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Collective defence and behavioural homogeneity during simulated territorial intrusions in banded mongooses (*Mungos mungo*)

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Abstract

Conflicts between stable social groups ("intergroup conflicts") can be damaging and exert a strong influence on within-group social behaviour. The success of groups during intergroup conflict may depend on the ability of individual group members to converge upon collective defence behaviour, such as approaching or attacking. In principle, collective defence can be achieved via a united front, in which each individual responds in the same way to an intergroup threat. We tested the impact of simulated intergroup conflicts on collective defence and individual behaviour in banded mongooses (*Mungos mungo*), a cooperatively breeding mammal in which intergroup conflict is particularly common and costly. We presented focal groups with scent markings, call playbacks and caged live animals from rival groups and compared their responses to these stimuli with their responses to own-group control stimuli. A greater proportion of group members approached the stimulus and acted defensively in response to rival stimuli as compared to controls, consistent with a unified collective defence response. However, counter to our expectation, groups exhibited lower behavioural homogeneity when presented with rival stimuli as compared to controls. A closer examination of the behaviours competitors used revealed that lower homogeneity was driven by a greater use, and diversity, of defensive behaviours relevant to repelling simulated rivals. Finally, group size affected responses: as group size increased, the proportion of members approaching the stimulus and behavioural homogeneity decreased. Our results lend support to the hypothesis that intergroup conflict leads to coordinated collective defence behaviour during the immediate threat of an intergroup conflict. However, collective defence need not mean that all group members execute the same behaviours.

KEYWORDS
banded mongoose, conflict, defence, intergroup contest, social carnivore, social evolution

1 | INTRODUCTION

Intergroup conflict, in which stable social groups of two or more individuals compete over access to limited resources like territory or food, is widespread (Green et al., 2020). Intergroup conflict (also termed between-group conflict, intergroup contests and intergroup contest competition) can result in costs to group members, including the death of adults and young (Batchelor & Briffa, 2011; Thompson et al., 2017; Wrangham et al., 2006). Groups can also benefit by winning intergroup conflicts, such as by gaining access to resources (Dyble et al., 2019; Markham et al., 2012). Under the selective pressure of intergroup conflict, individual and group social behaviour might be expected to evolve in a way that maximizes the (inclusive) fitness benefits and minimizes the costs of conflict.

Previous research on intergroup conflict in cooperative animal societies shows that group members often respond to intergroup conflict by increasing their investment in collective defence. For example, Christensen et al., (2016) presented groups of dwarf mongooses (*Helogale parvula*) with scent marks from rival groups. Compared to control conditions (own-group or herbivore scents), focal groups spent longer investigating rival group scents, a greater number of group members investigated rival group scents, and overall response levels (as measured by scent-marking effort) increased in response to rival group scents (Christensen et al., 2016). Increases in collective defence have also been shown in response to simulated intergroup conflict in other taxa: lions (*Panthera leo*) increase recruitment calling in the face of rival call playback (McComb et al., 1994); cichlid fish (*Neolamprologus pulcher*) are more aggressive towards simulated rivals than controls (Bruintjes et al., 2016); and green woodhoopoes (*Phoeniculus purpureus*) more quickly approach unfamiliar call playback as compared to familiar playback (Radford, 2005). Collective defence behaviours are thought to help groups defend resources like a territory, either through directly engaging with rivals (Grinnell et al., 1995; McComb et al., 1994) or by signalling the group's fighting ability to rivals (Christensen et al., 2016), among other possible functions.

In principle, we might expect collective defence to be most effective where group members act in unison to coordinate individual defence responses. Thus, we might expect behavioural homogeneity to increase in response to an outgroup threat, as different group members converge on a single unified behavioural response to amplify their individual defence capabilities. To our knowledge, however, no studies have investigated how behavioural homogeneity changes in response to an intergroup threat. For example, Bruintjes et al., (2016) found that cichlid fish increased defence behaviours when presented with simulated intergroup conflict, an effect driven by the dominant pair. However, this study did not differentiate between two major types of defensive behaviours, visual displays (e.g. opercula spreading) and physical attacks (e.g. biting), nor did it ask whether group members used the same, or different, behaviours as their group mates.

Here, we examined collective defence and behavioural homogeneity in banded mongooses exposed to intergroup conflict using simulated intrusion experiments. Banded mongooses live in stable groups of approximately 10–20 adults plus offspring that forage and sleep together, and that cooperate to rear young and defend against predators (Cant et al., 2016). Intergroup conflict in banded mongooses is common (Cant et al., 2002) and can be extraordinarily costly (Thompson et al., 2017): intergroup conflict mortality in this system is on par with that of chimps and small-scale human societies (Johnstone et al., 2020). Upon first encountering a rival group, group members produce collective calls, termed "war cries," that function to recruit group mates (Cant et al., 2002; Furrer & Manser, 2009; Müller & Manser, 2007). Most intergroup conflicts escalate to involve physical contact (Johnstone et al., 2020; Thompson et al., 2017). Members from opposing groups face off against each other in tight bunches (called "battle lines") before breaking out into chases and one-on-one fights. Groups may then retreat to mark each other with scents and reform battle lines before charging at each other again. This cycle continues until one group retreats from the area (Cant et al., 2002). Groups with more members usually win conflicts against groups with fewer members (Cant et al., 2002).

