distribution using the cumulative distribution function, so each cell of the raster contains the cumulative probability of use value for this location, indicating the probability that the cell is used across the home range time frame by the focal mongoose group. A cell value of 1 indicates a probability of 1 that the cell is used by a group, which suggests a core area that is frequently used, whereas a value of 0 indicates that there is a probability of 0 that the cell is used, suggesting a peripheral and rarely used area. The cumulative probability of use was extracted for each observed location from both the tablet and collar data GPS data during the experimental time period, using the *raster* and *move* packages in R (Hijmans, 2018; Kranstauber, Smolla and Scharf, 2019). These extracted values give an indication of whether mongoose groups were close to core areas of their territory or more peripheral areas.

Calculation of variables

Collar data and tablet data were analysed as separate datasets, however both datasets were manipulated in a similar way to calculate path characteristics and home range use characteristics.

To calculate path characteristics the distance (m) and speed (m/s) between each GPS fix was calculated using the *move* package in R (Kranstauber, Smolla and Scharf, 2019). These distances and speeds were then collated into path measures for each hour of behavioural observation (tablet GPS data) and for each day of the experimental trial (collar GPS data).

For tablet GPS data the total distance (sum of the distances between fixes); mean speed; the displacement (distance from first point in the path to final point); and tortuosity (a ratio of the total distance travelled and the displacement of the animal – this creates a tortuosity value of 1 for a straight line, and higher values indicate a more tortuous path) were calculated.

The collar GPS data were analysed not simply as path characteristics, but as path characteristics in relation to the area of the territory that the movement was taking place. In this analysis the GPS fix was categorised as either in the “core” of the territory (> 0.50 cumulative probability of use, which is equivalent to the 50% kernel distribution boundaries often defined as the core territory in other home range analyses (White and Garrott, 1990; Downs, Horner and Tucker, 2011; Fleming and Calabrese, 2017)) or in the “peripheral” area of the territory (<= 0.50 cumulative probability of use). The total distance for travel in the core and in the periphery was calculated as the sum of distances between fixes categorised as either core or peripheral. The mean speed was calculated as the mean speed value for fixes categorised as either core or peripheral. The dataset therefore comprised two values for each day of the experiment – one for movements undertaken in the core, and one for movements undertaken in the periphery of the territory. This analysis was undertaken to investigate whether path distance (m) or speed (m/s) differed according to the location in which they took place in relation to the home range of the group.

As with movement path characteristics, home range characteristics were brought together into one value to represent each hour of fine-scale tablet data, and each day of broad-scale collar data. In the case of home range data, the mean cumulative probability of use was used to represent the areas that mongooses used in relation to their home range, with a high value indicating that areas closer to the core of the territory were used and a low value indicating areas closer to the periphery were used. These data were also used to calculate how much time mongoose groups spent in either the “core” or the “periphery” of the territory. For each hour (tablet data) or each day (collar data) the percentage of time spent in the “core” territory was calculated. The difference between the starting location and the end location was also calculated (starting location cumulative probability of use – end location cumulative probability of use) to indicate whether a group moved closer to the core of the territory (indicated by a negative number) or closer to the periphery (indicated by a positive number) by the end of the observation. This was calculated for the tablet data only.

Statistical Analysis

Statistical analysis was performed in R 3.6.1 (R Development Core Team, 2019) using the *lme4* package (Bates and Maechler, 2009). Linear mixed models were constructed for each of the response variables of interest. Maximal models were created for each response variable, with treatment (control or simulated intrusion), time point (pre-experimental, experimental, or post-experimental), the starting location of the group (as a cumulative probability of use value from home range calculation – as this might affect the group's movements), and a three-way interaction between these variables, as explanatory variables of interest. The number of individuals in the group, breeding status of the group (oestrus, pregnancy, babysitting, escorting, non-breeding) and the mean rainfall (in the previous 30 days, as a proxy of food availability) were also included as fixed effects, as these could all potentially affect the movements of a group. The location of the presentation could not be included within the model, to account for differences in reactions between the core and periphery of a territory, as this was not recorded accurately. However, the starting location of the group on the day of the presentation gives an approximate location of each presentation. All models are summarised in Table 4.1, and explained in more detail below.

Question 1 – do mongooses move further and faster after simulated intergroup conflict to avoid further conflict?

Path characteristics were analysed from tablet GPS data over five days. Each of the path characteristics (total distance, displacement, mean speed, and path tortuosity for each hour of observation) was log-transformed to reduce residual heterogeneity and meet the assumptions of normality. Trial identity (to account for repeated measures), and mongoose group identity were included as random effects in models with these variables.

Question 2 – do mongooses move faster and further in the periphery after simulated intergroup conflict to avoid further conflict?

Path characteristics in specific areas of the home range (core vs. periphery) were analysed using collar GPS data over fifteen days. Mean speed for each day of the experiment was log transformed to reduce residual heterogeneity and meet the assumptions of normality, no transformation was required for the total distance travelled. Trial identity (to account for repeated measures), and group identity were included as random effects in models with these variables.

Question 3 – do mongooses spend more time in the core, and move closer to it after simulated intergroup conflict?

Home range characteristics were analysed from tablet GPS data over five days, and collar GPS data over fifteen days (except the change in home range use which was only analysed using tablet data). Percentage time spent in the core area was logit transformed to reduce residual heterogeneity and meet the assumptions of normality. The mean cumulative probability of use (from home range calculation) used in each hourly observation, and the change in home range use (starting location cumulative probability – end location cumulative probability) in each hourly observation were not transformed, as assumptions were met. Mongoose group identity was not included in these models as it did not explain any variance and caused singularity issues with the model fit. Trial identity (to account for repeated measures) was included as a random effect in models with these variables.

Table 4.1 – Details of the models fitted in each stage of the analysis in this chapter. *All models also include the number of individuals in the group, the breeding status of the group, and the mean rainfall in the previous 30 days as fixed effects.

Models predicting how intergroup conflict affects:	Measured as	Data source	Sample size	Random effects	Fixed effects*	Transformation
Path characteristics:						
Distance	The distance (m) groups travelled in each hour of observation	Tablet	414	Trial ID Group ID	Three-way interaction (treatment type, time point, starting location)	Log
Speed	The mean speed (m/s) groups travelled in each hour of observation	Tablet	414	Trial ID Group ID	Three-way interaction (treatment type, time point, starting location)	Log
Displacement	The distance (m) from the starting location to the ending location of each hour of observation	Tablet	414	Trial ID Group ID	Three-way interaction (treatment type, time point, starting location)	Log
Tortuosity	The ratio of the total distance travelled and the displacement of the group	Tablet	414	Trial ID Group ID	Three-way interaction (treatment type, time point, starting location)	Log
Path characteristics in relation to home range:						
Distance	The distance (m) groups travelled on each day of the experiment in core, or in peripheral areas of the territory	Collar	952	Trial ID Group ID	Three-way interaction (treatment type, time point, area)	None
Speed	The mean speed (m/s) groups travelled on each day of the experiment in core, or in peripheral areas of the territory	Collar	850	Trial ID Group ID	Three-way interaction (treatment type, time point, area)	Log

Home range characteristics:						
Time spent in the core vs the periphery	The percentage of time a group spent in the core territory (locations with > 0.50 cumulative probability of use)	Tablet	414	Trial ID	Three-way interaction (treatment type, time point, starting location)	Logit
		Collar	476			
Area of the home range used	Mean cumulative probability of use value of each location (each GPS fix) a group was located	Tablet	414	Trial ID	Three-way interaction (treatment type, time point, starting location)	None
		Collar	476			
Moving towards or away from the core	Change in cumulative probability of use value (staring CP – ending CP) for each hour of observation. A negative number indicates a group moved closer to the core of the territory and a positive value indicates they moved closer to the periphery	Tablet	414	Trial ID	Three-way interaction (treatment type, time point, starting location)	None

Model comparison

To assess the significance of each explanatory variable, we compare the likelihood ratio of the maximal model to that of the model without that explanatory variable (Bates *et al.*, 2015). Parameter estimates and standard errors are taken from the maximal models, rather than following a stepwise model reduction procedure, due to problems associated with this method (Whittingham *et al.*, 2006; Mundry and Nunn, 2009; Forstmeier and Schielzeth, 2011). We removed nonsignificant interaction effects from our maximal model prior to testing the main effects (Engqvist, 2005). Post-hoc tests were performed using the *emmeans* package in R, which calculates estimated marginal means from a model and contrasts them (Lenth, 2019).

Results

Question 1 - do mongooses move further and faster after simulated intergroup conflict to avoid further conflict?

Contrary to the predictions of either the conflict avoidance or the defence hypothesis the distance travelled, the displacement, the tortuosity and the mean speed of travel of mongoose groups each hour were not affected by treatment type, time point, start location, or an interaction between these factors. Distance travelled and mean speed were also not affected by any of the other explanatory variables (Table 4.2).

However, the displacement distance of a mongoose group in an hour was affected by the breeding status of the group ($X^2 = 18.31$, $p = 0.001$, see Table 4.2 for estimates). Displacement was smaller when groups were escorting (post-hoc test: estimate ± SE = -0.58 ± 0.17, $t = -3.43$, $p = 0.01$, Table A4.1), or babysitting (post-hoc test: estimate ± SE = -0.49 ± 0.16, z = -3.00, p = 0.04, Table A4.1) than when they were pregnant.

Similarly, the tortuosity of a mongoose group's path was also affected by the breeding status of the group ($X^2 = 18.89$, $p < 0.001$, see Table 4.2 for estimates). Tortuosity was higher (indicating more meandering paths) when groups were escorting than when they were in oestrus (post-hoc test: estimate ± SE = 0.75 ± 0.24, t = 3.16, p = 0.03, Table A4.2) or pregnant (post-hoc test: estimate ± SE = 0.49 ± 0.16, t = 3.15, p = 0.03, Table A4.2). Additionally, path tortuosity was lower, indicating that paths were more direct, when previous rainfall was higher (estimate ± SE = -0.12 ± 0.06, $X^2 = 4.38$, p = 0.04, Table 4.2).

Table 4.2 – Model comparison results for path characteristics. This table contains the results from four separate models, predicting (1) the total distance travelled by mongoose groups in one hour; (2) the displacement distance of mongoose groups in one hour; (3) the mean speed of movements by mongoose groups in one hour; and (4) the tortuosity of the path of a mongoose group in one hour. The table contains the estimates and standard errors from final models, and the chi-squared and p-values from model comparisons. The models are based on fine-scale GPS data collected using tablet computers, spanning five days.

Parameter		**Total distance**				**Displacement**				**Mean speed**				**Path tortuosity**			
		β	**SE**	**X^2**	**P**	**β**	**SE**	**X^2**	**P**	**β**	**SE**	**X^2**	**P**	**β**	**SE**	**X^2**	**P**
Treatment:Time:Start Location				4.28	0.12			3.63	0.16			4.27	0.12			4.71	0.09
Treatment:Time				0.02	0.99			0.60	0.40			0.02	0.99			0.69	0.71
Time:Start Location				2.26	0.32			1.42	0.49			1.43	0.49			2.05	0.36
Treatment:Start Location				0.01	0.93			0.05	0.83			0.04	0.85			0.06	0.80
Treatment type	Control	0.00	0.00	2.21	0.14	0.00	0.00	0.05	0.82	0.00	0.00	2.18	0.14	0.00	0.00	0.25	0.61
	Intrusion	0.08	0.06			4.32	0.29			0.08	0.06			0.05	0.16		
Time point	Pre-experimental	0.00	0.00	0.22	0.90	0.00	0.00	1.26	0.53	0.00	0.00	0.30	0.86	0.00	0.00	1.52	0.47
	Experimental	0.01	0.04			0.02	0.12			0.02	0.04			0.00	0.12		
	Post-experimental	-0.01	0.03			0.11	0.10			-0.01	0.03			-0.11	0.10		
Start Location		-0.07	0.01	1.59	0.21	-0.06	0.17	0.20	0.66	-0.08	0.05	2.34	0.13	0.00	0.16	0.02	0.90
Number in group		-0.01	0.01	1.56	0.21	-0.01	0.01	0.72	0.39	-0.01	0.01	1.71	0.19	0.00	0.01	0.47	0.49
Rainfall		-0.04	0.02	2.93	0.09	0.08	0.07	1.69	0.19	-0.03	0.02	2.14	0.06	-0.12	0.06	**4.38**	**0.04**
Breeding Status	Babysitting	0.00	0.00	7.37	0.12	0.00	0.00	**18.31**	**0.001**	0.00	0.00	9.02	0.06	0.00	0.00	**18.89**	**<0.001**
	Escorting	0.00	0.05			-0.09	0.16			0.00	0.05			0.09	0.15		
	Non-breeding	0.05	0.05			0.34	0.16			0.04	0.05			-0.31	0.15		
	Oestrus	-0.06	0.08			0.58	0.25			-0.07	0.08			-0.66	0.23		
	Pregnant	0.11	0.05			0.49	0.16			0.12	0.05			-0.40	0.15		

Question 2 - do mongooses' movement characteristics differ when they are in different parts of the home range, particularly after exposure to simulated intergroup conflict?

Contrary to our predictions there was no three-way interaction between treatment type, time point, and area of the home range when predicting the distance mongoose groups moved ($X^2 = 2.12$, $p = 0.35$, Table 4.3). However, there was an interaction between time point and area in relation to the total distance moved ($X^2 = 18.43$, $p < 0.001$, Figure 4.2C, Table 4.3), suggesting that there was some difference in movements between the core and the periphery after the presentations. The total distance travelled increased in core areas in the post-experimental phase compared to the pre-experimental phase (post-hoc test: pre-post in core territory, estimate ± SE = -200.77 ± 48.00, $t = -4.18$, $p < 0.001$, Table 4.3), but the distance travelled in peripheral areas did not change over the course of the trial (post-hoc test: pre-post in peripheral territory, estimate ± SE = 61.51 ± 48.00, $t = 1.28$, $p = 0.41$, Table 4.3). This suggests that on days after presentations mongoose groups were moving more when in the core areas, but there was no change in how far they travelled when in peripheral areas. This may be because they are spending more time in core areas after presentations, and points towards a conflict avoidance response. Treatment type, rainfall, breeding status of the group, number of individuals in the group, and interactions between treatment type and area, and treatment type and time point, did not affect total distance travelled (Table 4.3).

There was an interaction between treatment type and area ($X^2 = 10.41$, $p = 0.001$, Table 4.3) and an interaction between time and area ($X^2 = 18.23$, $p < 0.001$, Table 4.3) in relation to the mean speed groups moved. When travelling in peripheral areas there was an increase in mean speed in the post-experimental phase compared to the pre-experimental phase (post-hoc test: pre-post in peripheral territory, estimate ± SE = -0.26 ± 0.05, t = -4.98, p < 0.0001, Figure 4.2A, Table A4.4). In contrast, when travelling in core areas, there was no change in the mean speed in the experimental or post-experimental phase (post-hoc test: pre-post in core territory, estimate ± SE = 0.06 ± 0.05, t = 1.10, p = 0.51; pre-exp in core, estimate ± SE = 0.02 ± 0.11, t = 0.10, p = 0.98, Table A4.4). In control trials, there was no difference between the mean speed travelled in the core or peripheral areas of the territory (post-hoc test: core-periphery in control trials, estimate ± SE = 0.04 ± 0.06, t = 0.61, p = 0.54, Table A4.5), however, in intrusion trials the mean speed was higher in core areas than in peripheral areas (post-hoc test: core-periphery in intrusion trials, estimate ± SE = 0.27 ± 0.07, t = 4.10, p < 0.0001, Figure 4.2B, Table A4.5). This suggests that mongoose groups move faster in the peripheral areas of the home range after exposure to a presentation (either intrusion or control) and move faster in the core of the home range during intrusion trials than during control trials (both before and after presentations have taken place).

