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Network-level consequences of outgroup threats in banded mongooses: Grooming and aggression between the sexes

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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 predicted that social cohesion (specifically male-to-male and female-to-male grooming) would increase after conflict, and aggression would decrease, to minimize 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 2 days preceding a simulated intergroup conflict (pre-conflict network) and the 2 days after (post-conflict network).
4. We found no evidence of an increase in social cohesion after simulated conflicts, measured as grooming eigenvector centrality. Male-to-male, male-to-female and female-to-male grooming strength decreased after simulated intrusions compared to female-to-female grooming strength. 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 were 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 changes in the directionality of behaviour in response to intergroup encounters, and highlight how individual responses to conflict may scale up to affect

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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.

KEYWORDS

aggression, grooming, intergroup conflict, social cohesion, social network analysis

1 | INTRODUCTION

Intergroup conflict can be a major force driving evolution in social species (Choi & Bowles, 2007; Rusch & Gavrilets, 2016; Thompson, Marshall, Vitikainen, & Cant, 2017). Although intergroup conflict is widespread across social animals (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Golabek, Ridley, & Radford, 2012; Plowes & Adams, 2005; Thompson, Marshall, et al., 2017; Wilson & Wrangham, 2003), the costs and benefits of these conflicts to individual fitness remain poorly understood. Current theory borrows from dyadic animal contest theory, for example, Hawk-Dove evolutionary game theory (Maynard Smith, 1982) and theory of warfare, for example, 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 (Adams & Mesterton-Gibbons, 2003; Fearon, 1995; Johnson & Toft, 2014; Rusch & Gavrilets, 2016; Sherratt & Mesterton-Gibbons, 2013), although some recent theoretical work recognizes heterogeneity of groups (Bornstein, 2003; Gavrilets, 2015; Gavrilets & Fortunato, 2014; Pandit, Pradhan, Balashov, & Van Schaik, 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 and without offspring in the group (Arseneau, Taucher, van Schaik, & Willems, 2015; Boydston, Morelli, & Holekamp, 2001; Kitchen & Beehner, 2007; Mares, Young, & Clutton-Brock, 2012; Meunier, Molina-Vila, & Perry, 2012; Muller & Mitani, 2002; Thompson et al., 2020; Van Belle, Garber, Estrada, & Di Fiore, 2014; Van Belle & Scarry, 2015). Previous studies have shown that movement behaviour is affected by intergroup conflict (Christensen, Kern, Bennitt, & Radford, 2016; Crofoot, 2013), and this may, in turn, affect sociality. As groups are often heterogeneous, there can be internal conflict over investment in group territorial defence. Group members may potentially 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 maximizing fitness are different. A clear example is investment in territorial defence, which has different fitness benefits and costs for males versus females (as seen in vervet monkeys, Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017 and banded mongooses, Thompson, Marshall, et al., 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 species, including chimpanzees, meerkats, and Verraux's sifakas, males participate more than females in intergroup conflicts (Koch, Signer, Kappeler, & Fichtel, 2016; Mares et al., 2012; Muller & Mitani, 2002; Wilson et al., 2014), 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 in vervet monkeys, bonnet macaques, chimpanzees and free-ranging dogs (Arseneau et al., 2015; Cooper, Aureli, & Singh, 2004; Manson & Wrangham, 1991; 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 et al., 2001; Radford, 2003). In primates, the prevalence of sex-specific aggression likely reflects the reproductive costs that are posed by same-sex rivals from outside the group, or attempts to defend access to the group from potential same-sex joiners (Langergraber, Watts, Vigilant, & Mitani, 2017). In vervet monkeys, there are complex sex-specific changes in grooming as a result of conflict. Females increase grooming towards males in their own group who participate in conflicts (Arseneau-Robar et al., 2016), and have also been seen to receive less aggression from their new group if they participate in intergroup conflicts, potentially indicating more successful integration into this new social group (Hauser, Cheney, & 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. Similarly, there are differences in older and younger, and dominant and subordinate individuals, in their contributions to intergroup conflict (Arseneau et al., 2015; Arseneau-Robar et al., 2017; Bonanni, Valsecchi, & Natoli, 2010; Cant, Otali, & Mwanguhya, 2002; Hale, Williams, & Rabenold, 2003; Koch et al., 2016; Lazaro-Perea, 2001; Nunn & Deaner, 2004; Perry, 1996; Radford, 2003; Van Belle et al., 2014) which may equally affect individuals' post-conflict behaviour.