These observations suggest that collective defence, and potentially the homogeneity of (i.e. use of similar) behaviours, may be important during banded mongoose intergroup conflict. Prior studies in banded mongooses have shown increases in collective defence in response to simulated intergroup conflict. By playing back the war cries of rival groups, Furrer et al. (2011) showed that focal groups were more likely to move towards, and closely investigate, the calls of rivals when these calls occurred near the territory centre and when the focal group was large. Using scent markings (urine, faeces and anal gland excretions), Müller and Manser (2007) showed a similar result: when presented with scent markings from neighbouring groups, focal groups vocalized more and spent longer inspecting the stimuli than they did for scent markings from stranger groups. While these studies show heightened collective defence, they do not show whether and how behaviours varied within the group. Furthermore, they each used only a single stimulus (e.g. call playback or scent stimuli, but not both), a practice common in studies simulating intergroup conflict (Bruintjes et al., 2016; Christensen et al., 2016; McComb et al., 1994; Radford, 2005). In reality, an intruding group likely presents multiple stimuli: a group might first leave scent marks at a territory boundary, followed by vocalizations when a rival group inspects these scents, followed by invading the territory and starting an intergroup conflict. Understanding the function of collective defence and behavioural homogeneity requires experimental approaches that simulate all aspects of an intergroup conflict.

We tested the following predictions using our simulated intrusion experiments. First, we predicted that, compared to control (own-group) trials, groups would show higher levels of collective defence and more behavioural homogeneity in the presence of simulated rivals. We also expected responses to change relative to trial location: following prior work (Furrer et al., 2011), we predicted increased collective defence and behavioural homogeneity in response to simulated intrusions occurring in the territory core as compared to non-core (e.g. territory boundary) areas. Finally, we tested whether behaviours varied with focal group size (number of group members). Prior studies in this population have found both positive (Furrer et al., 2011) and no (Müller & Manser, 2007) relationship between-group size and responses to simulated conflict. We predicted that smaller groups would show increased collective defence and behavioural homogeneity than larger groups because smaller groups may be at a competitive disadvantage as compared to larger groups (Cant et al., 2002), but increased investment in defence and/or increased homogeneity might increase the success of smaller groups (Green et al., 2020).

2 | METHODS

Data for this study were collected 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. All field research was carried out under permit from Uganda Wildlife Authority (Ref. COD/96/02) and Uganda National Council for Science and Technology (NS 591). Ethical approval was received from Ethical Committee of the University of Exeter and is in line with the Guidelines for the Treatment of Animals of the Association for the Study of Animal Behaviour and the STRANGE framework (Webster & Rutz, 2020).

2.1 | Presentation trials

We performed 22 control and 22 stimulated intrusion trials to a total of five focal groups. The median number of control trials per group was 6 (range: 0–6), and the median number of intrusion trials per group was 4 (range: 2–6). Each group received repeated trials, with intrusion trials occurring before control trials; these were separated by at least two weeks. Each trial consisted of three different stimulus presentations: scents (faeces, urine, and scent marks from cheek and anal glands), calls and intruders. For logistical reasons, these were presented at different time points in the day, with scents and calls presented in the morning and intruders in the afternoon. Our rationale was to simulate how mongooses would encounter natural cues from rival groups, culminating in the presentation of multiple intruders. The median number of presentations per group was 22 (range: 9–28).

2.1.1 | Simulated intrusion trials

Scents from a neighbouring rival group (usually the largest neighbouring group) were presented to the focal group between 07:43 and 10:27 h East Africa Time (EAT). Scents were collected early on the same 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 to aid collection (these were washed thoroughly with soap and water between presentations). Samples were transferred as quickly as possible to the presentation site and presented within 2 h of collection (but usually much more quickly). The presentation site was placed in the foraging path of the focal group to ensure that focal group members 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 setting up scents in the focal group's foraging path, we filmed the group with either a handheld tablet computer (Samsung Galaxy Note 10.1, Samsung Group, South Korea) or a video camera (Panasonic HC-V520, Panasonic Corporation, Japan) from approximately 5 metres away, taking care to not disturb the group.

For presentations in non-core areas (i.e. near a territory boundary; see below for delineation of core and non-core areas), we did not control for the location of presentations relative to the location of the boundary between the focal and simulated rival group. A prior study in this population found that focal groups responded less strongly to rival group scent stimuli that were presented near the boundary opposite from that shared between the focal and rival group (Müller & Manser, 2007). However, other studies in this population, using both scent stimuli (Jordan et al., 2010) and call playback (Furrer et al., 2011), found no such effect. Because the present experiment was part of a larger study that involved tracking groups for two days before and two days after the experimental trial (Preston et al., 2020), it was necessary to conduct the trial where we found the focal group on the experimental day, irrespective of the group's location relative to the boundary with the rival group.

Three minutes after the focal group began moving toward the scents (earlier if the group began to move away from the area), we played back a recording of war cry vocalizations from the simulated rival group using an iHome IHM60 (iHome Audio, USA) portable speaker hidden in vegetation. War cries had been previously recorded (Zoom H1 recorder, Zoom Corporation, Tokyo; Sennheiser directional microphone, Sennheiser, Germany) from the same rival group more than one week prior to the trial; they were instigated by presenting the rival group with caged members of another group. The recordings were taken from 2 to 3 metres away, cut into 30-second sections during which vocalizing was occurring, and had their amplitude standardized to −1 dB using the normalize function in Audacity 2.1.2 (http://audacityteam.org). Recordings were never collected from a given group during the five-day period surrounding an experimental trial (two days before trial, day of trial, and two days after trial; Preston et al., 2020). Each 30-second playback clip was used only once to prevent habituation of the mongooses to particular recordings.

