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The combined effects of elevated within-group aggression and intergroup threat on dwarf mongoose behaviour

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Within-group aggression has well-established immediate effects on the contest-related behaviour of both participants and other group members (i.e. bystanders). However, we know far less about how within-group aggression influences behaviour not directly related to a contest and how cumulative information from contests can affect later behaviour. Moreover, it is unknown how any such behavioural changes are modified by the threat of intergroup contests, which are likely more costly and require a united response from groupmates, leaving an incomplete picture of how animals balance conflict at different scales. To test how individual and cooperative behaviours are affected by a general elevation in perceived within-group aggression, and how those behavioural responses change when there is an increase in the intergroup threat level, we ran a field experiment with groups of dwarf mongooses, *Helogale parvula*. Playback of simulated foraging displacements of subordinates by dominants led to bystanders avoiding close proximity with the seemingly aggressive individuals and reducing their cooperative sentinel contributions. The prospect of an intergroup contest (simulated by faecal and vocal presentations of a rival group) caused subordinates to return to close proximity with dominants, but sentinel contributions remained lower on days where elevated within-group aggression was simulated. This work highlights the potentially lasting effects of within-group aggression and how animals balance the threats of conflict from within and between groups.

In social species, conflict between group members affects both individual and cooperative behaviour. Animals living in groups often have disagreements over, for instance, foraging (Johnson et al., 2004; Sharpe et al., 2016), reproduction (Creel, 2005; Wong & Balshine, 2011) and movement (Dibnah et al., 2022; Papageorgiou & Farine, 2020) decisions. These conflicts can escalate to aggression, with time, energy and injury costs (Hardy & Briffa, 2013; Lane & Briffa, 2017; MacCormick et al., 2012), in addition to consequences for within-group relationships (Judge & Mullen, 2005; Morris-Drake, Kern, et al., 2021). Participants use a range of conflict-management strategies, such as reconciling with former opponents (Cools et al., 2008; Cords, 1992; Mallavarapu et al., 2006) and seeking comfort from other group members (Cools et al., 2008; Mallavarapu et al., 2006; Seed et al., 2007), to lower stress, restore relationships and reduce the chances of further aggression. Victims can also reduce the likelihood of receiving further aggression by distancing themselves from those who previously attacked them (Benkada et al., 2020; Kutsukake & Clutton-Brock, 2008). By contrast, targeted aggression is also used by dominants to solicit cooperative behaviour from subordinate groupmates, including contributions to nest defence against predators (Bergmüller & Taborsky, 2005; Zöttl et al., 2023) and territory defence against conspecifics (Arseneau-Robar et al., 2016; Hidaka et al., 2024). However, within-group aggressive contests do not only affect the subsequent behaviour of the participants but also other group members.

Individuals not directly involved in within-group contests, referred to as observers, bystanders or third-party individuals, often change their behaviour in response. Bystanders monitor the social interactions of others, either visually or by listening for acoustic signals and cues, to make informed behavioural decisions (Cheney et al., 2010; Radford et al., 2025; Tibbetts et al., 2020). For instance, bystanders can respond in the immediate aftermath of individual contests by affiliating with the participants or other third parties as a way of mediating stress, de-escalating conflict and repairing social relationships (Judge & Mullen, 2005; Schino & Sciarretta, 2015; Wittig & Boesch, 2010). However, we would also expect wider behaviour, outside that directly related to a recent contest, to be influenced by a higher level of within-group aggression. For instance, there could be greater wariness, with

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individuals both looking out for and avoiding those who are being aggressive (Hirsch, 2011; Kutsukake & Clutton-Brock, 2008). Moreover, if targeted aggression is used to punish noncooperators (Arseneau-Robar et al., 2016; Hidaka et al., 2024), other group members might choose to contribute more to avoid such actions (Bergmüller & Taborsky, 2005). Alternatively, if increased within-group aggression indicates instability or a breakdown in collective action, there might be a reduction in cooperative contributions, although this possibility has not been tested. The wider consequences of within-group aggression are important for a fuller understanding of social evolution, but our current knowledge is largely limited to relatively short time frames following individual contests, and studies of wild populations have generally relied solely on observational data.

Beyond the disagreements seen between groupmates, there is also conflict between groups that necessitates within-group cooperation. Groups of animals often collectively defend territories against neighbours to maintain exclusive access to key resources, including food and shelter (Bateman et al., 2015; Braga Goncalves et al., 2022). Within-group cooperation and social relationships have been demonstrated to be important across species in mitigating the potentially severe consequences of intergroup conflict (Arseneau-Robar et al., 2016; Braga Goncalves et al., 2022; Morris-Drake et al., 2022; Thompson et al., 2017). Defensive actions involve both signals of occupancy, such as vocal choruses and scent deposits (Radford, 2003; Sharpe et al., 2012), as well as direct antagonism when rivals are encountered, termed intergroup interactions (IGIs) (Green et al., 2022; Roth & Cords, 2016; Yi et al., 2020). Pre-emptive behavioural changes are therefore expected when encounters with other groups are more likely: for instance, the threat of an intergroup contest promotes within-group affiliation and cohesion in various species (mountain gorilla, *Gorilla beringei*: Mirville et al., 2020; green woodhoopoe, *Phoeniculus purpureus*: Radford, 2011; chimpanzee, *Pan troglodytes*: Samuni et al., 2020). Similarly, information gathering, such as moving to elevated locations, increases in chimpanzees and dwarf mongooses, *Helogale parvula*, when there is a greater likelihood of encountering rival groups (Lemoine et al., 2023; Morris-Drake et al., 2019). As intergroup conflict likely carries greater potential costs than within-group conflict, increased outsider threat might be expected to override any temporary perturbations in within-group relations, similar to postconflict reconciliation (Kutsukake & Clutton-Brock, 2008), to allow the group to defend itself effectively from rivals. Alternatively, changes in within-group behaviour could negatively impact the ability of groups to mitigate outsider threat, but these ideas have not been tested before.

