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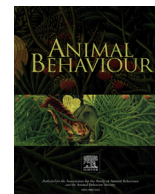
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## Factors affecting follower responses to movement calls in cooperatively breeding dwarf mongooses

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In social species, individuals maximize the benefits of group living by remaining cohesive and coordinating their actions. Communication is key to collective action, including ensuring that group members move together; individuals often produce signals when attempting to lead a group to a new area. However, the function of these signals, and how responses to them are affected by intrinsic characteristics of the caller and extrinsic factors, has rarely been experimentally tested. We conducted a series of field-based playback experiments with habituated wild dwarf mongooses, *Helogale parvula*, a cooperatively breeding and territorial species, to investigate follower responses to movement calls. In our first experiment, we found that focal individuals were more likely to respond to playback of 'movement calls' than control 'close calls', indicating movement calls function as recruitment signals. In a second experiment, we found that focal individuals responded similarly to the movement calls of dominant and subordinate groupmates, suggesting that dominance status (an intrinsic factor) does not influence receiver responses. In a final experiment, we found that individuals responded to the simulated presence of a rival group, but that this outgroup conflict (an extrinsic factor) did not affect responses to movement calls compared to a control situation. This may be because attention is instead focused on the potential presence of an imminent threat. By using playbacks to isolate the acoustic signal from physical movement cues, our results provide experimental evidence of how movement calls help leaders to attract followers and thus adds to our understanding of recruitment signals more generally.

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To maximize the benefits of group living (e.g. resource defence and reduced predation risk), group members need to act collectively; they must remain cohesive and coordinate with one another (Conradt & Roper, 2005; Krause & Ruxton, 2002; Ioannou et al., 2019). Since groups are composed of a heterogeneous mix of individuals whose interests do not perfectly align (Conradt & Roper, 2005), communication is often crucial to ensure collective action (Bradbury & Vehrencamp, 2011). Signals relating to collective movement can be produced at two stages of the process, which are not necessarily mutually exclusive. Individuals may produce a signal to indicate their readiness to move and/or when they attempt to initiate group movement, either following earlier signals of readiness or independently (Bousquet et al., 2011; Sperber et al.,

2017; Turbé, 2006). For instance, in wild dogs, *Lycaon pictus*, observational work indicates that a threshold of 'sneezing' individuals is needed to initiate group movements from a resting period (Walker et al., 2017), while 'moving calls' from several individuals are similarly required in meerkats, *Suricata suricatta*, for the group to change from one foraging patch to another (Bousquet et al., 2011). In some species, or certain contexts, a single individual may attempt to move elsewhere; attracting followers will avoid them becoming isolated and thus putative leaders may use movement signals to enhance the likelihood that they are joined. For example, meerkats also produce a distinct 'lead call', which is used when a potential leader attempts to initiate movement from a sleeping burrow to start foraging (Turbé, 2006). In white-faced capuchins, *Cebus capucinus*, backward glances seem to be important in recruiting others when shifting from resting to foraging, as the number of followers increases after a glance from a moving individual (Meunier et al., 2008). The faster 'grunt' rates of leaders

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compared to followers in redfronted lemurs, *Eulemur rufifrons*, when moving throughout the day suggests that this call may function as a movement signal (Sperber et al., 2017), and vocalizing when leaving the group increases the chances of an individual green woodhoopoe, *Phoeniculus purpureus*, being followed by its groupmates when changing foraging patches (Radford, 2004). While movement signals appear to be important in coordinating the actions of group members, there has been little experimental testing of the proposed function to recruit followers (for an exception, see Teixidor & Byrne, 1999), or of how follower responses differ depending on intrinsic characteristics of the signaller (e.g. their identity; but see Preston, 2020) and on extrinsic factors (e.g. the level of outgroup threat).

On hearing a movement signal, individuals might use information about the dominance status of the leader when deciding whether to follow. In principle, dominant individuals could be more likely to be followed if subordinates gain some benefit from doing so; for instance, if following increases future social tolerance or social-bonding opportunities (King et al., 2008; Smith et al., 2015). Dominant individuals could also be considered more reliable sources of information. For example, if they have greater knowledge of the environment, they may be more likely to lead individuals to better foraging patches (Brent et al., 2015; McComb et al., 2001). Alternatively, if group decisions are more evenly distributed across group members (Leca et al., 2003), then both dominants and subordinates could elicit similar responses from followers (Jacobs et al., 2011; Leca et al., 2003; Wang et al., 2016). Most work to date has investigated how dominance status affects the likelihood of leading. For example, in chacma baboons, *Papio ursinus*, the dominant individual tends to arrive at experimental food patches first, with subordinates following behind (King et al., 2008), while observations of Tibetan macaques, *Macaca thibetana*, suggest that dominance rank does not affect who leads the group away from depleted foraging patches (Wang et al., 2016). Far less work has examined how individuals respond to movement signals depending on the rank of the caller. One exception is an observational study of meerkats showing that dominant females producing a 'lead call' were more likely to be followed by group members than dominant males or subordinates producing the same call (Turbé, 2006), but experimental tests are needed.

Extrinsic factors can also affect follower decisions—for instance, simulated predator attacks on captive house sparrows, *Passer domesticus*, have been shown to reverse leader–follower positions relative to an exploratory context (Tuliozi et al., 2021)—but the influence of outgroup conflict in this regard has been little considered. Members of social species often interact with outside groups or individuals, which can pose a threat. For example, rival groups may be attempting to steal territory or resources (Dyble et al., 2019; Kelly, 2005), while individual outsiders may be seeking mating opportunities or a breeding position (Braga Goncalves & Radford, 2019; Mares et al., 2012). Contests with outsiders can have immediate consequences, such as physical injury or death (Dyble et al., 2019; Morris-Drake et al., 2022), while the threat of outgroup conflict can cause significant changes to within-group behaviour, including elevated levels of grooming, contact or aggression (Arseneau-Robar et al., 2018; Birch et al., 2019; Radford, 2008). Subsequent movement patterns and collective decision making have also been shown to be influenced by outgroup conflict (Christensen et al., 2016; Dyble et al., 2019; Morris-Drake, Linden et al., 2021; Radford & Fawcett, 2014). Deciding to follow another individual under conflict scenarios could have significant fitness implications; for instance, banded mongoose, *Mungos mungo*, males that follow a dominant female into violent contests suffer an increased mortality cost (Johnstone

et al., 2020). When there is the prospect of an imminent outgroup contest, group members may want to stay more cohesive due to heightened anxiety or to prime for battle (Birch et al., 2019; Morris-Drake et al., 2019), and thus could be more receptive to movement signals from leaders.