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 (Jones, Aplin, Devost, & Morand-Ferron, 2017; Krause, Croft, & James, 2007; Krause, Lusseau, & James, 2009; Kurvers, Krause, Croft, Wilson, & Wolf, 2014; Rozins et al., 2018; Shizuka & Johnson, 2020). 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 internal disturbance on social relationships (Formica, Wood, Cook, & Brodie, 2016; Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby, & Farine, 2018; Shizuka & Johnson, 2020; Wilson et al., 2015); however, the impact of an external intergroup conflict event (which does not necessarily disturb networks by removing individuals or shuffling groups) on internal group dynamics has not been studied. However, social network traits have been correlated to participation in group defence in female white-faced capuchins *Cebus capucinus* (Crofoot, Rubenstein, Maiya, & Berger-Wolf, 2011), but the impact of individual intergroup conflict events 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 (Bruintjes, Lynton-Jenkins, Jones, & Radford, 2015; Hellmann & Hamilton, 2019; Morris-Drake, Christensen, Kern, & Radford, 2019; Nunn & Deaner, 2004; Payne, Hallam, Lawes, & Henzi, 2003; Polizzi di Sorrentino, Schino, Massaro, Visalberghi, & Aureli, 2012; Radford, 2008a, 2008b), so we do not have concrete predictions surrounding age.

Banded mongooses live in stable multi-male, multi-female groups of between 10 and 30 individuals. Dispersal is relatively rare for both sexes: around 85% of males and females are born and die in the same group (Cant, Nichols, Thompson, & Vitikainen, 2016). Males sometimes disperse in groups voluntarily, but most dispersal occurs as a result of mass evictions, where groups of females (or, in mixed-sex evictions, groups of males and females) are attacked and forced out of their group by members of their own sex (Thompson, Cant, et al., 2017). Groups of mongooses are highly territorial, defending their territories from other groups during frequent, and sometimes lethal, intergroup conflicts (Nichols, Cant, & Sanderson, 2015; Thompson, Marshall, et al., 2017). Mongooses respond to sighting a rival group by standing alert and calling to other members of their group, they often congregate and stand 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 et al., 2002, 2016). Fighting is often highly aggressive involving biting and scratching, and sometimes individuals are held down and attacked by multiple rival mongooses.

On the basis of previous studies, we predict that intergroup conflict will be associated with increased social cohesion after conflict, represented by within-group affiliative behaviour (Bruintjes et al., 2015; Radford, 2008a, 2008b, 2011; Radford & Du Plessis, 2004; Schaffner & French, 1997). However, the concept of social cohesion is rarely defined explicitly, and could in theory be manifested as a reduction in within-group conflict, or reduced aggression (Reeve & Hölldobler, 2007; Thompson et al., 2020). We note, however, that previous studies have recorded no change in within-group aggression (Bruintjes et al., 2015; Morris-Drake et al., 2019; Nunn & Deaner, 2004), or an increased rate of within-group aggression following intergroup conflict (Bruintjes et al., 2015; Cooper et al., 2004; Polizzi di Sorrentino et al., 2012; Schaffner & French, 1997), 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 (F.J. Thompson, unpubl. data), whereas females can benefit from extra-group paternity (Nichols et al., 2015). If rival groups present no threat to females, we would not expect females to respond behaviourally in a manner that increases group social cohesion.

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.
3. Aggression will on average decrease after simulated encounters (following theory Reeve & Hölldobler, 2007). We predict that this decline will be particularly marked for aggression between males and females because males may seek to discourage dispersal by females after exposure to stimuli from rival males.

2 | MATERIALS AND METHODS

2.1 | Study site

Data were collected for this study from wild banded mongooses on the Mweya Peninsula in Queen Elizabeth National Park, Uganda (0°12′S, 29°54′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 Cant (2000), Cant et al. (2016) and Rood (1975).

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

2.2 | Data collection

2.2.1 | Experimental timeline

We adopted a controlled experimental approach in which we compared social networks before and after a simulated intergroup intrusion because it is difficult to predict when and where intergroup encounters will occur for any given study group. Trials took place over 5 days (see schematic in Figure 1). On the first and second days, we recorded baseline social interaction data that were 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. Hormonal changes are likely to lead to short-term behavioural changes via allo-grooming, preening and other affiliative behaviours (Crockford, Deschner, & Wittig, 2018; Dunbar, 2010; Madden & 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), additionally 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.

2.2.2 | 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. In natural encounters, mongooses will typically encounter indirect stimuli first, such as faeces or scent marks, which alert them to the potential presence of rival groups in the area, prior to any direct encounters. Since we did not know which of the many stimuli, or combination of stimuli, are most salient to simulate a natural encounter, we presented three major classes of sensory stimuli—olfactory, auditory and visual—in a single day, mirroring the sequence of exposures that characterize natural encounters. In total, we carried out 22 control presentations and 22 simulated intrusion presentations. Presentations to each focal group were separated by at least 2 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 hr). 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, and a standardized volume of faeces was used in each trial (100 × 137 mm ziplock bag). Samples were collected within 30 min, transferred as quickly as possible to the presentation site, and presented within 2 hr of collection, but generally much faster and as such were not stored on ice. 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 70–100 cm) as mongooses often use open patches for territorial marking (adapted from (Müller & Manser, 2007).