Here, we use dwarf mongooses as an experimental system to investigate how increases in within-group aggression affect individual and cooperative behaviour by bystanders, and how these behavioural changes are affected by a subsequent elevation in intergroup threat level. Dwarf mongooses are cooperative breeders, with group members moving together through a shared territory throughout the day (Arbon, Morris-Drake, Kern, Giuggioli, et al., 2024; Arbon, Morris-Drake, Kern, Howell, et al., 2024; Creel, 2013). Individuals forage for prey by digging in the ground and searching through the vegetation (Sharpe et al., 2010, 2016). Aggressive interactions within groups often occur over foraging resources such as large prey items or profitable foraging holes (Morris-Drake, Kern, et al., 2021; Sharpe et al., 2016). These foraging displacements usually include growls from an approaching dominant and submissive squeals from the displaced subordinate, with physical contact via ‘hip-slamming’ and occasionally biting or chasing (Morris-Drake, Kern, et al., 2021; Sharpe et al., 2016). While foraging, dwarf mongoose groups use a sentinel system where individuals coordinate their raised vigilance to look out for predatory and intergroup threats on behalf of their group (Kern & Radford, 2014; Rasa, 1986). Acting as a sentinel is a cooperative act because sentinels raise the alarm when danger is present (Kern & Radford, 2013, 2014), enable groupmates to reduce their personal vigilance while foraging (Kern et al., 2016) and sentinels cannot obtain food themselves while on duty (Kern & Radford, 2014). Mongooses socially monitor the cooperative contributions (Kern & Radford, 2018) and aggressive interactions (Morris-Drake, Kern, et al., 2021) of group members, retaining that information to inform grooming decisions at the evening sleeping burrow where cooperators are rewarded and aggressors avoided (Kern & Radford, 2018; Morris-Drake, Kern, et al., 2021).

Dwarf mongoose groups collectively defend their territories against neighbours (Christensen et al., 2016; Morris-Drake, Linden, et al., 2021). Nearly two-thirds of IGIs result in physical aggression such as chasing of outgroup individuals, while over a third result in intergroup fighting with occasional injury and even mortality (Morris-Drake et al., 2023). Both breeding and nonbreeding individuals participate in IGIs and there is no evidence to suggest differences in IGI participation between the monomorphic sexes (Arbon, Morris-Drake, Kern, Howell, et al., 2024), although the factors driving individual investment into IGIs are poorly understood. Mongoose groups have IGIs with each of their neighbours approximately twice a month (Morris-Drake et al., 2023), with each group often having two to four regularly encountered neighbours in addition to rarer interactions with non-neighbours (J. J. Arbon, personal observations). To protect against rivals, groups increase sentinel behaviour and scent marking when encounter likelihood increases (Christensen et al., 2016; Morris-Drake et al., 2019; Morris-Drake, Linden, et al., 2021).

In our field experiment, we simulated an increase in within-group aggression levels in the morning by playing back the sounds of aggressive foraging displacements of subordinates by dominants. We compared the afternoon behaviour of focal subordinate individuals in this elevated within-group aggression scenario with that on matched control days where we had played back nonaggressive vocalizations of the same group members in the morning. Having collected data on individual and cooperative behaviour, we simulated an increased intergroup threat level by initially presenting faecal samples from a rival group and then by playing back their vocalizations, on both aggression and control days. We collected the same individual and cooperative behavioural data from the focal individuals following intergroup presentations as from earlier in the afternoon. We predicted that increased within-group aggression would disrupt within-group behaviour, but intergroup threat would reset these disruptions to allow groups to repel dangerous rivals. Specifically, we predicted that, compared to control days, the simulation of elevated within-group aggression would result in subordinates exhibiting more personal vigilance, as they increased their monitoring of groupmates, and distancing themselves further from the dominants. We predicted that these subordinate bystanders would also reduce their cooperative contributions, here measured using contributions to sentinel behaviour (Kern & Radford, 2013, 2014). Sentinel contributions are rewarded with grooming in this species (Kern & Radford, 2018), so negative social interactions such as aggression may dampen contributions. Finally, we predicted that an increase in intergroup threat level would ‘reset’ changes in behaviour induced by within-group aggression, resulting in restored levels of cohesion and surveillance behaviour that mirror those seen on control days.