Between 16:35 and 18:18 h EAT on the same day as the scent and call playback presentations, we trapped (Tomahawk Live Trap Co., Tomahawk, WI, USA) four adult males from the rival group and presented them to the focal group for five minutes, following methods established in Cant et al. (2002). At all times, except during the presentation, we covered traps with a black cloth to minimize stress. After presenting the males, we returned them to their own group, usually within 10–20 min. All traps were washed with soap and water between trapping events.

2.1.2 | Control trials

Control trials followed the same protocol as simulated intrusion trials, except that stimuli were collected from the focal group. Scents were collected and re-presented to the focal group after they had moved away from the area of collection (with a similar gap between sample collection and presentation as simulated intrusion trials). For playbacks, war cries were replaced with close calls (a non-threatening communication call between group members; Jansen et al., 2012) from the focal group. 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 standardized in the same way as the war cry recordings. Live individual presentations used 4 adult males from the focal group that had been trapped, covered and moved to a safe, shaded location for 30 min before being presented to the rest of the focal group.

2.2 | Data collection

2.2.1 | Behavioural data

We quantified collective defence and behavioural homogeneity using three measures:

(1) We measured the proportion of group members approaching within 2 metres of the stimulus during a collective approach (Christensen et al., 2016; Grinnell et al., 1995). A greater proportion approaching the stimulus reflects greater investment in defence.

(2) We measured the proportion of group members acting defensively (defensive behaviours defined in Table 1), using behaviours similar to those in other studies of collective defence (Bruintjes et al., 2016; Christensen et al., 2016). Here, a greater proportion acting defensively would reflect greater defence behaviour.

(3) Finally, we measured behavioural homogeneity by quantifying the diversity of behavioural responses (see Table 1 for behaviours) within the group using the Shannon–Weiner diversity index, also known as the H-index (Shannon, 1948). The H-index quantifies the distribution of behavioural responses among individuals, where low values indicate less diversity (more homogeneity) in responses among group members and high values indicate high diversity (less homogeneity) in responses (see below). If groups responded in a more homogeneous manner to simulated intergroup conflict, we would expect a decrease in the H-index.

Behavioural data were collected by one observer (M.H.N.) from videos of the presentations. Because of logistical constraints, data could not be collected fully blind to treatment. To minimize bias, initial observations were conducted without audio, such that the observer was blind to the identity of the focal group and the location in which the treatment occurred, as well as to when in the video the call stimulus occurred (if applicable). Once behavioural data were collected, videos were re-watched with sound to record the time at which the call playback was performed.

We collected data only from group members that were at least six months old, defined as those who were at least two thirds of the size of the full-grown adults (Preston et al., 2020). To ensure we were not over- or underestimating the number of candidate individuals from which we recorded behavioural data, we compared the number of individuals older than six months in each video against the number of individuals older than six months that were recorded in the foraging group on the day of the presentation.

A summary of the data collection protocol is shown in Figure 1. We scan sampled group members at 30-second intervals, beginning 30 s after the time at which the first member came within two metres of the stimulus (defined as within 4 body lengths, tail included, as the average length of a banded mongoose is 0.5 m; Cant, 1998) and ending approximately 3 min 30 s from this time, unless the video ended beforehand. This sampling usually allowed for seven samples of intruder presentations and two to four samples each of scent and call presentations, as calls usually occurred between approximately 1 m 30 s and 2 m 30 s after sampling began in videos of the combined scent and call presentations. For scent and call presentation

TABLE 1 Ethogram of behaviours recorded from videos, including behaviour name, description, and whether the behaviour was coded as defensive or non-defensive

Behaviour	Description	Defensive/non-defensive
Stationary	Still; not exhibiting any other behaviours, such as standing upright.	Non-defensive
Walking/Running	Walking or running; not exhibiting any other behaviours, such as attacking.	Non-defensive
Digging	Pawing or digging at the ground around the stimulus; not foraging.	Non-defensive[a]
Vigilance	Standing upright on hind legs.	Defensive
Scent marking	Marking the ground or other group members with urine, faeces or scent marks (from anal or cheek glands rubbed along the surface).	Defensive
Attacking	Exhibiting aggressive behaviour towards (lunging at, scratching and biting) the stimulus.	Defensive

[a] Digging was categorized as a non-defensive behaviour as it was never observed during rival trials, only during control (own-group) trials. We interpreted this behaviour as attempting to “rescue” group mates.