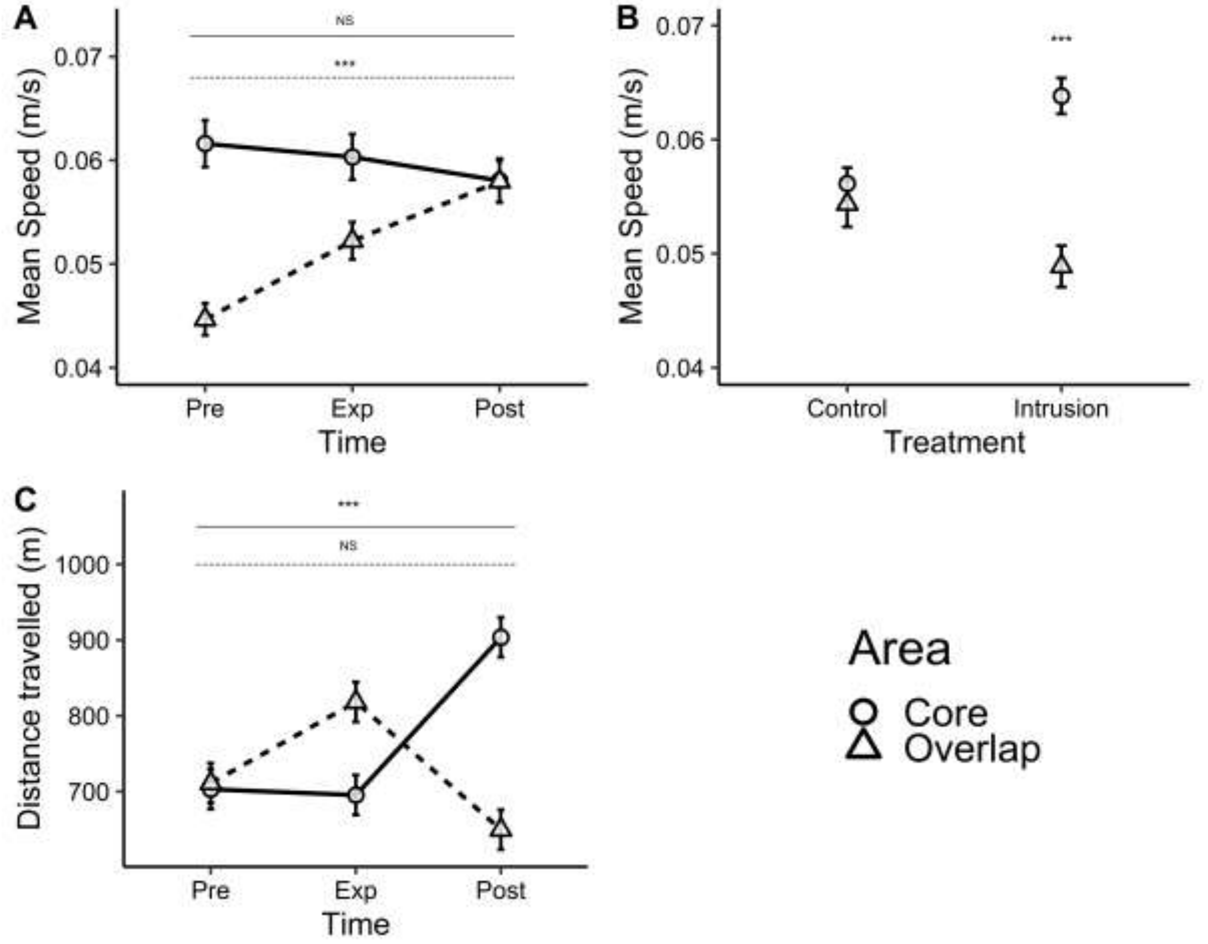

Figure 4.2 – Distance and speed travelled across core and peripheral areas of the territory. Means and standard errors of (A & B) the mean speed each day, and (C) the total distance travelled per day for the seven days before (Pre), the day of (Exp), and the seven days after (Post) a presentation. Empty triangles and dashed lines show distances and speeds in peripheral areas of the territory, and filled circles and solid lines show distances and speeds in core areas. Points show means from the LMMs ± SE. This figure shows interactions between the time point and area of the territory for mean speed (A) and total distance (C) which show that after presentations mongoose groups move faster (compared to before) in the periphery, and further in the core. This figure also shows an interaction between treatment type and area of the territory for mean speed (B) which shows that in intrusion trials mongooses move faster in the core than the periphery, whereas in control trials speeds are the same in both areas of the territory. For visualisation of the differences between intrusion and control trials see Figure A4.1.

Table 4.3 **–** Model comparison results for path characteristics in relation to area in the home range.This table contains the results from two separate models, predicting (1) the distance moved by mongoose groups in either core or peripheral areas; and (2) the mean speed mongoose groups travelled in either core or peripheral areas. The table contains the estimates and standard errors from final models, and the chi-squared and p-values from model comparisons. These models were based on broad-scale GPS data collected by collars, spanning 15 days.

Parameter		**Distance**				**Mean speed**			
		β	**SE**	**X^2**	**P**	**β**	**SE**	**X^2**	**P**
Treatment:Time:Area				2.12	0.35			0.48	0.79
Treatment:Time				0.71	0.70			1.43	0.49
Time:Area	Pre:Periphery	0.00	0.00	**18.43**	**<0.001**	0.00	0.00	**18.23**	**<0.001**
	Exp:Periphery	114.74	132.77			0.18	0.15		
	Post:Periphery	-262.29	67.79			0.32	0.07		
Treatment:Area	Core:Intrusion			2.75	0.10	0.00	0.00	**10.41**	**0.001**
	Periphery:Intrusion					-0.23	0.07		
Treatment type	Control	0.00	0.00	0.04	0.85	0.00	0.00	-	-
	Intrusion	15.24	61.64			0.13	0.09		
Time point	Pre-experimental	0.00	0.00	-	-	0.00	0.00	-	-
	Experimental	-7.47	93.90			-0.02	0.11		
	Post-experimental	200.77	48.03			-0.06	0.05		
Area	Core	0.00	0.00	-	-	0.00	0.00	-	-
	Periphery	8.16	47.12			-0.20	0.06		
Number in group		-7.02	6.03	1.60	0.21	-0.01	0.01	1.41	0.23
Rainfall		19.11	25.02	0.79	0.37	0.00	0.03	0.06	0.80
Breeding Status	Babysitting	0.00	0.00	9.10	0.06	0.00	0.00	6.16	0.19
	Escorting	-45.21	51.91			-0.03	0.06		
	Non-breeding	-14.33	59.76			0.01	0.08		
	Oestrus	111.76	93.75			0.14	0.13		
	Pregnant	-132.32	71.18			-0.13	0.10		

Question 3 - do mongooses use their core territory for longer, use areas closer to the core, and move closer to the core after exposure to simulated intergroup conflicts to avoid further conflict?

Contrary to our hypotheses neither the amount of time that mongoose groups spent in core areas, the mean cumulative probability of use value, nor the change in cumulative probability of use changed after exposure to simulated intergroup conflict (see Tables 4.4, 4.5 and 4.6).

The percentage time spent in the core areas of the territory was higher in the experimental phase than in the pre-experimental phase ($X^2 = 6.22$, $p = 0.04$; post-hoc tests: pre-exp, estimate ± SE = -0.09 ± 0.04, $t = -2.47$, $p = 0.04$, Figure 4.3, Table 4.6) for the fine-scale tablet data spanning five days of the trial, but this occurred across both intrusion and control trials, suggesting that this was not just a response to simulated intergroup conflict. However, the starting location (the cumulative probability of use value of the first GPS fix in the hour/day) was strongly associated with the time spent in the core in both analyses (fine-scale analysis: estimate ± SE = 1.20 ± 0.05, $X^2 = 365.68$, $p < 0.001$; broad-scale collar GPS data analysis: estimate ± SE = 2.85 ± 0.26, $X^2 = 108.13$, $p < 0.001$, Table 4.4). If mongoose groups started closer to the core, they then spent more of their time in the next hour/day in the core areas of the territory, as expected with autocorrelation. Time spent in the core was not affected by the treatment type, rainfall, the number of individuals in the group or any interactions between treatment type, time point and start location in either scale of analysis (Table 4.4).

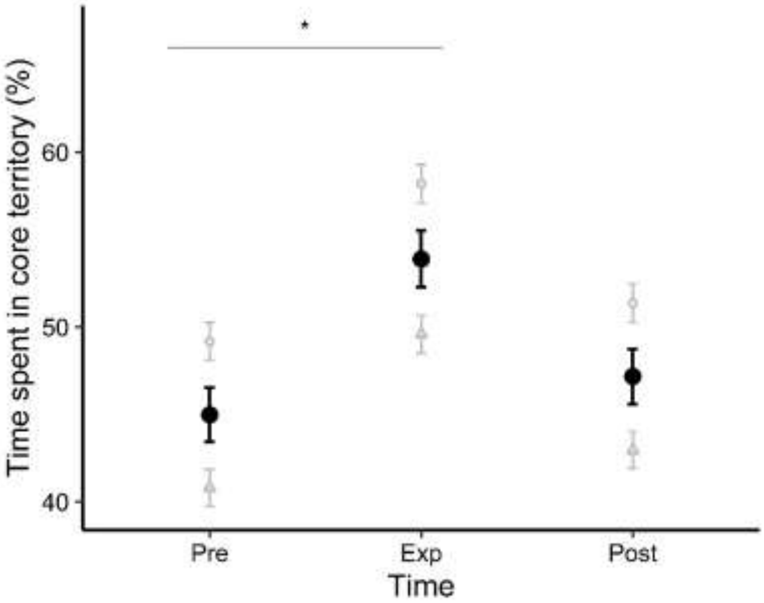

Figure 4.3 – The percentage of time that mongoose groups spent in the core of their territories after presentations. Core territory includes locations with a cumulative probability of use > 0.5. Points show means from the LMM ± SE. Means for control trials (circles) and intrusion trials (triangles) are also shown in grey. * $P < 0.05$; asterisks refer to post hoc comparison of means across all three categories.

The mean cumulative probability of use value of locations that mongoose groups used was not affected by treatment type, rainfall, breeding status, number of individuals in the group or any interactions between treatment type, time point and starting location (Table 4.5). However, the starting location was strongly associated with the mean cumulative probability of use value in both analyses (fine-scale analysis: estimate ± SE = 0.79 ± 0.03, $X^2 = 470.98$, $p < 0.001$; broad-scale analysis: estimate ± SE = 0.30 ± 0.03, $X^2 = 108.28$, $p < 0.001$, Table 4.5). If mongoose groups started closer to the core, they then used areas that were closer to the core in the next hour/day in the core areas of the territory, as expected from autocorrelation.

Similarly, the starting location was strongly associated with the change in home range area (estimate ± SE = 0.23 ± 0.04, $X^2 = 38.80$, $p < 0.001$, Table 4.6). If mongoose groups started closer to the core, they had a positive change in home range location, which indicates that they moved closer to the edge of the territory by the end of the hour.

Table 4.4 **–** Model comparison results for time spent in core areas of the territory. This table contains the results from two separate models, predicting (1) the percentage time mongoose groups spent in the core for fine-scale hourly data; (2) the percentage time mongoose groups for broad-scale daily data. The table contains the estimates and standard errors from final models, and the chi-squared and p-values from model comparisons. The models are based on fine-scale GPS data (spanning five days) collected using tablet computers and from broad-scale GPS data (spanning fifteen days) collected by collars.

Parameter		**% Time spent in core (fine-scale)**				**% Time spent in core (broad-scale)**			
		β	**SE**	**X^2**	**P**	**β**	**SE**	**X^2**	**P**
Treatment:Time:Start location				1.28	0.14			1.65	0.44
Treatment:Time				0.34	0.85			1.12	0.57
Time:Start Location				0.81	0.67			0.36	0.55
Treatment:Start Location				0.20	0.65			2.42	0.30
Treatment type	Control	0.00	0.00	3.29	0.07	0.00	0.00	0.29	0.59
	Intrusion	-0.03	0.02			-0.16	0.30		
Time point	Pre-experimental	0.00	0.00	**6.01**	**0.05**	0.00	0.00	1.88	0.39
	Experimental	0.03	0.01			0.39	0.29		
	Post-experimental	0.01	0.01			0.07	0.15		
Start location		**0.40**	**0.02**	**359.59**	**<0.001**	2.85	0.26	**108.13**	**<0.001**
Number in group		0.00	0.00	0.57	0.45	0.00	0.02	0.01	0.91
Rainfall		0.01	0.01	1.91	0.17	0.00	0.12	0.01	0.91
Breeding Status	Babysitting	0.00	0.00	2.46	0.65	0.00	0.00	0.91	0.92
	Escorting	-0.02	0.02			0.18	0.26		
	Non-breeding	-0.02	0.02			-0.03	0.31		
	Oestrus	-0.01	0.02			0.02	0.49		
	Pregnant	-0.01	0.02			0.04	0.34		

Table 4.5 – Model comparison results for mean cumulative probability of use. This represents the area of the home range that the mongooses spent most time in – a high value indicates that areas close to the core of the territory were used, and a low value indicates that areas in the periphery that are rarely used by the group were used. This table contains the results from two separate models, predicting (1) the mean cumulative probability of use of mongoose groups for fine-scale hourly data; and (2) the mean cumulative probability of use of mongoose groups for broad-scale daily data. The table contains the estimates and standard errors from final models, and the chi-squared and p-values from model comparisons. The models are based on fine-scale GPS data (spanning five days) collected using tablet computers and from broad-scale GPS data (spanning fifteen days) collected by collars.

Parameter		**Mean cumulative probability of use (fine-scale)**				**Mean cumulative probability of use (broad-scale)**			
		β	**SE**	**X^2**	**P**	**β**	**SE**	**X^2**	**P**
Treatment:Time:Start location				0.55	0.76			3.39	0.18
Treatment:Time				0.60	0.74			1.40	0.50
Time:Start Location				2.39	0.30			2.50	0.29
Treatment:Start Location				0.01	0.93			0.01	0.94
Treatment type	Control	0.00	0.00	0.12	0.73	0.00	0.00	0.00	0.95
	Intrusion	-0.01	0.02			0.00	0.03		
Time point	Pre-experimental	0.00	0.00	2.60	0.27	0.00	0.00	2.24	0.32
	Experimental	0.03	0.02			0.04	0.03		
	Post-experimental	0.01	0.02			0.01	0.02		
Start location		**0.79**	**0.03**	**470.98**	**<0.001**	**0.30**	**0.03**	**108.28**	**<0.001**
Number in group		0.00	0.00	0.64	0.42	0.00	0.01	0.07	0.79
Rainfall		0.00	0.01	0.11	0.75	0.00	0.01	0.10	0.75
Breeding Status	Babysitting	0.00	0.00	2.70	0.61	0.00	0.00	3.11	0.54
	Escorting	-0.03	0.02			0.03	0.02		
	Non-breeding	-0.01	0.02			0.02	0.03		
	Oestrus	-0.02	0.04			0.01	0.05		
	Pregnant	-0.02	0.02			0.00	0.03		

Table 4.6 – Model comparison results for change in the area of home range that was used. This was calculated as the cumulative probability of use value at the start location - the cumulative probability of use value at the end location. A positive value indicates that the group moved closer to the edges of the territory, and a negative value indicates that they moved closer to the core. This table contains the results from a model predicting the change in home range area of a mongoose group from the start to the end of the hour. The table contains the estimates and standard errors from final models, and the chi-squared and p-values from model comparisons. The models are based on fine-scale GPS data collected on tablet computers, spanning five days.

Parameter		**Change in home range area**			
		β	**SE**	**X^2**	**P**
Treatment:Time:Start location				0.30	0.86
Treatment:Time				0.03	0.99
Time:Start location				1.35	0.51
Treatment:Start location				0.46	0.50
Treatment type	Control	0.00	0.00	0.23	0.63
	Intrusion	0.01	0.04		
Time point	Pre-experimental	0.00	0.00	1.71	0.42
	Experimental	-0.03	0.03		
	Post-experimental	-0.01	0.02		
Start location		0.23	0.04	38.80	<0.0001
Number in group		0.00	0.00	1.32	0.25
Rainfall		0.00	0.01	0.00	0.96
Breeding Status	Babysitting	0.00	0.00	2.13	0.71
	Escorting	0.04	0.03		
	Non-breeding	0.00	0.03		
	Oestrus	0.01	0.05		
	Pregnant	0.02	0.03		

Discussion

Question 1 - do mongooses move further and faster after simulated intergroup conflict to avoid further conflict?

We predicted that mongoose group movements would change after exposure to intergroup conflict, either increasing their speed and distance and travelling more directly to avoid conflict, or moving more slowly over shorter or more meandering paths as a form of patrolling or territory defence. We found no evidence that any of the path characteristics we measured were affected by exposure to intergroup conflict – suggesting that mongooses are not adjusting their movements, and not conforming to the predictions of either the conflict avoidance or defence hypotheses. These results contrast with previous studies which found that groups do alter their movement characteristics after exposure to real or simulated conflict. Capuchin monkeys moved faster and further after losing a conflict (Crofoot, 2013), suggesting they might be following a conflict avoidance response, which in the context of losing a conflict may be more beneficial than active defence. Dwarf mongooses show the opposite style of response and moved slower and over shorter distances after simulated intergroup conflicts than after control presentations (Christensen *et al.*, 2016), which fits the predictions of a patrolling style response.

Other factors like the breeding status of the group, rainfall or resource availability could also affect movement behaviours via changes to foraging or other behaviours. We found that path characteristics were only affected by the breeding status of the group (displacement and path tortuosity) and previous rainfall (path tortuosity), and not by exposure to conflict. Breeding status and resource availability (which rainfall is a proxy for) may affect movement patterns more than intergroup conflict in banded mongooses as conflict is frequent, and mongooses may not respond to single intergroup encounters. Breeding status may affect movement patterns, as at different stages of the breeding cycle pups may be foraging with the group affecting the speed and distance a group can travel. Other examples of breeding status affecting movement include: babysitting, when the group may be using one den and returning to this den each day; or during oestrus when females may seek different areas of the territory for maximal fitness from mating with in- or out-group males. These factors are not always controlled for in other studies (Markham, Alberts and Altmann, 2012; Crofoot, 2013; Christensen *et al.*, 2016), although Christensen *et al.* did include pup presence or absence as an explanatory factor, and found no difference in movement patterns between these categories. Using pre- and post-experimental measures also helps to account for these potentially confounding factors.

Question 2 - do mongooses' movement characteristics differ when they are in different parts of the home range, particularly after exposure to simulated intergroup conflict?

