



Collective close calling mediates group cohesion in foraging meerkats via spatially determined differences in call rates

Sabrina Engesser ^{a,*,1} , Marta B. Manser ^{a, b, c}

^a Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

^b Kalahari Research Centre, Kuruman River Reserve, Van Zylsrus, Northern Cape, South Africa

^c Mammal Research Institute, University of Pretoria, Pretoria, South Africa

ARTICLE INFO

Article history:

Received 29 April 2021

Initial acceptance 1 July 2021

Final acceptance 11 November 2021

Available online 25 January 2022

MS. number: 21-00272R

Keywords:

close call
contact call
group cohesion
group movement
Suricata suricatta
vocal hotspot

During group movements, many socially living and group-foraging animals produce contact calls. Contact calls typically function to coordinate and maintain cohesion among group members by providing receivers with information on the callers' location or movement-related motivation. Previous work suggests that meerkats, *Suricata suricatta*, also produce short-range contact calls, so-called 'close calls', while foraging to maintain group cohesion. Yet, the underlying mechanism of how meerkats coordinate cohesion via close calling is unclear. Using a combination of field observations and playback experiments we here show that foraging meerkats adjusted the call rates of their continuously produced close calls depending on their spatial position to group members. Specifically, meerkats called at higher rates when foraging at a closer distance to and when surrounded by conspecifics; however, the number of calling individuals or their call rates did not affect a subject's close call rate. Overall, close call playbacks elicited a call response in receivers and attracted them to the sound source. Our results suggest that differences in individual close call rates are determined by a meerkat's proximity to other group members, being assessed through their vocal interactions. We discuss how local differences in individual call rates may extrapolate to the group level, where emerging 'vocal hotspots' indicate areas of high individual density, in turn attracting and potentially guiding group members' movements. Hence, the described pattern illustrates a so far undocumented call mechanism where local differences in the call rates of continuously produced close calls can generate a group level pattern that mediates the cohesion of progressively moving animal groups.

© 2021 The Authors. Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Socially living animals rely heavily on vocal signals and produce different types of contact calls to coordinate their diverse group activities (Boinski & Garber, 2000; Fichtel & Manser, 2010). Of these, 'close calls', soft, short-range contact calls, have gained particular interest in the field of animal behaviour due to their central role in the mediation of collective movement decisions, specifically the maintenance of group cohesion during foraging movements (Fichtel & Manser, 2010). The precise vocal mechanism through which cohesion among group-foraging individuals is achieved varies among species, with different calling strategies resulting in different patterns of spatial structure and movement dynamics at the group level (Boinski & Garber, 2000; Fichtel & Manser, 2010). Such patterns usually emerge from simple

interindividual interactions related to spatial arrangements based on either attraction or repulsion among group members (Couzin et al., 2002, 2005; Gall & Manser, 2017). Accordingly, in many species close calls serve to attract or keep in vocal contact with group members. This is typically reflected in individuals emitting calls when initiating or leading group movements, or increasing call rates when at a closer distance to group members (Boinski & Garber, 2000; Engesser et al., 2017; Neumann & Zuberbühler, 2016; Sperber et al., 2017; Walker et al., 2017). Alternatively, individuals might increase calling when they risk getting separated from the group, for example, at the end of a group's progression or with increasing distance to group members (Cheney et al., 1996; Hedwig et al., 2015; Koda et al., 2008; Pfluger & Fichtel, 2012; Uster & Zuberbühler, 2001). In other cases, interindividual spacing patterns may be regulated by a combination of repulsive and attractive interactions among callers. Accordingly, while on the larger group level close calls function to maintain group cohesion, on a local,

* Corresponding author.

E-mail address: sabrina.engesser@outlook.com (S. Engesser).

¹ Present address: Department of Behavioural and Cognitive Biology, University of Vienna, Vienna, Austria.

individual scale they maintain the individual distance among group members to reduce foraging competition, with call rates increasing when at a closer distance to or when surrounded by more foraging competitors (Boinski & Campbell, 1996; Palombit, 1992; Radford, 2004; Radford & Ridley, 2008).

Here, we investigated the function of close calls in meerkats, *Suricata suricatta*, a small carnivore that inhabits the semiarid region of the Kalahari Desert (Clutton-Brock et al., 1998; Clutton-Brock & Manser, 2016). Meerkats are cooperative breeders that live in groups of up to 50 individuals including a dominant breeding pair and subordinate helpers (Clutton-Brock et al., 2001, 2005; Doolan & Macdonald, 1999; Griffin et al., 2003). They have evolved a sophisticated communication system, relying heavily on vocal signals to keep track of their social and ecological environment (Manser, 1998). First, this can be attributed to meerkats inhabiting rather dense habitats, where visual contact between individuals can be easily obscured by vegetation such as scrub, tufts of grass or deadwood (Doolan & Macdonald, 1996). Second, meerkats constantly probe the substrate and dig in the soil for prey in a head-down position, so that any scans of the environment would involve costly interruptions of the foraging activity (Doolan & Macdonald, 1996). During the day, meerkat groups move progressively as a cohesive unit through their 0.85–5 km² territory while foraging, typically with a clear direction and at a constant pace, with individuals frequently transitioning between different positions and moving around within the group as it progresses (Bousquet et al., 2011; Doolan & Macdonald, 1996; Kranstauber et al., 2020).

Throughout foraging periods, all members of a group continuously produce close calls at varying call rates, with on average five to six calls/min and sometimes up to 20 calls and more (Mausbach et al., 2017; Wyman et al., 2017). Previous work has shown that subtle variation in the acoustic structure of close calls encodes finely graded contextual information (Reber et al., 2013; Townsend et al., 2011). For example, throughout foraging, meerkats produce short 'foraging close calls'. These continuously produced 'foraging close calls' can be replaced by a single, less frequently produced long 'guarding close call' when meerkats interrupt scrabbling activities for a brief bipedal guarding activity to scan the surroundings for predators (Townsend et al., 2011). Alternatively, 'foraging close calls' can be substituted by rarer broadband 'aggression close calls' which are occasionally produced upon too close approach of conspecifics, typically involving physical contact, while digging for or processing prey (Manser, 1998). Yet, the overall function of meerkat close calls and, specifically, the factors that underlie variation in close call rates have not been investigated systematically. Recent work suggests that during foraging movements meerkats tend to head towards the location with the highest close call production, that is, the 'moving vocal hotspot', an area where many individuals are close calling and/or where individuals call at higher rates (Gall & Manser, 2017). While close calls in meerkats appear to function to maintain group cohesion by guiding a group's movement via a vocal hotspot (Gall & Manser, 2017), how this newly described group level calling mechanism may emerge from more local differences in individual call rates is unclear. Here, we systematically investigated the spatial factors that affect individual close call rates in meerkats and how they emerge from attractive and/or repulsive interactions among calling group members. We further discuss how the resulting calling pattern may lead to the emergence of 'moving vocal hotspots'.