METHODS

Study System and Site

We conducted the experiment on a wild, habituated population of dwarf mongooses at Sorabi Rock Lodge, Limpopo Province, South Africa (-24.203°, 30.782°) between 14 July and 31 August 2023. The field site is within Africa's Savanna biome, with the habitat characterized by a mixture of open areas, low-lying shrubs and acacia woodland (Kern & Radford, 2013); at the time of the experiment, heavy and extended summer rains had resulted in dense grass cover across much of the study site. Dwarf mongooses are territorial, group-living mammals found throughout East and Southern Africa (Arbon, Morris-Drake, Kern, Giuggioli, et al., 2024; Arbon, Morris-Drake, Kern, Howell, et al., 2024; Creel, 2013). Reproduction is largely monopolized by a dominant pair, who raise young with the assistance of subordinate adult helpers of both sexes; subordinates can be both natal individuals and immigrants (Arbon, Morris-Drake, Kern, Howell, et al., 2024; Rood, 1990). Groups defend territories against neighbours through habitual scent marking of latrine sites as well as direct interactions (Christensen et al., 2016; Morris-Drake et al., 2023; Morris-Drake, Kern, et al., 2021; Sharpe et al., 2012). Dwarf mongoose sentinel behaviour has been shown to be state dependent (Arbon et al., 2020) and used in both antipredator (Arbon et al., 2020) and intergroup (Morris-Drake et al., 2019) contexts. Aggressive foraging displacements within groups were previously reported at a mean of 2.6 per 3 h observation session (range 0–10) (Morris-Drake, Kern, et al., 2021). At the time of the experiment, the study population had been constantly monitored since 2012, with each individual uniquely identified by blond hair-dye marks applied to its fur (Kern & Radford, 2013). Individual age and dominance status were known from detailed life history and behavioural observations (Arbon, Morris-Drake, Kern, Howell, et al., 2024). Experimental groups contained a mean (± SE) of 7.8 ± 1.3 adults (individuals over one year) and 4.5 ± 2.2 juveniles born in the previous breeding season.

Experimental and Data Collection Protocol

We conducted two treatments in counterbalanced order on nine subordinate adult mongooses (five males, four females) in four groups. The aggression treatment entailed increasing the perceived level of within-group aggression through the playback of vocalizations associated with foraging displacements, while the control treatment involved the playback of the same number of close calls (given while foraging) of the same individuals used in the matched aggression treatment. Experimental manipulation and data collection took one full day per treatment; experimental days with the same focal individual were a median of 3 days apart (range 2–11 days). Trial pairs to different focal individuals within the same group occurred ~3 weeks apart. We did not experiment on days when IGIs occurred, and group composition was required to be the same for the two treatments to the same individual to preserve the paired nature of the experiment. Groups were always followed from emergence at their morning sleeping burrow until they entered their evening sleeping burrow, and all observed naturally occurring aggressive interactions were noted.

Both aggression and control trial days followed an identical schedule as shown in Fig. 1: we carried out a playback session in the morning (0930–1230 hours) followed by data collection in the afternoon (1230–1630 hours). Playback sessions comprised the playing of eight, 40 s tracks over a 2 h period while the group was foraging; each track was spaced by approximately 15 min. In both treatments, each playback track featured a series of 10 alternating close calls (also referred to in the literature as contact calls) between one of the dominant pair and a nonfocal subordinate group member. In the aggression treatment, this sequence finished with three aggressive growls from the dominant individual and a single submissive squeal from the subordinate, simulating an aggressive interaction (in line with Morris-Drake, Kern, et al., 2021). On control days, the sequence of close calls ended with three more repeated close calls from the dominant (instead of the growls) and one from the subordinate (instead of the squeal) to simulate a nonaggressive interaction between the pair. This represented the only difference between the experimental and control days; there was no significant difference between treatments in the number of natural aggression occurrences throughout the day ($P = 0.879$; Supplementary Table S1a), with all subsequent data collection identical. Each individual of the dominant pair was featured in four of the eight tracks played during the morning of a trial, with multiple subordinates featured in the eight tracks in a trial. The combinations of dominants and subordinates within tracks were the same for the matched aggression and control treatments conducted on the same focal individual, whereas different original recordings and combinations of individuals were used for playbacks to different focal individuals in the same group. Playbacks were not commenced if the individuals whose calls were to be played back were foraging in close proximity to the focal individual. All calls that were used in playback tracks had been recorded in the previous 3 months using a Sennheiser MKE 600 microphone (Sennheiser, Wademark, Germany) and Tascam DR-

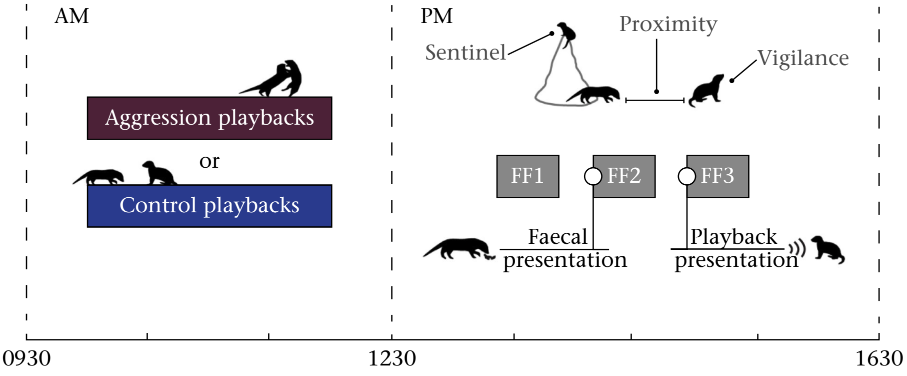

Figure 1. Schematic showing the schedule of an experimental day. One of two within-group playback treatments was conducted in the morning (AM) session. In the afternoon (PM) session, there were three focal follows (FF1–FF3), interspersed with a faecal presentation and a playback presentation to simulate an increased intergroup threat. Filled bars are to scale with the timeline. The three main response behaviours recorded in each FF are depicted: sentinel contributions, proximity to groupmates and personal vigilance.