Mongoose groups moved further in core areas after presentations, but not in peripheral areas. This was the case in both control and intrusion trials, suggesting that this might not be a reaction to intergroup conflict. Additionally, mean speed was higher after presentations exclusively in peripheral areas, and was higher generally in intrusion trials than control trials. The location of the group represents potential risk from intergroup conflict, with the risk rising in peripheral areas, suggesting that movement behaviour may be affected by risk, rather than directly by exposure to conflict. This reaction might represent moving away from and avoiding risky areas in the edge of the territory, and moving quickly when in those areas of risk. This result follows some of the predictions of the conflict avoidance hypothesis, but according to the risk in the current location rather than as a response to conflict directly. Intergroup conflict could be an aspect to the “landscape of fear” for banded mongooses (Brown, Laundre and Gurung, 1999), and influence their movements more indirectly. This might have consequences for territory use and potentially fitness, especially if key resources (for example, fresh water which is mostly found at the edge of the peninsular on the boundary of territories, or human waste sources which are often in overlapping areas) are in peripheral areas of the territory. Previous studies have not investigated differences in movement behaviour in different parts of the home range (Markham, Alberts and Altmann, 2012; Crofoot, 2013; Christensen *et al.*, 2016), but this could be an important part of responses to intergroup conflict, or of more general movement ecology in species that experience intergroup conflict.

Question 3 - do mongooses use their core territory for longer, use areas closer to the core, and move closer to the core after exposure to simulated intergroup conflicts to avoid further conflict?

Similarly to other measures we did not find evidence to support either the conflict avoidance or the defence hypothesis when investigating changes to home range use. Home range use measures were mostly explained by the starting location of the group. If groups started in core areas they then spent a larger percentage of their time in the core, and moved (on average) in areas closer to the core than when they started the hour or day further away from the core. The closer a group started to the core of their territory the larger the change in cumulative probability of use value they experienced – this means that they were closer to the edge of the territory than when they started the day.

These results can be explained by autocorrelation, as starting close to the core means by definition that groups must pass through more core areas in their movements, and are more likely to end up closer to the edge than they started.

However, we did find that mongoose groups spent more time in the core areas of their territory (> 0.5 cumulative probability of use) during the experimental phase than during the pre-experimental phase when analysing fine-scale data (2 hours immediately after each presentation). This result was not found when analysing broad-scale data (whole day of the presentation). This suggests that if mongoose groups' home range use is affected by simulated intergroup conflict, it is affected only in the few hours after conflict takes place. Studies that have investigated home range use over longer time scales have found that longer-term use predicted victory, and was more important than recent use (Markham, Alberts and Altmann, 2012). However, group behaviour is also affected in the same way in control trials, casting doubt on whether this effect is due exclusively to intergroup conflict, or due to the experimental set-up. If this result is interpreted as an effect of intergroup conflict then mongoose groups seem to use the core areas of their territory more, taking a more conflict avoidance style response to intergroup conflict, although this evidence is only tentative due to similar patterns in control trials.

Detectable home range use changes seem to be limited to the relatively short term (if at all), similarly to social behaviour (see Chapter 2). These presentations represent a one off incursion into the territory, and a more sustained and systematic boundary push may be needed to impact the longer term home range use of mongoose groups, perhaps repeated presentations at territory boundaries over a series of weeks. Other studies show that some groups are impacted by single conflict events (Crofoot, 2013; Christensen *et al.*, 2016), but the high prevalence of intergroup encounters in banded mongooses (mean encounter rate per group = 0.8 per week (non-oestrus periods) to 2.9 per week (group oestrus); data from 12 groups (Cant, Otali and Mwanguhya, 2002)) may mean that one event is not enough to impact mongoose movement behaviours further than a few hours. More extreme circumstances may be required to truly impact home range use – for example demographic change of the group that leads to changing between-group dynamics, whether demographics are initially impacted by intergroup conflict (Mitani, Watts and Amsler, 2009) or other causes (Scarry and Tujague, 2012).

There was no evidence that mongoose groups moved closer or further away from the core in either control or intrusion trials. We expected that if mongooses were performing patrolling-style behaviours, like chimpanzees (Watts and Mitani, 2000), that we would detect movement towards the periphery after simulated intergroup encounters. However, defence of the core areas of their territory may be more important to banded mongoose groups than active patrolling, and previous research has shown that they are more likely to defend against simulated intruders in the core areas of their territory (Furrer *et al.*, 2011). This balance might change in times of group or neighbouring group instability, and more aggressive boundary pushing behaviour could follow (Mitani, Watts and Amsler, 2009; Scarry and Tujague, 2012). This is a potentially interesting area for further study, involving more sustained or aggressive boundary pushing simulations.

Table 4.7 – Summary of results. Ticks indicate evidence for the hypothesis, crosses indicate no evidence for the hypothesis, and question marks indicate tentative evidence for the hypothesis.

Measure	**Conflict avoidance**	**Defence**	**Null**

Path characteristics:			
Distance	✗	✗	✓
Speed	✗	✗	✓
Displacement	✗	✗	✓
Tortuosity	✗	✗	✓
Path characteristics in relation to home range:			
Distance	?	✗	?
Speed	?	✗	?
Home range characteristics:			
Time spent in the core vs the periphery	?	✗	?
Area of the home range used	✗	✗	✓
Moving towards or away from the core	✗	✗	✓

Conclusions

Several of our analyses showed that movement changed over the course of the experiment (see summary of results in Table 4.7). However, the changes we observed were similar for both intrusion and control trials. After both types of trial, banded mongooses spent more time in the core areas of their territory, and moved further but slower whilst in core areas. The similarity between responses in intrusion and control trials is puzzling because in previous chapters I have shown that immediate behavioural responses to these two treatment types are very different (see Chapter 2), and that intrusion (but not control) trials have lasting effects on individuals and network-level behaviour (see Chapter 2 and 3). There are two possible explanations for the observed impacts of intrusion and control trials on movement patterns. First, it may indicate that the movement patterns of mongoose groups were not affected by the experimental presentations *per se*, but by some other correlate of the experiment, such as the presence of human observers or a vehicle, on the five central days of the trial. However, this would be surprising, given the differential effects of control versus intrusion presentations that were measured in Chapters 2 and 3. Second, our findings may indicate that mongooses were reacting to the control trials either as if they were intrusion trials, or as a different, but similar form of disturbance to their movement and home range use patterns. Traps were cleaned between presentations to try and avoid transferring rival scents into control trials, but some residual scent may have remained that impacted mongoose movement behaviour. Additionally, some rival scents may be carried to the experimental area on the research vehicle, as mongooses from all groups tend to scent mark on the vehicle. Alternatively, the trapping of males from the focal group during control trials may have impacted group movement and home range use. Although mongooses are trapped regularly and habituated to this procedure, and care was taken to minimise stress, this procedure could still impact the movement behaviour of the group. The impact of trapping on physiology and behaviour has been investigated in a number of mammal species (see Table 1 in (Kukalová, Gazárková and Adamík, 2013)), and some studies have detected changes in movement patterns as a consequence of capture or trapping by researchers (Cattet *et al.*, 2008; Morellet *et al.*, 2009).

Although the location of each experimental presentation was not recorded, and could therefore not be included as a factor in the statistical models, this is unlikely to change these conclusions. It is unlikely that there is any systematic bias in location of each trial either on the day of the presentation in control and treatment trials, or in the pre and post-trial periods, and the starting location acts as a proxy for the trial location. However, due to the limitations of the experimental design, comparisons between control and intrusion trials should be interpreted with some caution. Each experimental trial contains its own within trial control, the pre-experimental period, which helps to alleviate these concerns, but as control and intrusion trials differed in their observers, and were undertaken in blocks rather than fully randomised, some caution is needed in interpreting these results.

However, despite control trials not differing from intrusions, the pre-experimental phase of the trial also acts as a second, internal control, and changes across time within trials indicate that the animals change their movement patterns in response to the presentation of stimuli, even if this response is not contingent on whether the stimuli derived from mongooses in their own versus other groups. These changes persist for between two and seven days after simulated conflicts, suggesting that perceived intergroup conflict may have lasting effects on both movement characteristics and home range use of mongoose group. This is longer than movement characteristic changes detected in previous studies, (Crofoot, 2013; Christensen *et al.*, 2016), suggesting that animal movement might be affected by intergroup conflict in the longer term. Home range use has been shown to be affected, at least by losing intergroup conflicts, for up to 12 months (Markham, Alberts and Altmann, 2012), so there may also be even longer-term consequences than investigated here. These changes to movement behaviour may impact reproduction and fitness, as moving faster and further is energetically demanding (and may also represent a reduction in foraging behaviour) (Crofoot, 2013) and increased use of core areas may impact pup care and defence. These tentative conclusions should be confirmed with further work, possibly including alternative control trials that do not involve presentations of stimuli, or trapping of individuals.

These questions surrounding the effect of intergroup conflict on movement behaviour are of importance in bridging the gap between short-term responses to intergroup conflict and longer-term responses that impact on survival, reproduction and fitness. The impact of intergroup conflict on group level social behaviour seems to be very short-lived (Chapter 2), with slightly longer-term impacts on social behaviour between individuals (Chapter 3), and here we show that there is tentative evidence for some longer-term consequences for movement and home range use. Behaviour across timescales seems to be affected by intergroup conflicts, suggesting that it may have shaped the evolution of this species, and have ongoing impacts on behaviour, reproduction and fitness. This study also shows that the reactions may vary across the home range in line with the risk in the area, which could underpin much longer term “landscapes of fear” (Brown, Laundre and Gurung, 1999) induced changes to movement behaviour and home range use. This could lead to the formation of “landscapes of *intergroup* fear” that influence not only movements, but also within-group social behaviour and other behaviours that are influenced by intergroup conflict.

Chapter 5:

Leadership and the risk of intergroup encounters in banded mongooses

Abstract

Leadership emerges in social groups for many reasons, for example, to coordinate group responses and maintain cohesion within groups. Theory, and human research, suggests that patterns of leadership are affected by intergroup conflict, and that the risk of conflict may influence the type of individuals that group members are willing to follow. But these potential impacts on leadership have not been studied in cooperative animal societies. We used banded mongooses as a model system to explore the factors involved in a successful leadership bid, using both natural observations and playback experiments. We observed natural leadership attempts by individuals of different age and sex categories in three groups of wild banded mongooses, and performed an experiment on the same groups using playbacks of lead calls in both the core and periphery of the group's home range. We found that leadership bids by females and younger individuals were more likely to be followed by other group members, and that compared to males leadership by females was particularly successful in more peripheral areas of the home range. However, in responses to playback experiments there was no such interaction between the sex and the area of the home range in which it was played. In the playback experiments responses depended strongly on the breeding status of the group. These exploratory results do give some evidence for increased female leadership, particularly in areas of greater risk from conflict with other groups, but the general patterns of leadership in banded mongooses are still not clear. Further work is needed to investigate which individuals directly lead groups into intergroup conflict, and in other contexts.

Introduction

Leadership – the phenomenon of individuals affecting group behaviour and influencing group decisions – has been studied extensively in both the biological and social sciences (House and Aditya, 1997; Van Vugt, Hogan and Kaiser, 2008; Dyer *et al.*, 2009; King, Johnson and Van Vugt, 2009; Smith *et al.*, 2016). Recent work has focused on leadership from an evolutionary perspective considering questions that include: why leadership evolves; whether leadership is generalizable across contexts; and which individuals tend to lead (Smith *et al.*, 2016). Leadership is one way to coordinate group responses and maintain cohesion within groups – and may be important in the evolution of cooperation, personality differences and intergroup conflict (Van Vugt, 2006; Van Vugt, Hogan and Kaiser, 2008; King, Johnson and Van Vugt, 2009; Johnstone and Manica, 2011; Gavrilets and Fortunato, 2014). Animal leaders are often: dominant or older individuals (Radford, 2004; Bonanni *et al.*, 2010; Nagy *et al.*, 2010; McComb *et al.*, 2011; Brent *et al.*, 2015; Smith *et al.*, 2015; Langergraber *et al.*, 2017); those with valuable knowledge (Lusseau and Conradt, 2009; Nagy *et al.*, 2010; Bousquet and Manser, 2011; Brent *et al.*, 2015); or those in need, e.g. hungry individuals (Fischhoff *et al.*, 2007; Furrer, Kunc and Manser, 2012). The emergence of leadership in animal groups has several theoretical explanations or mechanisms: heterogeneity among individuals leading to spontaneous leaders and followers (including consistent differences in personality or motivation) (Johnstone and Manica, 2011; Smith *et al.*, 2016; Pruitt *et al.*, 2018); ecological hardship (Brent *et al.*, 2015); and overcoming collective action problems, including those that occur during within-group and between-group conflicts, via punishment or differential fitness payoffs (Gavrilets and Fortunato, 2014; Smith *et al.*, 2016).

Theoretical work suggests that intergroup conflict can affect leadership – both helping it to emerge within groups – and affecting the types of leadership that individuals use (Van Vugt, Hogan and Kaiser, 2008; Smith *et al.*, 2016). These theories predict that intergroup conflict will lead to increasingly despotic leadership within a group, with fewer individuals contributing to leading (Van Vugt, Hogan and Kaiser, 2008; Smith *et al.*, 2016). Theory also predicts that leadership may be an important way to overcome the collective action problem of participating in intergroup conflict (Gavrilets and Fortunato, 2014), and that leadership allows individuals to control movement, and engagement in intergroup conflict, to increase their fitness (Petit and Bon, 2010). During times of relative peace, theory predicts that leadership should return to a more democratic model with more individuals leading, and voting or other consensus decision-making within a group rather than dictatorial leadership by one group member (Van Vugt, 2006). Empirical research has investigated the impact of intergroup conflict on human leadership during warfare (Campbell, Hannah and Matthews, 2010), and in the lab (Gleibs and Haslam, 2016), but little research has been done in non-human animals, particularly animals living under natural conditions.

Conflict over leadership itself might also occur due to heterogeneity of individuals within groups. Individuals with different biological traits, personalities, motivation or knowledge may have conflicting preferences for movement, foraging or engaging in intergroup conflicts (Petit and Bon, 2010). These differences may lead to conflict over leadership – particularly when the differential costs and benefits for different individuals are high (Van Vugt, 2006). Heterogeneity of individuals is known to lead to the spontaneous emergence of leaders and followers – but when conflict over leadership is high, leadership breaks down as many individuals attempt to lead, and none follow (Johnstone and Manica, 2011). This breakdown of leadership needs to be avoided to maintain group cohesion. Sex is one of the key forms of heterogeneity in animal groups, and males and females may experience different costs and benefits of leadership. These costs and benefits may in turn be affected by the impact of intergroup conflict on these classes of individuals, which also varies widely. Benefits associated with leadership include no compromise for the individual, which can decide when are where to forage or move to maximise their own fitness, however costs may arise from maintaining leadership, particularly if leadership is associated with the dominance hierarchy, or if there is conflict within the group over where to forage or move that results in conflict over leadership of the group that determines this. Intergroup conflict may be one situation in which leadership is important to facilitate a rapid response, but there are also high levels of conflict over leadership, due to differential costs and benefits associated with engagement in conflict between the heterogeneous individuals that make up a group.

In this preliminary study we explore the impact of intergroup conflict risk on banded mongoose (*Mungos mungo*) leadership. Banded mongooses engage in intergroup conflict regularly (mean encounter rate per group = 0.8 per week (non-oestrus periods) to 2.9 per week (group oestrus); data from 12 groups (Cant, Otali and Mwanguhya, 2002)). Additionally, banded mongoose groups are made of individuals which differ in their fitness benefits and costs associated with conflict (males, females, different age classes, different relatedness levels) making them an ideal candidate for studying leadership and intergroup conflict. Female banded mongooses can gain extra-group paternity during intergroup conflicts, which is especially important to individuals in groups in which there is a high risk of inbreeding (Nichols, Cant and Sanderson, 2015). In contrast, despite potential gains from extra-group paternity, male banded mongooses experience a high cost of intergroup conflict due to skewed mortality risk during encounters (long term data, Banded Mongoose Research Project).

Here we aim to use the banded mongoose as a model system to begin to explore leadership in heterogeneous groups in the context of intergroup conflict. This study aims to test whether leadership attempts (intentional or not) by males and females differ in their success, particularly in relation to the area of the home range in which they are performed (as a proxy for risk of intergroup encounters). Given the differing costs and benefits of intergroup conflict for males and females we predict that females will attempt to lead more, and be followed more, in areas of potential conflict, because they can gain extra-group paternity and attempt to lead the group towards other neighbouring groups, and exert more influence in these areas as they are more motivated to lead. In contrast, we also predict that males will attempt to lead more, and be followed more, in areas of potential conflict, because they can avoid costly conflict with other groups, and attempt to lead the group away from risky areas. Individuals may be followed preferentially by other individuals of the same sex, who also wish to avoid the costs or gain the benefits of conflict and avoid, or move towards, these areas of risk.

Methods

Study Site

Data from banded mongooses were collected for this study between October and December 2017 on the Mweya Peninsula in Queen Elizabeth

National Park, Uganda (0º12’S, 29º54’E). The study was performed on banded mongoose groups that are part of a long-term study population. In depth descriptions of the study site can be found in (Rood, 1975; Cant, 2000; Cant, Vitikainen and Nichols, 2013).