After 3 min of exploring the scent marks, or slightly before if the animals began to move away from the area, a playback of war cries (that had been recorded earlier 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. These war cries were recorded in advance using an H1 Zoom recorder attached to a Sennheiser directional microphone, and were emitted in response to rival mongooses presented in traps.

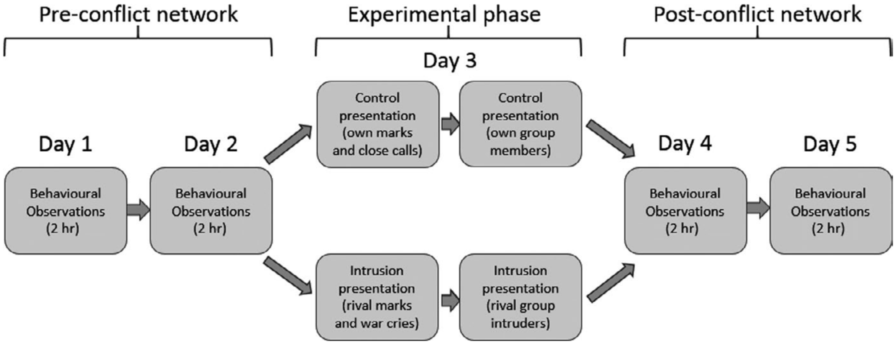

FIGURE 1 A schematic diagram of the timeline of each trial, showing the process in both control (top row) and intrusion (bottom row) trials

These recordings were made when individuals from the rival group were vocalizing at rival mongooses that were presented in traps (see Supporting Information for an example). The recordings were taken from 2 to 3 m away from the mongooses, and recorded calls from multiple individuals as the group were calling together. The recordings were cut into 30 s sections in which vocalizing was occurring, and the amplitude of each clip was standardized using the normalize function in Audacity 2.1.2 to −1 dB (http://audacityteam.org). Each 30 s 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 hr), 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 minimize 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 5 min, the rival males were removed (and the traps re-covered with the cloth) then returned to their own group, to minimize stress levels.

Mongooses appear to react to these simulated intergroup encounters in a similar manner to their reaction to natural encounters, despite their artificial nature. Banded mongooses assess their rivals by approaching, either in battle lines in natural encounters, or by approaching caged animals in simulated encounters. Once they have engaged, they then split their time between group scent marking slightly away from the rivals and engaging with the rival group (either direct fighting, or snapping at and moving around cages)—this happens in both simulated and natural encounters.

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 standardized 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.

2.2.3 | Social data collection

Social interaction data were collected during observations of the focal group for 1 hr in the morning (between 07:00 and 12:00 hr) and for 1 hr in the afternoon (between 16:00 and 19:30 hr) on each day when mongooses had moved away from the den and begun foraging. Banded mongooses spent time foraging, moving and resting during these periods, but changed activity regularly, and there was no systematic difference between observations. Throughout the observation, every affiliative and aggressive interaction between individuals was recorded. This was possible in this system as banded mongooses forage at ground level in cohesive groups in relatively open habitat so all individuals could be seen by either one, both or all of the observers at any one time. A minimum of two observers were present during each observation. All affiliative interactions, that is, grooming and 'nubbing' (mutual genital sniffing) were recorded by noting the identity of the individuals involved and the direction of the interaction (see Table 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 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 2 days before the presentation day (total 4 hr of observations) were pooled to create a pre-conflict grooming and a pre-conflict aggressive social network. Social interaction data

TABLE 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 backward and forward motion. One bout of grooming was defined as active grooming between the same pair of individuals with short breaks of no longer than 30 s of rest. If 30 s 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 s of rest (no grooming of any partner) occurred Nubbing—wo mongooses perform 'nubbing' behaviour—a mutual genital sniff with raised tails which may also include marking each other and vocalizing
Aggressive interaction	One mongoose is aggressive to another mongoose. This can include lunging, biting, growling or snarling vocalizations, 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 s between aggressive behaviours (e.g. lunging, vocalizing)

from 2 days after the presentation day (total 4 hr of observations) were pooled to create a post-conflict grooming and a post-conflict aggressive social network.