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100 MKIII solid-state recorder (Tascam, Tokyo, Japan). We played all tracks through a Bose SoundLink micro loudspeaker (Bose, Framingham, MA, U.S.A.) at natural amplitudes (55 dB at 1 m for close calls and growls, 65 dB at 1 m for squeals), assessed using a sound pressure level meter (Arbon et al., 2020; Morris-Drake, Kern, et al., 2021). We placed the loudspeaker at a height of 10 cm in a visually obscured location approximately 10 m from the focal individual.

In the afternoon session of a trial day, we conducted three identical 30 min observations of our focal individual (termed focal follows; FFs) and simulated two separate increases in intergroup threat (Fig. 1). First, we conducted FF1 to assess behavioural differences between treatments before simulation of an elevated intergroup threat, testing the effects of the earlier simulated increase in within-group aggression. We then presented the focal individual with intergroup faecal samples, which was immediately followed by FF2. Once complete, we then presented the group with a playback simulating the presence of intergroup individuals, which was followed by FF3. FFs were conducted as close in time to each other as conditions allowed, with FF1 and the two subsequent presentations only proceeding if there had been no alarm behaviour in the preceding 10 min and no latrine behaviour in the preceding 30 min. These conditions prevented individual behaviour being disrupted by extraneous threats, reducing the noise in our data set.

We collected identical data in each 30 min FF (Fig. 1). For a 5 min period, taken at the earliest point of the FF where the focal individual was reliably foraging, we recorded the occurrence and duration of each separate bout of head-up vigilance (as in Kern et al., 2016). At every fifth minute, excluding minute zero, we conducted a neighbour proximity scan, noting the identity of all adult groupmates within 5 m of the focal individual; this was the largest distance that could be accurately and practically recorded given vegetation density. We also recorded the occurrence and duration of all sentinel bouts by the focal individual during the whole FF. All data were dictated by the observer onto a Sony ICD-PX370 recorder (Sony, Tokyo, Japan) and later transcribed.

For the intergroup faecal presentations, we used samples from non-neighbouring groups to the focal to reduce the potential confound of groups responding differently to different known rivals (Radford, 2003); previous work has shown mongooses do not react differently to simulated intrusions by neighbours versus strangers (Christensen et al., 2016). On collection, we immediately placed faecal samples on ice until they were transferred to a freezer (~ -20 °C) later in the day. All samples were presented within 1 week of collection. In a trial, we presented the faeces of four adults, including at least one dominant, simultaneously on bare earth against a flat rock to simulate the structure of usual latrine deposits (Christensen et al., 2016). Faecal samples were presented in a way that ensured that the focal individual was the only one to interact with the sample. We recorded all interactions between the focal individual and the faecal sample. Mongooses spent a mean (± SD) of 6.4 ± 4.8 s interacting with the presented intergroup faecal sample, with no significant difference between the aggression and control treatments ($P = 0.164$; Supplementary Table S2a). After the interaction ceased, we covered the sample with a rock; the subsequent focal follow (FF2) was commenced as soon as the focal individual returned to foraging.

For the intergroup playbacks, we created tracks by combining the movement calls, close calls and lost calls (calls given to facilitate spatial coordination) of four adults (including at least one dominant) to simulate the usual call combinations observed during the build-up to IGIs (Morris-Drake, Linden, et al., 2021). All calls had been recorded in the previous 3 months. For a given focal individual, we used recordings from the same non-neighbouring group as the faecal presentation. We played tracks through a pair of Bose SoundLink micro loudspeakers that were placed in the stereo setting once the loudspeakers had been linked in ‘Party mode’ and positioned 5 m apart. Due to an experimental trial taking multiple hours to run and the mobility of dwarf mongoose group, capable of covering their entire home range in a single day (Arbon, Morris-Drake, Kern, Giuggioli, et al., 2024), we could not control the precise location of either presentation. However, IGIs have been witnessed throughout the ranges of groups, including core areas (J. J. Arbon, personal observations), and therefore the presentations were ecologically relevant. Tracks were constructed so that calls from two individuals came from each loudspeaker, such that calls simultaneously came from multiple locations to increase the realism of the manipulation. We obscured the loudspeakers in vegetation close to the foraging group to minimize their detection. Before the playback, we used a small amount of crumbed hard-boiled egg, which is routinely used to obtain body weights and dye-mark individuals (Kern & Radford, 2014), to centre the group ~20 m from the loudspeakers to increase the standardization of playback exposure. A mean (± SD) of 5.2 ± 3.4 individuals approached each intergroup intrusion playback within 10 m, with no significant difference between the aggression and control treatments ($P = 0.416$; Supplementary Table S2b). Once the focal individual had recommenced foraging, we immediately began the final focal follow (FF3).