In line with previous work on other species (Boinski & Campbell, 1996; Boinski & Garber, 2000; Palombit, 1992; Radford & Ridley, 2008), and particularly work on meerkats (Gall & Manser, 2017), we predicted that meerkats adjust their individual calling rates in relation to their spatial position to other group members. Specifically, we predicted that meerkats call at higher rates when foraging at a closer distance to and when surrounded by

more conspecifics, such as at the middle part of a group's progression. As a consequence, higher calling rates should emerge at areas with a high density of conspecifics, which would ultimately enable other group members to orient themselves towards the emerging vocal hotspot and the central part of the group. To assess their spatial position to group members, meerkats might themselves attend to the neighbours' close calls rather than visually monitor their physical location. Particularly, considering that meerkats forage in a head-down position, often in dense habitat, and move dynamically around within the group, visual information is typically not easily accessible for meerkats, hence requiring vocal mechanisms to efficiently coordinate group activities and to maintain contact acoustically (Bousquet et al., 2011; Doolan & Macdonald, 1996; Manser, 1998). Accordingly, a meerkat might adjust its own call rate with respect to its own distance and arrangement to other group members, with its own position being assessed through the close call output of and vocal interactions with neighbouring individuals. In line with these predictions, playing back 'foraging close calls' of a group member should, in contrast to background noise, elicit a call response in test subjects. Moreover, if meerkats call at higher rates when foraging closer to neighbouring group members and in areas of higher individual density, then a higher call response might be elicited when (1) playing back 'foraging close calls' at higher rates (compared to low rates) simulating close group members, when (2) playing back 'foraging close calls' of several individuals, compared to one individual, and/or when (3) playing back 'foraging close calls' of several individuals from opposite sides of a test subject compared to playbacks from only one side.

While all these predictions fall in line with meerkats adjusting their individual calling rates according to their spatial proximity to group members, to disentangle whether on the local scale close calls attract or alternatively keep group members away we played back 'foraging close calls' from a stationary loudspeaker. In line with previous work experimentally demonstrating that meerkats follow the simulated close call hotspot (Gall & Manser, 2017), we predicted that 'foraging close calls' have an attracting effect on group members. However, the less frequent 'aggression close calls', produced by digging and food-processing individuals when other meerkats approach too close, might in fact serve to keep conspecifics away. Accordingly, playing back 'foraging close calls' should result in meerkats approaching the loudspeaker, and 'aggression close calls' should keep individuals away from the sound source. In addition, background noise should neither attract nor keep individuals away.

To empirically test our predictions, we conducted observations on naturally foraging meerkats and three different types of playback experiments (see Appendix Table A1 for an overview of the study design). Observations aimed to determine how a meerkat's spatial position (i.e. distance to group members and location within the group progression) affect close call rates. Experiment A investigated the effect of played back 'foraging close calls' of varying call rates and varying numbers of simulated callers on a test subject's close call rate. Experiment B investigated the effect of the arrangement of simulated callers (opposite sides versus same side) on a test subject's close call rate. Lastly, experiment C tested whether 'foraging close calls' (in comparison to 'aggression close calls' and background noise) attract or keep test subjects away.

METHODS

Study Site and Subjects

Behavioural observations and playback experiments were conducted between July 2010 and January 2011 on 10 groups of wild,

but habituated, meerkats at the Kalahari Meerkat Project, South Africa (see below and [Tables A1 and A2](#) for sample size structure; [Clutton-Brock et al., 1998](#); [Clutton-Brock & Manser, 2016](#)). The study population is part of a long-term project established in 1998, and meerkats are habituated to close observations by human observers enabling audio recordings and experiments within 1 m of the animal ([Clutton-Brock et al., 1998](#)). Each meerkat at the study site was identifiable through a transponder ID chip and individual dye marks ([Clutton-Brock et al., 2001](#)).

Behavioural Observations on Naturally Foraging Meerkats

Procedure and parameters

To investigate whether a meerkat's close call rate is affected by its distance to its closest neighbouring group member and its spatial location within the group progression, we conducted 5 min focal observations on individual meerkats during foraging. During the behavioural observations, we instantaneously recorded the close calls (irrespective of close call variant) a focal individual produced, as well as changes in its distance to the closest neighbour (0–1, 1–2, 2–5, 5–10 and > 10 m) and its spatial location within the moving group's progression (front, middle and last third; see [Fig. 1](#)). Since meerkats move around within the group during foraging, changes in the nearest-neighbour distance and location within the group are frequent. The observational data were directly entered into a handheld data logger (PSION Organizer II, Model LZ64). All observations were conducted by the same observer, providing consistent distance and location assessments across observations.

Test subjects and sample size structure

In each group, we conducted 5 min observations on each of a group's dominant male and female, one subordinate adult male and one subordinate adult female (age > 12 months), as well as one subadult male and one subadult female (age 6–12 months). However, in one of the 10 test groups no subordinate adult female was available, while in another group the subadult female was never foraging at a clear position within the group's progression resulting

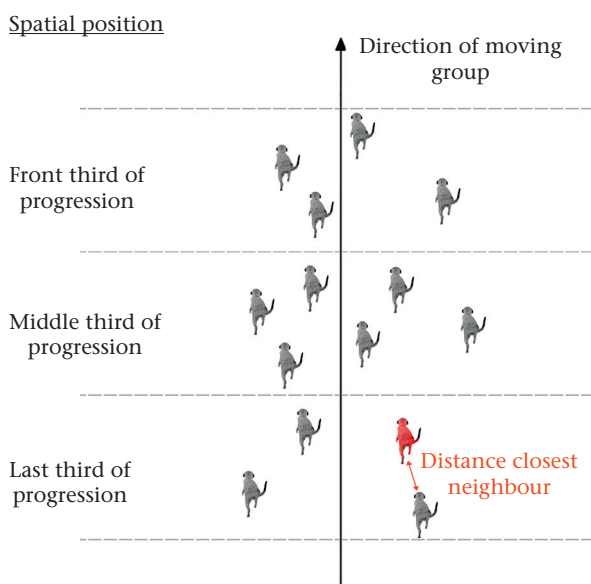


Figure 1. Spatial position of a foraging meerkat within the moving group. Schematic represents the partitioning of a subject's position within the moving group's progression into front, middle and last third. The red image represents a meerkat foraging in the last third of the progression, as well as the hypothetical distance to its closest neighbour. Group sizes during the study period ranged from 14 to 29 individuals (25% quantile = 19, 50% quantile = 23, 75% quantile = 26, $N = 10$).

in its exclusion from analysis due to ambiguity (in all other cases, location within the group's progression could be reliably assessed). We conducted two additional observations on a subordinate adult male and a subordinate adult female from two of the 10 test groups with the aim of balancing data collection with respect to the represented age categories. All individuals were observed only once, totalling 60 5 min observations from 60 individuals originating from 10 groups (see [Table A2](#)). Individuals belonging to the same group were observed in a randomized order in one morning, and with the earliest observation beginning 30 min after the group left the sleeping burrow and started foraging with a clear movement direction.