2.3 | 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 & 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 hr 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. To test the robustness of these networks, we ran Mantel tests in three pilot control trials pre- and post-conflict grooming and aggression matrices, which were significantly correlated (Mantel tests: all $p < 0.05$), suggesting that the observed social interactions were stable over the study period. We also ran bootstrapping methodology (adapted from Lusseau, Whitehead, & Gero, 2008). Mean deviation of each mongooses eigenvector centrality from 1,000 bootstrapped samples of the raw data was 0.062 ± 0.20 in the grooming networks and 0.055 ± 0.21 in the conflict networks. Modal deviation was 0 in both grooming and conflict networks. These methods are based on those available (Lusseau et al., 2008; Whitehead, 2008), but so far there are no specific methods for addressing robustness of networks when there is more than one network, and for interaction rather than association data. These should be developed more in the future.

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, for example, male–male for an interaction from a male towards another male, or female–male for an interaction from a female directed to a male. All network metrics analysed were chosen a priori based on the predictions and hypotheses outlined in the introduction, and again below.

2.4 | 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, that is, 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, that is, 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 & Faust, 1994). Indirect centrality measures have been used to assess social cohesion in a number of studies, and eigenvector centrality is appropriate for use as a cohesion measure in this study as there are no sub-groups (Blumstein, Wey, & Tang, 2009; Brent, 2015; Kanngiesser, Sueur, Riedl, Grossmann, & Call, 2011; Makagon, McCowan, & Mench, 2012; Wiszniewski, Lusseau, & Möller, 2010). An increase in eigenvector centrality indicates that an individual mongoose is more connected either directly or indirectly in the network, suggesting that grooming interactions surrounding that individual are increasing. This indicates social cohesion through increased grooming, as seen in previous studies that have recorded an increase in other affiliative interactions after intrusions (Bruintjes et al., 2015; Radford, 2008a, 2008b, 2011; Radford & Du Plessis, 2004; Schaffner & French, 1997). In contrast, a reduction of an individual's grooming eigenvector centrality suggests that the network is less connected, and less grooming is being directed at or given by the focal individual and its direct connections—this might indicate less grooming in general, or less grooming among certain parts of the network, for example older females. These changes will give us an insight into how cohesive and well connected the network is following intrusions.

This model contained the change in eigenvector centrality of each individual, in each trial (857 observations from 100 individual mongooses in five 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. Individual identity nested in group identity was included as a random factor. We then used AIC model selection to select the best model, and remove unnecessary interaction effects, while retaining biologically relevant interactions. Models within ΔAIC < 2 of the model with the lowest AIC value were considered (Burnham & 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.

2.5 | 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 1,714 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. Individual identity nested in group 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.

2.6 | 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 2,571 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. Individual identity nested within group 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.

2.7 | 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. Node label permutations in this case meant that the node labels of each observed network (e.g. pre-experimental observations of group 1 in trial 1) were shuffled, to separate individual identity from the age or sex of an individual and test for the effect these factors had on their social relationships. 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, Madden, Franks, and James (2011), Farine and Whitehead (2015)]. Model coefficients stabilized at 5,000 permutations, tested using the method from Bejder, Fletcher, and Brager (1998). We therefore ran 5,000 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 randomized model coefficients that were larger/smaller than the observed model coefficient. Here, we used $\alpha = 0.025$ 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 treatments). Simple linear mixed models (with individual identity nested in group identity as a random effect) of the variables of interest were then run, for example, 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 to extract randomized 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: four post-hoc tests, $\alpha = 0.006$; grooming and aggression strength: six post-hoc tests, $\alpha = 0.004$). 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 to extract randomized model coefficients used to calculate *p* values for these post-hoc tests (female grooming eigenvector centrality: one post-hoc test, $\alpha = 0.025$; grooming and aggression strength: three post-hoc tests, $\alpha = 0.008$). 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 & Maechler, 2009).

Additional permutations which randomized the treatment label were also performed. These permutations meant that the treatment type label (control or intrusion) was randomized within group, within paired experiment, within period (before or after), and within individual. Change in network metric was then recalculated after randomization so that treatment type was separated from the network metric value. Models were then re-run on subsets of the data for each sex, or edge sex, but included only Treatment type and, as a random factor, individual identity. Age could not be included in these models as individuals changed their age (measured as a continuous variable) between paired control and intrusion experiments, and labels were shuffled between these paired experiments, leading to mismatches in age when recalculating change in network metric.