Ethical Note

Work was conducted under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001CPM403-00013), ethical approval from the University of Pretoria, South Africa (Animal Ethics Committee: NAS321/2022) and the University of Bristol, U.K. (Animal Welfare and Ethics Review Body: UIN/17/074), and in line with ASAB/ABS guidelines for the ethical treatment of animals (ASAB/ABS, 2020).

Analytical Methods

We conducted analyses in R version 4.4.0. Linear and generalized linear mixed models (LMMs/GLMMs) were run using the ‘lme4’ R package (Bates et al., 2015) with diagnostics checked using tools from the DHARMa R package (Hartig, 2022). We ran all models with treatment (aggression, control) and trial order (first, second) as fixed factors, and focal individual identity as a random factor to capture the paired nature of the experiment. We modelled responses in each FF period separately. The number of vigilance bouts (in a 5 min period) and the number of sentinel bouts (in the whole FF) were modelled as Poisson GLMMs with log link functions. Models of the number of sentinel bouts contained an offset term for the log of the duration of the FF period, as this period was curtailed in some instances by strong alarm calls given to observed potential predators. Models analysing the mean vigilance bout duration and all models analysing neighbour proximity scans (response variables: mean number of neighbours within 5 m per scan, proportion of scans with a dominant within 5 m, proportion of scans with a subordinate within 5 m) were run as LMMs. We assessed significance using likelihood ratio tests between the full model and the same model without the term of interest. For a subset of models (details in Supplementary Tables), we specified a weak Bayesian prior to aid with the fitting of the random effects structure of the model using the ‘blmer()’/‘bglmer()’ functions from the ‘blme’ package (Chung et al., 2013). These act as wrapper functions for ‘lme4’ models (LMMs and GLMMs), fitting a weakly informative prior to the covariance matrix (here a Wishart

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distribution), helping to avoid singular model fit and estimate random-term variance as nonzero.

RESULTS

During the first focal follow of the afternoon (FF1), focal mongooses had 0.4 (95% CI = 0.1–0.6) fewer adult groupmates within 5 m per scan on days where elevated within-group aggression was simulated in the morning, compared to control days ($P = 0.006$; Supplementary Table S3a). This was driven by a 36% (11–60%) lower likelihood of being found within 5 m of a dominant individual in a given scan on aggression treatment days compared to control days ($P = 0.004$; Fig. 2a, Supplementary Table S3b); there was no significant difference between treatments in the likelihood of the focal individual foraging within 5 m of another subordinate ($P = 0.189$; Fig. 2b, Supplementary Table S3c). There were no significant differences in the number ($P = 0.677$; Fig. 2c, Supplementary Table S3d) or mean duration ($P = 0.834$; Supplementary Table S3e) of head-up vigilance bouts between treatments. However, compared to control days, mongooses were 2.5× (1.1–6.1×) less likely to perform sentinel bouts when elevated within-group aggression was simulated in the morning ($P = 0.020$; Fig. 2d, Supplementary Table S3f).

Table 1
Model estimates, 95% confidence interval of the estimate and *P* values for the main effect of playback treatment (aggression, control) on the set of response variables following the intergroup faecal and playback presentations

Response	Estimate	95% CI	*P*
Following faecal presentation			
Number of adults within 5 m	−0.004	−0.278, 0.269	0.973
Probability of a dominant within 5 m	−0.116	−0.305, 0.074	0.201
Probability of a subordinate within 5 m	0.023	−0.122, 0.167	0.734
Number of vigilance bouts	−0.760	−1.183, −0.349	**<0.001**
Mean vigilance bout duration	0.284	−0.160, 0.729	0.189
Number of sentinel bouts	−0.926	−1.714, -0.109	**0.017**
Following playback presentation			
Number of adults within 5 m	−0.247	−0.665, 0.172	0.216
Probability of a dominant within 5 m	−0.176	−0.421, 0.069	0.140
Probability of a subordinate within 5 m	0.124	−0.089, 0.337	0.226
Number of vigilance bouts	−0.830	−1.322, -0.366	**<0.001**
Mean vigilance bout duration	−0.311	−0.881, 0.259	0.267
Number of sentinel bouts	−2.551	−4.403, -1.307	**<0.001**

All models contained trial order as a fixed effect and individual ID as a random effect (Supplementary Tables S4–S5). Models of the number of sentinel bouts contain an offset for the duration of the focal follow. *N* = 9 individuals.