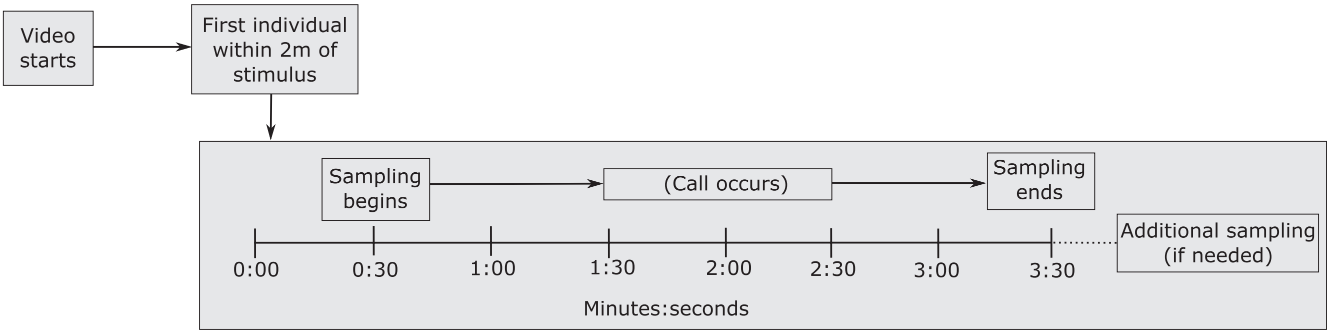

FIGURE 1 Summary of data collection protocol, as detailed in text. Boxes with text indicate relevant timepoints during sampling protocol. "(Call occurs)" box indicates timeframe at which calls usually occurred during scent and call playback trials (no calls occurred during intruder presentations). "Additional sampling (if needed)" box indicates videos for which data were collected at 30 s time intervals beyond the usual 3 m 30 s timeframe

videos in which calls occurred much later than 2 m 30 s after sampling began, we extended our sampling timeframe beyond 3 m 30 s. This allowed us to ensure that at least two samples were collected for each stimulus type (scents, calls and intruders). We discarded any presentations in which there were fewer than two samples for each stimulus type.

At each sampling point, we collected data on the number of group members within and outside 2 m of the stimulus and the number of members exhibiting each of six behaviours (Table 1). The six behaviours we identified were informed by prior observations in banded mongooses (Cant et al., 2002; Jansen et al., 2012; Jordan et al., 2010; Preston et al., 2020) and were an exhaustive list of the behaviours we could reliably identify from the videos. From these behavioural data, we calculated the number of group members acting defensively and non-defensively (see Table 1 for which behaviours were considered "defensive" and "non-defensive"), and the H-index of the group, which quantifies the behavioural homogeneity of group members (see below). If group members were outside the field of view of the camera, we recorded these members as being outside 2 m of the stimulus and recorded "NA" for the type of behaviour each group member was exhibiting. For call stimuli, we did not record the number of individuals within 2 m of the stimulus because the speaker was hidden and it was impossible to know when individuals were within or outside of 2 m of the speaker.

Behavioural metrics were calculated at each 30-second sampling point and then averaged across all 30-second sampling points of the stimulus. The proportion of group members within 2 m of the stimulus (hereafter "proportion approaching") was calculated by dividing the number of group members within 2 m of the stimulus by the sum of all group members seen in the video. The proportion of group members acting defensively (hereafter, "proportion acting defensively") was calculated by dividing the number of group members exhibiting behaviours we coded as "defensive" (Table 1) by the total number of group members for which we could observe their behaviour. The H-index was calculated following Cheney (1992) and Cronin and Ross (2019), as

$$H = -\sum\nolimits_{i=1}^{R}(p_i \ln p_i)$$

where R represents the complete set of behavioural categories and p_i represents the proportion of individuals exhibiting the i^{th} behaviour. Greater values of H indicate a greater diversity of behaviours (less homogeneity), while lower values of H indicate a lower diversity of behaviours (more homogeneity).

2.2.2 | Location data

We determined the location of each presentation in the home range of the focal group using two GPS sources. We calculated home ranges from GPS collars deployed on up to 2 individuals in each group (Gipsy4 and Gipsy5 collars, Technosmart, Italy). We estimated the location of presentations relative to home ranges using GPS locations collected by Samsung Galaxy Note 10.1 tablet computers (via the Mongoose2000 app; Marshall et al., 2018).

To gather GPS data for home range calculation, GPS collars were scheduled to take a burst of 10 locations ("fixes") every 30 min between 07:00–12:00 and 15:00–19:00 h EAT. To maximize battery life, GPS collars did not attempt to take GPS fixes between 12:00 and 15:00 h EAT, when groups rest in the shade (in their den or under bushes), or 19:00–07:00 h EAT, when groups are sleeping in their den and are outside of satellite range (Cant et al., 2016). Fixes were filtered for accuracy and removed if they had fewer than 4 satellites in range, an HDOP value of greater than 4, or if they fell outside of the boundary of the Mweya peninsula (Langley, 1999). After filtering, if multiple fixes were still associated with a scheduled fix time, the final fix in the burst was used since it is likely to be the most accurate (*personal communication*, C. Catoni, Technosmart). From these GPS collar data, we calculated the home range of each group for the three months preceding the day of each presentation (mean number of GPS fixes per group ± SE = 804 ± 31, range = 133–1184) by applying an autocorrelated kernel density estimate using the *ctmm* package (Calabrese et al., 2016) in R version 4.0.2 (R Core Team, 2020). Three months represents approximately one breeding