Banded mongooses are small (< 2 kg) diurnal herpestids that live in stable multi-male, multi-female groups of between 10 and 30 individuals. Groups are territorial and defend their territories from other groups during frequent, and sometimes lethal, intergroup conflicts (Nichols, Cant and Sanderson, 2015; Thompson, Marshall, Vitikainen and Cant, 2017). Banded mongooses in the study site almost exclusively engage in physically violent inter-group interactions, with very few interactions between groups that are neutral, peaceful, or involve only signalling between groups with no physical interaction, e.g. war dances, or vocal defence. Fighting can be highly aggressive involving biting and scratching, and sometimes individuals are held down and attacked by multiple rival group members.

All mongooses in the study population are individually marked using unique hair-shave patterns and are habituated to close observation from 2-4 metres. One to two mongooses in each group are fitted with a radio collar weighing 26-30 g (Sirtrack Ltd, Havelock North, New Zealand) with 20-cm whip antenna (Biotrack Ltd, Dorset, UK) to allow the groups to be located. One to two additional individuals are fitted with a GPS collar weighing 24-41g (Gipsy4 and Gipsy5, Technosmart, Italy), to allow group movements to be recorded. Three focal groups, which were habituated to close observation, were used in this study.

Data Collection

Behavioural observations of natural leadership bids

One hour behavioural observation sessions were carried out for the three mongoose groups, and all movement leadership attempts were recorded ad-lib. A leadership attempt was defined as one (or a small coalition of) individual(s) moving purposely away from the rest of the group (a minimum distance of 2 metres away), alert and with the head up. Individuals involved in a leadership attempt often made moving or leadership calls, but calling while moving was not a requirement for our definition of a leadership attempt.

For each leadership attempt, the following were recorded:

- the identity of the leader(s)
- whether the leader was making any moving or leadership calls
- the speed of the group (forage – slow or no movement whilst feeding; walk – slow movement by > 75% of the group, run – faster movement by > 75% of the group)
- the area of territory the group was in (cumulative probability of use value – calculated from three month home ranges, see details below)
- the length of time spent attempting to lead
- whether the leadership attempt was successful (i.e. did the group follow the direction of the leader > 80% required for success).

We also recorded the direction of the leadership attempt in relation to the core of the group's territory (towards the core, away from the core, parallel to the core), as a proxy for moving towards or away from a neighbouring group or a risky area where conflict might take place. The breeding status of the group was also recorded for each observation (non-breeding; oestrus; babysitting & oestrus; babysitting; pregnant; pregnant & escorting).

Experimental playbacks

To investigate the effect of territory position and sex on leadership further, playbacks of either male or female leadership calls were played in either core areas of the territory or areas which were in the periphery and may have overlapped with other groups' territories. A factorial design was used, with each focal group tested with male playbacks in core areas, male playbacks in peripheral areas, female playbacks in core areas and female playbacks in peripheral areas.

Audio clips for playback were recorded using an H1 Zoom recorder attached to a Sennheiser directional microphone. Recordings were made when individuals were making clear leadership calls and leading the group into a new area. The recordings were taken from 1-2 metres away from the focal mongoose, and closer to the focal mongoose than any following individuals to avoid recording calls from multiple individuals. However, due to the preliminary nature of this research it is not yet known whether mongooses can distinguish between male and female leadership calls. It is likely that these calls have an individual identity element, as seen with other banded mongoose calls, including moving calls (Müller and Manser, 2008; Jansen, Cant and Manser, 2012, 2013), but this has not been explicitly tested for leadership calls (a subsection of moving calls).

Each playback clip was made up of nine calls, each separated by one second of silence, including three calls from each of the three oldest individuals of the target sex that were present in the group at the time of the experimental trial. The amplitude of each clip was standardised using the normalize function in Audacity 2.1.2 to -1dB (http://audacityteam.org). The recordings were conducted using a portable USB speaker (iHome IHM60) attached to the leg of the researcher at mongoose height. The researcher positioned themselves at a distance of 4-5 metres from the focal group, in the direction of travel, to simulate a leadership attempt. Each playback clip was used only once to prevent habituation of the mongooses to particular recordings.

Each focal group was played 20 different playbacks, 10 of female leadership calls, and 10 of male leadership calls. Approximately half of the playbacks from each sex were performed in the core areas of the territory, and half in the peripheral areas of territory. Groups were followed for at least half an hour before playbacks were performed, to ensure that in the half an hour before the trial the group was not disturbed by humans, predators, or another group of mongooses.

During the 5 minute observation after the playback, the following were recorded:

- whether any individuals approached the speaker
- which individuals approached the speaker
- whether any individuals responded with moving calls
- which individuals responded with moving calls
- whether the direction of the group changed (towards the speaker, away from the speaker, on the same path)
- the speed of the group (forage, walk, run) before the playback, and after the playback, to assess any change in movement speed.

Home Range Calculation

Home ranges were calculated from data collected by GPS collars in the focal group. Data were collected between 07:00 and 19:00 at 30 minute intervals, with a gap between 12:00 and 15:00. These times correspond with mongoose activity, which begins after sunrise, drops in the middle of the day when they rest during the hottest part of the day, and ends at sunset. GPS collars took a burst of 10 fixes at each scheduled fix time, and these were then filtered for accuracy. To filter for accuracy all GPS fixes with fewer than 4 satellite connections and fixes with an HDOP (horizontal dilution of precision) value of over 4 were removed. Additionally fixes with unrealistic longitude (< 28.85 or > 29.95), latitude (< -0.21 or > -0.15), or altitude (< 800m or > 1100m) values for the study site were removed. Finally, data were restricted to the Mweya peninsula, using a shape file of the area, to remove fixes that fell in the lake. If multiple fixes were still associated with a scheduled fix time, the final fix in the burst was used to ascertain the likely position of the collar, as the final fix is likely to be the most accurate. GPS fixes were also collected by tablet computers (through the Mongoose2000 app (Marshall *et al.*, 2018), on Samsung Galaxy Note 10.1 tablets) at the site of each observation or experimental playback.

Home ranges were calculated for the three months preceding the day of each playback, or behavioural observation, using the collar GPS data. Three months represents approximately one breeding cycle of the group (from oestrus to oestrus), and should therefore account for any differential use of the home range across the breeding cycle. Each home range was calculated using the *ctmm* package in R, which uses autocorrelated kernel density estimation (Fleming and Calabrese, 2019). Rasters were created for each home range utilisation distribution using the cumulative distribution function, so each cell of the raster contains the cumulative probability of use value for this location, indicating the probability that the cell is used across the home range time frame by the focal mongoose group. A cell value of 1 indicates a probability of 1 that the cell is used by a group which suggests a core area that is frequently used, whereas a value of 0 indicates that there is a probability of 0 that the cell is used, suggesting a peripheral and rarely used area. The cumulative probability of use was extracted for each observed location of a leadership bid, and each location of an experimental playback, using the *raster* and *move* packages in R (Hijmans, 2018; Kranstauber, Smolla and Scharf, 2019). These extracted values give an indication of whether mongoose groups were close to core areas of their territory or more peripheral areas. Values were analysed as a continuous variable for observation data analysis, and were categorised as either “core” territory (> 0.50) or “peripheral” territory (<= 0.50) for the experimental playback data analysis.

Statistical Analysis

Observations of natural leadership bids

Statistical analysis was performed in R 3.6.1 software (R Development Core Team, 2019). A linear mixed model was constructed for the binary response variable indicating whether individuals were successful in their leadership bid (i.e. more than 80% of the group followed the leader(s) or not). We used model averaging for linear mixed models ((Anderson, 2008) as described by (Grueber *et al.*, 2011)). A model averaging approach was taken due to the large number of potential influencing variables, and no strong hypotheses associated with most of these variables. Model averaging allows many variables to be investigated simultaneously as an exploratory method of finding potentially important factors influencing leadership success. The method also allows for model uncertainty by creating an averaged model (Grueber *et al.*, 2011). Home range location (cumulative probability of use value from *ctmm* home range), leader sex, leader age, production of moving calls, direction of travel in relation to core territory (towards, away from, parallel to), time spent leading, whether the leader was in a coalition (i.e. leading with others), number in the coalition, speed of the group (forage, walk, run) and breeding status (non-breeding; oestrus; babysitting & oestrus; babysitting; pregnant; pregnant & escorting) were included as fixed effects. Additionally a three-way interaction between home range location, sex and age was included as a fixed factor. Leader identity nested within group identity was included as a random factor. The *glmer* function in the *lme4* package (Bates and Maechler, 2009) was used to fit this model. A binomial error structure was used in the model to reduce residual heterogeneity due to the binary nature of the response variable.

Experimental playbacks

Linear models were constructed for each of the responses to the experimental playback – percentage of individuals that approached the speaker, percentage of males present that approached, percentage of females present that approached, percentage of individuals that responded with moving calls, percentage of males that made calls, percentage of females that made calls. Percentage response variables were logit transformed, to reduce residual heterogeneity. Change in group direction was analysed using a general linear model, with a binomial error structure, as the change in group direction was binary: either mongoose groups moved towards the speaker, or did not change their direction. Change in group speed was analysed using a cumulative link model for ordinal regression using the *ordinal* package (Christensen, 2019), to reduce residual heterogeneity due to the ordinal nature of the response variable.

Maximal models were created for each response variable, with playback call type (male or female), area of the territory (core or periphery), an interaction between playback type and area, and breeding status of the group (non-breeding; oestrus; babysitting & oestrus; babysitting; pregnant; pregnant & escorting) included as fixed effects. To assess the significance of each explanatory variable, we compare the likelihood ratio of the maximal model to that of the model without that explanatory variable (Bates *et al.*, 2015). Parameter estimates and standard errors are taken from the maximal models, rather than following a stepwise model reduction procedure, due to problems associated with this method (Whittingham *et al.*, 2006; Mundry and Nunn, 2009; Forstmeier and Schielzeth, 2011). We removed nonsignificant interaction effects from our maximal model prior to testing the main effects (Engqvist, 2005). Post-hoc tests were performed using the *emmeans* package in R, which calculates estimated marginal means from a model and contrasts them (Lenth, 2019). This frequentist modelling approach was taken as there were clear predictions and hypotheses about the variables.

Results

Observations of natural leadership bids

There were 1336 leadership attempts recorded during 29.5 hours of observation. A number of variables were related to leadership success (i.e. whether potential leaders were followed or not), including sex and age of the possible leader, time spent attempting to lead and the direction and location of the leadership attempt (see Table 5.1 for model averaged parameters).

Leadership context

Leadership success increased with the length of time spent attempting to lead (estimate = 0.99, confidence intervals (CI) = 0.65 – 1.33). However, leadership success did not increase with the production of moving calls (estimate = 0.04, CI = -0.19 – 0.28). There was also no relationship between the speed that the group was moving and the likelihood that a leadership bid would be successful (rest: estimate = -23.23, CI = -2848 – 2786; walk: estimate = -13.42, CI = -2785 – 2758; trot: estimate = -11.12, CI = -2783 – 2761; run: estimate = -11.13 CI = -2848 – 2802). Leadership success was not influenced by breeding status of the group (babysitting and oestrus: estimate = 0.09, CI = -0.45 – 0.64; oestrus: estimate = 0.14, confidence intervals = -0.65 – 0.92; pregnant: estimate = 0.05, confidence intervals = -0.29 – 0.39; pregnant and escorting: estimate = 0.02, confidence intervals = -0.26 – 0.30; non-breeding: estimate = 0.09, confidence intervals = -0.41 – 0.61). In addition there was no effect of being in a coalition (estimate = -0.10, CI = -0.44 – 0.25) or the size of the coalition (estimate = -0.02, CI = -0.16 – 0.12)

Leadership identity

Females were followed more than males (estimate = -0.73, CI = -1.18 – -0.28), and younger individuals were slightly more likely to be successful leaders than older individuals (estimate = -0.43, CI = -0.85 – -0.02). However, there was no interaction between sex and age in relation to leadership success (estimate = -0.15, CI = -0.82 – 0.51).

Leadership location

Leadership attempts that were parallel to the core territory (i.e. neither moving towards nor away from the core territory) were less likely to be successful than leadership attempts away from the core territory (estimate = -

0.58, CI = -0.88 – -0.29). However, there was no difference between leadership attempts towards the core or away from the core territory (estimate = -0.32, CI = -0.71 – 0.07).

There was no relationship between the location in the territory (cumulative probability of use value) and leadership success (estimate = -0.19, CI = -0.47 to 0.09). But, there was an interaction between sex and area – male leadership attempts did not differ in success according to the area of the territory that they took place, however females were more likely to be followed in areas of the territory that were used less frequently, than in areas closer to the core territory (estimate = 0.82, CI = 0.24 – 1.40, Figure 5.1). This difference was small, both males and females were followed across the full range of home range values, but when females were followed the mean cumulative probability of use was 0.58, and when they were not followed it was 0.71, whereas for males the respective values were 0.60 and 0.59 (higher values indicate areas that were used more).

Table 5.1 – Model averaged parameter estimates for factors affecting leadership success of banded mongooses. Only parameters included in the model set are reported. *Effect size has been standardized using R (see Grueber et al. 2011). **Relative importance is calculated according to the number of models that include the variable, and their weighting within the models

Variable		Estimate*	Confidence intervals		Relative importance**
Sex:location		**0.82**	**0.24**	**1.40**	**1.00**
Sex		**-0.73**	**-1.18**	**-0.28**	**1.00**
Direction	**Parallel to core**	**-0.58**	**-0.88**	**-0.29**	**1.00**
	Towards core	-0.32	-0.71	0.07	1.00
Speed	Rest	-23.23	-2848	2786	1.00
	Walk	-13.42	-2785	2758	1.00
	Trot	-11.12	-2783	2761	1.00
	Run	-11.13	-2848	2802	1.00
Age		**-0.43**	**-0.85**	**-0.02**	**1.00**
Location – cumulative probability of use		-0.19	-0.47	0.09	1.00
Time spent leading		**0.99**	**0.65**	**1.33**	**1.00**
Coalition		-0.10	-0.44	0.25	0.36
Sex:age		-0.15	-0.82	0.51	0.31
Moving calls produced		0.04	-0.19	0.28	0.23
Coalition size		-0.02	-0.16	0.12	0.16
Breeding status	Babysitting/oestrus	0.09	-0.45	0.64	0.14
	Oestrus	0.14	-0.65	0.92	0.14
	Pregnant	0.05	-0.29	0.39	0.14
	Pregnant/escorting	0.02	-0.26	0.30	0.14
	Non-breeding	**0.09**	**0.41**	**0.61**	**0.14**

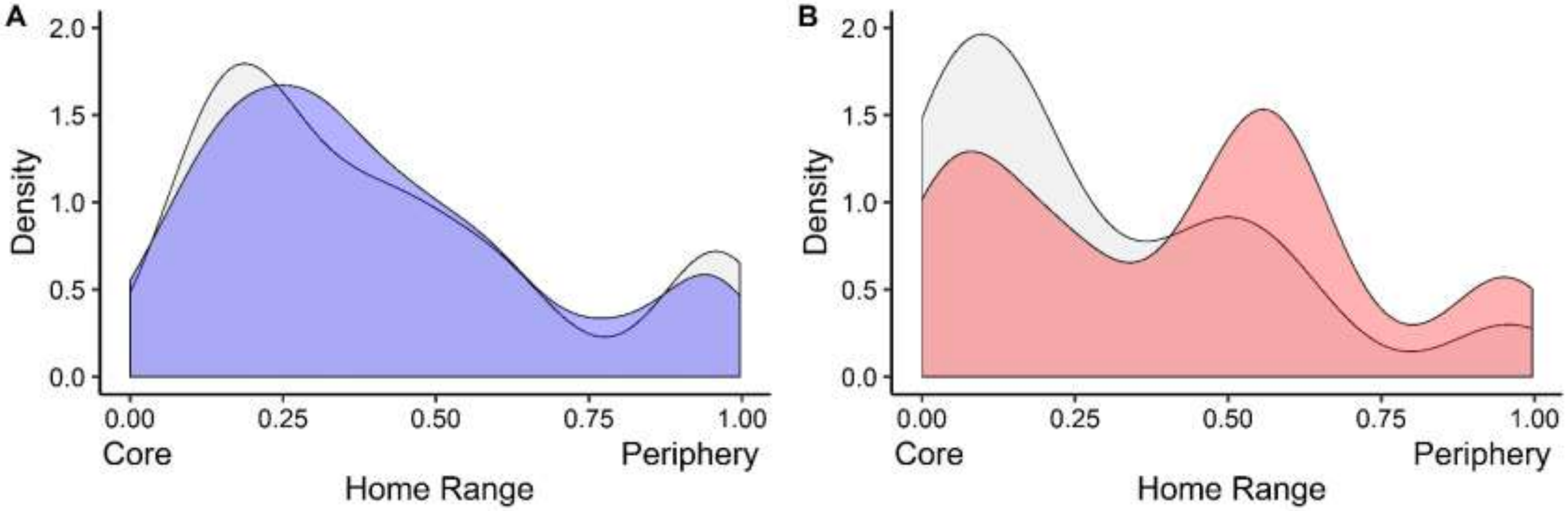

Figure 5.1 – Leadership success in relation to sex and location within the home range. Density shows leadership bids for (A) male leadership bids and (B) female leadership bids. Grey-filled densities indicate unsuccessful leadership bids (not followed by the group) and colour-filled densities indicate successful leadership bids (followed by the group). Low values of home range indicate areas regularly used by the group (high cumulative probability of use), and high values indicate areas used rarely. The home range values have been inverted for presentation graphically.