Results for the FF periods following the intergroup faecal and playback presentations (FF2 and FF3, respectively) were qualitatively the same, so are presented together in the text with mean effect sizes and confidence intervals (split summary outputs in Table 1, full outputs in Supplementary Tables S4–S5). There was mild evidence for habituation to the intergroup presentations, with significant trial order effects seen for 1/4 of the response measures (Supplementary Tables S4–S5). In contrast to FF1, there

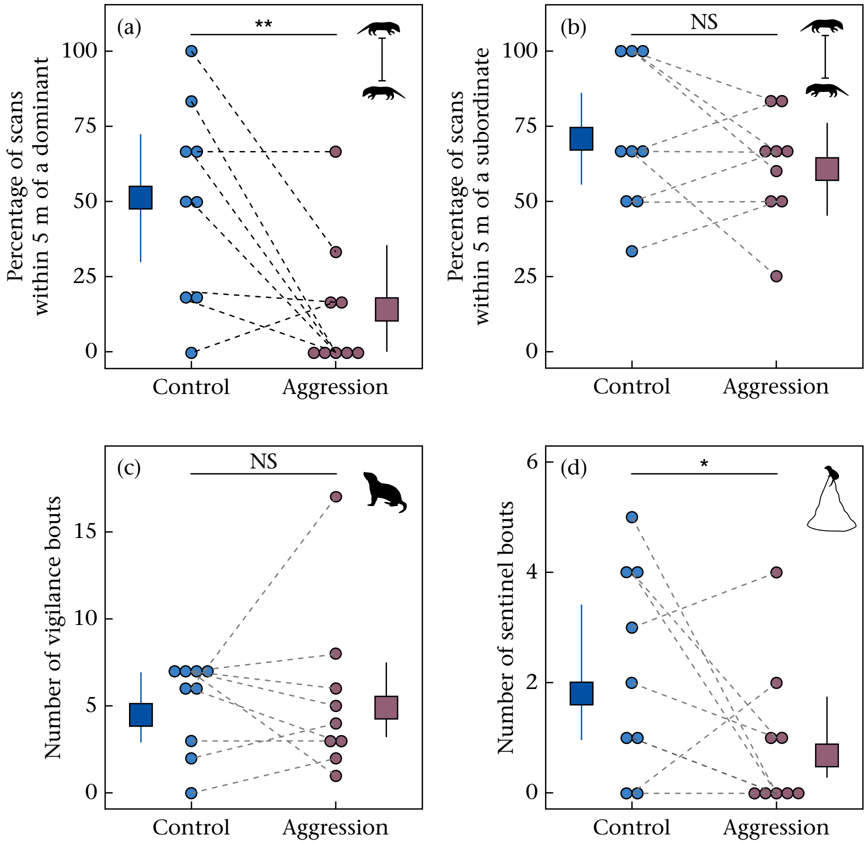

Figure 2. Differences in behaviour during the first focal follow (FF1), before the simulated elevation of intergroup threat level. The likelihood of the focal individual being within 5 m of (a) a dominant or (b) a subordinate groupmate in a neighbour proximity scan, (c) the number of head-up vigilance bouts conducted in a 5 min period and (d) the number of sentinel bouts conducted in the FF by the focal individual. Raw data plotted with lines connecting paired trials to the same focal individuals; lines have partial opacity to help visualize overlapping data. Boxes and arms are model estimated means and 95% confidence intervals. *N* = 9 individuals. **P* < 0.05; ***P* < 0.01.

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was no significant difference between treatments in the number of adults found within 5 m of the focal individual. This was because, while there was still no significant difference in the likelihood of being found within 5 m of a subordinate groupmate, there was no longer a significant treatment difference in the likelihood of the focal individual being found within 5 m of a dominant individual (Fig. 3a, b). Focal individuals were, however, 2.2× (CI: 1.44–3.5×) less likely to conduct bouts of personal vigilance on aggression treatment days (Fig. 3c, d); there was no significant difference in the duration of these vigilance bouts. A pair of follow-up linear mixed models comparing FF1 vigilance bout durations to the pooled mean of FF2 and FF3 periods showed no significant difference in the aggression treatment ($P = 0.400$), but a significant difference ($P = 0.040$) for increased vigilance in FF2/FF3 relative to