Dwarf mongooses, *Helogale parvula*, are an ideal species in which to investigate experimentally the responses of group members to movement calls. They live in cooperatively breeding groups that each defend a year-round territory (Rasa, 1987), with group members spending most of the day foraging together throughout their territory before returning to a communal burrow to sleep (Rasa, 1987). Dwarf mongooses are highly vocal, maintaining contact during foraging by producing sporadic 'close' calls (Rasa, 1987). When departing or returning to a sleeping burrow, and when moving from one foraging patch to another, individuals move cohesively at a heightened pace, usually following a leader that has initiated the movement while producing a 'movement call'—a fast burst of multiple close calls. Prior to movement from a resting position (e.g. from a sleeping burrow) there is also a gradual increase in the frequency of close calls, which may indicate an increasing willingness to move (Sperber et al., 2017). By contrast, when dwarf mongoose groups move from one foraging patch to another, there is no obvious predeparture behaviour; instead, an individual attempts to initiate group movement by moving at pace while producing a movement call. We focus on the latter behaviour in this paper.

Dwarf mongoose groups comprise a dominant breeding pair and subordinate helpers (all other adults); group members can obtain information about dominance status and individual identity from various calls (Kern et al., 2016; Morris-Drake, Kern et al., 2021; Sharpe et al., 2013). Previous work reported that dwarf mongoose movement decisions are despotic in nature, with the dominant female always leading the group (Rasa, 1987), but recent observations show that over half of group movements are led by subordinates (Cobb et al., 2022). Groups come into conflict with conspecific rivals, both neighbours and those from further afield (Christensen et al., 2016; Rasa, 1987), on average once every 2 weeks in the study population (Cobb, 2022); groups encounter faecal deposits of rival groups much more regularly (Christensen et al., 2016). Intergroup interactions (IGIs) involve a combination of group members looking at each other, vocalizing and, on some occasions, escalation to physical fights (Rasa, 1987). Individuals forage closer to their nearest neighbour after the simulated threat of a rival group (Morris-Drake et al., 2019), which could proximately be a response to heightened anxiety about imminent conflict (Radford et al., 2016), and ultimately represent priming behaviour to ensure the most collective response to outsiders (Birch et al., 2019; Radford, 2011).

We investigated subordinate group member responses to dwarf mongoose movement calls in three related field experiments. First, we tested whether the call functions to attract followers. We predicted that, compared to control close calls, movement calls would elicit a 'follow' response, with the focal individual becoming more vigilant, vocalizing and moving towards the loudspeaker. Second, we tested whether individuals respond differently to movement calls from dominant and subordinate group members, predicting either a stronger response to movement calls from dominant individuals, or for there to be no clear difference in response to movement calls from dominant versus subordinate individuals. Third, we tested how the threat of a nearby rival group affects the response to movement calls. We predicted that, compared to a control stimulus, the simulation of an intergroup threat would result in heightened responses to movement calls, such that the group would remain cohesive in case a contest occurred imminently.

## METHODS

### Study Site and Population

We carried out the research at the Dwarf Mongoose Research Project (DMRP) in Limpopo Province, South Africa (24°11'S, 30°46'E); see [Kern and Radford \(2013\)](#) for more details. Eight wild but habituated groups, each comprising 4–12 adults (individuals >1 year old), were used in experiments during the study period (April–August 2020). Groups are habituated to close human presence (<5 m) and individuals are uniquely dye-marked ([Kern & Radford, 2013](#)). The dominance status (dominant or subordinate; identifiable from the outcome of aggressive interactions such as foraging displacements) and sex (identifiable from anogenital grooming bouts) of all individuals is known from the long-term observations ([Kern & Radford, 2013, 2016](#)). We considered only adults for playback experiments because individuals less than 1 year old rarely lead the group ([Cobb, 2022](#)).

### Experimental Overview

We conducted three playback experiments to investigate the responses of focal subordinate individuals to the movement call of another group member. In experiment 1 (10 April–8 June 2020), we determined the baseline responses to the movement call of a dominant individual by comparing them to the responses elicited by close calls (given while foraging) of the same dominant group member. In experiment 2 (27 April–25 June 2020), we tested whether responses differed depending on the dominance status of the caller, comparing those elicited by movement calls of dominant and subordinate group members of the same sex (the focal individual was not necessarily sex-matched to the signallers). In experiment 3 (10 July–16 August 2020), we tested how the simulated presence of a rival group affected responses to movement calls. Experiment 3 involved two parts: an initial playback of close calls and 'lost' calls (high-pitched vocalizations usually produced while foraging, particularly when an individual becomes isolated) from a non-neighbouring rival group or control herbivore sounds, and then playback of the same movement call of a dominant group member. All three experiments had matched-pairs designs, with each focal subordinate in an experiment receiving two treatments in a counterbalanced order ( $N = 18$  individuals from six groups for experiment 1 and 2;  $N = 16$  individuals from eight groups for experiment 3).

### Recordings and Playback Tracks

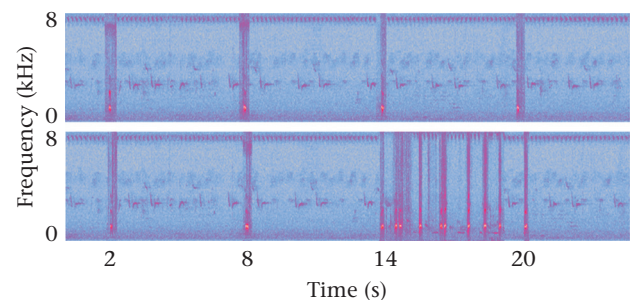
We recorded calls ad libitum within 3 m of an individual in calm conditions, using a Marantz PMD661MKII solid-state recorder (Marantz, Kanagawa, Japan) and a Sennheiser MKE600 shotgun microphone (Sennheiser, Wedemark, Germany) coupled with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, U.K.). As all groups are well habituated to close human presence, the behaviour and vocalizations of individuals were not impacted during recordings. We recorded individual close and lost calls while groups were foraging throughout the day, and we recorded individual movement calls when a group moved collectively (sometimes excluding individuals such as babysitters; B. Cobb, personal observation) from a sleeping burrow to a foraging site, from one foraging patch to another, or to a sleeping burrow before sundown (example recordings available in Supplementary Material). Collective group movements are initiated by one individual moving quickly away from the group while producing a movement call; those following often produce movement calls too.