3 | RESULTS

3.1 | Prediction 1: Social cohesion will increase following encounters

There was a significant interaction between treatment type and sex (estimate = −0.099, p = 0.025, Table 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 = 0.002, Table A1; Figure 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 = 0.013, p = 0.06, Table A2]. Additionally, following treatment type permutations, the change in female eigenvector centrality did not differ between control and intrusion trials (estimate = 0.033, p = 0.26). 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 = −0.052, p = 0.41, Table A1; treatment permutations: estimate = −0.019, p = 0.63]. 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 = 0.075, p = 0.02; intrusion data, female–male = −0.032, p = 0.81, Table A1]. There was no relationship between change in grooming eigenvector centrality and either age, or an interaction between treatment type and age (Table 2). This suggests that there is no evidence for the first prediction that social cohesion (represented by eigenvector centrality) will increase following encounters.

TABLE 2 Model parameter estimates from the grooming eigenvector centrality model, and p values from network permutations (p values are calculated as a proportion of randomized 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 nested in group identity as a random intercept (LMM, N = 857 observations (274 = female, 583 = male) across 100 individuals in five 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	−0.048	
Treatment	**0.112**	**0.0004**
Age	0.0006	0.439
Sex	**0.075**	**0.022**
Treatment:Sex	**−0.099**	**0.025**
Treatment:Age	−0.018	0.911

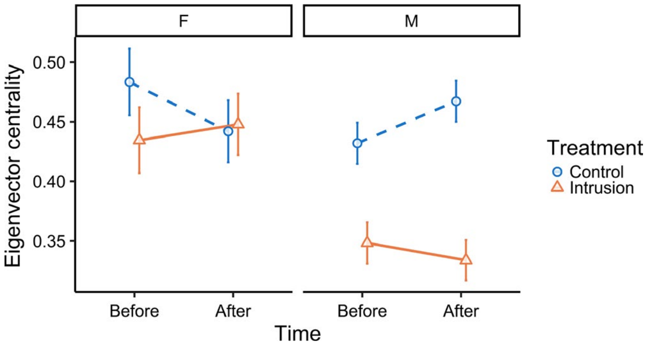

FIGURE 2 The change in mongoose individual grooming eigenvector centrality from before presentations to after presentations for males and females in intrusion (orange triangles and solid lines) and control (blue circles and dashed lines) trials. The figure shows that for female mongooses intrusion trials 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 five groups and 44 trials

3.2 | Prediction 2: Grooming directed towards males will increase following encounters

There was a significant interaction between treatment type and edge sex (intrusion:MM estimate = −0.935, p = 0.010; intrusion:MF estimate = −0.593, p = 0.006; intrusion:MF estimate = −1.152, p = 0.001, Table 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 = −0.858, p = 0.001, Table A3], male-to-female [post-hoc test (α = 0.004): MF data control-intrusion estimate = −0.526, p = 0.000, Table A3] and female-to-male relationships [post-hoc test (α = 0.004): FM data control-intrusion estimate = −1.006, p = 0.000, Table A3; Figure 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 = −1.075, p = 0.00; MF data, intrusion estimate = −0.788, p = 0.00; FM data, intrusion estimate = −1.536, p = 0.00, Table A4]. The change in male-to-male and male-to-female grooming strength was also confirmed to be decreasing in intrusion trials compared to

TABLE 3 Model parameter estimates from the grooming strength model, and *p* values from network permutations (*p* values are calculated as a proportion of randomized model coefficients that are larger/smaller than the observed model coefficient, $\alpha = 0.025$ as these were two-tailed tests). Model was fitted with individual identity nested in group identity as a random intercept (LMM, $N = 1{,}714$ observations (FF = 274, MM = 583, MF = 583, FM = 274) across 100 individuals from five 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	**0.600**	**0.006**
Age	−0.036	0.310
MM	0.278	0.080
MF	0.142	0.200
FM	−0.127	0.527
Treatment:MM	**−0.935**	**0.010**
Treatment:MF	**−0.593**	**0.006**
Treatment:FM	**−1.152**	**0.001**
Treatment:Age	**−0.157**	**0.004**

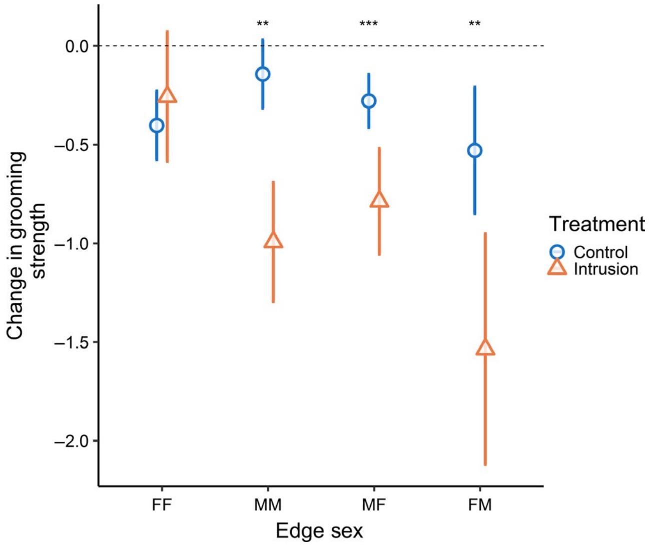

FIGURE 3 The change in mongoose individual grooming strength from before presentations to after presentations for males and females in intrusion (orange triangles) and control (blue circles) trials. This figure shows that female–female grooming is not affected by intergroup conflict, but male–male, male–female and female–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. $N = 1{,}714$ observations (FF = 274, MM = 583, MF = 583, FM = 274) across 100 individuals from five groups in 44 trials. $^{**}p < 0.01$, $^{***}p < 0.001$