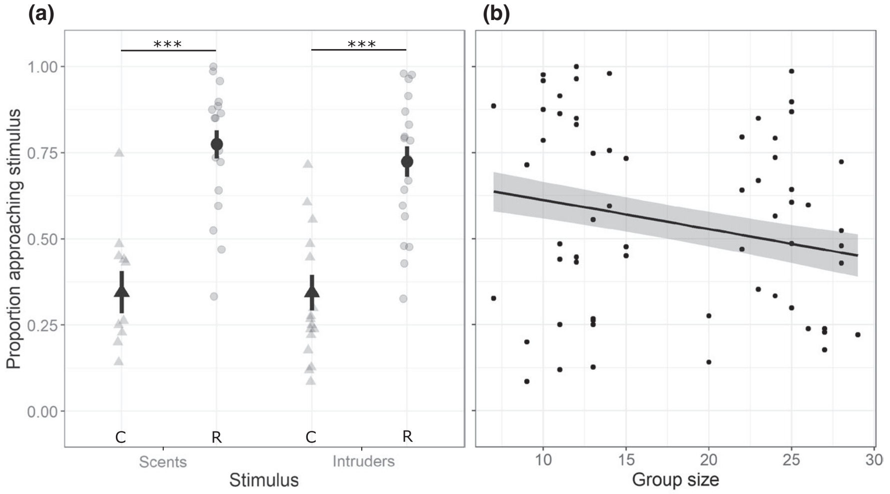

FIGURE 2 The proportion of group members approaching the stimulus was affected by (a) stimulus type (control stimuli = triangles, “C”; rival stimuli = circles, “R”) and (b) group size. Y-axis is the same in (a) and (b). In (a), small, semi-transparent points show raw data and have their positions randomly jittered for clarity. Large, filled points show mean estimates from GLMM; vertical lines show standard error. Lines with asterisks show statistical comparisons as described in main text (*** = $p < .001$). In (b), points show raw data, solid line indicates predicted relationship from LMM, shaded area shows standard error

cycle of the group (Cant, 2000) and should therefore account for differences in home range across the breeding cycle. We defined the core area of activity as the 50% most occupied area (the area containing 50% of locations).

We determined the location of each presentation using GPS fixes taken by tablet computers. The tablet computers took GPS locations every minute; we used the location closest in time to the presentation as the GPS location of the presentation. We defined a presentation as occurring in the “core” if it was within the 50% area of activity calculated (from the GPS collar data) over the preceding 3 months, and “non-core” if it was outside of this area.

2.3 | Data analysis

We tested how each of our three metrics (proportion approaching, proportion acting defensively and H-index) was correlated with three predictor variables: (1) the type of stimulus presented to the focal group (control scents, rival scents, control calls, rival calls, control intruders and rival intruders), (2) the location of the presentation (core and non-core), and (3) focal group size (the number of individuals older than six months recorded in the foraging group on the day of the presentation).

We built linear mixed-effects models (LMMs) and generalized linear mixed-effects models (GLMMs) using the glmmTMB package (Brooks et al., 2017) in R. For each analysis, we first fitted a full model including all fixed effects and two-way interactions. All models also included a random effect of group identity to account for repeated measures from the same group.

For the models predicting proportion approaching the stimulus and proportion acting defensively, we applied the following transformation to the response variable:

$$y' = \frac{[y(N-1)+0.5]}{N}$$

where y is the response variable and N is the sample size. This transformation compressed the data such that values of exactly 0 or 1 could be analysed in a beta regression model (Smithson & Verkuilen, 2006). These response variables were then used in GLMMs with beta error distributions and logit link functions (Brooks et al., 2017). The model predicting H-index had a Gaussian error distribution. In the model predicting the proportion approaching the stimulus, we did not include data for call stimuli (see above).

After fitting a full model, we used the “drop 1” function in R to compare the likelihood ratio of the full model to a model without each fixed effect in turn. We removed non-significant interactions to test the main effects, but did not remove non-significant main effects to avoid problems with stepwise model reduction (Mundry & Nunn, 2009). Where we found a significant effect of stimulus type, we ran post hoc tests with user-defined contrasts and single-step adjusted p-values ("glht" function in the multcomp package in R; Hothorn et al., 2008) to test the significance of the treatment *versus* control comparison within each stimulus.

3 | RESULTS

3.1 | Summary statistics

We could not gather location data for seven presentations and we could not hear at what point during a scent/call trial the call playback was played for six presentations. We excluded these 13 presentations from the data set, resulting in a final data set of 86 presentations. Tables S1-S6 detail the results of the statistical models.

3.2 | Proportion approaching stimulus

A greater proportion of group members approached rival stimuli as compared to own-group controls ($\chi^2_3 = 47.56$, $p < .001$, Table S1). More members approached rival scents as compared to control scents (rival scent mean ± SE = 0.76 ± 0.19, control = 0.36 ± 0.18; $\beta = 1.88$, SE = 0.33, $z = 5.72$, adjusted $p < .001$) and rival intruders as compared to control intruders (rival intruder mean ± SE = 0.71 ± 0.20, control = 0.32 ± 0.18; $\beta = 1.62$, SE = 0.28, $z = 5.82$, adjusted $p < .001$, Figure 2a, Table S2). There was also an effect of group size that was independent of stimulus type: as group size increased, the proportion of members approaching the stimulus decreased ($\beta = -0.04$, SE = 0.02, $\chi^2_1 = 5.50$, $p = .02$, Figure 2b, Table S1).