To construct playback tracks, we used Audacity 2.3.3. For all tracks, we superimposed good-quality recordings of calls (e.g. no overlapping sounds such as conspecific calls) onto recordings of ambient sound recorded in calm conditions in the centre of a group's territory when no dwarf mongooses were present. We used a HandyMAN TEK 1345 sound meter (Metrel U.K. Ltd; Epsom, Surrey, U.K.) to standardize playback volume of calls to match natural vocalizations, as well as amplifying calls in Audacity where needed. We applied a high-pass filter (filtering out frequencies below 300 Hz) in all tracks to improve signal-to-noise ratio and to standardize background sound. The same ambient-sound recording was used for both playbacks within a pair (i.e. the two treatments to a focal individual in a given experiment). Movement calls, which are composed of fast-repeating close call elements, are often preceded by infrequent close calls ([Maier et al., 1983](#)). To replicate this combination and to standardize track length, movement call tracks for all three experiments consisted of 25 s of ambient sound, with two close calls (one at 2 s and one at 8 s after the start of the track) followed by a movement call commencing 14 s from the start of the track ([Fig. 1](#), bottom). We standardized movement calls to be 10 close call elements within 6–7 s based on early analysis of a subset of recordings during the field season (mean  $\pm$  SE call rate =  $1.5 \pm 0.1$  close call elements/s, range 0.4–3.6); thus, the movement call playback rate ranged from 1.4 to 1.6 close call elements/s. For all experiments, both female and male vocalizations were used for playbacks. The same calls were sometimes used across experiments.

In experiment 1, we compared responses to movement call and control tracks from the same dominant individual. Control tracks comprised 25 s of ambient sound with four close calls at 2, 8, 14 and 20 s from the start of the track ([Fig. 1](#), top). We standardized both close calls and movements calls to 50–55 dB from 1 m. Within the experiment, a given individual was used as a source of calls no more than three times (mean = 1.8), and a given call was only used once in playback tracks.

In experiment 2, we compared responses to movement call tracks from a dominant and subordinate individual. A given individual was used as a source of calls no more than three times (mean = 1.4). We standardized calls to 50–55 dB from 1 m, and used a given call once within the experiment. The two playbacks to a focal individual were of calls from individuals of the same sex as each other (e.g. a dominant male and a subordinate male) to ensure the sex of the caller had no effect on responses.

Experiment 3 involved two parts. For part 1 (the rival group or herbivore control playback), we created tracks using similar methodology to [Morris-Drake et al. \(2019\)](#); call rates within tracks matched those heard naturally. Herbivore tracks were made up of herbivore feeding sounds available from previous work, and included plains zebras, *Equus quagga*, blue wildebeest,



**Figure 1.** Spectrogram of close call control track (top) and movement call track (bottom). Blue indicates low-amplitude noise; red indicates higher-amplitude noise. Taken and adapted from Audacity 2.3.3.

*Connochaetes taurinus*, giraffe, *Giraffa camelopardalis giraffe*, and waterbuck, *Kobus ellipsiprymnus*. We pasted four herbivore sounds onto 12 s of ambient sound, to create four different sequences. We then pasted these sequences into a 1 min track (one sequence being used twice) in a random order, which we duplicated to make a 2 min herbivore track. Rival group tracks each contained calls from a single other group: close calls from four individuals, including at least one dominant, and lost calls from two individuals. We inserted four close calls (one from each individual) into a 3 s sequence. Four sequences were constructed, each with a randomized order of caller. We then inserted these four sequences into 12 s blocks of ambient sound, to make five 12 s blocks, with each block having a randomized sequence order. These blocks were then combined to make a 1 min track, and five calls were removed at random to create a call rate of 75/min, as per the natural call rate of a foraging group and in line with previous experimental work (Morris-Drake et al., 2019; Sharpe et al., 2013). In this 1 min segment, four lost calls from two individuals (two each) were then inserted into the track at random time stamps within the first 30 s, alternating between individuals. As lost calls are difficult to predict and record, some recordings from previous field seasons from individuals no longer in the group were used. As we were playing back calls from non-neighbouring groups, we did not expect this to affect responses of the focal group. We then duplicated each 1 min track to make 2 min tracks. We faded rival group tracks so that the maximum amplitude (50–55 dB at 1 m for close calls and 60–65 dB at 1 m for lost calls) was reached at 1 min, to simulate a rival group approach. Previous work has shown that individuals are able to distinguish between calls of their own group and those of a rival group (Morris-Drake et al., 2019).

Some close calls and herbivore sounds were used more than once within part 1 of the experiment, but the component parts of each track were arranged randomly in a different order to generate unique tracks. We used the same group for playback construction no more than four times (mean = 2.3), with a maximum of three focal individuals per group receiving playbacks (mean = 2). The same rival group was used for playback on a maximum of two focal individuals from the same group. As rival tracks were from non-neighbouring groups (and thus all rivals were unknown outsiders from the perspective of a focal group), it is unlikely that group identity affected focal responses, and a 2-week gap was left between trials on different individuals within the same group to avoid habituation to the calls (see [Experimental Protocol](#) below for further details).

For part 2 (the movement call playback), a given individual was used as a source of call no more than twice (mean = 1.2), with different calls used for different focal individuals. Calls were standardized to 50–55 dB from 1 m. After receiving the playback track in part 1, a focal individual received a movement call track from a given dominant individual within its group. The same movement call track was used following a herbivore or rival group track to ensure differences in movement calls had no effect on responses.

### Experimental Protocol

For all three experiments, we conducted trials during the day when the group was foraging, in calm weather conditions and at least 10 min after a group movement, latrine behaviour, snake mob or other disturbance. If an IGI occurred, at least 30 min was left before running a trial in experiments 1 and 2; for experiment 3, trials were carried out on a different day to IGIs. We started trials when the focal individual was foraging at least 2 m from other individuals.

We carried out experiments 1 and 2 using a similar experimental protocol. We placed a loudspeaker (Rokono B10 or Rokono

BASS+ Mini, Boundless Technology Limited, Devon, U.K.) connected to an MP3 device (either a Moto G 5 phone; Motorola Inc, Chicago, IL, U.S.A., or a Kubik Evo; Kubik Digital Electronics) 3 m perpendicular from the focal individual (chosen randomly before visiting the group), hidden in vegetation. Trials to the same individual were separated by at least 1 day and performed at a similar time of day. Within a group, at least 30 min was left between trials on different individuals. If a trial was disturbed (e.g. due to conspecific alarm calls or the focal individual moving into vegetation and out of view), it was abandoned (experiment 1:  $N = 4$ ; experiment 2:  $N = 7$ ) and repeated that day or at a later date, but with the order of the treatments reversed. The playback track in the abandoned trial was therefore not used more than once on the same day, to avoid habituation.