control trials by treatment permutations (MM estimate = −0.850, $p = 0.01$; MF estimate = −0.508, $p = 0.016$), but not in female-to-male grooming strength change (FM estimate = −1.006, $p = 0.92$).

Female-to-female grooming strength did not differ between control and intrusion trials [post-hoc test ($\alpha = 0.004$): FF data control-intrusion estimate = 0.146, $p = 0.07$, Table A3; Figure 3; treatment permutations estimate = 0.146, $p = 0.53$]. In control trials, there was no difference in the response of each edge sex [post-hoc tests ($\alpha = 0.004$): control data, FF-MM estimate = 0.207, $p = 0.12$; FF-MF estimate = 0.071, $p = 0.28$; FF-FM estimate = −0.127, $p = 0.52$, Table A3]. In contrast, in intrusion trials, both female-to-male grooming decreased compared to female-to-female grooming [post-hoc tests ($\alpha = 0.004$): FF-FM estimate = −1.279, $p = 0.00$, Table A3]. 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) than younger individuals after intrusion trials (Table 3; Figure 4), and this slope was significantly different from zero [post-hoc test ($\alpha = 0.0125$): intrusion data, age estimate = −0.222, $p = 0.00$, Tables A5 and A6]. In control experiments, there was no change in grooming strength across age classes [post-hoc test ($\alpha = 0.0125$): control data, age estimate = −0.046, $p = 0.84$, Table A5].

3.3 | 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 4; post-hoc test ($\alpha = 0.004$): MF data control-intrusion estimate = −0.468, $p = 0.00$, Table A7; Figure 5]. This decrease in male-to-female aggression

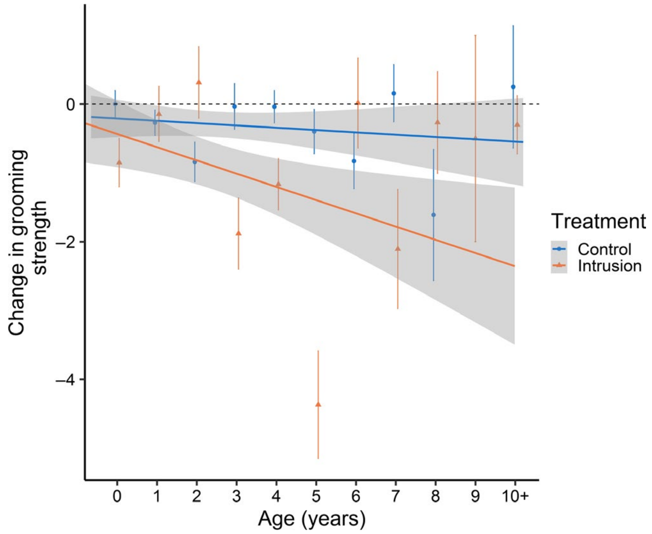

FIGURE 4 The change in mongoose individual grooming strength from before presentations to after presentations in intrusion (orange triangles) and control (blue circles) trials. This figure shows that in intrusion trials older individuals reduce their grooming more than younger individuals. Points shown are raw data binned into categories (statistical analysis used a continuous measure) and lines are predictions from the raw data. $N = 1{,}714$ observations across 100 individuals from five groups in 44 trials

TABLE 4 Model parameter estimates from the aggression strength model, and p values from network permutations (p values are calculated as a proportion of randomized model coefficients that are larger/smaller than the observed model coefficient, $\alpha = 0.025$ as these were two-tailed tests). Model was fitted with individual identity nested in group identity as a random intercept (LMM, $N = 2{,}571$ observations (FF = 857, MM = 857, MF = 583, FM = 274) across 100 individuals in five groups for 44 trials). Significant terms are given in bold