Experimental playbacks

Approaching the speaker

Contrary to our expectations the percentage of individuals, either males or females, who approached the speaker was not affected by the type of playback call (all: estimate ± SE = 0.90 ± 0.51, F_1 = 3.09, p = 0.08, males: estimate ± SE = 0.95 ± 0.51, F_1 = 3.37, p = 0.07, females: estimate ± SE = 0.92 ± 0.57, F_1 = 2.64, p = 0.11), the area of the territory the playback was performed in (all: estimate ± SE = -0.66 ± 0.51, F_1 = 1.66, p = 0.20, males: estimate ± SE = -0.73 ± 0.52, F_1 = 1.98, p = 0.17, females: estimate ± SE = -0.50 ± 0.57, F_1 = 0.77, p = 0.38), an interaction between the area and the call type (all: F_1 = 0.02, p = 0.89, males: F_1 = 0.18, p = 0.68, females: F_1 = 0.06, p = 0.81), or the breeding status of the group (all: F_4 = 0.52, p = 0.72, for estimates see Table A5.1, males: F_4 = 0.45, p = 0.77, for estimates see Table A5.2, females: F_4 = 0.76, p = 0.56, for estimates see Table A5.3).

Vocal response

Similarly, the percentage of individuals, males or females, responding by making moving calls was not affected by either the type of playback call (all: estimate ± SE = 0.13 ± 0.34, F_1 = 0.14, p = 0.71; males: estimate ± SE = 0.38 ± 0.38, F_1 = 1.00, p = 0.32; females: estimate ± SE = 0.08 ± 0.39, F_1 = 0.04, p = 0.84), the area in which the playback took place (all: estimate ± SE = -0.09 ± 0.33, F_1 = 0.08, p = 0.78; males: estimate ± SE = -0.05 ± 0.37, F_1 = 0.02, p = 0.90; females: estimate ± SE = 0.17 ± 0.39, F_1 = 0.18, p = 0.67), or an interaction between these two variables (all: F_1 = 0.17, p = 0.69, Table A5.4; males: F_1 = 0.16, p = 0.69, Table A5.6; females: F_1 = 0.18, p = 0.67, Table A5.8).

However, this response was affected by the breeding status of the group ($F_4 = 3.79$, $p = 0.01$, Table A5.4). Groups that were pregnant and escorting had a higher percentage of individuals responding with moving calls than either groups in a non-breeding state (post-hoc test, $t = -2.84$, $p = 0.04$, Table A5.5) or only pregnant (post-hoc test: $t = -4.07$, $p < 0.001$, Table A5.5), but other breeding stages did not respond differently (Table A5.5). Groups that were pregnant and escorting also had a higher percentage of males responding with moving calls than either groups that were babysitting and in oestrus ($F_4 = 3.83$, $p = 0.01$, Table A5.6; post-hoc test: $t = -3.00$, $p = 0.03$, Table A5.7) or pregnant (post-hoc test: $t = -3.45$, $p = 0.01$ Table A5.7), but other breeding stages did not respond differently (Table A5.7). The percentage of females responding with moving calls was lower during both non-breeding periods and when females were pregnant than when groups were pregnant and escorting ($F_4 = 3.79$, $p = 0.01$, Table A5.8, post-hoc tests: non-breeding-pregnant and escorting $t = -2.58$, $p = 0.02$, pregnant-pregnant and escorting $t = -2.44$, $p = 0.02$, Table A5.9).

Movement response

Any change in direction in response to the playback was not affected by the type of call used in the playback (estimate ± SE = 0.57 ± 0.59, $X^2_1 = 0.92$, $p = 0.34$, Table A5.10), the area of the territory where the playback occurred (estimate ± SE = -0.87 ± 0.60, $X^2_1 = 2.16$, $p = 0.14$, Table A5.10), an interaction between playback type and location ($X^2_1 = 0.17$, $p = 0.68$, Table A5.10), or the breeding status of the group ($X^2_4 = 6.83$, $p = 0.15$, see Table A5.10 for estimates).

Similarly, the change in speed of a mongoose group did not differ between call types (estimate ± SE = -0.12 ± 0.61, $X^2_1 = 0.04$, $p = 0.84$, Table A5.11). In contrast, the change in speed was higher when the playback occurred in the core areas of the territory compared to the periphery (estimate ± SE = -1.65 ± 0.65, $X^2_1 = 7.21$, $p = 0.01$, Table A5.11). There was no change in speed across breeding statuses ($X^2_4 = 3.87$, $p = 0.42$, for estimates see Table A5.11). There was no effect of an interaction between call type and location on speed change ($X^2_1 = 0.05$, $p = 0.83$, Table A5.11).

Discussion

Observations of natural leadership bids

This exploratory data showed that in natural leadership events females and younger individuals were more likely to be followed when they made a leadership bid, and females were more likely to be followed in more peripheral areas of the home range compared to males. Thus we found evidence that females lead, and were followed, in riskier areas of the territory. This is consistent with the hypothesis that females have an incentive to gain extra-group paternity.

Female banded mongooses were more likely to be followed after leadership bids than males, despite the fact that females made fewer bids than males. Females have been reported to lead groups in many species, including horses (*Equus ferus caballus*) (Welsh, 1975), lemurs (*Propithecus* and *Eulemur* sp.) (Erhart and Overdorff, 1999; Kappeler, 2000), monkeys (Boinski, 2000), Verraux's sifakas (*Propithecus verreauxi*) (Trillmich, Fichtel and Kappeler, 2004), lions (*Panthera leo*) (Schaller, 1972) and hyenas (*Crocuta crocuta*) (Holekamp, Boydston and Smale, 2000). Females may lead because they are more energetically motivated, e.g. lactating female zebras with greater energy requirements (Fischhoff *et al.*, 2007); or because the species is female-bonded (Erhart and Overdorff, 1999), among other reasons. Attempts to gain extra-group paternity might also explain why females lead, however in this case there was no evidence that breeding status influenced the success of leadership bids as might be expected under this scenario. Younger individuals were also followed more than older individuals in the group – which is more surprising – as most studies have shown that dominant, or older, more experienced individuals tend to lead groups (Radford, 2004; Bonanni *et al.*, 2010; Nagy *et al.*, 2010; McComb *et al.*, 2011; Brent *et al.*, 2015; Smith *et al.*, 2015; Langergraber *et al.*, 2017). These observations may be confounded by the fact that leadership was measured from the edge, or “front”, of a group, and leadership may also emerge from the centre – which could mask leadership from older individuals foraging at the centre. Central leadership is difficult to detect, and measure, but new technologies that can monitor multiple individuals’ fine-scale movements simultaneously are starting to be used to measure leadership from any position within a group (Nagy *et al.*, 2010; Strandburg-Peshkin *et al.*, 2015). Future work, using similar technology could help reveal whether true leadership is taking place from the edge, or the centre, of mongoose groups.

Female banded mongooses were more likely to be followed in more peripheral areas of the territory, in contrast, males were less likely to be followed in these peripheral areas. The distribution of the data shows that males make more leadership attempts in regularly used areas and are roughly equally likely to be followed or not, they also show a small increase in leadership bids in very rarely used areas – but are less likely to be followed here. In contrast females are less likely to be followed in regularly used areas, despite a relatively large number of attempts to lead, this balance shifts in areas of around 0.5 probability of use, with females being followed in these locations more. Females are also more likely to be followed in extremely rarely used areas.. This might also suggest that females lead the group into riskier areas of the territory – perhaps to gain extra-group paternity, although as noted before they do not do this differentially across different stages of the breeding cycle, and the effect is not extreme. Alternatively, females may be more likely to be followed in peripheral areas, perhaps by males attempting to mate-guard them in these risky areas. Previous studies have found correlations between leadership in group movement scenarios and participation in intergroup fighting (Bonanni *et al.*, 2010; Bonanni, Valsecchi and Natoli, 2010; Van Belle, 2015) – however in this case we observe female leadership, but male mortality (indicating greater participation in intergroup fighting) which might indicate a lack of correlation between leadership during group movements and participation in intergroup conflicts in banded mongooses. Further research should address which individuals lead groups into intergroup encounters, and whether this is influenced by breeding opportunities for females, or defence of the territory by males.

Experimental playbacks

In contrast to natural leadership events, the leadership response to experimental playbacks did not provide any evidence that group members are more likely to follow females, whether in the core or the periphery of the territory. There was also no evidence that individuals respond more strongly to leadership bids by their own sex. Experimental playbacks had a greater impact on vocal responses and the speed of movement of the group, than on a direct follow (approaching the speaker and proceeding in the direction of the leadership calls). The change in speed following a playback was partially explained by the location of the playback in the territory, with larger changes in speed seen in core areas than peripheral ones.

A vocal response towards a leadership bid could indicate voting and support of the leadership bid (Conradt and Roper, 2003, 2005), like sneezing in African wild dogs (Walker *et al.*, 2017), or moving calls in meerkats leading to group departure (Bousquet, Sumpter and Manser, 2011). However, an increased vocal response could indicate disagreement, or conflict over the leadership bid, with moving calls increasing but voting for different options. Alternatively, a vocal response, but no direct follow, might indicate confusion over the leadership calls, as the playbacks were incongruent, and calls were apparently being made from places where the caller was not present. Incongruent calls in other studies have elicited more attention from focal individuals than congruent calls (Townsend, Allen and Manser, 2012; Gilfillan *et al.*, 2016) – and thus these results may not mirror the patterns seen when observing natural leadership behaviour. However, as all the playbacks were incongruent (all individuals recorded were present at the time of playback) there should be no systematic difference between different classes of playback, or locations in which these took place. Similarly, there may simply be no discrimination of calls made by males and females, either because this is not encoded in the call, or more likely because this is not seen as relevant information by the mongooses, as seen in previous studies of individual discrimination between adult banded mongooses (Jansen, Cant and Manser, 2013).

An additional limitation of the experimental playbacks is that they were made up of calls from the three oldest individuals of each sex in the group, and observations revealed that younger individuals were more likely to be followed.

Additionally, leadership calls were not crucial in a successful leadership bid: in natural events production of leadership or moving calls was not associated with whether individuals followed a potential leader or not. Leadership is complex, and may be cryptic. Leadership does not always occur from the front of the group (as measured in observations, and simulated in the experimental playbacks) and it may be that leadership calls alone with no additional context, e.g. body language, orientation or movement of an individual, are not enough to influence other members of the group. Future experiments with banded mongooses might build on the information gleaned during these observations – focusing on length of the attempted leadership bid, rather than a coalition of older individuals (as neither coalitions nor older individuals were more successful leaders), and using more realistic playbacks that are not incongruent and incorporate body postures etc. by using model banded mongooses.

Conclusion

In conclusion, the pattern of leadership in relation to risk from intergroup conflict is still not clear in banded mongooses. Exploratory observations of natural leadership bids and experimental leadership playbacks revealed different responses to leadership attempts – with some evidence for increased female leadership, particularly in areas of greater risk from conflict with other groups. Further work is needed to confirm how leadership is affected by intergroup conflict in banded mongooses, potentially exploring whether mongooses discriminate between leaders, who leads into fights directly, and which individuals support and follow them, and whether this leadership is correlated to other leadership (e.g. in group movements) and to fitness costs and benefits of intergroup conflicts.

Chapter 6:

General Discussion

Overview

Intergroup conflict in animals is a topic of great interest in evolutionary biology, because of its potential to explain patterns of cooperation and social behaviour. A great deal of research has focused on the behaviour of primates, for example studying individual participation in conflicts, and when and where these conflicts occur, to investigate the ultimate and proximate reasons for intergroup conflict. Some studies have begun to investigate the behavioural consequences of intergroup conflict, to assess the impact that intergroup conflict has on groups and individuals, and expanded the taxonomic reach of intergroup conflict research. However, these behavioural impacts have previously only been measured over short time scales (Table 1.1). Moreover, unlike social mongooses, very few primates are cooperative breeders in which there are conspicuous examples of altruism and helping. In this thesis I measured behavioural changes over longer time scales from 5 minutes after simulated intrusions up to seven days after intrusions in wild banded mongooses. Some behavioural changes were very short-lived, including reduced group-level grooming in the 5-60 minutes after intrusions (**Chapter 2**), but others persisted into the days after a simulated intrusion, including reduced grooming from male mongooses to others, and from females back to males, and reduced aggression from males directed towards females, particularly from older males (**Chapter 3**). These results add to the body of evidence that within-group social behaviours are affected by intergroup conflict (Radford, 2008b, 2008a; Bruintjes *et al.*, 2015; Morris-Drake *et al.*, 2019). However, in banded mongooses we found evidence for reduced (rather than increased) affiliation and aggression, which to our knowledge contrasts with all previous studies of social vertebrates (Table 1.1).

The studies that measure the longest term impacts of intergroup conflict focus on movement behaviour and home range use, rather than social behaviours (e.g. (Markham, Alberts and Altmann, 2012)). These studies found different responses to conflict – some studies found defensive responses, with groups relocating from the area the conflict took place and moving directly and at speed (Markham, Alberts and Altmann, 2012; Crofoot, 2013), other studies found a more attacking response, with evidence of patrolling group boundaries and searching for rival groups (Watts and Mitani, 2000; Mitani, Watts and Amsler, 2009). We found that despite the high frequency of intergroup conflicts, and their violent nature in banded mongooses, their impact on movement and home range use was unclear (**Chapter 4**). However, despite this lack of evidence for direct impacts on movement behaviour, the *risk* of intergroup conflict may be affecting movement, as leadership success differs across the home range (**Chapter 5**).

Sex and age differences in participation in conflict have been seen in many species (Perry, 1996; Saito *et al.*, 1998; Boydston, Morelli and Holekamp, 2001; Lazaro-Perea, 2001; Cant, Otali and Mwanguhya, 2002; Muller and Mitani, 2002; Radford, 2003; Hale, Williams and Rabenold, 2003; Nunn and Deaner, 2004; Harris, 2010; Zhao and Tan, 2011; Mares, Young and Clutton-Brock, 2012; Meunier, Molina-Vila and Perry, 2012; Shaffer, 2013; Van Belle *et al.*, 2014; Wilson *et al.*, 2014; Arseneau *et al.*, 2015; Pal, 2015; Koch *et al.*, 2016a), suggesting that these differences might persist in behavioural responses. Individual differences in traits such as sex or age, lead to differing costs and benefits associated with participating in, and winning or losing intergroup conflicts, which may affect individuals responses to conflict. A limited number of studies have found differences in responses between dominant and subordinate individuals (Radford, 2008b, 2008a, 2011; Bruintjes *et al.*, 2015), and this thesis adds evidence that not only age but sex differences in responses are present in banded mongooses (**Chapter 3**). Additionally, movement consequences may be affected by individual differences, as females are more successful leaders in risky, peripheral areas of the home range (**Chapter 5**), which may lead to increased likelihood of intergroup conflict. Leadership seems to be affected by risk of intergroup conflict, however, the key question of whether leadership is more despotic or democratic in intergroup conflict remains unanswered.

Do groups become more cooperative or cohesive in the face of intergroup conflict?

One of the key questions in animal intergroup conflict research is whether intergroup conflict can lead to increased cooperation, or social cohesion within a group, as has been suggested for humans (Choi and Bowles, 2007; Bowles and Gintis, 2013). Several studies have discovered that in post-conflict periods within-group affiliation increases (Schaffner and French, 1997; Payne, Hallam, Lawes and Henzi, 2003; Radford, 2008b, 2008a; Bruintjes *et al.*, 2015), but it is not yet known how widespread this type of response is. All previous studies have found that either affiliation increases, or there is no change in this type of behaviour, but we found that affiliative behaviour decreased (**Chapter 2**). This was only a short-lived effect of simulated intergroup encounters, and affiliative behaviour returned to pre-experimental levels after an hour (**Chapter 2**), however, this is strikingly different to behavioural responses seen in other species. Not only was group-level affiliation reduced, but rates of grooming between males and other mongooses, and from females back to males were also reduced after exposure to simulated intergroup conflict, compared to those relationships before the conflict (**Chapter 3**). Additionally there was no overall increase in eigenvector centrality (often interpreted as social cohesion) after simulated encounters (**Chapter 3**). These results are the opposite to those measured in any previous studies, suggesting that increased within-group affiliative behaviour is not a universal response to intergroup conflict, and that it can induce the opposite response.