For experiment 3, we used two loudspeakers, one for each part. To avoid disturbing the focal individual during loudspeaker set-up, a small amount of egg was used to attract it to an area where the two loudspeakers were already positioned. When playback started, the focal individual was thus 5 m from the first loudspeaker (used to broadcast either the rival group or herbivore track) (Morris-Drake et al., 2019). The second loudspeaker (used for the movement call playback) was placed diagonally ca. 3 m from the first loudspeaker so that, if the focal individual approached the first loudspeaker, the second loudspeaker would be positioned to one side of the individual. Following initial playback of a rival group or herbivore track, the movement call track was started at least 30 s, and no more than 5 min, later. Variation in time between playbacks was due to individuals moving out of view, for example into dense vegetation, before the movement call track could be started, but there was no difference between treatments (mean  $\pm$  SE time after a rival group track =  $110 \pm 22$  s, herbivore track =  $112 \pm 21$  s). Trials to the same focal individual were separated by at least 1 day, and at least 2 weeks were left before conducting trials on another individual in the same group, to avoid habituation. Trials abandoned due to disturbances (e.g. alarm calls or the focal individual going out of view) were repeated with different rival group or herbivore tracks at least 2 days later ( $N = 7$ ).

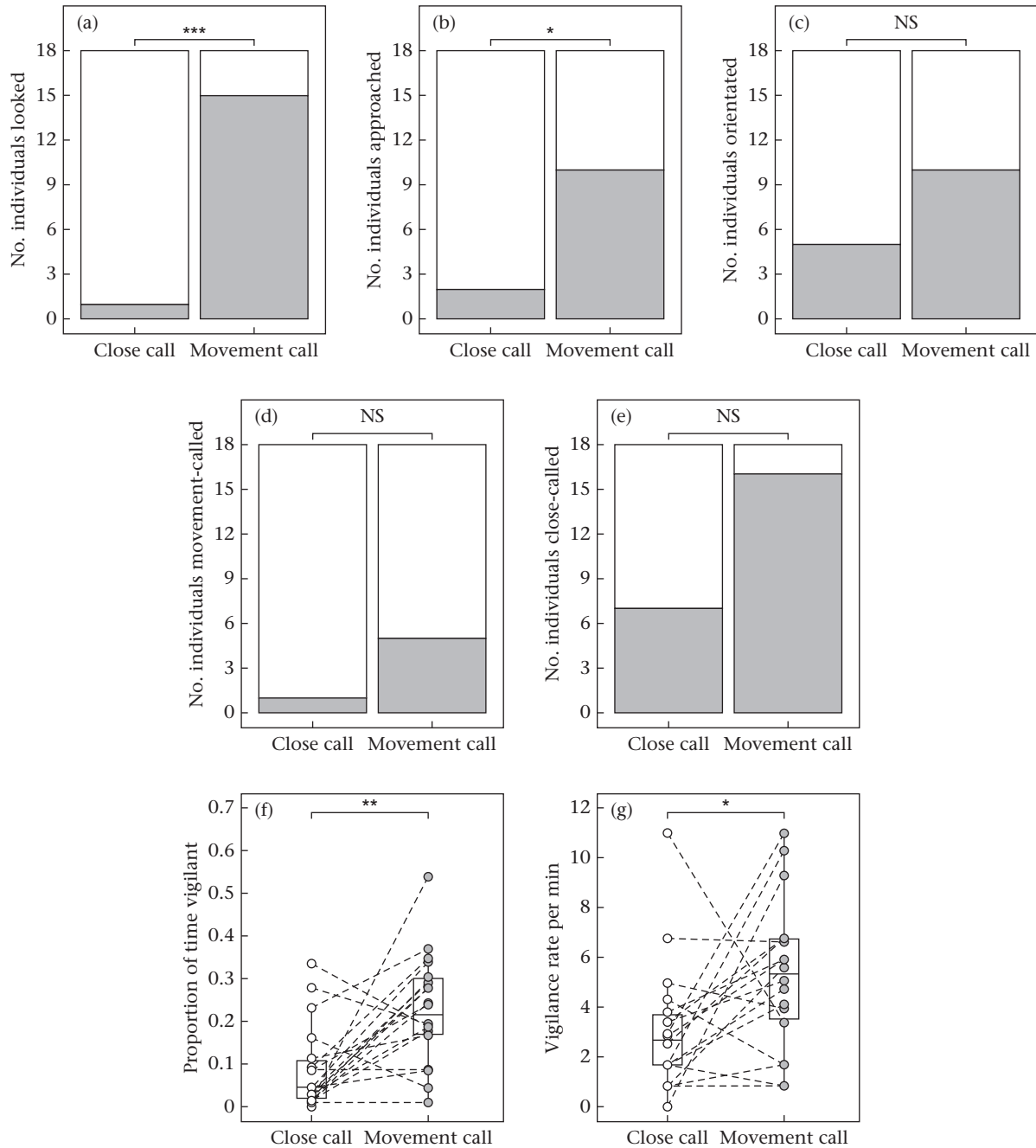
For all experiments, we recorded the following responses to movement calls (and close calls in experiment 1): (1) whether the focal individual looked (head raised and directed towards the loudspeaker), orientated (whole body turned to face the loudspeaker) and/or approached (after orientating, moved at least 50 cm towards the loudspeaker); (2) whether they vocalized (gave either close calls and/or movement calls); (3) the rate and proportion of time spent vigilant (head raised). These responses were collected from 14 s after the start of the playback (i.e. once the movement call period had commenced; see [Recordings and Playback Tracks](#)), and focal individuals were observed for a minimum of 25 s after the playback finished. We analysed data for a maximum of 60 s response time, as we assumed that individuals would not be responding to movement calls after this point. Chi-square tests were performed to show that there were no differences between treatments in the response time analysed: experiment 1 ( $\chi^2_1 = 0$ ,  $P = 1$ ), experiment 2 ( $\chi^2_1 = 1.45$ ,  $P = 0.229$ ) and experiment 3 ( $\chi^2_1 = 0$ ,  $P = 1$ ). For part 1 of experiment 3 (the rival group or herbivore playback), we recorded whether the individual looked, orientated and approached the loudspeaker during the 2 min playback period, to ensure individuals were responding to rival group calls as expected from Morris-Drake et al. (2019). All trials were filmed using a GoPro Hero 7 strapped to the head of the observer, who also narrated responses into a Dictaphone (Sony ICD-PX370) while standing ~3 m away from the focal individual and loudspeaker to avoid disturbances.

Ethical Note

All work was conducted with permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013), the Ethical Committee of the University of Pretoria, South Africa and the Ethical Review Group of the University of Bristol, U.K. (University Investigator Number: UIN/17/074). Only those individuals comfortable with close presence of experimenters were included in the study. To minimize anxiety, rival group playbacks were limited to a maximum of three focal individuals per group.