Variable (Reference)	Estimate	p value
Intercept	0.020	
Treatment (Control)	−0.181	0.931
Age	−0.030	0.620
MM (FF)	0.008	0.716
MF (FF)	−0.082	0.711
FM (FF)	0.276	0.200
Treatment:MM (Control:FF)	0.289	0.028
Treatment:MF (Control:FF)	**−0.443**	**0.000**
Treatment:FM (Control:FF)	−0.157	0.825
Treatment:Age (Control:Age)	0.061	0.037
Age:MM (Age:FF)	0.004	0.396
Age:MF (Age:FF)	**0.078**	**0.002**
Age:FM (Age:FF)	−0.103	0.906

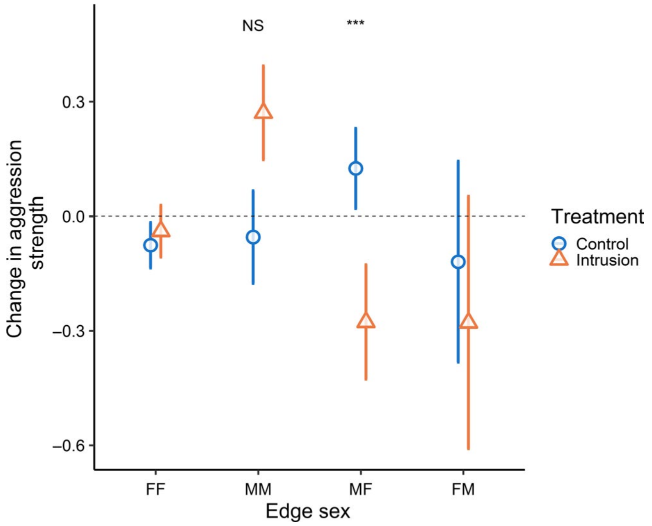

FIGURE 5 The change in mongoose individual aggression strength from before presentations to after presentations for males and females in intrusion (orange triangles) and control (blue circles) trials. This figure shows that male–female aggression decreases in intrusion, but not control trials. Points shown are means from the raw data and error bars are standard errors on these means. $N = 2{,}571$ observations (FF = 857, MM = 857, MF = 583, FM = 274) across 100 individuals in five groups for 44 trials. ***$p < 0.001$

in intrusion trials was significantly different from zero, suggesting a decrease in real terms [post-hoc test ($\alpha = 0.008$): MF data, intrusion estimate = −0.308, $p = 0.00$, Table A8]. The change in male-to-female aggression was also confirmed to be decreasing in intrusion trials compared to control trials by treatment permutations (estimate = −0.411, $p = 0.01$). 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; Figure 5). Treatment permutations confirmed that male-to-male and female-to-male aggression did not differ between intrusion and control trials (MM estimate = 0.479, $p = 0.07$, FM estimate = −0.126, $p = 0.69$).

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). Specifically, male-to-female

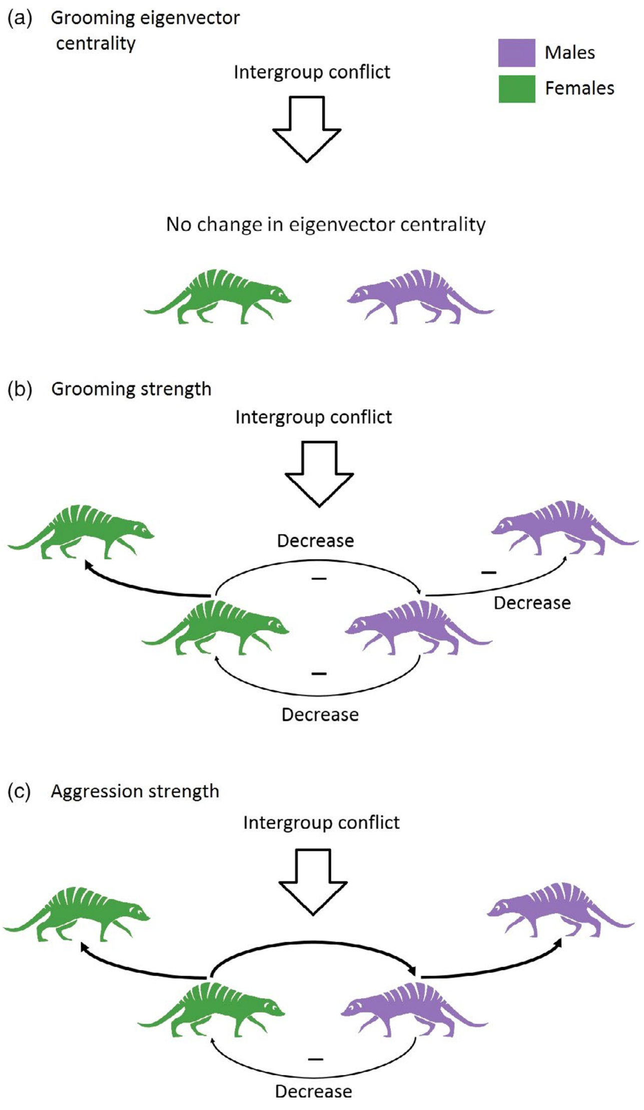

FIGURE 6 Summary of the effect of intrusion trials on grooming and aggression networks (a) grooming eigenvector centrality does not change; (b) grooming strength decreases in male–male, male–female and female–male relationships; and (c) aggression strength decreases in male–female relationships. Female 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