3.3 | Proportion acting defensively

The proportion of individuals acting defensively was higher for rival stimuli as compared to controls ($\chi^2_5 = 70.44$, $p < .001$, Table S3). This effect was driven by scent and intruder stimuli, but not call stimuli. Groups showed a greater proportion of individuals acting defensively to rival scents as compared to control scents (rival scent mean ± SE = 0.46 ± 0.13, control = 0.12 ± 0.10; $\beta = 1.62$, SE = 0.34, $z = 4.79$, adjusted $p < .001$) and to rival intruders as compared to control intruders (rival intruder mean ± SE = 0.54 ± 0.23, control = 0.07 ± 0.10; $\beta = 2.48$, SE = 0.31, $z = 8.03$, adjusted $p < .001$), but not to rival calls as compared to control calls (rival call mean ± SE = 0.23 ± 0.16, control = 0.09 ± 0.10; $\beta = 0.89$, SE = 0.44, $z = 2.01$, adjusted $p = .13$, Figure 3, Table S4).

3.4 | H-Index

There was a significant effect of stimulus type on H-index ($\chi^2_5 = 28.99$, $p < .001$, Table S5); the direction of this effect was opposite of what we predicted. Groups showed higher behavioural diversity (less homogeneity) in response to presentations of rival scents as compared to control scents (rival scent mean ± SE = 0.80 ± 0.14, control = 0.61 ± 0.23; $\beta = 0.21$, SE = 0.09, $z = 2.39$, adjusted $p = .049$) and rival intruders as compared to control intruders (rival intruder mean ± SE = 0.85 ± 0.26, control = 0.52 ± 0.22; $\beta = 0.35$, SE = 0.07, $z = 5.12$, adjusted $p < .001$, Figure 4a, Table S6). There was also an effect of group size that was independent of stimulus type: as group size increased, H-index increased ($\beta = 0.01$, SE = 0.01, $\chi^2_1 = 4.25$, $p = .04$, Figure 4b, Table S5).

Because the H-index results were counter to our predictions (we predicted lower, not higher H-index values for rivals compared to controls), we further investigated the effects of the stimulus type on behavioural homogeneity. We calculated the proportion of group members showing each of six behaviours we coded from videos of trials (see Methods and Table 1) and plotted these proportions as a function of treatment. This plot (Figure 4c) revealed that higher H-index values were driven by a greater use, and diversity, of defensive behaviours. For example, groups responded to rival intruder stimuli (as compared to control intruder stimuli) by using attacking behaviours and by increasing scent marking. Similarly, in response to rival scent stimuli (as compared to control scent stimuli), groups increased scent-marking behaviour while decreasing walking/running and stationary behaviours.

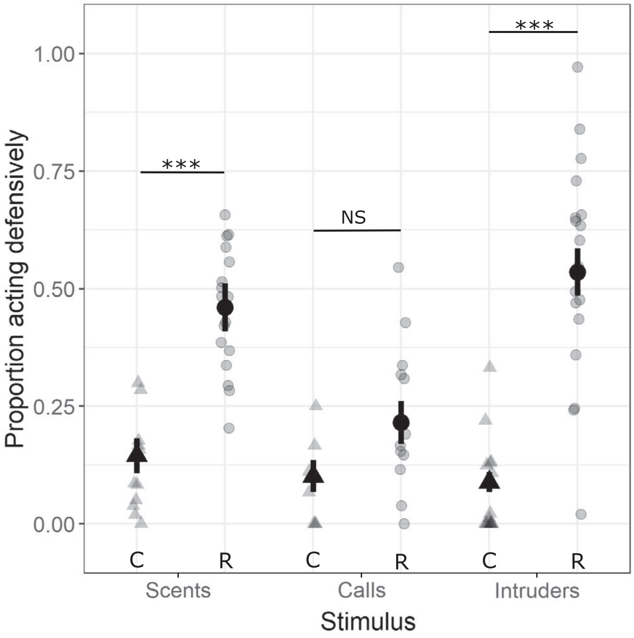

FIGURE 3 The proportion of group members acting defensively was affected by stimulus type (control stimuli = triangles, "C"; rival stimuli = circles, "R"). Small, semi-transparent points show raw data and have their positions randomly jittered for clarity. Large, filled points show mean estimates from GLMM; vertical lines show standard error. Lines with asterisks show statistical comparisons as described in main text (*** = $p < .001$, NS = not significant)

4 | DISCUSSION

We tested whether banded mongoose groups showed increased collective defence and behavioural homogeneity during simulated intergroup conflicts. In line with our predictions, groups showed greater defensive responses towards simulated rivals as compared to controls: a greater proportion of group members approached the stimulus and acted defensively. However, our measure of behavioural homogeneity—the H-index—showed opposite results to what we predicted: groups displayed less behavioural homogeneity toward rival stimuli than controls. Investigating the types of behaviours used by groups suggested that these counterintuitive results were driven by a greater use, and diversity, of defensive behaviours during rival treatments (as compared to controls). Finally, as group size increased, both the proportion of group members approaching the stimulus decreased and behavioural homogeneity decreased.