Playback Experiments: Stimuli and General Procedure

Playback stimuli

For the playback treatments, we recorded 'foraging close calls' and 'aggression close calls' from subordinate adult male meerkats (see [Fig. 2](#) for spectrograms of typical 'foraging' and 'aggression close calls'). In each test group, we recorded 'foraging close calls' of two subordinate adult male group members (for experiments A and B), and additional 'aggression close calls' from one of the recorded males (for experiment C). Calls of subordinate adult males were chosen, first, because this was the strongest represented social category during the study period, second, to avoid any conflicting factors that may arise when playing back vocalizations of potentially eviction-facing females, and third, to aim for consistency and to control for any further potential social- and age-related features encoded in the calls that could affect playback outcomes (e.g. vocalizations of dominant or subadult individuals could intensify or weaken observed behaviours, hence blurring responses). Calls were recorded at about 1 m (range 0.5–1.5 m) to the animal by using a Sennheiser directional microphone (ME66/K6) connected to a Marantz solid-state recorder (PMD660, sampling frequency 48 kHz, 16-bit accuracy). Playback tracks were created with CoolEdit 2000 1.1 (Syntrillium Software Corporation, Scottsdale, AZ, U.S.A.) selecting vocalizations with a high signal to noise ratio. For each of the 10 test groups, individual, group-specific tracks were created such that only calls of group members were played back.

Playback experiments and treatments

We conducted three different types of playback experiments (A–C), two composed of 'foraging close call' and background noise treatments (experiments A and B), and one of 'foraging close call', 'aggression close call' and background noise treatments (experiment C) (see below and [Table A1](#) for more details). For 'foraging' and 'aggression close call' treatments, each playback track was composed of at least six different 'foraging close calls', or 'aggression close calls' respectively, of one individual. The calls were repeated in a randomized order at equal time intervals with silence in between (for time intervals/broadcast call rates and playback

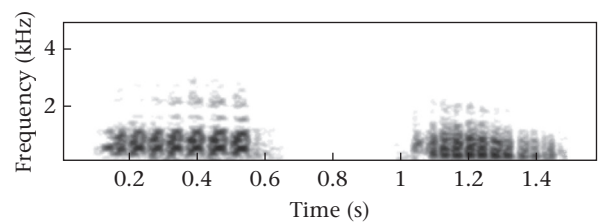


Figure 2. Spectrograms of a 'foraging close call' (left) and an 'aggression close call' (right) of a subordinate male meerkat used in the playback experiment. Spectrograms were drawn in a Hamming window (fast Fourier transformation, length 512, 75% overlap).

duration see details on experiments A–C below), and stimuli were normalized and played back at a naturally occurring amplitude using a portable loudspeaker suitable for broadcasting low-amplitude, close-range vocalizations (JBL On Tour; broadcast amplitude was adjusted by ear to fit the close call amplitude of group members). For the background noise treatments six different sound files were created by recording the background noise in the meerkats' natural habitat at the field site, while ensuring there were no conspicuous sounds such as singing or alarm-calling birds or artificial noises. The six background noise tracks were randomly assigned to the test subjects and had the same duration as the counterpart test treatments.

Test subjects/groups

All three types of playback experiments (A–C) were conducted once in the 10 test groups, and in each group a minimum of 1 week was left between different experiment types to avoid habituation of meerkats to the playback procedure. However, for each group, the single treatments of a given experiment type were conducted on the same day, broadcast in a randomized order, and with a break of at least 1 min between treatments (although in reality, the breaks between treatments were typically longer, on average 11 min, to ensure playback requirements were met at each playback onset, see below).

Response variables

During playbacks, a test subject's close call production (irrespective of close call variant) and the distance to its closest neighbour (0–1, 1–2, 2–5, 5–10 and > 10 m; experiments A and B) or its distance to the loudspeaker (experiment C) were documented and recorded with a digital video camera (JVC Everio GZMG150) or a digital compact camera (Canon PowerShot SX20 IS) by the same experimenter. Call production and distance changes were noted instantaneously as they occurred. Videos were coded afterwards using Quick Time Player (Apple Inc.).

Playback Experiment A: Effect of Call Rate and Number of Callers

Playback treatments

To test whether played back close calls elicit a close call response and whether a meerkat's close call rate is affected by the close call rate of neighbouring individuals and/or the number of neighbouring callers, the following four treatments were played back, each lasting 5 min. (1) To investigate whether close calls elicit a call response 'foraging close calls' of a single group member were played back with a low call rate of 4 calls/min. (2) As a control, background noise was broadcast. (3) To test whether the rate of played back close calls affects a test subject's close call rate, we played back 'foraging close calls' with a high call rate of 20 calls/min and compared the response to that elicited by the low-rate (4 calls/min) playback. The call rate of 4 against 20 calls/min was chosen to achieve an informative difference between call rates, yet reflecting the natural close call rate of subordinate adult male meerkats when the closest neighbour is foraging within 1–2 m based on the 5 min observations on the naturally foraging meerkats (close calls/min: range 0–22.5, 25% quantile = 4.7, 50% quantile = 5.3, 75% quantile = 10.6, $N = 10$). (4) To test whether the number of calling individuals affects a subject's close call rate, we played back 'foraging close calls' of two different individuals, each with a call rate of 10 calls/min (resulting in an overall call rate of 20 calls/min) and with the calls of the two broadcast individuals being alternated.

Test subjects and sample size structure

In each group ($N = 10$), the four playback treatments were conducted on one subordinate male individual using a within-

subject design. Playbacks were only conducted on subordinate male meerkats to warrant consistency among playback treatments and to control for age and social factors that could affect call rates and playback responses. Individuals were followed at 1–2 m with the loudspeaker attached to the experimenter's leg at the height of a foraging meerkat (5–10 cm above ground). To avoid interference with vocalizations produced by close-by group members playbacks were typically conducted when subjects were foraging at the edge of the group. This experimental approach, where calling individuals have been simulated next to test subjects despite the absence of close-by group members, has been used in earlier work on meerkats confirming that it does not confound playback manipulations since meerkats primarily rely on vocal rather than visual information (Gall & Manser, 2017; Manser, 1998; Reber et al., 2013; Townsend et al., 2011).

Playback Experiment B: Effect of Caller Spatial Arrangement

Playback treatments

To test whether the spatial arrangement to other calling group members influences a meerkat's close call rate, experiments simulating two calling individuals on one side versus two individuals on opposite sides of a test subject were conducted. The playbacks were carried out by two experimenters, each carrying a loudspeaker around the lower leg. Each experimenter played back 'foraging close calls' of either one of the two simulated group members, alternating the calls of the two broadcast individuals at equal time intervals. Calls of each simulated individual were played back at a rate of 6 calls/min and for 2 min. A constant distance of 2 m to the subject was maintained by following its movement. When calls were played back from the same side, the two experimenters were located side-by-side between the subject and the group centre. When playing back calls from opposite sides, one experimenter was positioned between the subject and the group's centre and the second experimenter opposite the subject but in line with the test subject and the first experimenter (Fig. 3).