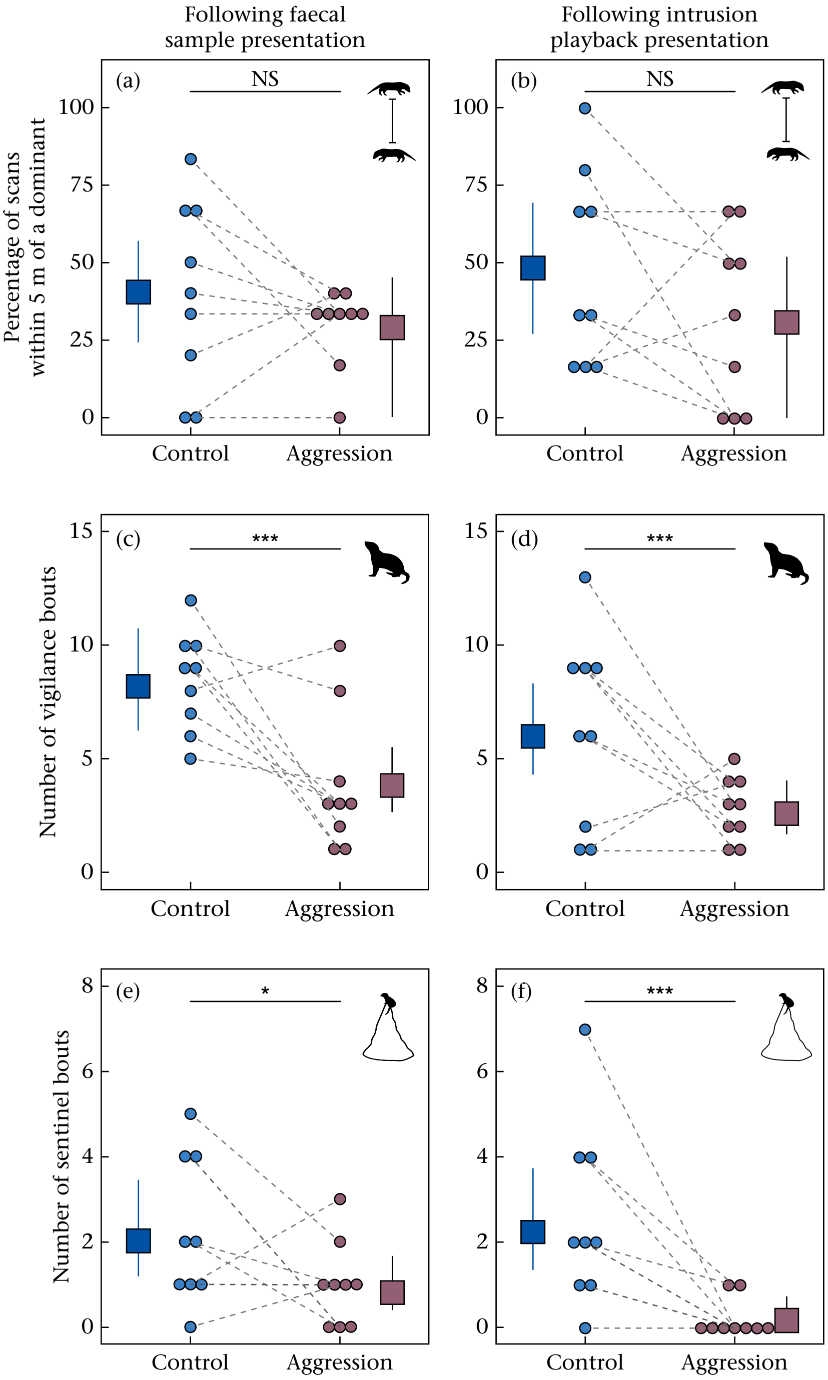

Figure 3. Differences in behaviour during the second and third focal follows (FF2 and FF3), after simulation of an elevated intergroup threat, on aggression and control days. The likelihood of the focal individual being (a, b) within 5 m of a dominant in a neighbour proximity scan, (c, d) the number of head-up vigilance bouts conducted in a 5 min period and (e, f) the number of sentinel bouts conducted in the FF by the focal individual in the sampling periods after intergroup threat presentations. Raw data plotted with lines connecting paired trials to the same focal individuals; lines have partial opacity to help visualize overlapping data. Boxes and arms are model estimated means and 95% confidence intervals. $N = 9$ individuals. *$P < 0.05$; ***$P < 0.001$.

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FF1 in the control treatment (Supplementary Table S6). As in FF1, there was a treatment difference in the likelihood that individuals performed sentinel bouts: following the simulation of elevated intergroup threat, focal individuals performed 7.7× fewer bouts (2.4—43.8×) on days where elevated within-group aggression was simulated relative to control days (Fig. 3e, f).

DISCUSSION

Our experimental results demonstrate how a perceived increase in within-group aggression alters the individual and cooperative behaviour of bystander groupmates, while the threat of intergroup conflict resets some, but not all, of these behavioural changes. Bystanders distanced themselves from seemingly aggressive dominants and contributed less to sentinel behaviour when they detected increased levels of within-group conflict from vocal cues. Following the simulation of an elevated intergroup threat level, bystanders no longer avoided dominants on days where there had been simulated increases in within-group aggression. However, cooperative sentinel contributions remained lower than in control conditions and personal vigilance became lower on days when there had been the simulation of elevated within-group aggression. Together, our findings highlight how acoustic social monitoring of within-group aggression can have consequences for individual and cooperative behaviours, and how those responses can be modified by intergroup threat.

The simulation of increased within-group aggression affected foraging proximity between group members. Bystanders that heard aggression by dominants were more likely to be found distanced from those individuals, exhibiting similar avoidance behaviours seen by meerkats, *Suricata suricatta*, and rooks, *Corvus frugilegus*, that had received direct aggression (Benkada et al., 2020; Kutsukake & Clutton-Brock, 2008). Avoiding aggressive individuals will reduce the costs associated with being attacked and of being displaced from a foraging patch or losing a prey item. As bystanders have been shown to seek affiliation with groupmates in primate systems (Judge & Mullen, 2005; Schino & Sciarretta, 2015), the lack of a difference in proximity to other subordinates in our study may appear surprising. However, given that the aggressive playbacks occurred long before data collection, immediate responses to aggression (e.g. seeking support from others) are likely to have decayed. The increase in distancing from dominants may explain the initially consistent levels of personal vigilance between treatments; while we predicted increased social monitoring of dominants through head-up vigilance, reducing the proximity to potential aggressors could be a viable alternative to minimize risk. While there was sufficient power to find a significant treatment effect on the number of vigilance bouts, we must remain cautious on our interpretation of the mechanism responsible, although results suggest an increase in head-up vigilance on control days that was not seen on days where aggression within the group was simulated. Collecting data from more individuals, or sampling vigilance over a longer time frame, would potentially reveal further nuances in this behaviour not found in this study. It is also possible that social monitoring in dwarf mongooses is a predominantly vocal affair; mongooses live in a dense bushveld habitat with limited lines of sight, often foraging with their head to the ground (Kern et al., 2016; Sharpe et al., 2010). Future work may therefore find differences in vocal responses in addition to any vigilance-based metrics. Our experimental finding that bystanders reduce proximity to perceived aggressors of earlier simulated foraging displacements, but not other group members, adds to evidence of vocal recognition across contexts in this species (Kern & Radford, 2018; Morris-Drake, Kern, et al., 2021; Sharpe et al., 2013).