Statistical Analysis

We extracted data using Boris 7.9.19 (Friard & Gamba, 2016). Video footage from GoPro recordings was used where quality was sufficient, but where recordings failed, or quality was poor (e.g. due to dense vegetation), only Dictaphone audio was used for both treatments in a pair. We used R v.4.0.3 for statistical analyses (R Core Team, 2020) and 'ggplot2' to construct figures (Wickham, 2016). McNemar tests (with continuity corrections) were used for paired responses with a binary outcome. Paired *t* tests were used for continuous response variables where assumptions were met



**Figure 2.** Number of individuals that (a) looked, (b) approached and (c) orientated towards the loudspeaker, and that gave (d) movement calls and (e) close calls in response to playback of close calls and movement calls. White bars indicate no response, grey bars show a positive response. (f) Proportion of time spent vigilant and (g) vigilance rate in response to playback of close calls and movement calls. Box plots show medians and quartiles, whiskers show upper and lower quartiles ( $\pm 1.5$  times the interquartile range). Dotted lines link data points from the same individuals in the two treatments (circles). \**P* < 0.05; \*\*\**P* < 0.001. *N* = 18 individuals receiving paired trials.

(paired differences and residuals being normally distributed, checked visually with histograms and Q–Q plots). Where assumptions were violated, Wilcoxon signed-rank exact tests were performed. To compensate for an increased likelihood of type I error due to multiple testing, we used sequential Bonferroni corrections (Rice, 1989) for tests within three grouped response variables for each experiment: (1) physical response (look, orientate, approach); (2) vocal response (close call, movement call) and (3) vigilance response (proportion of time vigilant, vigilance rate). Adjusted  $\alpha$  levels are given within each grouping where at least one significant result is reported. The data and R code used for analysis is available in Supplementary Material.

## RESULTS

### Experiment 1

In response to movement call playback, focal individuals were significantly more likely to look (McNemar's test:  $\chi^2_1 = 12.07$ ,  $P < 0.001$ , adjusted  $\alpha = 0.017$ ; Fig. 2a) and approach ( $\chi^2_1 = 6.13$ ,  $P = 0.013$ ,  $\alpha = 0.025$ ; Fig. 2b), but not orientate ( $\chi^2_1 = 2.29$ ,  $P = 0.131$ ; Fig. 2c), towards the loudspeaker than in close call (control) trials. There was no significant difference between treatments in the number of individuals that gave movement calls ( $\chi^2_1 = 2.25$ ,  $P = 0.137$ ; Fig. 2d). Individuals were more likely to give close calls in response to movement call playbacks than in response to close call playbacks, but this was not significant after Bonferroni correction ( $\chi^2_1 = 4.92$ ,  $P = 0.027$ ,  $\alpha = 0.025$ ; Fig. 2e). Movement call playback resulted in significantly greater vigilance than in control trials (paired  $t$  test, proportion of time spent vigilant:  $t_{17} = 3.39$ ,  $P = 0.004$ ,  $\alpha = 0.025$ , mean difference = 0.14, 95% CIs = 0.05–0.22; Fig. 2f; vigilance rate:  $t_{17} = 2.24$ ,  $P = 0.039$ ,  $\alpha = 0.05$ , mean difference = 2.18 look-ups per min, 95% CIs: 0.13–4.24; Fig. 2g).

### Experiment 2

There was no significant difference in the number of individuals that looked (McNemar's test:  $\chi^2_1 = 0.13$ ,  $P = 0.724$ ; Appendix, Fig. A1a), orientated ( $\chi^2_1 = 1.5$ ,  $P = 0.221$ ; Appendix, Fig. A1b) or approached ( $\chi^2_1 = 0$ ,  $P = 1$ ; Fig. 3a) towards the loudspeaker in response to playback of movement calls from dominant versus subordinate group members. There was also no significant treatment difference in the number of individuals that gave movement calls ( $\chi^2_1 = 0.8$ ,  $P = 0.371$ ; Appendix, Fig. A1c) or close calls

( $\chi^2_1 = 0.17$ ,  $P = 0.683$ ; Fig. 3b). Finally, neither the proportion of time spent vigilant (paired  $t$  test:  $t_{17} = 0.22$ ,  $P = 0.827$ , mean difference = 0.02, 95% CIs:  $-0.14$ – $0.17$ ; Appendix, Fig. A1d) nor the vigilance rate ( $t_{17} = 0.12$ ,  $P = 0.903$ , mean difference = 0.14 look-ups per min, 95% CIs:  $-2.23$ – $2.51$ ; Fig. 3c) differed significantly between treatments.

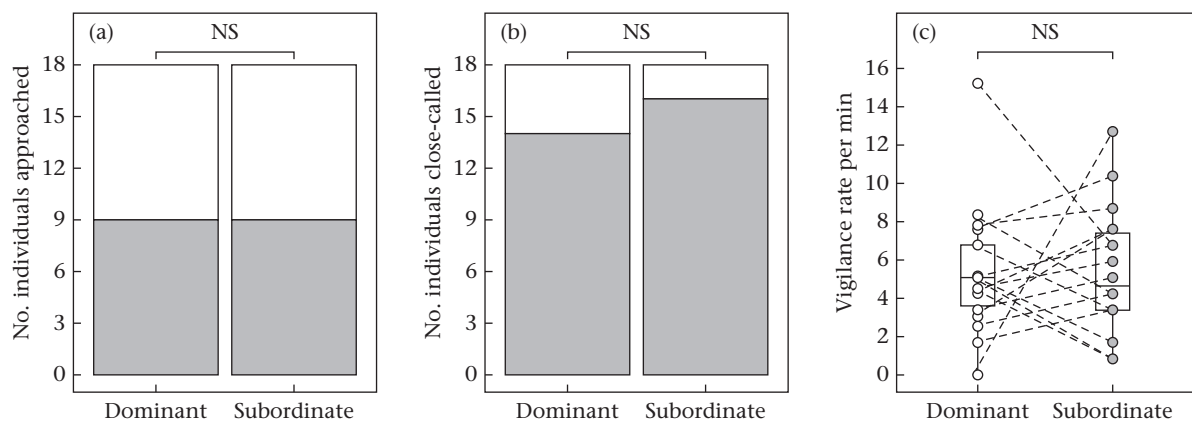
### Experiment 3

In part 1 of experiment 3, individuals were significantly more likely to look (McNemar's test:  $\chi^2_1 = 6.13$ ,  $P = 0.013$ ,  $\alpha = 0.017$ ; Fig. 4a), orientate ( $\chi^2_1 = 4.9$ ,  $P = 0.027$ ,  $\alpha = 0.05$ ; Fig. 4b) and approach ( $\chi^2_1 = 5.82$ ,  $P = 0.016$ ,  $\alpha = 0.025$ ; Fig. 4c) towards the loudspeaker in response to rival group playback than in response to playback of herbivore control sounds.