Test subjects and sample size structure

In line with experiment A, playbacks were conducted when the test subject foraged in a more segregated part of the group, and in each test group ($N = 10$) both treatments were played back to one subordinate male individual using a within-subject design.

Playback Experiment C: Effect on Approach Behaviour

Playback treatments

To test whether 'foraging close calls' function either to attract or to maintain individual spacing between group members, 'foraging close calls' were broadcast from a stationary loudspeaker. As a

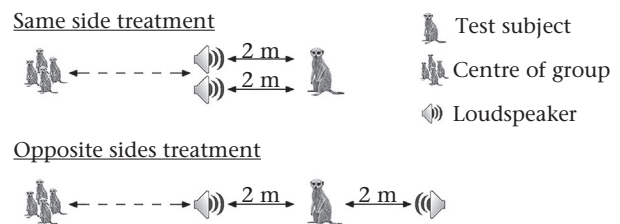


Figure 3. Set-up of experiment B. Close calls of two individuals were broadcast from two different loudspeakers. In the 'same side treatment' the two experimenters were positioned between the subject and the centre of the group. In the 'opposite sides treatment' one experimenter was positioned between the test subject and the centre of the group, and the second experimenter was on the opposite side of the subject and the first experimenter.

direct counterpart we played back 'aggression close calls' to serve as a negative stimulus presumed to keep individuals away from the sound source, and background noise to serve as a neutral control stimulus. Each of the three treatments lasted 2 min, and 'foraging close calls' or 'aggression close calls' were broadcast at a rate of 6 calls/min.

Test subjects and sample size structure

For each treatment in each test group ($N = 10$), the loudspeaker was placed 15 m in front of the group, ensuring that the group member whose calls were presented in the playback was not the one closest to the speaker. As soon as the first adult, irrespective of sex and dominance status due to limited controllability, was within 10 m of the loudspeaker the playback was started, and the proportion of time (during the 2 min playback) this individual spent within 2 m of the speaker was recorded.

Statistical Analysis of Observations during Natural Foraging

To investigate whether the distance to the closest neighbour and the location within the group's progression affected a meerkat's close call rate, as well as to test for a potential interaction effect, we assessed the number of close calls a focal individual produced during the time it spent at either of the 15 possible progression distance categories (i.e. front third and 0–1 m, front third and 1–2 m, front third and 2–5 m, front third and 5–10 m, front third and > 10 m, middle third and 0–1 m, middle third and 1–2 m, middle third and 2–5 m, middle third and 5–10 m, middle third and > 10 m, last third and 0–1 m, last third and 1–2 m, last third and 2–5 m, last third and 5–10 m, last third and > 10 m). During foraging, individuals frequently transitioned between different locations of the group (e.g. from the back to the middle third of the progression), combined with constant and rapid changes in closest-neighbour distances. Accordingly, multiple data points could exist for individual subjects, which represent call rates produced at different progression distance categories. Since these movement transitions could occur rapidly, and in line with previous work showing that meerkats produce a close call on average every 10–12 s (Mausbach et al., 2017; Wyman et al., 2017), we included intervals when individuals spent at least 12 s at a particular progression distance category. We fitted a generalized linear mixed model (GLMM) with a Poisson distribution and the number of close calls produced by a focal individual during the time it spent within a certain progression distance category as response variable. A focal individual's distance to its closest neighbour and its position within the group's progression, as well their interaction term, were fitted as explanatory variables. Individual identity nested within an individual's group affiliation and a focal individual's social category (dominant female, dominant male, subordinate adult female, subordinate adult male, subadult female, subadult male) were set as random terms. To account for differences in the time subjects spent in each of our predefined progression distance categories we fitted the logarithm of the duration as an offset term. Overdispersion due to an overrepresentation of periods with no call production was controlled for by adding an observation level random term (Bolker et al., 2009; Harrison, 2014). Potential multicollinearity among predictor variables was assessed using the *vif.mer* function designed for mixed-effects models and could be ruled out (Frank, 2011). All models were fitted using R (version 5.0.5) and the *lme4* package (Bates et al., 2014). Significances of fixed effects were assessed using likelihood ratio tests comparing the full model with the model without the factor of interest, and 95% confidence intervals were obtained through parametric bootstrapping with 500 iterations. To investigate the differences between factor levels, the 95% confidence intervals of the difference (bootstrapped with 500

iterations) were compared across the levels, with those not crossing zero representing significant contrasts between levels (Burnham & Anderson, 2002).

Statistical Analysis of Playback Experiments

To investigate differences in meerkats' responses to the different treatments in each of the three types of playback experiments, linear mixed-effect models (LMM) were fitted. Specifically, the following models were fitted. To investigate the effect of the treatment type in experiments A and B (explanatory variable) on a subject's close call rate (response variable), we calculated the close calls produced per min during the playback period (see below) and square-root transformed the response variable to achieve normality. A subject's identity was fitted as a random term to control for repeated measurements due to the within-subject design of the playbacks. To investigate the effect of the treatment type in experiment C (explanatory variable) on a subject's likelihood to approach the loudspeaker, we calculated the proportion of time the first approaching individual spent within 2 m of the loudspeaker during the playback period and square-root transformed the response variable to achieve normality. A subject's group identity was fitted as a random term to control for repeated measurements per group. Significances for treatment effects were assessed by conducting likelihood ratio tests comparing the full model with and without the treatment factor. To investigate the differences between playback treatments, the 95% confidence intervals of the difference (bootstrapped with 500 iterations) were compared between playback conditions, again, with those not crossing zero representing significant contrasts (Burnham & Anderson, 2002). Since playbacks A and B were conducted by following the focal individual from 1–2 m, only periods when no other neighbouring individuals were within 2 m of the test subject were included for the analyses, as otherwise the presence of closer group members might have falsified the playback results. To account for and outweigh the effect any other close-by group members might have had on the playback outcome, we calculated a test subject's close call rate separately during periods when another individual was at any of the remaining distance categories (2–5, 5–10 and > 10 m), and subsequently averaged them to receive the overall close call rate. Furthermore, although each playback experiment was conducted on 10 subjects, one test subject in the low-rate close call treatment of experiment A was never over 2 m from the closest neighbour resulting in a posterior exclusion and in a sample size of nine for that treatment.

Observer Biases

To rule out observer biases, a second observer blind-coded 50% of the videos of all experimental trials, which were randomly selected. Interobserver reliability tests showed a high level of agreement for close call rates (Spearman rank correlations: $r_s = 0.959$, $N = 30$, $P < 0.001$) over all experimental trials of experiments A and B, as well as for the time individuals spent within 2 m of the loudspeaker in experiment C (Spearman rank correlation: $r_s = 1$, $N = 15$, $P < 0.001$).