In contrast to previous studies we also found a reduced rate of aggression, from males towards females, after exposure to conflict (**Chapter 3**). Previous studies that measured within-group aggression found that it either increased (Schaffner and French, 1997; Cooper, Aureli and Singh, 2004; Polizzi di Sorrentino *et al.*, 2012), or did not change (Nunn and Deaner, 2004; Bruintjes *et al.*, 2015; Morris-Drake *et al.*, 2019). Reduced aggression could be interpreted as indicating social cohesion, by reducing internal conflict within groups. This might suggest that intergroup conflict does promote social cohesion in banded mongooses, but that this is mediated through reduced aggression rather than through affiliative interactions. Reducing internal conflict is not discussed much in the “parochial altruism” evolutionary model in humans, which focuses instead on group membership and cooperation (Choi and Bowles, 2007; Bowles and Gintis, 2013), however, research on major evolutionary transitions and other multi-level selection theories suggest that both increasing cooperation and reduced internal conflict are important factors (Maynard Smith and Szathmary, 1995; Frank, 2003; Reeve and Hölldobler, 2007; Queller and Strassmann, 2009). Whilst some studies have measured within-group aggression in post-conflict scenarios, a number of studies, including influential work on green wood-hoopoes, have not measured this behaviour (Schaffner and French, 1997; Payne, Hallam, Lawes and Henzi, 2003; Radford, 2008b, 2008a; Radford and Fawcett, 2014). Within-group affiliation may only be half of the story, and within-group aggression and the internal conflict this represents, may be equally as important in the influence of intergroup conflict on social cohesion and group behaviour.

Different species, populations, and groups appear to respond to intergroup conflict in different ways. Some of this variation may be explained by the different risks associated with neighbours vs. strangers in different species. For some social species neighbours are a larger and more constant threat, either to territory, resources, or to paternity (Müller and Manser, 2007; Gill *et al.*, 2012), which is the case for banded mongooses (Müller and Manser, 2007). In many other social species, “stranger” or unfamiliar groups or individuals are seen as a larger threat, often because they are more likely to displace a dominant individual, rather than erode territory (Stanford, 1991; French *et al.*, 1995; Radford, 2005, 2008b; Palphramand and White, 2007; Wich and Sterck, 2007). Perhaps when risk from neighbours is high, social groups respond by reducing internal conflict, as they are likely to encounter neighbours frequently, and this response is less time consuming than increasing affiliation (which often requires resting for longer periods). In contrast, if the risk from strangers is high, social groups may respond with increased affiliation between group members, to consolidate social relationships, which may reduce defection, and immigration, or acceptance of a new dominant individual. Strangers are presumably less frequently encountered than neighbours, and these encounters may also be concentrated in a breeding or dispersal season, so the high cost of spending more time performing affiliative interactions rather than foraging etc. occurs less frequently and may be balanced by the benefits of maintaining dominance and the high reproductive success this brings. Green wood-hoopoes face a greater threat from strangers (Radford, 2005), and do indeed increase affiliative interactions after intergroup encounters. This increase in affiliation is attributed mainly to increasing affiliation by dominants towards subordinates (Radford, 2008a, 2008b), which follows the hypothesis that affiliation may consolidate relationships in order to reduce defection, or acceptance of a new dominant, as this would be more important for the dominant individuals in the group. In contrast, banded mongooses face a greater threat from neighbouring groups (Müller and Manser, 2007), and appear to respond by reducing internal conflict rather than increasing affiliation (**Chapter 3**), these changes are affected by both the age and sex of the individual, with older males reducing aggression the most, suggesting that paternity, or mortality risk, may be important. These are just two anecdotal examples, but there may be a widespread effect of the risk of neighbours vs. strangers on post-conflict behaviour, which needs investigating further.

How long do the behavioural consequences of intergroup conflict last?

One of the gaps in animal intergroup conflict research is the length of time that intergroup conflicts affect the behaviour of groups, and individuals in those groups for. Previous studies have measured social behaviour change in the minutes, and occasionally hours after a conflict has taken place, but not for any longer than later on the same day that an intergroup conflict occurred (Table 1.1). In this thesis I measured social behaviour responses over the day of a simulated intergroup encounter, and for two days afterwards, greatly expanding the length of time studied for post-conflict social behaviour (**Chapter**

2 & 3). I also measured movement behavioural responses in the two to seven days after an encounter took place (**Chapter 4**), expanding on the time scale at which changes to movement path characteristics have been studied (Crofoot, 2013; Christensen *et al.*, 2016).

I found mixed evidence for longer-term impacts of intergroup conflict on group behaviour. The rate of collective alarm calling and scent marking were unaffected by simulated intergroup encounters even within the first few minutes and hours after they occurred (**Chapter 2**). However, grooming at a mean group level was found to decrease in the 5 to 60 minutes after an encounter took place (**Chapter 2**). Grooming then appeared to recover to pre-experimental levels in the days after the conflict on a group level (**Chapter 2**), but this masked subtle changes to individual grooming in this two day period after exposure to conflict (**Chapter 3**). Male mongooses reduced their grooming to both females and other males, with females responding by reducing their grooming towards males (**Chapter 3**). Similarly group-level aggression was not affected exclusively by intergroup conflict, although was reduced in the first five minutes following an encounter (**Chapter 2**). Aggression then returned to pre-experimental levels in the next 55 minutes and remained at this level in the two days after an encounter (**Chapter 2**), but this again masked subtle changes to individual aggressive relationships (**Chapter 3**). In the two days after an encounter males reduced the aggression that they directed towards females, and this was particularly pronounced for older males (**Chapter 3**). This gives evidence that animal social relationships are affected by intergroup conflicts in the longer term, for at least two days after they experience this conflict. However, this impact is not necessarily detectable at a group level, but through differential changes to individuals' social relationships.

Social behaviour is not the only type of behaviour which is affected by intergroup conflict. Some studies have also investigated the impact of intergroup conflict on group movement, in order to assess the potential energetic or resource costs of intergroup conflicts (Crofoot, 2013; Christensen *et al.*, 2016). These studies were also short term, following groups of capuchins and dwarf mongooses for the rest of the day after they were involved in either a natural or simulated intergroup encounter. In **Chapter 4** I measured similar path characteristics (distance, speed, displacement, and path tortuosity) over not only the day of the simulated encounter but for seven days afterwards. However, I did not find any evidence that intergroup conflict *per se*, impacted the movement behaviour of banded mongooses, as groups responded similarly in both control and intrusion trials (**Chapter 4**). Although there is tentative evidence that groups move faster when in the periphery, and further when in the core of their territory after intrusions (**Chapter 4**). This may suggest that risk of, rather than exposure to, conflict is more important in influencing movement. I also investigated the impact of simulated intergroup conflicts on home range use, and similarly found that mongoose groups responded to control and intrusion trials in the same way. However, there is tentative evidence that mongoose groups spend more time in core areas after intrusions (**Chapter 4**). Home range use has already been studied over the longer term (up to 12 months after intergroup conflicts) in some studies, and specifically losing conflicts has led to avoidance of previously used areas (Markham, Alberts and Altmann, 2012). In this research there was no distinction between “winning” or “losing” as the conflicts were simulated, and winner or loser effects may be more important than simply experiencing intergroup conflict, in determining movement patterns and home range use.

The impacts of intergroup conflict on leadership have not yet been studied empirically in animal groups. In this thesis, leadership behaviour was not directly linked to length of time since any previous intergroup conflict, however, leadership success was linked to the area of the home range leadership was attempted in (**Chapter 5**). Female mongooses were more successful leaders in the peripheral areas of the home range than male mongooses (**Chapter 5**) which might mean that intergroup conflicts have a long term impact on how mongooses move, as leadership is affected by the risk of intergroup conflict in the area. Intergroup conflict may contribute to a “landscape of fear” for banded mongooses, having a long term impact on leadership, movement and home range use. Further research is needed to investigate this possibility based on home range use in relation to winning or losing natural intergroup encounters.

Do different individuals respond differently to intergroup conflicts?

An emerging question in this research area is whether individuals respond differently to intergroup conflict. Many studies have shown that individuals differ in how much they participate in intergroup conflict, whether this is based on their sex (e.g. Wilson *et al.*, 2014; Pal, 2015; Koch *et al.*, 2016b), age (e.g. Perry, 1996; Nunn and Deaner, 2004; Koch *et al.*, 2016a; Arseneau-Robar *et al.*, 2017), or simply individual “personality” differences (e.g. Grinnell, 2001). This suggests that individuals might also differ in their response to intergroup conflict, and indeed some studies in cichlid fish (Bruintjes *et al.*, 2015; Hellmann and Hamilton, 2019), green wood-hoopoes (Radford, 2008b, 2008a) and primates (Payne, Hallam, Lawes and Henzi, 2003), have indicated that dominants and subordinates do react differently to intergroup conflict. This is not the case in dwarf mongooses, ring-tailed lemurs or capuchin monkeys, where no difference in response between dominant and subordinate individuals, or males and females, was detected (Nunn and Deaner, 2004; Polizzi di Sorrentino *et al.*, 2012; Morris-Drake *et al.*, 2019). In **Chapter 3** we show that banded mongooses react differently to intergroup encounters, at least in terms of their social interactions, according to both their sex, and their age class.

There are currently no clear patterns in the responses of dominants and subordinates to intergroup conflict. In cichlid fish dominant individuals *receive* more affiliation from other group members than subordinates (Bruintjes *et al.*, 2015; Hellmann and Hamilton, 2019), whereas in green wood-hoopoes, the dominant individuals *give* more affiliation to subordinates (Radford, 2008b, 2008a). Dominant cichlid fish increased aggression towards subordinates, and subordinates increased affiliation to dominants when exposed to neighbours (Hellmann and Hamilton, 2019), a pattern which was not seen in banded mongooses (**Chapter 3**). Additionally, lower ranked female monkeys groomed less than high rank females after intergroup encounters (Payne, Hallam, Lawes and Henzi, 2003). Banded mongooses seem to add to this variation, as we found that older males reduced their aggression towards females more than younger males (**Chapter 3**). This reduction in aggression between the sexes may not be unique to banded mongooses, as cichlid fish were also seen to adjust their behaviour in a sex specific way (Hellmann and Hamilton, 2019). However, cichlid fish were more aggressive to their own sex (and similarly sized group members) after exposure to another group (Hellmann and Hamilton, 2019), rather than repressing between sex aggression.

Most studies did not detect a difference in the responses of male and female individuals to intergroup conflict (Payne, Hallam, Lawes and Henzi, 2003; Nunn and Deaner, 2004; Radford, 2008b, 2008a; Polizzi di Sorrentino *et al.*, 2012; Bruintjes *et al.*, 2015; Morris-Drake *et al.*, 2019). The exception, is a study by Hellman & Hamilton (2019), which also detected a reduction of aggression between males and females (**Chapter 3**), specifically from dominant males to the dominant female. This might suggest that reducing internal conflict between the sexes, particularly between the oldest or most dominant individuals is more widespread. This is the case for banded mongooses, as males reduced aggression directed to females (**Chapter 3**). Reduced aggression after intergroup conflict has not been detected, and different aggressive responses to intergroup conflict between the sexes have not been measured, in any other previous studies, but this could be an important social dynamic after intergroup conflicts, particularly if between-sex conflict is high. We also found reduced grooming from males to other mongooses, and from females back to males – only female to female grooming was unaffected by exposure to intergroup conflict (**Chapter 3**). This appears to be not only the first detection of reduced within-group affiliative behaviours after exposure to intergroup conflict, but among the first to detect differences between male and female affiliative responses to intergroup conflict. This is surprising, as a large number of studies have shown that males and females show different rates of participation in conflicts due to differential costs and benefits of entering into intergroup fights, and these costs and benefits might also affect post-conflict behaviour. Previous studies in vervet monkeys have shown that males and females respond to intergroup conflicts by “rewarding” or “punishing” the opposite sex for either participating or not participating in intergroup conflicts during the conflicts in different ways, but it is unclear whether these different within-group social responses during a conflict continue into the post-conflict phase (Arseneau-Robar *et al.*, 2016, 2018).

Although not a direct response to intergroup conflict, we also found differences in leadership behaviour between individuals. Males made many more leadership attempts than females, but females were more likely to be followed (**Chapter 5**). In areas where the risk of conflict was higher (areas at the edge of the territory) females were much more likely to be followed than males, whereas close to the core of the territory males were more likely to be followed than females (**Chapter 5**). This suggests that intergroup conflict, or at least the risk of conflict occurring, might also affect leadership, and particularly the individuals that attempt, and are successful at leadership. We also found that younger individuals were more likely to be followed, although this did not vary with the risk of intergroup conflict (**Chapter 5**). The next stage of this research is to link leadership more directly to intergroup conflict, investigating which individuals lead the group towards rival groups, which individuals lead during the conflict, and which individuals lead after the conclusion of the conflict.

Future directions for research

There are still many more questions to answer about intergroup conflict, and how social groups respond to rival groups. Here I outline some of the research questions that are still unanswered, particularly for the banded mongoose study system.

We detected changes to social relationships after exposure to simulated intergroup encounters, but we standardised these encounters in an attempt to present a stimulus of consistent magnitude. There are a number of factors that might affect a response to, and therefore the post-conflict behaviour after, a simulated intergroup conflict. Firstly, the exposure to a neighbour versus a stranger group has been seen to elicit different responses (Stanford, 1991; French *et al.*, 1995; Radford, 2005; Müller and Manser, 2007; Palphramand and White, 2007; Wich and Sterck, 2007; Gill *et al.*, 2012; Christensen and Radford, 2018), and indeed different post-conflict behaviour (Radford, 2008b). Banded mongooses react more to neighbours than to strangers (Müller and Manser, 2007), but it is unclear what impact this has on post-conflict behaviour. Further research could investigate the impacts of neighbour vs stranger conflicts, and whether this differs systematically across species according to risk type, greatest threat, or other traits of the species. Similarly, groups have been seen to respond differently according to whether they won or lost an intergroup conflict (Radford, 2008a; Markham, Alberts and Altmann, 2012; Crofoot, 2013), and it has been suggested that this might influence post-conflict behaviour (Radford, 2008a; Polizzi di Sorrentino *et al.*, 2012). As the conflicts in this thesis were simulated there was no clear winner or loser, but the outcome of a conflict could feasibly impact post-conflict behaviour. Further research could measure behaviour before and after natural intergroup encounters and the outcome of the encounter, to determine if there is any impact of the outcome on post-conflict behaviour, and if that varies across species.

We detected changes to the social network for at least two days after a simulated intergroup encounter (**Chapter 3**). Future research could investigate how long these changes persist, or if they are permanent changes to the network after disruption. New analysis techniques, including dynamic network analysis could be used to track changes across time more accurately in terms of the length of time they persist, and whether they return to the original pre-conflict network, or if relationships are changed in the long term. Investigating how long these changes persist, and whether changes are permanent could give greater insight into the link between short term social behavioural change and the spread of cooperation and cohesion predicted in evolutionary models.

In this research we investigated responses to conflict based on the sex and age of individual mongooses, but there are many other factors which might affect how or whether individuals respond to intergroup conflict. One of the key factors explored in animal intergroup conflict is the strength of participation of the individual in the encounter, and this itself may also affect the individual’s post-conflict behaviour. Individuals who participate in intergroup conflict are often those with the lowest cost (large body size, low energetic cost) and the largest potential benefit (dominant individuals defending mates, resources or offspring, males with high change of paternity, females with high quality in-group males, individuals seeking extra-group mating). They may also therefore be most affected in the post-conflict period, perhaps rewarding others who participated, punishing those who did not, driving an affiliative response (or repression of internal conflict), or simply performing stress-relieving behaviours. Some evidence of this has been seen in vervet monkeys, in which individuals reward and punish others according to their participation (or lack thereof) during intergroup conflict (Arseneau-Robar *et al.*, 2016, 2018). The level of participation in intergroup fighting of an individual may have a large impact on how the individual responds in the post-conflict period, and deserves further research. Participation in intergroup conflict has also been linked to social network position (Crofoot *et al.*, 2011), which might also influence the changes to social relationships post-conflict. Further research combining information on participation, and social network position before and after intergroup conflicts could help reveal whether, and how, participation affects social relationship changes.

Another factor of interest, especially in the banded mongoose system, is the relatedness of individuals to each other, or to the group. The relatedness of the group could impact the response of the group to intergroup conflict. In banded mongooses, groups become more closely related as time goes on, due to high levels of inbreeding (Nichols, Cant and Sanderson, 2015; Sanderson *et al.*, 2015) and seek extra-group paternity more (Nichols, Cant and Sanderson, 2015), this could affect how groups behave post-conflict but has not yet been investigated. Additionally, an individual's relatedness in relation to the rest of the group could impact the individual's social response to conflict. Immigrant females that participate in intergroup conflict have been seen to receive more grooming and less aggression than those who don't (Hauser, Cheney and Seyfarth, 1986), which suggests that individuals who are less related may use participation, or indeed post-conflict behaviour to consolidate social bonds and group membership. Individuals may also be more or less likely to seek extra-group mating opportunities, according to their relatedness to the group. Seeking extra-group mating might affect post-conflict behaviour through punishment of this behaviour, or reconciliation between those who have mated with out-group individuals and in-group individuals of the opposite sex.

The link between leadership and intergroup conflict is also a topic for further research. This thesis finds some links between leadership and risk of intergroup conflict, but more evidence is needed to link leadership to natural intergroup encounters. Areas of interest include which individuals lead into the areas where intergroup encounters actually occur, which individuals lead during the fighting itself, and which individuals lead after encounters are resolved.

These individuals may be consistent across these categories, but may also differ – for example, females leading into areas with rival groups (to gain extra-group mating), males leading the fighting itself (to defend mates), and then dominant individuals leading after the intergroup encounter (to defend offspring and move away from the area). Another area to explore is not only which individuals are leading, and the traits that might affect this, but to explore how democratic versus despotic leadership becomes. Theory suggests that despotic leadership occurs in war (Van Vugt, Hogan and Kaiser, 2008; Smith *et al.*, 2016), and this remains to be tested in the animal world.