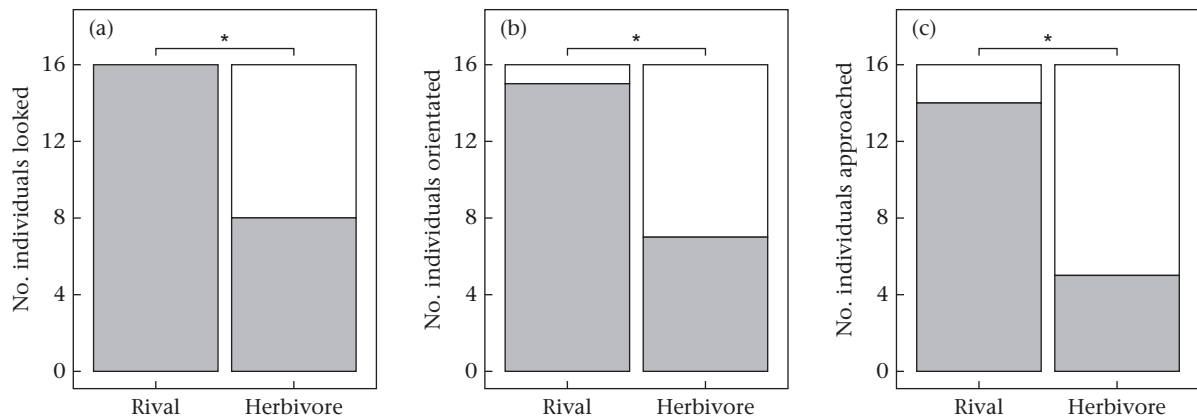
During part 2 (playback of a movement call), there was no significant difference between treatments (following either rival group or herbivore playback) in the number of focal individuals that looked (McNemar's test:  $\chi^2_1 = 0$ ,  $P = 1$ ; Appendix, Fig. A2a), orientated ( $\chi^2_1 = 1.5$ ,  $P = 0.221$ ; Appendix, Fig. A2b) or approached ( $\chi^2_1 = 0.13$ ,  $P = 0.724$ ; Fig. 5a) towards the loudspeaker. Similarly, there was no significant difference between treatments in the number of individuals that gave movement calls ( $\chi^2_1 = 0$ ,  $P = 1$ ; Appendix, Fig. A2c) or close calls ( $\chi^2_1 = 1.5$ ,  $P = 0.221$ ; Fig. 5b). There was also no significant treatment difference in the proportion of time spent vigilant (Wilcoxon signed-rank exact test with continuity correction:  $V = 93$ ,  $N = 16$ ,  $P = 0.211$ ; Appendix, Fig. A2d) or in vigilance rate of individuals ( $V = 46.5$ ,  $N = 12$ ,  $P = 0.583$ ; Fig. 5c).

## DISCUSSION

In response to movement call playbacks compared to control playbacks, dwarf mongoose individuals were more likely to look and approach the loudspeaker and were more vigilant (experiment 1), suggesting movement calls function as recruitment calls. Focal subordinates responded similarly to playbacks of movement calls from dominants and subordinates (experiment 2), suggesting that the dominance rank of the caller (an intrinsic factor) may not influence a decision on whether to follow another individual. The playback of a rival group caused individuals to look, orientate and approach the loudspeaker more than when played a control herbivore track, but this heightened outgroup conflict (an extrinsic factor) did not translate into a difference in response to movement calls (experiment 3). Using playback experiments allowed us to



**Figure 3.** Number of individuals that (a) approached and (b) gave close calls, and (c) the vigilance rate of individuals in response to playback of dominant and subordinate movement calls. For (a) and (b), white bars indicate no response, grey bars show a positive response. For (c), box plots show medians and quartiles, whiskers show upper and lower quartiles ( $\pm 1.5$  times the interquartile range) and dotted lines link data points from the same individuals in the two treatments (circles).  $N = 18$  individuals receiving paired trials.



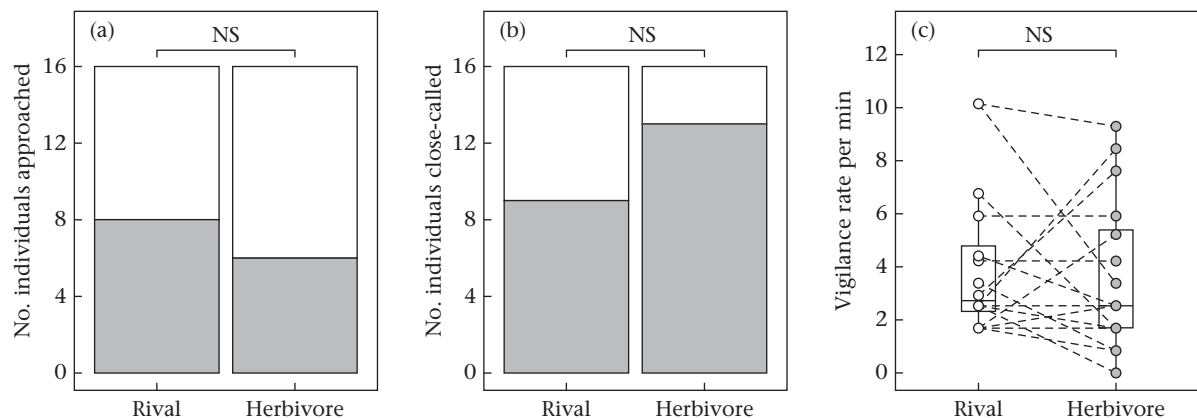
**Figure 4.** Number of individuals that (a) looked, (b) orientated and (c) approached towards the loudspeaker in response to playback of rival group or herbivore sounds. White bars indicate no response, grey bars show a positive response.  $*P < 0.05$ .  $N = 16$  individuals receiving paired trials.

eliminate confounding factors, such as physical movement cues, and thus isolate the importance of the acoustic movement call in follower decision making.