Ethical Note

The study was conducted under the permission of the ethical committee of the University of Pretoria and the Northern Cape Conservation, South Africa (EC011-10). We confirm that our research adheres to the ASAB/ABS guidelines for the use of animals in research, the legal requirements of South Africa as the country in which the work was carried out, and any other institutional

guidelines. Our observations and playback experiments on wild, naturally foraging meerkats had no impact on the animals' welfare or their environment, and no individuals were trapped or handled for the study.

RESULTS

Behavioural Observations on Naturally Foraging Meerkats

Close call rates were significantly affected by a meerkat's distance to the closest neighbour, but not by its relative location within the group's progression. There was no significant interaction between the two factors (GLMM: distance: $\chi^2_4 = 19.2$, $P < 0.001$; progression: $\chi^2_2 = 3.7$, $P = 0.155$; distance*progression: $\chi^2_8 = 11.1$, $P = 0.195$; $N = 246$ data points from 60 individuals of 10 groups; Fig. 4). Specifically, meerkats called at higher rates when foraging at a closer distance to the nearest group member. Albeit decreasing with increasing neighbour distance, at over 10 m to the closest neighbour call rates did not differ from those at any other distance categories (Fig. 4, Table A3).

Playback Experiment A: Effect of Call Rate and Number of Callers

The close call rate of test subjects differed when playing back background noise, a low rate or high rate of 'foraging close calls' of a single individual and 'foraging close calls' of two individuals equalling the high rate of a single individual (LMM, square-root transformation: treatment: $\chi^2_3 = 15.9$, $P = 0.001$, $N = 39$ data points from 10 individuals; Fig. 5). Post hoc comparisons of the 95% confidence intervals of the difference further revealed that, while subjects did not differ in their close call rates in response to 'foraging close calls' at a low rate or a high rate or to calls of two individuals, individuals produced more close calls in response to any of the three close call playback treatments compared to playbacks of background noise (Fig. 5, Table A4).

Playback Experiment B: Effect of Caller Spatial Arrangement

Test subjects called at higher rates when 'foraging close calls' of two individuals were played back from opposite sides of a subject compared to when these calls were played back from the same side (LMM, square-root transformation: treatment: $\chi^2_1 = 6.9$, $P = 0.009$, $N = 20$ data points from 10 individuals; Fig. 6, Table A4).

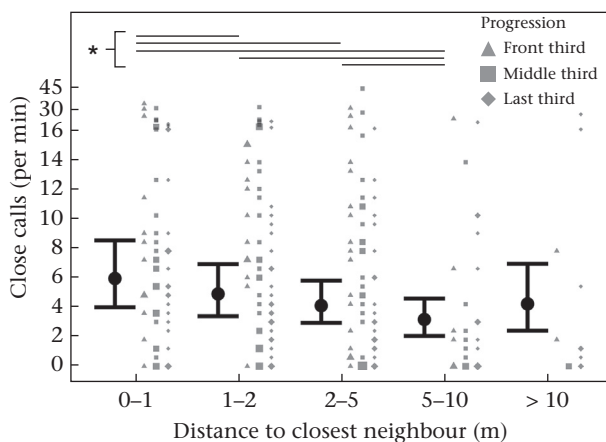


Figure 4. Effect of a meerkat's distance to the closest neighbour on its close call rate. Dark dots represent the means and bars the 95% confidence intervals of the back-transformed model estimates. Pale dots represent the raw data, with the size corresponding with the frequency of occurrence (largest equals a frequency of $N = 9$). Asterisk indicates significant contrast according to the 95% confidence intervals of the difference (see Table A3). For a better representation of the data the Y axis is squeezed above 16 calls/min.

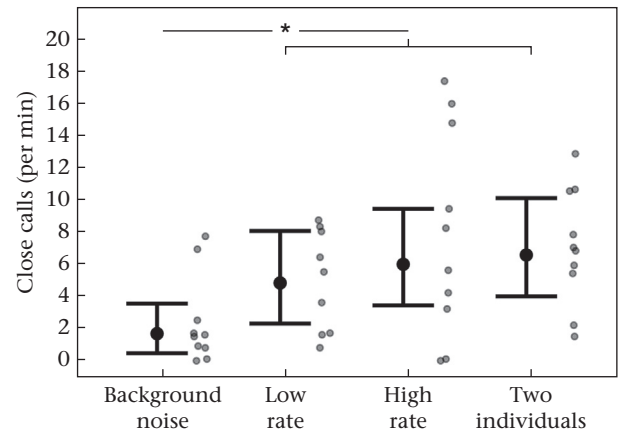


Figure 5. Effect of played back background noise and 'foraging close calls' of a single individual at a low or high rate, and of two individuals with the high rate of a single individual on a test subject's close call rate. Dark dots represent the means and bars the 95% confidence intervals of the back-transformed model estimates; pale dots represent the raw data. Asterisk indicates significant contrast according to the 95% confidence intervals of the difference (see Table A4).

Playback Experiment C: Effect on Approach Behaviour

When 'foraging close calls', 'aggression close calls' or background noise were played back from a stationary loudspeaker, test subjects spent different amounts of time within 2 m of the sound source (LMM, square-root transformation: treatment: $\chi^2_2 = 23.8$, $P < 0.001$, $N = 30$ data points from 10 groups; Fig. 7). Specifically, post hoc comparisons of the 95% confidence intervals of the difference revealed that subjects spent more time within 2 m of the loudspeaker in response to 'foraging close calls' than both 'aggression close calls' and background noise. No difference was found in how long subjects spent within 2 m of the loudspeaker in response to 'aggression close calls' and background noise playbacks (Fig. 7, Table A4).

DISCUSSION

Observations and playback experiments on free-ranging meerkats suggest that individuals attended to the continuously produced close calls of their group members and adjusted their own call rate depending on their proximity and spatial arrangement to

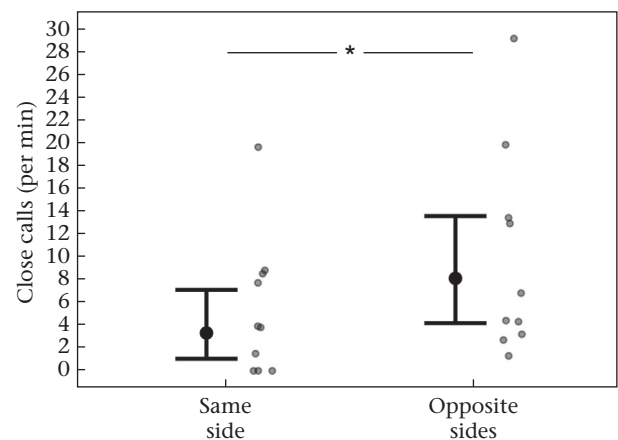


Figure 6. Effect of 'foraging close calls' played back from the same side and the opposite sides on a subject's close call rate. Dark dots represent the means and bars the 95% confidence intervals of the back-transformed model estimates; pale dots represent the raw data. Asterisk indicates significant contrast according to the 95% confidence intervals of the difference (see Table A4).