Conclusions

In conclusion, this thesis adds to the body of research on post-conflict behaviour after intergroup encounters, extending the time period over which these were detected, and finding differences in the responses of different sex and age classes. The key findings are that affiliation and aggression are reduced after intergroup conflict, and that these effects are short-lived at the group level, but last into the longer term as individual responses. Individuals differ in their responses to intergroup conflict, but these differences are masked in many group-level measures of behaviour, which highlights the importance of measuring individual as well as group behaviour. Group-level behaviour returns to pre-conflict levels quickly, whereas individual subtle responses to intergroup conflict last into the longer-term, although how long is not yet known. The impact of intergroup conflict on banded mongoose group movements is unknown, but it may cause an increased amount of time spent in core areas of the territory, and cause groups to move further and slower in the core than in the peripheral areas of their territory. This seems to be a conflict avoidance style response by banded mongooses, but these results are not conclusive. Leadership may also be linked to intergroup conflict, although this has not yet been confirmed directly. How far these results can be extrapolated to other animal species, or even humans is unclear, but many of these results contrast with those seen even in other cooperatively breeding species. There may be much more variation in animal responses to intergroup conflict and post-conflict behaviour than has been measured so far. This variation in responses is worth exploring further, as patterns in responses may be revealed and provide new insights into the causes and consequences of intergroup conflict for animal societies. There are many additional interesting research questions that build on, or complement, this research in both banded mongooses and beyond.

APPENDICES

Appendix – Chapter 2

Table A2.1 – Distribution of experimental trials across focal mongoose groups.

Group	Intrusion Trials	Control Trials
1B	6	6
1H	6	6
11	4	3*
2	4	0*
26	2	7*

* Group 2 dissolved before any successful control trials could take place. The female group members merged with group 11 males to create group 26 – all remaining trials for these groups took place with group 26.

Table A2.2 – Model predicting the frequency of grooming interactions during an observation, based on data from the day of the presentation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Intercept		-2.47	0.54		
Treatment type:Stimulus type:Time point				-0.44	1.00
Stimulus type	Intruder	0.00	0.00	0.73	0.39
	Marks/playback	-0.16	0.19		
Treatment type: Time point	Intrusion:5-60 minutes	-0.97	0.38	**6.19**	**0.01**
Rainfall		-0.02	0.14	0.03	0.87
Group Size		0.07	0.02	**11.01**	**<0.001**
Breeding status	Babysitting	0.00	0.00	8.51	0.07
	Escorting	0.18	0.31		
	Non-breeding	-0.14	0.32		
	Oestrus	0.04	0.55		
	Pregnant	0.80	0.33		

Table A2.3 – Model predicting the frequency of aggression interactions during an observation, based on data from the day of the presentation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Intercept		-4.38	0.70		
Treatment type:Stimulus type:Time point				0.69	0.41
Treatment type:Time point				0.01	0.94
Stimulus type	Intruder	0.00	0.00	0.37	0.54
	Marks/playback	0.14	0.23		
Treatment type	Control	0.00	0.00	**13.32**	**<0.001**
	Intrusion	1.72	0.45		
Time point	0-5 minutes	0.00	0.00	**11.67**	**<0.001**
	5-60 minutes	0.83	0.26		
Rainfall		-0.34	0.18	3.37	0.07
Group Size		0.06	0.02	**6.46**	**0.01**
Breeding status	Babysitting	0.00	0.00	9.01	0.06
	Escorting	0.63	0.39		
	Non-breeding	0.37	0.41		
	Oestrus	-1.58	0.81		
	Pregnant	0.35	0.44		

Table A2.4 – Model predicting the frequency of collective scent marking during an observation, based on data from the day of the presentation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Intercept		-2.40	0.46		
Treatment type:Stimulus type:Time point				0.35	0.56
Treatment type:Time point				0.04	0.85
Stimulus type	Intruder	0.00	0.00	0.35	0.55
	Marks/Playback	-0.09	0.15		
Treatment type	Control	0.00	0.00	0.73	0.39
	Intrusion	0.25	0.29		
Time point	0-5 minutes	0.00	0.00	0.43	0.51
	5-60 minutes	-0.14	0.21		
Rainfall		-0.02	0.12	0.04	0.85
Group Size		-0.02	0.02	2.16	0.14
Breeding status	Babysitting	0.00	0.00	0.75	0.95
	Escorting	-0.16	0.28		
	Non-breeding	-0.05	0.28		
	Oestrus	0.18	0.42		
	Pregnant	-0.08	0.29		

Table A2.5 – Model predicting the frequency of collective alarm calling during an observation, based on data from the day of the presentation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Intercept		-2.21	0.49		
Treatment type:Stimulus type:Time point				0.03	0.85
Treatment type:Time point				0.03	0.86
Stimulus type	Intruder	0.00	0.00	0.17	0.68
	Marks/Playback	0.07	0.32		
Treatment type	Control	0.00	0.00	**4.71**	**0.03**
	Intrusion	0.71	0.32		
Time point	0-5 minutes	0.00	0.00	0.80	0.37
	5-60 minutes	-0.20	0.22		
Rainfall		-0.13	0.13	0.96	0.33
Group Size		-0.04	0.02	**4.60**	**0.03**
Breeding status	Babysitting	0.00	0.00	4.16	0.38
	Escorting	-0.37	0.30		
	Non-breeding	-0.35	0.30		
	Oestrus	-0.05	0.44		
	Pregnant	-0.57	0.31		

Table A2.6 – Model predicting the immediate behavioural reaction score of mongooses following a presentation. Model was fitted using a cumulative link mixed model for ordinal regression, (CLMM, N = 86 videos from 44 trials). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Treatment type	Intrusion	0.00	0.00	**83.01**	**<0.001**
	Control	47.55	250.16		
Stimulus type	Intruder	0.00	0.00	0.03	0.87
	Marks/playback	0.09	0.59		

Table A2.7 – Model predicting the frequency of grooming interactions during an observation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and group ID, trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Intercept		-1.60	0.33		
Treatment type:Time point	Intrusion:Pre	0.00	0.00	**11.59**	**0.01**
	Intrusion:0-5	0.42	0.31		
	Intrusion:5-60	-0.58	0.27		
	Intrusion:Post	-0.32	0.26		
Treatment type	Control	0.00	0.00		
	Intrusion	-0.09	0.26		
Time point	Pre	0.00	0.00		
	0-5 minutes	-0.33	0.22		
	5-60 minutes	-0.07	0.19		
	Post	-0.05	0.18		
Rainfall		0.01	0.08	0.22	0.64
Group Size		0.05	0.01	**4.19**	**0.04**
Breeding status	Babysitting	0.00	0.00	9.33	0.06
	Escorting	0.01	0.18		
	Non-breeding	-0.22	0.18		
	Oestrus	-0.19	0.29		
	Pregnant	0.32	0.18		

Table A2.8 – Post-hoc tests investigating differences in the frequency of grooming between time points in different treatment types.

Contrast		Estimate	Standard Error	Z	P
Control vs Intrusion	Pre-experimental	0.09	0.26	0.34	0.73
	0-5 minutes	-0.33	0.30	-1.1	0.27
	5-60 minutes	**0.67**	**0.27**	**2.49**	**0.01**
	Post-experimental	0.41	0.26	1.59	0.11
Pre vs 0-5	Control	0.33	0.22	1.54	0.42
	Intrusion	-0.09	0.22	-0.42	0.98
Pre vs 5-60	Control	0.07	0.19	0.40	0.98
	Intrusion	**0.66**	**0.20**	**3.34**	**0.005**
Pre vs Post	Control	0.05	0.18	0.25	0.99
	Intrusion	0.37	0.19	1.99	0.19
0-5 vs 5-60	Control	-0.26	0.22	-1.18	0.64
	Intrusion	**0.75**	**0.23**	**3.30**	**0.005**
0-5 vs Post	Control	-0.29	0.22	-1.33	0.55
	Intrusion	0.46	0.22	2.10	0.15
5-60 vs Post	Control	-0.03	0.19	-0.16	1.00
	Intrusion	-0.29	0.20	-1.46	0.46

Table A2.9 – Model predicting the frequency of aggressive interactions during an observation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Intercept		-3.13	0.35		
Treatment type:Time point				2.63	0.45
Treatment type	Control	0.00	0.00	**9.48**	**0.002**
	Intrusion	0.79	0.24		
Time point	Pre	0.00	0.00	**22.12**	**<0.001**
	0-5 minutes	-0.67	0.17		
	5-60 minutes	-0.17	0.12		
	Post	0.05	0.10		
Rainfall		-0.06	0.10	0.45	0.50
Group Size		0.07	0.01	**23.11**	**<0.001**
Breeding status	Babysitting	0.00	0.00	5.12	0.27
	Escorting	0.27	0.23		
	Non-breeding	-0.02	0.23		
	Oestrus	-0.59	0.38		
	Pregnant	0.01	0.24		

Table A2.10 – Post-hoc tests investigating differences in the frequency of aggression between time points.

Contrasts	Estimate	Standard Error	Z	P
Pre vs 0-5	**0.67**	**0.17**	**3.92**	**0.001**
Pre vs 5-60	0.17	0.12	1.46	0.46
Pre vs Post	-0.06	0.11	-0.54	0.95
0-5 vs 5-60	**-0.50**	**0.17**	**-2.88**	**0.02**
0-5 vs Post	**-0.72**	**0.17**	**-4.26**	**0.0001**
5-60 vs Post	-0.23	0.12	-1.96	0.20

Table A2.11 – Model predicting the frequency of collective scent marking during an observation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Intercept		-2.77	0.29		
Treatment type:Time point				6.19	0.10
Treatment type	Control	0.00	0.00	0.002	0.97
	Intrusion	0.01	0.20		
Time point	Pre	0.00	0.00	0.96	0.81
	0-5 minutes	0.16	0.19		
	5-60 minutes	0.004	0.10		
	Post	0.06	0.09		
Rainfall		-0.001	0.08	0.0001	0.99
Group Size		-0.01	0.01	0.63	0.43
Breeding status	Babysitting	0.00	0.00	0.37	0.98
	Escorting	0.06	0.19		
	Non-breeding	-0.04	0.19		
	Oestrus	0.10	0.30		
	Pregnant	0.04	0.19		

Table A2.12 – Model predicting the frequency of collective alarm calling during an observation. Model was fitted using a poisson error structure and a log link function, with observation times as an offset term, and trial ID and observation-level as random intercepts (GLMM, N = 44 trials in 5 groups). Significant terms are given in bold.

Parameter		**Estimate**	**Standard Error**	**X^2**	**P**
Intercept		-2.71	0.32		
Treatment type:Time point				2.79	0.42
Treatment type	Control	0.00	0.00	2.05	0.15
	Intrusion	0.33	0.22		
Time point	Pre	0.00	0.00	1.26	0.74
	0-5 minutes	0.24	0.20		
	5-60 minutes	0.03	0.10		
	Post	0.03	0.09		
Rainfall		-0.03	0.09	0.09	0.76
Group Size		-0.02	0.01	3.35	0.07
Breeding status	Babysitting	0.00	0.00	3.02	0.55
	Escorting	-0.14	0.21		
	Non-breeding	-0.38	0.22		
	Oestrus	-0.09	0.34		
	Pregnant	-0.16	0.22		

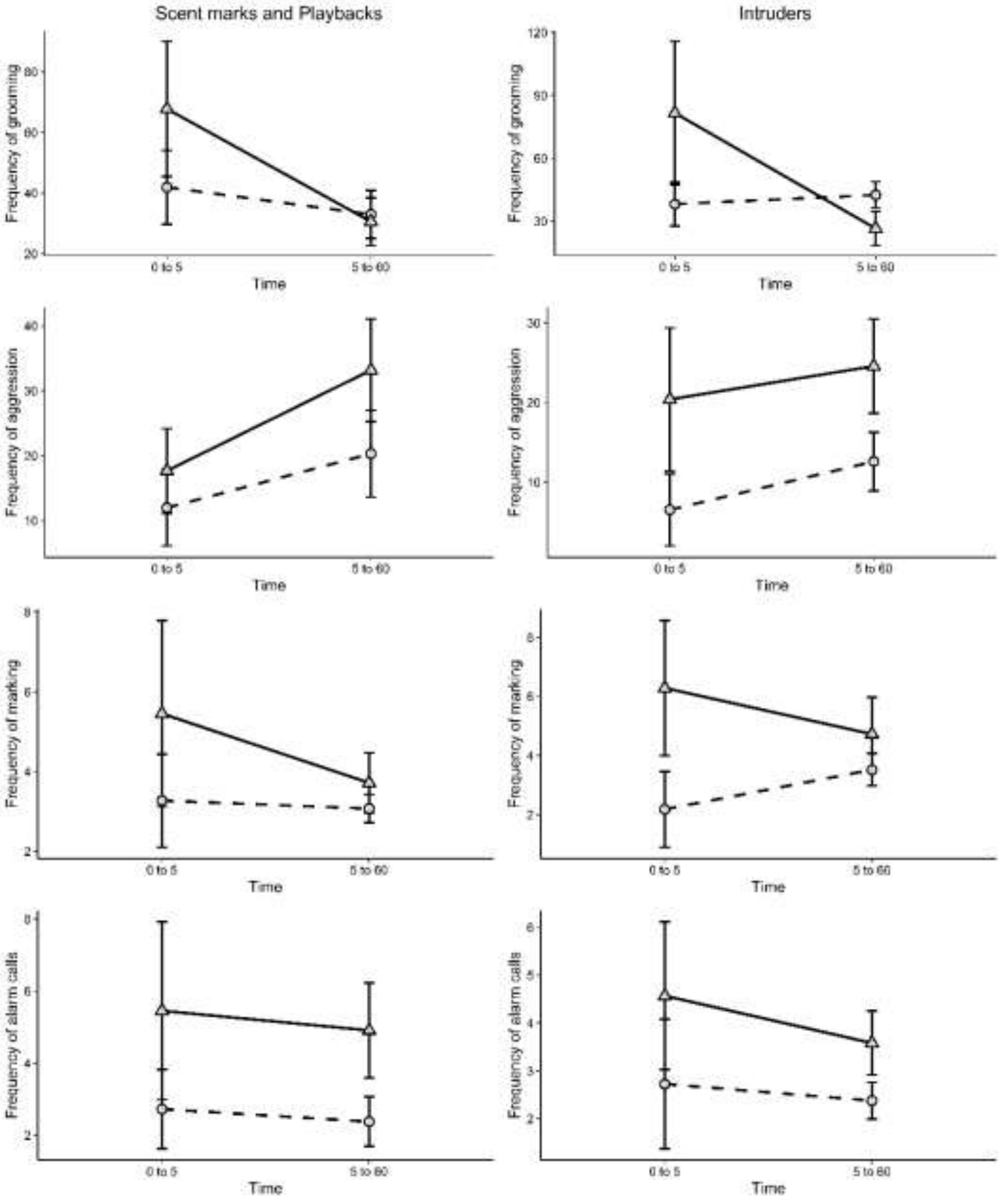

Figure A2.1 – Means and standard errors across time points after mark and playback and intruder presentations. Open triangles and solid lines show intrusion presentations, open circles and dashed lines show control presentations. Responses to scent mark, faeces and playback presentations are shown on the left, and responses to intruder presentations are shown on the right.