Much observational work suggests that signals are important in coordinating group movements in a variety of taxa (Conradt & Roper, 2005; Sperber et al., 2017). Here, we have shown experimentally that a movement call alone is sufficient to elicit a movement response in a nearby group member. While foraging for prey, dwarf mongooses spend the majority of their time with their heads down (Rasa, 1989), and vegetation can be dense, meaning that purely visual cues of a lead attempt may be obscured or missed. Thus, a salient acoustic signal of recruitment is likely useful in attracting the attention of other group members and increasing the likelihood of recruiting followers so that the putative leader is not left isolated. Similar vocalizations have been observed in other species and may be important for both recruiting followers and in coordinating movement among group members (Sperber et al., 2017); distinct vocalizations may exist for these somewhat different functions. In meerkats, for example, a 'lead call' is produced by a potential leader seemingly to attract followers (Bousquet et al., 2011); this is similar in context to the dwarf mongoose movement call that we studied. Meerkats also exhibit predeparture behaviour when changing foraging patches, with several group members giving 'moving calls', possibly to ensure a foraging patch is depleted before leaving (Bousquet et al., 2011). In

dwarf mongooses, any potential 'voting' process, whereby individuals contribute to a group decision, is perhaps more likely to occur when changing activities, rather than when moving during foraging (the context that we investigated): prior to leaving a sleeping burrow or returning in the evening, there is a gradual increase in the frequency of close calls before an individual first produces a movement call and moves off (B. Cobb, personal observation). In our first experiment, there was a nonsignificant tendency for individuals to produce close calls more in response to movement call playbacks than in response to close call playbacks. This might be an indication that followers are signalling to the leader their intention to follow, although individuals did not produce movement calls more in response to movement call playbacks than in response to close call playbacks. The lack of a strong vocal response might perhaps be due to the use of a static loudspeaker in our experiment, which likely represents a weaker stimulus than a natural lead event involving a physical cue too; future experimental work could use a moving loudspeaker (Gall & Manser, 2017). Interactive playbacks (King, 2015) could also help our understanding of how followers and leaders vocally interact with one another to coordinate movements; for example, whether vocal feedback from followers is required to initiate a group movement (Bousquet et al., 2011).

In experiment 2, we found no significant differences in response to dominant versus subordinate movement calls, but responses for



**Figure 5.** Number of individuals that (a) approached and (b) gave close calls, and (c) the vigilance rate of individuals in response to playback of movement calls following playback of either rival group or herbivore sounds. For (a) and (b), white bars indicate no response, grey bars show a positive response. For (c), box plots show medians and quartiles, whiskers show upper and lower quartiles ( $\pm 1.5$  times the interquartile range) and dotted lines link data points from the same individuals in the two treatments (circles).  $N = 16$  individuals receiving paired trials.



both were similar to those in the movement call treatment of experiment 1. In principle, one explanation could be that movement calls do not convey information on individual identity or dominance status. However, previous work on dwarf mongooses has shown that individuals respond differently to sentinel calls depending on the dominance status of the caller (Kern et al., 2016). Furthermore, Sharpe et al. (2013) showed that, in response to close calls of higher-ranked versus lower-ranked individuals of similar ages, focal individuals with a food item were more vigilant, suggesting discrimination based on social rank. We therefore suggest that individuals were still responding to movement calls, but with no preference in following individuals of different dominance status. Where within-group conflict is frequent, such as in chacma baboons, dominant leadership patterns have been observed, and following a dominant and maintaining social bonds with them could ease anxiety or reduce the chance of receiving aggression (Kalbitzer et al., 2015; King et al., 2008). In dwarf mongooses, there are relatively low levels of within-group conflict, perhaps in part because aggressors receive less grooming at the evening sleeping burrow (Morris-Drake, Kern et al., 2021). Rather than dominance status per se, other factors such as nutritional requirements may be more important (Sueur et al., 2013). If movement calls are a form of honest signal, in that they are often produced by individuals with the highest needs (Conradt et al., 2009; Rands et al., 2003), then other group members could respond to them regardless of the relative social rank of the caller due to inclusive fitness benefits (Hamilton, 1964). As playbacks were conducted while foraging, the experiments could mimic a situation whereby the caller is motivated to move to another foraging patch due to the current one being depleted. If the receiver's foraging success was low at the time, it could also be in their best interest to respond to movement calls, in anticipation of a richer foraging patch. Alternatively, other individual attributes regardless of status could be important. For example, individuals could be more likely to respond to those groupmates to whom they are more strongly bonded, as previous work in dwarf mongooses has demonstrated for snake mob calls (Kern & Radford, 2016).

For our final experiment, which entailed an initial playback of either a rival group track or control herbivore track, we found a stronger response towards the former in line with previous work (Morris-Drake et al., 2019). But, we found no difference in response towards a subsequent dominant movement call, in contrast to our prediction of a heightened response. One explanation is that there could be no increase in response towards a movement call after simulated rival group presence due to heightened anxiety and alertness for rivals; rather than being more likely to respond to a movement call, the immediate threat of a rival group demands more attention from a given individual and thus movement calls might not elicit a different response, or even a weaker response. It would be interesting to conduct similar experiments during the breeding season, in which we might expect a stronger response to rival group calls. In pied babblers, *Turdoides bicolor*, for example, groups respond to rival group calls more strongly in the breeding season, likely due to increased food availability and having more energy to invest (Golabek et al., 2012). However, the lack of difference between treatments in our experiment could also be due to methodological reasons. In contrast to experiments 1 and 2, movement call playback in our control treatment elicited a weaker response. This could be due to the use of egg prior to playback to get focal individuals into position – it is possible individuals were less likely to respond to a movement call in both treatments if they anticipated more food in the area. The presence of a rival group would clearly demand more immediate responses from individuals despite the presence of food, which we found, but responses to a subsequent movement call may have been subdued. We also found

no difference in vigilance levels during the movement call playback, despite previous work showing increased vigilance following rival group playback (Morris-Drake et al., 2019). As we gave egg to a single individual, rather than to the whole group as in Morris-Drake et al. (2019), the incentive for food may have been larger in our study and affected behaviour more. Conflict has previously been shown to affect movement decisions across taxa, with groups or individuals either staying in an area to defend their territory, or moving elsewhere to avoid any further costly contests (Christensen et al., 2016; Descovich et al., 2012; Radford & Fawcett, 2014; Yi et al., 2020). As costs and opportunities of contests differ between group members, conflict is likely to affect leaders and followers differently (Johnstone et al., 2020). Further work should look to use these conflicts of interests to investigate variation in responses to movement signals, and communication more generally, while under threat.