The simulated increase in within-group aggression also reduced the cooperative contributions of bystanders to sentinel behaviour. Cooperative contributions have previously been documented to increase following instances of aggressive coercion or punishment (Arseneau-Robar et al., 2016; Zöttl et al., 2023), but these represent direct, targeted responses to individual actions (or lack of action). Our work instead shows that general increases in within-group aggression can have negative effects on contributions to group level public goods. The observed decrease in mongoose cooperation could be due to a breakdown in social relationships within the group; we know that more grooming is given to those that conduct more sentinel behaviour (Kern & Radford, 2018), and it is therefore possible sentinel behaviour is suppressed in environments where reward benefits are less likely. Individuals may also perceive the increased aggression as an indicator that others are not likely to contribute their portion of sentinel protection, resulting in a breakdown in collective action, and therefore downregulate their own contribution. In principle, the decrease in sentinel bouts could also be explained through an indirect pathway. As sentinel behaviour is state dependent (Arbon et al., 2020), decreases in foraging efficiency due to an increase in social monitoring could result in reduced contributions to sentinel behaviour; we did not, however, detect a difference in personal vigilance between treatments before the simulation of elevated intergroup threat, so this explanation is unlikely. Regardless of the mechanism, the observed reduction in sentinel behaviour will be costly for all through a group level decrease in surveillance or for the aggressive individuals that may have to pick up the shortfall (Kern et al., 2023); dominant individuals already contribute more to sentinel behaviour than subordinates (Kern et al., 2016), so increased dominant aggression may skew these contributions further.

The elevation of intergroup threat level altered the pattern of bystander behaviours relative to the aggression treatment, but only partially ‘reset’ focal behaviour to levels seen on control days. First, bystanders appeared to return to foraging within closer proximity of dominants at levels not significantly different to control days; we do not have the statistical power to assess whether this lack of significant difference represents a true behavioural reset to baseline behaviour or smaller, incomplete compensation. Such proximity could represent increased cohesion in the face of an imminent outside threat. Dominant individuals usually have disproportionate leadership influence (Averly et al., 2022) and are often the largest, most experienced individuals and are therefore likely to be better fighters (Green et al., 2022); both of these attributes will make them preferable associates when an intergroup contest may be imminent. An elevated intergroup threat level did not, however, result in sentinel contribution rates seen in the control treatment. Despite an upregulation in sentinel behaviour being reported at the group level in response to an intergroup threat (Christensen et al., 2016; Morris-Drake et al., 2019), bystanders remained far less likely to contribute on days with a simulated elevation in within-group conflict. This could highlight pervasive and prolonged consequences of within-group aggression and an unwillingness for individuals to pay the costs of becoming a sentinel, even when the need for surveillance increases. The observed pattern of greater sentinel activity by bystanders on control days was also mirrored in personal vigilance decisions: on control days, the threat of outsiders raised personal vigilance, potentially as a mechanism to detect rivals, while this increase was not seen following the aggression treatment. When within-group aggression is raised, individuals may be less likely to contribute to monitoring outsiders on behalf of the group. Whether the disharmony that results from elevated within-group aggression would translate into differences in contest

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contributions were an escalated IGI to emerge is a question for future studies.

Our experimental findings highlight the effects of within-group aggression on the behaviour of bystanders that could negatively affect both the individual and the wider group across contexts. This work also demonstrates the power of social monitoring to shape behaviour at timescales much longer than the immediate aftermath of observed interactions. Although dominant breeders monopolize reproduction through aggressive coercion within oft-called ‘despotic’ social groups (Cant, 2012; Creel, 2005), it may be important for dominants in some systems to withhold a level of aggression to ensure cohesion and the continued supply of public goods from their subordinate groupmates. The partial ‘reset’ in behaviour observed following an elevation in the intergroup threat level highlights the strength of conflict with outsiders as a force for shaping individual behaviour, but the fact it was incomplete points to longer-lasting effects of within-group aggression than predicted. Together, our work demonstrates potential lasting impacts of within-group aggression, with consequences for both within- and between-group behaviour.

Author Contributions

Josh J. Arbon: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Amy Morris-Drake:** Project administration, Methodology, Conceptualization. **Julie M. Kern:** Resources, Project administration. **Andrew N. Radford:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Data and Code Availability

All data and code required to reproduce analyses and plots in this manuscript are available as Supplementary Material.

Declaration of Interest

The authors declare no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2026.123474.

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