aggression increased in older males following presentations, but not in younger males [Table 3, post-hoc test ($\alpha = 0.006$): MF data, age estimate = 0.095, $p = 0.0006$, Tables A9 and A10]. The change in aggression between other edge types was not related to age [post-hoc tests ($\alpha = 0.006$): FF data, age estimate = −0.014, $p = 0.95$; FM data, age estimate = −0.069, $p = 0.87$; MM data, age estimate = −0.004, $p = 0.69$, Table A9]. There was therefore mixed evidence for the third prediction, that between-sex aggression strength would decrease, as male-to-female aggression decreased, but female-to-male aggression was not affected by simulated intergroup conflict (Figure 6).

4 | 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 increased in older males compared to younger ones. These results highlight both sex and age differences in the responses of banded mongooses to intergroup encounters.

4.1 | 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 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. Social cohesion may be masked by this measure if there is increased spatial cohesion of individuals, but these individuals are more vigilant or otherwise not interacting with each other. This could be investigated in the future if individuals can be followed and spatial structure of the group and interactions measured simultaneously.

4.2 | 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 for their participation (Arseneau-Robar et al., 2016; Cooper et al., 2004). 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. Previous studies in dwarf mongooses have found that vigilance behaviour increases after exposure to a simulated intergroup conflict (Morris-Drake et al., 2019); however, we found no evidence of increased alarm calling or scent marking at a group level (Preston, 2019). It is possible that males contribute more to alarm calling or scent marking that is not clear when measuring group-level behaviour but unfortunately, these behaviours were only recorded at a group and not individual level in this study. It seems plausible though, that 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 investing in internal relationships. Females may then reciprocate grooming less, as males are not grooming them, leading to a by-product reduction in female–male grooming. Individual differences in behaviour may also be attributed to individual contributions to intergroup conflicts, for example in this case males contributing more than females. In this study, it was not possible to separate out contributions of individuals, even by sex and age class, to intergroup conflicts, as almost all individuals interacted with presented stimuli and detailed individual behaviour could not be followed accurately during presentations. Future work aims to address this using technology to disentangle contributions and link these to behavioural change at an individual level. 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, & 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* (Mares et al., 2012). Males chased intruders more than females as they suffer a greater threat from the intruders, and reduced pup care when intruders were present (Mares et al., 2012). Our results also provide evidence that males are affected more by intergroup encounters than females, as all grooming strength changes involving males were significantly 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 (Nichols, Jordan, Jamie, Cant, & Hoffman, 2012). 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 (Arseneau et al., 2015; Van Belle et al., 2014).

4.3 | 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 (Cooper et al., 2004; Polizzi di Sorrentino et al., 2012; Schaffner & French, 1997), or no change (Bruintjes et al., 2015; Morris-Drake et al., 2019; Nunn & Deaner, 2004), 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 & 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 et al., 2004). Males may simply be spending more time on other activities and reducing all social interactions, but aggressive interactions are quick and do not require as much time investment as affiliative grooming interactions. Additionally, male banded mongooses suffer higher rates of mortality from intergroup aggression than females (F.J. Thompson, unpublished data), and females can even benefit from extra-group mating opportunities (Nichols et al., 2015), which could create conflict between males and females over engagement in intergroup encounters. This between-sex conflict 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, Hodge, Bell, Gilchrist, & Nichols, 2010). Alternatively, 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. Indeed, male-to-male aggression appears to increase slightly, and although this is not statistically significant, this is worth investigating in the future in case this trend represents re-directed aggression from out-group members to within-group males. Same-sex aggression may serve to encourage participation in future conflict, or to relieve tension from losing a conflict (Radford, Majolo, & Aureli, 2016).

5 | 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 suggests 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 recognizing 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 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.

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AUTHORS' CONTRIBUTIONS

E.F.R.P. carried out field work and data analysis, designed the study and drafted the manuscript; F.J.T. carried out pilot fieldwork, and critically revised the manuscript; S.E. assisted with data analysis and critically revised the manuscript; S.K. collected field data and critically revised the manuscript; D.P.C. co-supervised the work, assisted with data analysis and critically revised the manuscript; M.A.C. supervised the work, managed the long-term project and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.12744992 (Preston et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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