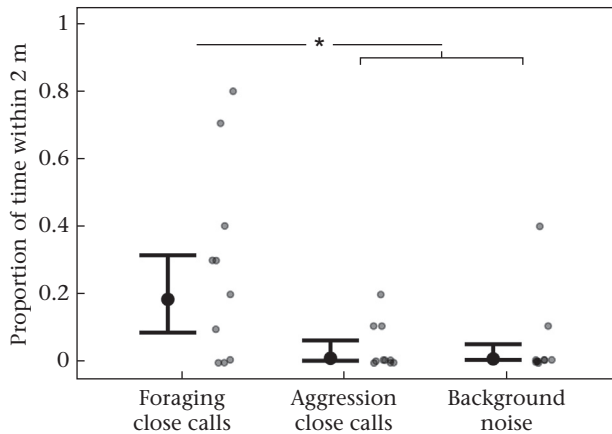


Figure 7. Proportion of time that subjects spent within 2 m of the loudspeaker in response to 'foraging close calls', 'aggression close calls' or background noise. Dark dots represent the means and bars the 95% confidence intervals of the back-transformed model estimates; pale dots represent the raw data. Asterisk indicates significant contrast according to the 95% confidence intervals of the difference (see [Table A4](#)).

neighbouring group members. Close call rates were higher when individuals were foraging at a closer distance to the nearest neighbour. Playing back 'foraging close calls', compared to background noise, elicited a close call response in test subjects, and call rates were higher when the simulated calling individuals were on opposite sides, rather than on one side, of the test subject. Furthermore, individuals spent more time within 2 m of a stationary loudspeaker in response to 'foraging close calls' compared to 'aggression close calls' or background noise. Playing back 'foraging close calls' with different call rates or of two compared to one individual did not affect test subjects' close call rate; neither did the location within the group's progression.

Our work supports the overall hypothesis that meerkat close calls serve to maintain cohesion among foraging group members. The variations in close call rates were found to have arisen primarily from spatially mediated interactions among calling neighbouring individuals. Specifically, our findings suggest that close calls overall elicit a call response in receivers, and that calling rates are affected by the spatial proximity and arrangement to group members, but not by a neighbour's close call rate or the number of calling neighbouring individuals. Accordingly, meerkats increased call rates when they were closer to or more surrounded by neighbours, that is, in meerkat-dense areas. The lack of an increase in call rate in response to high-rate close calls or more calling individuals, originally intended to simulate a closer distance to and higher density of conspecifics respectively, indicates that meerkats might assess the distance and arrangement to neighbouring group members more actively through distance-related spectral degradation and directionality of the calls, rather than simply through the neighbours' call rates.

In line with previous work indicating that meerkats follow the 'moving close call hotspot' ([Gall & Manser, 2017](#)), we further found that playing back 'foraging close calls' attracted meerkats to the sound source. Hence, 'foraging close calls' are attractive and serve to keep group members close by, rather than keeping them away. We did not find that meerkats spent less time within 2 m of the loudspeaker in response to 'aggression close calls' compared to background noise. Yet, we do not rule out that 'aggression close calls', which are typically produced when other group members approach too close, might still serve to repel conspecifics to avoid food competition. However, our playback was not suitable to test for this function. Of future interest might be how subtle variation encoded in different close call variants might affect individual spacing and a group's overall spatial organization. In further

support of an attractive function of 'foraging close calls', we also found that, albeit decreasing with increasing distance to the closest neighbour, call rates did not decrease further when individuals foraged more than 10 m away from the closest group member. This finding might suggest that besides being affected by spatial factors, close call rates might be increased particularly to attract group members to a certain area and/or to prevent group members from moving away, although further work is required to confirm this.

While we cannot disentangle with certainty whether increased close calling rates are primarily the result of increased proximity or alternatively whether increased proximity results from increased calling, our results are more suggestive of the former (although we do not rule out a fine interplay and interaction among both potential mechanisms). Specifically, if meerkats solely increased call rates to attract group members, a more dichotomous difference rather than a gradual variation in call rates should have been observed, and the location of simulated callers (or indeed close call playbacks overall) should not have affected subjects' call rates. In contrast, our work suggests that meerkats primarily adjust their close call rates with respect to their spatial proximity to neighbouring individuals, with spatial information being assessed via vocal interaction between callers. That is, close calls elicit a call response in receivers, so that both the caller and receivers receive information regarding their spatial distance and arrangement to each other. This information is likely to be deduced from call directionality and spectral call features and in turn affects an individual's own call rate. As a result, individual call rates increase in closer proximity to other group members, probably resulting in a calling pattern where high (total) call rates emerge in meerkat-dense areas, that is, when individuals cluster and forage closer together. In line with previous work on meerkat 'vocal hotspots' ([Gall & Manser, 2017](#)), individual call rate differences on the local scale might extrapolate to the group level where the emerging group level pattern can give rise to a close call hotspot that allows meerkats to orient their individual movements towards the central part of the group where most individuals are concentrated and calling. In a nutshell, spatially determined variations in individual call rates might generate a group level call pattern where group cohesion in foraging meerkat groups is maintained through attractive caller interactions that enable individuals to assess the group's spatial structure and monitor its 'moving vocal hotspot'. While here we applied observational and experimental tools to investigate how spatial factors affect meerkat close call rates, future modelling approaches and network analyses, tracking individual meerkats' movements and their call rates, could yield further detailed insights into the mechanisms underlying meerkat close calling. For example, agent-based modelling approaches could be applied to investigate how individual close call differences extrapolate to the group level and result in the manifestation of vocal hotspots and could help to disentangle how precisely differences in call rates affect an individual meerkat's, and the group's, overall movement and vice versa.

From a comparative perspective, our findings on meerkat close calling are in line with studies on other species where close calls, more broadly labelled 'contact calls', serve to maintain group cohesion, although our work also reveals intriguing differences. In other, particularly forest-living, species contact calls are typically only produced situationally when individuals initiate movements of, or risk separation from, the group ([Boinski & Garber, 2000](#)). Meerkats, on the other hand, produce close calls continuously, and it is the changes in call rates that encode spatial information. This difference might be due to the species' different locomotion styles. Specifically, while forest-living species (e.g. forest-living monkeys) move in a more saltatory fashion and dwell in places for longer ([Boinski & Garber, 2000](#)), meerkats continuously move amoeba-like through their territory during foraging periods. Hence, meerkats are likely to rely more strongly on constant vocal feedbacks provided through

continuously produced vocalizations, in turn giving rise to the so-called 'moving vocal hotspot'. Future work investigating contact calling patterns in species with similar foraging styles as meerkats might help to reveal how common this newly described call mechanism is. In this respect, a call system that resembles that of meerkats can be found in pied babblers, *Turdoides bicolor*, a cooperatively breeding bird that inhabits the same habitat as meerkats, feeds on similar prey and has similar socioecological characteristics (Clutton-Brock & Manser, 2016; Ridley, 2016). The major difference between the call systems of meerkats and pied babblers is that pied babbler close calls, on the local scale, act to repulse rather than to attract group members (Radford & Ridley, 2008). At this point, we can only speculate about the causes of this difference, although one explanation might be differences in the species' social tolerance/food sharing preferences or the presence/lack of further specified vocalizations. Yet, these similarities and differences in close call functions illustrate that there are still many open questions with respect to the factors that lead to the emergence of different calling strategies, and they highlight the need for future comparative research to deepen our knowledge on the mechanisms and characteristics of vocally mediated collective group activities in social animals.