Our findings that a greater proportion of group members approached and acted defensively towards rival stimuli as compared to controls match prior work suggesting that the immediate threat

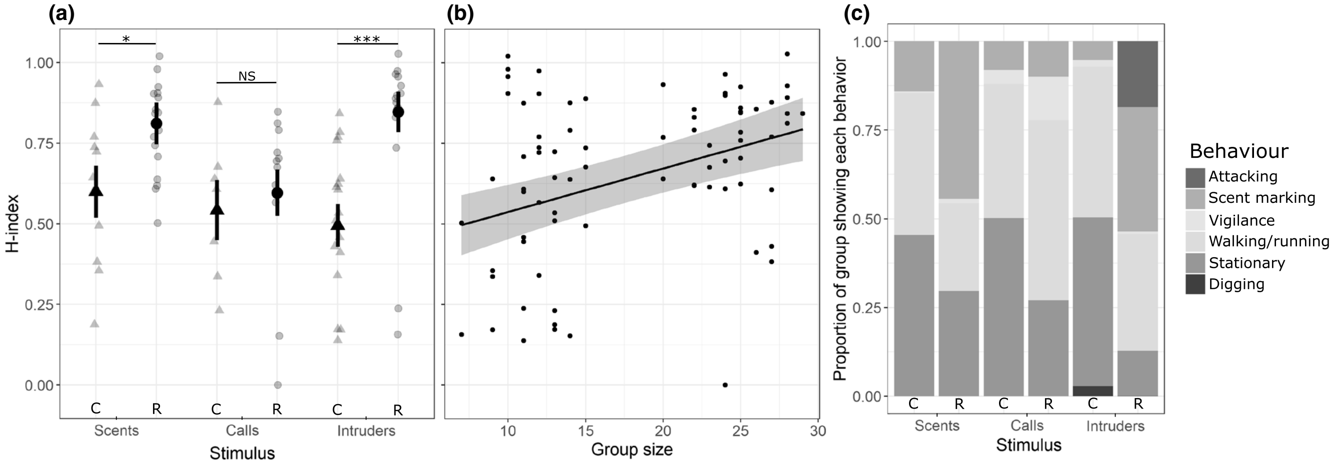

FIGURE 4 The effects of (a) stimulus and (b) group size on H-index, and of (c) stimulus on the proportion of group members showing each of six behaviours. In (a), control stimuli = triangles, "C"; rival stimuli = circles, "R." Small, semi-transparent points show raw data and have their positions randomly jittered for clarity. Large, filled points show mean estimates from LMM; vertical lines show standard error. Lines with asterisks show statistical comparisons as described in main text (*** = $p < .001$, * = $p < .05$, NS = not significant). Y-axis is the same for (a) and (b). In (b), solid line indicates predicted relationship from LMM; shaded area shows standard error. In (c), stacked barplots show the proportion of group members showing each of six behaviours (see legend). Orange colours reflect behaviours we considered "defensive," while purple colours reflect behaviours we considered "not defensive" (see Table 1). Left-side bars for each stimulus show control treatment, while right-side bars show rival treatment, indicated by "C" and "R," respectively

of an intergroup conflict heightens collective defence responses. In banded mongooses, previous studies have shown that groups exhibit stronger responses (e.g. greater investigatory or attacking behaviour) towards scent marks from neighbouring rival groups as compared to scent marks from stranger rival groups (Müller & Manser, 2007), rival group calls as compared to own-group calls (Furrer et al., 2011) and caged rival intruders as compared to caged group mates (Cant et al., 2002). Other studies in dwarf mongooses (Christensen et al., 2016), termites *Zootermopsis angusticollis* (Thompson et al., 2020), ants *Messor barbarus* (Birch et al., 2019), lions (Grinnell et al., 1995; McComb et al., 1994), cichlid fish (Bruintjes et al., 2016) and vervet monkeys *Chlorocebus aethiops pygerythrus* (Arseneau-Robar et al., 2016) also support the hypothesis that collective defence behaviours increase during an intergroup conflict.

One explanation for our results is that they do not reflect collective defence, but instead that individuals acted without consideration of their group mates and individual behaviours simply tended to coalesce to a common type (i.e. defensive behaviours) in the face of a threat. Such an explanation is unlikely to explain the behavioural changes we observed. For example, a single focal individual would be at a clear competitive disadvantage by approaching and acting defensively toward (e.g. attacking) four members of a rival group. In contrast, by collectively increasing defensive behaviours, the focal group likely increases its chances of repelling rivals. We suggest that our results—that a greater proportion approached and acted defensively towards rivals as compared to controls—reflect increased collective defence on the part of the group toward the goal of repelling rivals.

Our measure of behavioural homogeneity—the H-index—showed opposite results from what we expected. We predicted that simulated rival intrusions would lead to groups expressing more homogeneous behaviours; however, our results found that group members showed less homogeneous behaviours in response to rival scents and intruders. Our detailed investigation of behavioural responses showed that this increase in H-index was driven by an increase in the use and diversity of defensive behaviours. When presented with rival intruders as compared to control intruders, group members more frequently used behaviours like attacks and scent marking. While we naively expected that group members should all use the same behaviours when under the threat of a conflict, banded mongoose groups might instead adopt different roles or tasks to achieve competitive success. For example, when presented with rival intruders, groups might assess the size of the rival group (in our experiment, four males) and respond with an appropriate number of group members attacking while the remaining individuals complete other tasks (e.g. scent mark or other behaviours).