Our current work has focused on movement decisions, but recruitment signals are widespread in the animal kingdom and occur in a variety of contexts. In dwarf mongooses alone, three different recruitment signals exist: in addition to the movement call investigated here, there is a lost call and a snake mob call (Kern & Radford, 2016; Rubow et al., 2017). Different calls likely exist because different responses are required from the receivers in each context. Across species, there are a variety of other contexts in which recruitment signals may be produced, such as attracting groupmates to foraging patches (Hauser et al., 1993; Radford & Ridley, 2006). Similar or different intrinsic and extrinsic factors could affect how individuals respond to different recruitment signals. As we learn more about recruitment signals and follower responses, comparative studies will allow us to investigate this variety in more detail.

### Author Contributions

**Benjamin Cobb:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - Original draft, Visualisation. **Amy Morris-Drake:** Conceptualization, Methodology, Writing - Review & editing, Supervision. **Patrick Kennedy:** Writing - Review & editing, Supervision. **Megan Layton:** Investigation, Writing - Review & editing. **Julie M. Kern:** Methodology, Writing - Review & editing. **Andrew N. Radford:** Conceptualization, Methodology, Writing - Original draft, Supervision, Project administration, Funding acquisition.

### Declaration of Competing Interest

None.

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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.2022.07.009>.

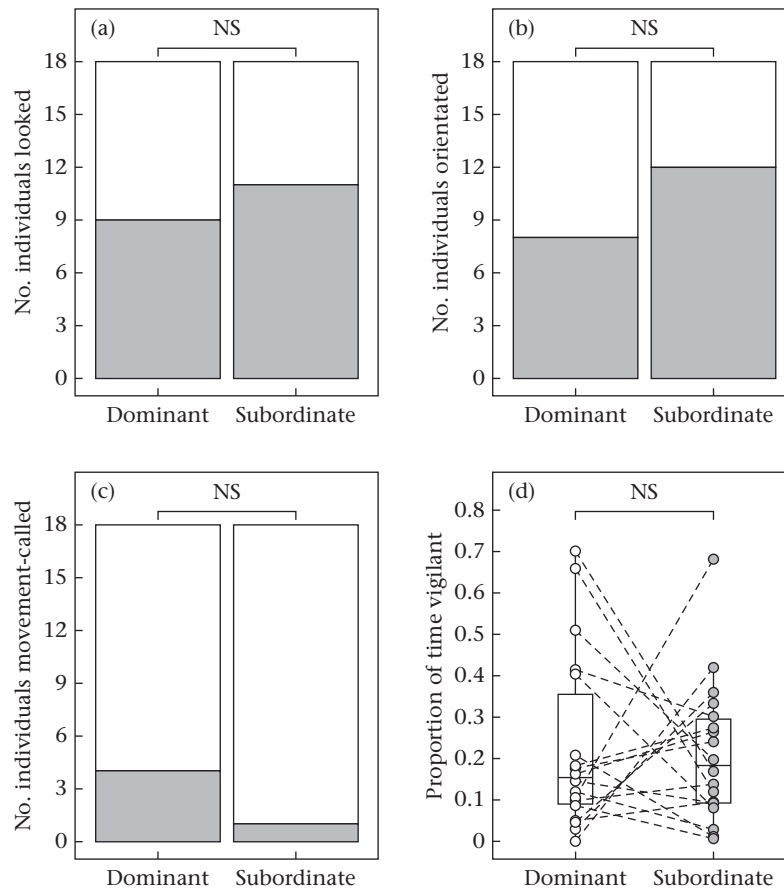
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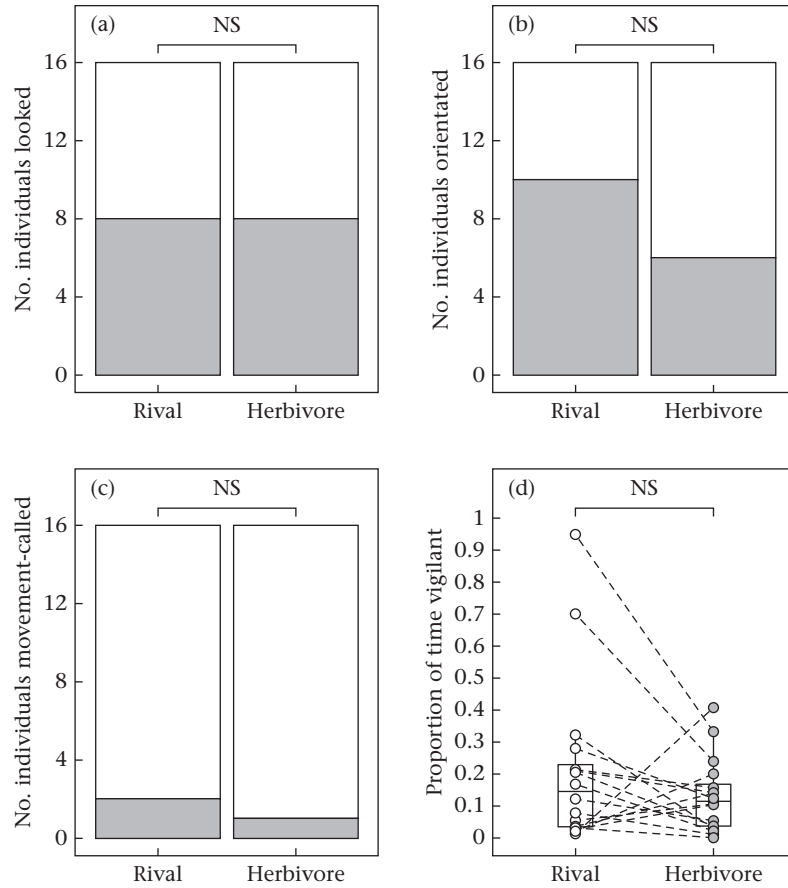
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## Appendix



**Figure A1.** Number of individuals that (a) looked and (b) orientated towards the loudspeaker and (c) that gave a movement call in response to playback of dominant and subordinate movement calls. White bars indicate no response, grey bars show a positive response. (d) Proportion of time spent vigilant in response to playback of close calls and movement calls. Box plots show medians and quartiles, whiskers show upper and lower quartiles ( $\pm 1.5$  times the interquartile range). Dotted lines link data points from the same individuals in the two treatments (circles).  $N = 18$  individuals receiving paired trials.



**Figure A2.** Number of individuals that (a) looked and (b) orientated towards the loudspeaker, and (c) that gave a movement call in response to playback of movement calls following playback of either rival group or herbivore sounds. White bars indicate no response, grey bars show a positive response. (d) Proportion of time spent vigilant in response to playback of movement calls following playback of either rival group or herbivore sounds. Box plots show medians and quartiles, whiskers show upper and lower quartiles ( $\pm 1.5$  times the interquartile range). Dotted lines link data points from the same individuals in the two treatments (circles).  $N = 16$  individuals receiving paired trials.