Author Contributions

Sabrina Engesser: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing—Original draft, Writing—Reviewing & Editing, Visualization, Project administration. **Marta B. Manser:** Conceptualization, Methodology, Resources, Data Curation, Writing—Original draft, Writing—Reviewing & Editing, Supervision, Funding acquisition.

Data Availability

Data related to this work have been deposited on the Open Science Framework (<https://osf.io/v48dh/>; DOI 10.17605/OSF.IO/V48DH).

Acknowledgments

We thank T. Clutton-Brock, the Kalahari Research Trust, the families de Bruin and Kotze for access to land and logistics; the volunteers of the Kalahari Meerkat Project for maintaining habituation of the study population and collecting life history data; Elizabeth Wiley for assistance with playback experiments; Sandra Balmer for blind coding of the data; and Ramona Rauber, Ariana Strandburg-Peshkin and Vlad Demartsev for valuable comments and discussions. The study was financed by the University of Zurich, and the running costs of the long-term field site of the Kalahari Meerkat Project were covered by the Universities of Cambridge and Zurich. S.E. was further funded by the Swiss National Science Foundation (grant no. P400PB_183863).

References

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>

Boinski, S., & Campbell, A. F. (1996). The huh vocalization of white-faced capuchins: A spacing call disguised as a food call? *Ethology*, 102(10), 826–840. <https://doi.org/10.1111/j.1439-0310.1996.tb01204.x>

Boinski, S., & Garber, P. (2000). *On the move: How and why animals travel in groups*. The University of Chicago Press.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>

Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2011). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the*

Royal Society B: Biological Sciences, 278(1711), 1482–1488. <https://doi.org/10.1098/rspb.2010.1739>

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer.

Cheney, D. L., Seyfarth, R. M., & Palombit, R. (1996). The function and mechanisms underlying baboon 'contact' barks. *Animal Behaviour*, 52, 507–518. <https://doi.org/10.1006/Anbe.1996.0193>

Clutton-Brock, T. H., Brotherton, P. N. M., Russell, A. F., O'Riain, M. J., Gaynor, D., Kansky, R., et al. (2001). Cooperation, control, and concession in meerkat groups. *Science*, 291(5503), 478–481. <https://doi.org/10.1126/Science.291.5503.478>

Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A. D. C., McIlrath, G., Chadwick, P., et al. (1998). Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society B: Biological Sciences*, 265(1392), 185–190. <https://doi.org/10.1098/rspb.1998.0281>

Clutton-Brock, T. H., & Manser, M. (2016). Meerkats: Cooperative breeding in the Kalahari. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: studies in ecology, evolution and behavior* (pp. 294–317). Cambridge University Press.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., & Jordan, N. R. (2005). 'False feeding' and aggression in meerkat societies. *Animal Behaviour*, 69, 1273–1284. <https://doi.org/10.1016/j.anbehav.2004.10.006>

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, 433(7025), 513–516. <https://doi.org/10.1038/nature03236>

Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology*, 218(1), 1–11. <https://doi.org/10.1006/jtbi.2002.3065>

Doolan, S. P., & Macdonald, D. W. (1996). Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology*, 239, 697–716. <https://doi.org/10.1111/j.1469-7998.1996.tb05472.x>

Doolan, S. P., & Macdonald, D. W. (1999). Co-operative rearing by slender-tailed meerkats (*Suricata suricatta*) in the southern Kalahari. *Ethology*, 105(10), 851–866. <https://doi.org/10.1046/j.1439-0310.1999.00461.x>

Engesser, S., Ridley, A. R., & Townsend, S. W. (2017). Element repetition rates encode functionally distinct information in pied babbler 'clucks' and 'purrs'. *Animal Cognition*, 20(5), 953–960. <https://doi.org/10.1007/s10071-017-1114-6>

Fichtel, C., & Manser, M. B. (2010). Vocal communication in social groups. In P. Kappeler (Ed.), *Animal behaviour: Evolution & mechanisms* (pp. 29–54). Springer.

Frank, A. F. (2011). R-hacks/mer-utils.R. <https://github.com/auf frank/R-hacks/blob/master/mer-utils.R>. (Accessed 28 April 2021).

Gall, G. E. C., & Manser, M. B. (2017). Group cohesion in foraging meerkats: Follow the moving 'vocal hot spot'. *Royal Society Open Science*, 4(4), 170004. <https://doi.org/10.1098/rsos.170004>

Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., McIlrath, G., Gaynor, D., Kansky, R., et al. (2003). A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioral Ecology*, 14(4), 472–480. <https://doi.org/10.1093/Beheco/Arg040>

Harrison, X. A. (2014). Using observation-level random effects to model over-dispersion in count data in ecology and evolution. *PeerJ*, 2, Article e616. <https://doi.org/10.7717/peerj.616>

Hedwig, D., Mundry, R., Robbins, M. M., & Boesch, C. (2015). Audience effects, but not environmental influences, explain variation in gorilla close distance vocalizations—A test of the acoustic adaptation hypothesis. *American Journal of Primatology*, 77(12), 1239–1252. <https://doi.org/10.1002/ajp.22462>

Koda, H., Shimooka, Y., & Sugiura, H. (2008). Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (*Macaca fuscata*). *American Journal of Primatology*, 70(11), 1055–1063. <https://doi.org/10.1002/ajp.20597>

Kranstauber, B., Gall, G. E. C., Vink, T., Clutton-Brock, T., & Manser, M. B. (2020). Long-term movements and home-range changes: Rapid territory shifts in meerkats. *Journal of Animal Ecology*, 89(3), 772–783. <https://doi.org/10.1111/1365-2656.13129>

Manser, M. B. (1998). *The evolution of auditory communication in suricates, Suricata suricatta*. University of Cambridge. Ph.D. dissertation.