We were unable to individually identify or sex group members in videos, but the variation we saw in behavioural responses may be related to sex, dominance status, or other factors. A recent study suggested that oestrus female banded mongooses incite conflicts between groups in order to escape mate guarding males from their own group and obtain extra-group matings (Johnstone et al., 2020). Offspring sired by outgroup males are heavier and have higher survival than ingroup offspring (Nichols et al., 2015), and female lifetime reproductive success increases with the number of intergroup conflicts in which their group is involved (Johnstone et al., 2020). During rival intruder trials, when defensive behaviours were most common, approximately 50% of group members were walking, running or stationary (Figure 4c); it could be that these individuals were overwhelmingly female and may have been searching for other males, that is, mating opportunities. However, only three of our 44 trials occurred while focal group females were in oestrus, and the data from these trials were not outliers. Therefore, it is unlikely that the reproductive status of the focal group influenced our results. Another way in which individuals might vary in responses is related to dominance status. Cant et al., (2002) found that subordinate males, who had not mate-guarded in the previous mating attempt, were most aggressive in response to caged rival intruders, while dominant individuals were comparatively less aggressive. Perhaps, we would have found similar results had we been able to individually identify group members.

Our results suggest banded mongooses may assess the number of members in their group relative to that of a rival group, but further work on this topic is needed. As the size of the focal group increased, the proportion of group members approaching the stimulus and behavioural homogeneity decreased. Previous research has shown that banded mongoose groups with more members have a competitive advantage over groups with fewer members (Cant et al., 2002), a finding that is common to many taxa that engage in intergroup conflict (Green et al., 2020). However, if greater investment in collective defence enhances competitive success, small, yet more aggressive, groups may be able to overcome a group size disadvantage, leading to selection on individuals in smaller groups to invest more in collective defensive. This may occur, for instance, in wood ants (*Formica rufa*): members of smaller groups act more aggressively during intergroup conflicts than members of larger groups, and greater aggression in focal groups leads to lower focal group attrition (Batchelor & Briffa, 2011). In banded mongooses, smaller groups may devote a proportionately larger share of their members to the task of investigating (i.e. approaching) a threat. Larger groups can thereby use a greater diversity of behaviours because proportionately fewer members are required to investigate the threat. This effect in larger groups might be driven by a collective action problem, in which individuals in (especially larger) groups are incentivized to avoid fighting and allow their group mates to incur any costs of competition (Olson, 2009). Supporting this idea, the lower behavioural homogeneity we saw in large groups was not driven by defensive behaviours: there was no significant relationship between group size and the proportion of members acting defensively (Table S3). However, alternative explanations may be more parsimonious. For example, it might simply take longer for information to spread through a large group than a small group: by the time some individuals in a large group come to investigate a stimulus, the first-arriving group members may have already moved off. Future work, potentially utilizing techniques from studies of assessment in dyadic contests (Green et al., 2020), might help grasp if and how banded mongoose groups assess relative group size.

Our investigation of collective defence and behavioural homogeneity connects to a related topic that has received focus in the sociology literature. The "conflict-cohesion hypothesis" posits that intergroup conflict should lead to an increase in social cohesion within a group (Benard & Doan, 2011; Stein, 1976). "Cohesion" is defined in sociology as a tendency for the group to be united in pursuing a shared objective, such as winning a sporting match (Carron et al., 2002; Okasha, 2018). Studies in non-human animals have suggested that increases in affiliative behaviour (e.g. allogrooming) after intergroup conflict reflect increased cohesion within the group, thereby supporting the conflict-cohesion hypothesis (reviewed in, e.g., Radford et al., 2016). Increased collective defence behaviours *during* an intergroup conflict may similarly reflect a group's unity in pursuing the goal of winning the conflict, thereby showing links between conflict and cohesion, not just after, but also during non-human animal intergroup conflict (see also Thompson et al., 2020). Future work in animal behaviour might use related research in the social sciences to establish general metrics of cohesive behaviour (e.g. Carron & Brawley, 2000) and to investigate whether there are unifying principles that explain variation in intergroup conflict behaviour in human and non-human animal societies.

Finally, our results suggest an important practical point to future studies using simulated intrusions to study conflict behaviour. While we did not explicitly test for differences in responses to rival scent markings *versus* live, caged rivals, responses to these stimuli were quite similar. Both rival scent markings and live rivals also appeared to lead to differences in group member behaviour as compared to rival calls. These differences might be methodological: calls were played only ~3min after the presentation of scents. This experimental design was intended to heighten group responses to calls, but it is possible that the short interval between the two stimuli depressed any independent response to calls. Additionally, though group members frequently made alarm call vocalizations in response to rival call stimuli (E.F.R.P., *personal observation*), for methodological reasons we could not collect data on the number of individuals producing alarm calls. Nonetheless, the similarity between responses to rival scents and rival intruders suggests that future work in this species need not use caged rival intruders to stage simulated intrusions. Caging and presenting rival intruders is much more time- and labour-intensive than presenting scent markings. In addition, though we know of no negative impacts of caging individuals and presenting them in this way, avoiding presenting caged intruders reduces human impact on this population. Future work in this and other social mammals might use only scent markings to study conflict behaviour.

Our results show how collective defence behaviours increase in the presence of an immediate threat, thereby supporting ties between social behaviour and intergroup conflict. Our study also highlights that, while defence often involves collective behaviour, it does not necessarily mean that all individuals need to act in the same way.

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AUTHOR CONTRIBUTIONS

E.F.R.P., D.P.C., F.J.T. and M.A.C. designed the experiment, which E.F.R.P. carried out. M.H.N. collected video data. M.H.N., P.A.G., E.F.R.P. and F.J.T. analysed the data. P.A.G., F.J.T., D.P.C. and M.A.C. supervised research. M.A.C. and F.J.T. managed the field project. P.A.G. and M.A.C wrote the manuscript. All authors contributed feedback and approve the final version.

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SUPPORTING INFORMATION

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

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