Appendix – Chapter 3

Table A3.1 – Post-hoc tests investigating differences in grooming eigenvector centrality between sexes and treatment types. Significant contrasts are shown in bold (α = 0.006)

Data	Contrasts	Estimate	P
Females	**Control-Intrusion**	**0.055**	**0.0008**
Males	Control-Intrusion	-0.050	0.379
Controls	Female-Male	0.077	0.017
Intrusions	Female-Male	-0.028	0.785

Table A3.2 – Post-hoc tests investigating difference from zero in grooming eigenvector centrality in females in each treatment type. Significant contrasts are shown in bold (α = 0.0125)

Data	Treatment type	Estimate	P
Females	**Control**	**-0.041**	**0.003**
	Intrusion	0.008	0.10

Table A3.3 – Post-hoc tests investigating differences in grooming strength between edge sexes and treatment types. Significant contrasts are shown in bold (α = 0.004)

Data	Contrasts	Estimate	P
Female-to-female	Control-Intrusion	0.146	0.063
Female-to-male	**Control-Intrusion**	**-1.006**	**0.0006**
Male-to-female	**Control-Intrusion**	**-0.508**	**0.0002**
Male-to-male	**Control-Intrusion**	**-0.850**	**0.002**
Controls	FF – MM	0.260	0.088
	FF – MF	0.221	0.123
	FF – FM	-0.127	0.527
Intrusions	FF – MM	-0.736	0.027
	FF – MF	**-0.530**	**0.002**
	FF – FM	**-1.279**	**0.000**

Table A3.4 – Post-hoc tests investigating difference from zero in grooming strength in each treatment type. Significant contrasts are shown in bold (α = 0.008)

Data	Treatment type	Estimate	P
Female-to-male	**Control**	**-0.530**	**0.005**
	Intrusion	**-1.536**	**0.000**
Male-to-female	**Control**	**-0.279**	**0.001**
	Intrusion	**-0.787**	**0.000**
Male-to-male	Control	-0.143	0.449
	Intrusion	**-0.993**	**0.000**

Table A3.5 – Post-hoc tests investigating differences in grooming strength by age in each treatment type. Significant contrasts are shown in bold (α = 0.0125)

Data	Parameter	Estimate	P
Control	Age	-0.034	0.834
Intrusion	**Age**	**-0.192**	**0.000**

Table A3.6 – Post-hoc tests investigating difference from zero in grooming strength by age in each treatment type. Significant contrasts are shown in bold (α = 0.0125)

Data	Parameter	Estimate	P
Control	**Age**	**-0.068**	**0.000**
Intrusion	**Age**	**-0.240**	**0.000**

Table A3.7 – Post-hoc tests investigating differences in aggression strength between edge sexes and treatment types. Significant contrasts are shown in bold (α = 0.004)

Data	Contrasts	Estimate	P
Female-to-female	Control-Intrusion	0.041	0.423
Female-to-male	Control-Intrusion	-0.126	0.819
Male-to-female	**Control-Intrusion**	**-0.411**	**0.000**
Male-to-male	**Control-Intrusion**	**0.325**	**0.004**
Controls	FF – MM	0.021	0.718
	FF – MF	**0.195**	**0.002**
	FF – FM	-0.029	0.594
Intrusions	FF – MM	0.310	0.024
	FF – MF	**-0.248**	**0.0006**
	FF – FM	-0.218	0.957

Table A3.8 – Post-hoc tests investigating difference from zero in aggression strength in each treatment type. Significant contrasts are shown in bold (α = 0.008)

Data	Treatment type	Estimate	P
Male-to-female	**Control**	**0.147**	**0.0004**
	Intrusion	**-0.264**	**0.0000**
Male-to-male	Control	-0.055	0.912
	Intrusion	0.271	0.010

Table A3.9 – Post-hoc tests investigating differences in aggression strength by age in each edge sex. Significant contrasts are shown in bold (α = 0.006)

Data	Parameter	Estimate	P
Female-to-female	Age	-0.017	0.954
Female-to-male	Age	-0.088	0.876
Male-to-female	**Age**	**0.079**	**0.0008**
Male-to-male	Age	-0.019	0.736

Table A3.10 – Post-hoc tests investigating difference from zero in aggression strength by age in male-to-female interactions. Significant contrasts are shown in bold (α = 0.025)

Data	Parameter	Estimate	P
Male-to-female	**Age**	**0.079**	**0.0008**

Appendix – Chapter 4

Table A4.1 – Post-hoc tests investigating differences in displacement of mongooses in one hour, between breeding stages. Data from fine-scale analysis – using GPS from tablets over 5 days.

Contrast	Estimate	Standard Error	t	P
Babysitting vs. Escorting	0.09	0.16	0.54	0.98
Babysitting vs. Non-breeding	-0.34	0.16	-2.13	0.23
Babysitting vs. Oestrus	-0.58	0.25	-2.34	0.16
Babysitting vs. Pregnant	**-0.49**	**0.16**	**-3.00**	**0.04**
Escorting vs. Non-breeding	-0.43	0.17	-2.57	0.10
Escorting vs. Oestrus	-0.67	0.26	-2.62	0.09
Escorting vs. Pregnant	**-0.58**	**0.17**	**-3.43**	**0.01**
Non-breeding vs. Oestrus	-0.24	0.25	-0.98	0.86
Non-breeding vs. Pregnant	-0.15	0.16	-0.97	0.86
Oestrus vs. Pregnant	0.09	0.24	0.38	1.00

Table A4.2 – Post-hoc tests investigating differences in path tortuosity of mongooses in one hour, between breeding stages. Data from fine-scale analysis – using GPS from tablets over 5 days.

Contrast	Estimate	Standard Error	t	P
Babysitting vs. Escorting	-0.13	0.16	-0.80	0.93
Babysitting vs. Non-breeding	0.26	0.16	1.63	0.49
Babysitting vs. Oestrus	0.52	0.28	1.90	0.34
Babysitting vs. Pregnant	0.32	0.17	1.90	0.34
Escorting vs. Non-breeding	0.39	0.16	2.42	0.13
Escorting vs. Oestrus	0.65	0.28	2.36	0.15
Escorting vs. Pregnant	0.44	0.16	2.71	0.07
Non-breeding vs. Oestrus	0.26	0.27	1.00	0.85
Non-breeding vs. Pregnant	0.06	0.15	0.37	1.00
Oestrus vs. Pregnant	-0.21	0.27	-0.79	0.93

Table A4.3 – Post-hoc tests investigating differences in total distance moved by mongooses in core or peripheral areas between time points. Pairwise comparisons between pre-experimental, experimental and post-experimental phases in core or peripheral areas. Data from broad-scale analysis – using GPS collars over 15 days.

Contrast		**Estimate**	**Standard Error**	**t**	**P**
Core area	Pre vs. Exp	7.47	93.90	0.08	1.00
	Pre vs. Post	**-200.77**	**48.00**	**-4.18**	**<0.001**
	Exp vs. Post	-208.24	94.30	-2.21	0.07
Peripheral area	Pre vs. Exp	-107.27	93.90	-1.14	0.49
	Pre vs. Post	61.51	48.00	1.28	0.41
	Exp vs. Post	168.78	94.30	1.79	0.17

Table A4.4 – Post-hoc tests investigating differences in mean speed of mongooses in core or peripheral areas between time points. Pairwise comparisons between core or peripheral areas and time points. Data from broad-scale analysis – using GPS collars over 15 days.

Contrast		**Estimate**	**Standard Error**	**t**	**P**
Core area	Pre vs. Exp	0.02	0.11	0.19	0.98
	Pre vs. Post	0.06	0.05	1.10	0.51
	Exp vs. Post	0.04	0.11	0.35	0.93
Peripheral area	Pre vs. Exp	-0.16	0.10	-1.55	0.27
	Pre vs. Post	**-0.26**	**0.05**	**-4.98**	**<0.0001**
	Exp vs. Post	-0.10	0.10	-1.02	0.56

Table A4.5 – Post-hoc tests investigating differences in mean speed of mongooses in core or peripheral areas between treatment types. Pairwise comparisons between intrusion and control trials in core or peripheral areas. Data from broad-scale analysis – using GPS collars over 15 days.

Contrast		**Estimate**	**Standard Error**	**t**	**P**
Control	Core vs. Periphery	0.04	0.06	0.61	0.54
Intrusion	**Core vs. Periphery**	**0.27**	**0.07**	**4.10**	**<0.0001**

Table A4.6 – Post-hoc tests investigating differences in time spent in the core home range in one hour, between time points. Data from fine-scale analysis – using GPS from tablets over 5 days.

Contrast	**Estimate**	**Standard Error**	**t**	**P**
Pre vs. Exp	**-0.03**	**0.01**	**-2.43**	**0.04**
Pre vs. Post	-0.01	0.01	-0.75	0.73
Exp vs. Post	0.02	0.01	1.84	0.16

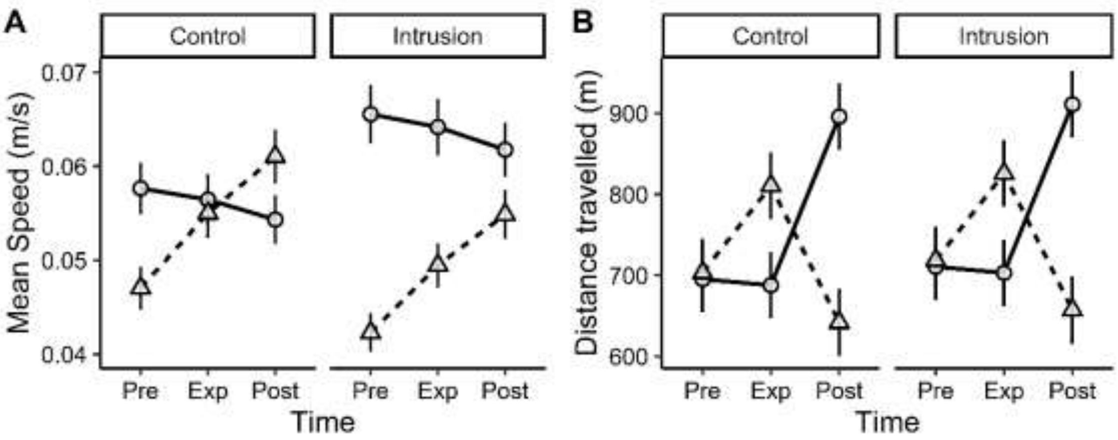

Figure A4.1 – Distance and speed travelled across core and peripheral areas of the territory in different treatment types. Means and standard errors of (A) the mean speed each day, and (B) the total distance travelled per day for the seven days before (Pre), the day of (Exp), and the seven days after (Post) a presentation. Empty triangles and dashed lines show distances and speeds in peripheral areas of the territory, and filled circles and solid lines show distances and speeds in core areas. Points show means from the LMMs ± SE. This figure shows data split between control and intrusion trials to show differences, however, there was no significant interaction between time, treatment type and area.

Appendix – Chapter 5

Table A5.1 – Model predicting the percentage of individuals approaching the playback speaker. Model was fitted to logit transformed data, (LM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		**Estimate**	**Standard Error**	**F**	**P**
Intercept		-2.51	0.66		
Call type:Location				0.02	0.89
Call type	Female	0.00	0.00	3.09	0.08
	Male	0.90	0.51		
Location		-0.66	0.51	1.66	0.20
Breeding status	Babysitting	0.00	0.00	0.52	0.72
	Babysitting & oestrus	0.48	1.24		
	Non-breeding	0.78	0.76		
	Pregnant	0.05	0.72		
	Pregnant & escorting	-0.27	1.03		

Table A5.2 – Model predicting the percentage of male individuals approaching the playback speaker. Model was fitted to logit transformed data, (LM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		**Estimate**	**Standard Error**	**F**	**P**
Intercept		-2.54	0.67		
Call type:Location				0.18	0.68
Call type	Female	0.00	0.00	3.37	0.07
	Male	0.95	0.51		
Location		-0.73	0.52	1.98	0.17
Breeding status	Babysitting	0.00	0.00	0.45	0.77
	Babysitting & oestrus	0.15	1.25		
	Non-breeding	0.66	0.76		
	Pregnant	0.02	0.72		
	Pregnant & escorting	-0.45	1.04		

Table A5.3 – Model predicting the percentage of female individuals approaching the playback speaker. Model was fitted to logit transformed data, (LM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		**Estimate**	**Standard Error**	**F**	**P**
Intercept		-2.54	0.73		
Call type:Location				0.06	0.81
Call type	Female	0.00	0.00	2.64	0.11
	Male	0.92	0.57		
Location		-0.50	0.57	0.77	0.38
Breeding status	Babysitting	0.00	0.00	0.76	0.56
	Babysitting & oestrus	0.66	1.38		
	Non-breeding	0.84	0.84		
	Pregnant	-0.05	0.79		
	Pregnant & escorting	-0.79	1.14		

Table A5.4 – Model predicting the percentage of individuals making moving calls in response to the playback. Model was fitted to logit transformed data, (LM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		**Estimate**	**Standard Error**	**F**	**P**
Intercept		-1.74	0.43		
Call type:Location				0.17	0.69
Call type	Female	0.00	0.00	0.14	0.71
	Male	0.13	0.34		
Location		-0.09	0.33	0.08	0.78
Breeding status	Babysitting	0.00	0.00	**3.57**	**0.01**
	Babysitting & oestrus	-0.87	0.80		
	Non-breeding	-0.74	0.49		
	Pregnant	-1.00	0.46		
	Pregnant & escorting	1.23	0.72		

Table A5.5 – Post-hoc tests investigating differences in the percentage of individuals responding by making moving calls between different breeding statuses.Significant contrasts are given in bold.

Contrast	Estimate	Standard Error	t	P
Babysitting vs Babysitting & oestrus	0.87	0.80	1.08	0.81
Babysitting vs Non-breeding	0.74	0.49	1.51	0.56
Babysitting vs Pregnant	1.01	0.46	2.17	0.21
Babysitting vs Pregnant & escorting	-1.23	0.72	-1.72	0.43
Babysitting & oestrus vs Non-breeding	-0.13	0.75	-0.17	1.00
Babysitting & oestrus vs Pregnant	0.14	0.75	0.18	1.00
Babysitting & oestrus vs Pregnant & escorting	-2.10	0.94	-2.24	0.18
Non-breeding vs Pregnant	0.26	0.40	0.66	0.96
Non-breeding vs Pregnant & escorting	**-1.97**	**0.69**	**-2.87**	**0.05**
Pregnant vs Pregnant & escorting	**-2.24**	**0.66**	**-3.41**	**0.01**

Table A5.6 – Model predicting the percentage of male individuals making moving calls in response to the playback. Model was fitted to the logit transformed data, (LM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	F	P
Intercept		-2.25	0.48		
Call type:Location				0.16	0.69
Call type	Female	0.00	0.00	1.00	0.32
	Male	0.38	0.38		
Location		-0.05	0.37	0.02	0.90
Breeding status	Babysitting	0.00	0.00	**3.83**	**0.01**
	Babysitting & oestrus	-1.63	0.90		
	Non-breeding	-0.60	0.55		
	Pregnant	-1.01	0.52		
	Pregnant & escorting	1.54	0.81		

Table A5.7 – Post-hoc tests investigating differences in the percentage of male individuals responding by making moving calls between different breeding statuses. Significant contrasts are given in bold.

Contrast	Estimate	Standard Error	t	P
Babysitting vs Babysitting & oestrus	1.64	0.90	1.81	0.38
Babysitting vs Non-breeding	0.60	0.55	1.08	0.82
Babysitting vs Pregnant	1.01	0.52	1.94	0.31
Babysitting vs Pregnant & escorting	-1.54	0.81	-1.91	0.33
Babysitting & oestrus vs Non-breeding	-1.04	0.84	-1.23	0.73
Babysitting & oestrus vs Pregnant	-0.63	0.85	-0.74	0.95
Babysitting & oestrus vs Pregnant & escorting	**-3.17**	**1.06**	**-3.00**	**0.03**
Non-breeding vs Pregnant	0.41	0.45	0.92	0.89
Non-breeding vs Pregnant & escorting	-2.13	0.77	-2.76	0.06
Pregnant vs Pregnant & escorting	**-2.55**	**0.74**	**-3.45**	**0.01**

Table A5.8 – Model predicting the percentage of female individuals making moving calls in response to the playback. Model was fitted to the logit transformed data, (LM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	F	P
Intercept		-1.72	0.50		
Call type:Location				0.18	0.67
Call type	Female	0.00	0.00	0.04	0.84
	Male	0.08	0.39		
Location		0.17	0.39	0.18	0.67
Breeding status	Babysitting	0.00	0.00	**3.79**	**0.01**
	Babysitting & oestrus	-1.38	0.93		
	Non-breeding	-1.25	0.57		
	Pregnant	-1.10	0.54		
	Pregnant & escorting	1.33	0.83		

Table A5.9 – Post-hoc tests investigating differences in the percentage of female individuals responding by making moving calls between different breeding statuses. Significant contrasts are given in bold.

Contrast	Estimate	Standard Error	t	P
Babysitting vs Babysitting & oestrus	1.38	0.93	1.48	0.58
Babysitting vs Non-breeding	1.25	0.57	2.19	0.20
Babysitting vs Pregnant	1.11	0.54	2.05	0.26
Babysitting vs Pregnant & escorting	-1.34	0.83	-1.61	0.50
Babysitting & oestrus vs Non-breeding	-0.13	0.87	-0.15	1.00
Babysitting & oestrus vs Pregnant	-0.27	0.88	-0.31	1.00
Babysitting & oestrus vs Pregnant & escorting	-2.71	1.09	-2.49	0.11
Non-breeding vs Pregnant	-0.14	0.47	-0.31	1.00
Non-breeding vs Pregnant & escorting	**-2.58**	**0.80**	**-3.24**	**0.02**
Pregnant vs Pregnant & escorting	**-2.44**	**0.76**	**-3.21**	**0.02**

Table A5.10 – Model predicting the change in direction in response to the playback. Model was fitted using a general linear model, with a binomial error structure, (GLM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Call type:Location				0.17	0.68
Call type	Female	0.00	0.00	0.92	0.34
	Male	0.57	0.59		
Location		-0.87	0.60	2.16	0.14
Breeding status	Babysitting	0.00	0.00	6.83	0.15
	Babysitting & oestrus	16.94	1380.49		
	Non-breeding	0.27	0.86		
	Pregnant	0.21	0.80		
	Pregnant & escorting	-1.35	1.34		

Table A5.11 – Model predicting the change in speed in response to the playback. Model was fitted using a cumulative link model for ordinal regression, (CLM, N = 60 trials in 3 groups). Significant terms are given in bold.

Parameter		Estimate	Standard Error	X^2	P
Call type:Location				0.05	0.83
Call type	Female	0.00	0.00	0.04	0.84
	Male	-0.12	0.61		
Location		-1.65	0.65	**7.21**	**0.01**
Breeding status	Babysitting	0.00	0.00	3.87	0.42
	Babysitting & oestrus	0.03	1.47		
	Non-breeding	-0.18	0.89		
	Pregnant	-0.47	0.83		
	Pregnant & escorting	-2.86	1.75		

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