Mausbach, J., Braga Goncalves, I., Heistermann, M., Ganswindt, A., & Manser, M. B. (2017). Meerkat close calling patterns are linked to sex, social category, season and wind, but not fecal glucocorticoid metabolite concentrations. *PLoS One*, 12(5), Article e0175371. <https://doi.org/10.1371/journal.pone.0175371>

Neumann, C., & Zuberbühler, K. (2016). Vocal correlates of individual sooty mangabey travel speed and direction. *PeerJ*, 4, e2298. <https://doi.org/10.7717/peerj.2298>

Palombit, R. A. (1992). A preliminary study of vocal communication in wild long-tailed macaques (*Macaca fascicularis*). 2. Potential of calls to regulate intra-group spacing. *International Journal of Primatology*, 13(2), 183–207. <https://doi.org/10.1007/BF02547840>

Pfluger, F. J., & Fichtel, C. (2012). On the function of redfronted lemur's close calls. *Animal Cognition*, 15(5), 823–831. <https://doi.org/10.1007/s10071-012-0507-9>

Radford, A. N. (2004). Vocal mediation of foraging competition in the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*). *Behavioral Ecology and Sociobiology*, 56(3), 279–285. <https://doi.org/10.1007/s00265-004-0785-6>

Radford, A. N., & Ridley, A. R. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal Behaviour*, 75, 519–527. <https://doi.org/10.1016/j.anbehav.2007.05.016>

Reber, S. A., Townsend, S. W., & Manser, M. B. (2013). Social monitoring via close calls in meerkats. *Proceedings of the Royal Society B: Biological Sciences*, 280(1765), Article 20131013. <https://doi.org/10.1098/Rspb.2013.1013>

Ridley, A. R. (2016). Southern pied babblers: The dynamics of conflict and cooperation in a group-living society. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: studies in ecology, evolution and behavior* (pp. 115–132). Cambridge University Press.

Sperber, A. L., Werner, L. M., Kappeler, P. M., Fichtel, C., & Wright, J. (2017). Grunt to go-Vocal coordination of group movements in redfronted lemurs. *Ethology*, 123(12), 894–905. <https://doi.org/10.1111/eth.12663>

Townsend, S. W., Zöttl, M., & Manser, M. B. (2011). All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behavioral Ecology and Sociobiology*, 65(10), 1927–1934. <https://doi.org/10.1007/s00265-011-1202-6>

Uster, D., & Zuberbühler, K. (2001). The functional significance of diana monkeys 'clear' calls. *Behaviour*, 138(6), 741–756. <https://doi.org/10.1163/156853901752233389>

Walker, R. H., King, A. J., McNutt, J. W., & Jordan, N. R. (2017). Sneeze to leave: African wild dogs (*Lycan pictus*) use variable quorum thresholds facilitated by sneezes in collective decisions. *Proceedings of the Royal Society B: Biological Sciences*, 284(1862). <https://doi.org/10.1098/rspb.2017.0347>

Wyman, M. T., Rivers, P. R., Muller, C., Toni, P., & Manser, M. B. (2017). Adult meerkats modify close call rate in the presence of pups. *Current Zoology*, 63(3), 349–355. <https://doi.org/10.1093/cz/zox029>

Appendix

Table A1
Study design and statistical information

	Behavioural observations	Playback experiment A	Playback experiment B	Playback experiment C
Aim	Effect of distance to closest neighbouring individual and location within the group progression on focal individuals' close call rate	Effect of close calls, close call rate and number of simulated callers on test subjects' close call rate	Effect of spatial arrangement to simulated callers on test subjects' close call rate	Effect of played back close calls on test subjects' approach behaviour
Focal/test subject/s	In each of 10 groups: dominant female, dominant male, 1 subordinate adult female, 1 subordinate adult male, 1 subadult female, 1 subadult male (two exceptions, see text)	In each of 10 groups: 1 subordinate male (within-subject design)	In each of 10 groups: 1 subordinate male (within-subject design)	In each of 10 groups: first approaching individual, irrespective of social category (within-group design)
Procedure	Following subjects and documenting call production and changes in closest neighbour distance and location within group progression	Following subjects while broadcasting playbacks and documenting call production and changes in closest neighbour distance	Broadcasting playbacks from a stationary loudspeaker and documenting the duration the first approaching individual spent within 2 m to the loudspeaker	Broadcasting playbacks from a stationary loudspeaker and documenting the duration the first approaching individual spent within 2 m to the loudspeaker
Factor levels /playback treatments	Distance to closest neighbour: 0–1 m, 1–2 m, 2–5 m, 5–10 m, > 10 m Location within group progression: front third, middle third, last third	Background noise Low-rate foraging close calls High-rate foraging close calls Foraging close calls of 2 individuals	Foraging close calls of 2 individuals played back from one side of test subject Foraging close calls of 2 individuals played back from opposite sides of test subject	Background noise Foraging close calls Aggression close calls
Response variable	Number of close calls (count) produced when located at particular distance*progression category (see text) per time spent at that particular distance*progression category (time controlled for via offset term, resulting in close calls/min)	Call rate in close calls/min (calculated by dividing the number of calls produced per playback duration, but averaging call rates at different nearest-neighbour distances and excluding times when another individual was within 2 m)		Proportion of time within 2 m of the loudspeaker during playback period (calculated by dividing the duration within 2 m by the playback duration)
Explanatory variable/s	Distance to closest neighbour (5 levels) * Location within group progression (3 levels)	Treatment type (4 levels)	Treatment type (2 levels)	Treatment type (3 levels)
Random/control variable/s	Individual identity nested within group identity Social category (6 levels)	Individual identity	Individual identity	Group identity
Model	GLMM with Poisson distribution and observation time at distance*progression category as offset	LMM (square-root transformed response variable)	LMM (square-root transformed response variable)	LMM (square-root transformed response variable)

Table A2
Sample size structure of the behavioural observations and playback experiments

Group	Behavioural observations			Experiment A	Experiment B	Experiment C					
						Foraging close calls	Aggression close calls	Background noise			
AZ	VWF063	VVM032	VAZF018	VAZM021	VAZF007	VAZM006	VAZM013	VAZM013	VWF063	VVM032	VAZF015
D	VDF115	VDM108	VDF140	VDM141	VDF133	VDM134	VDM138	VDM136	VDM134	VDM108	VDM141
F	VFF138	VDM102	VFF165	VFM164	VFF144	VFM145	VFM163	VFM161	VFM127	VDM102	VDM102
JX	VLf102	VJXM005	VJXF022	VJXM023	VJXF017	VJXM016	VJXM014	VJXM015	VJXM016	VJXM023	VLf102
KU	VGGF014	VWM085	NA	VKUM029	VKUF020	VKUM023	VKUM021	VKUM026	VKUM016	VGGF014	VKUF028
L	VLf111	VWM120	VLf167	VLM166	VLf152	VLM153	VLM155	VLM153	VLM151	VGLM151	VLf164
SQ	VCDF002	VCBM001	VSQF017	VSQM015	VSQF005	VSQM007	VSQM018	VSQM018	VCDF002	VSQM007	VSQM015
TY	VWF106	VTYM003	VTYF030	VTYM028	VTYF020	VTYM021	VTYM025	VTYM027	VTYM011	VTYM011	VTYF024
VH	VWF093	VVHM001	VVHF029	VVHM028	NA	VVHM017	VVHM022	VVHM018	VVHM018	VWF093	VVHM019
W	VWF095	VLM114	VWF145	VVM143	VWF133	VVM131	VVM144	VVM132	VWF140	VWF140	VWF140
Social category	Dominant female	Dominant male	Subordinate adult female	Subordinate adult male	Subadult female	Subadult male	Subordinate adult male	Subordinate adult male	First individual approaching loudspeaker irrespective of social category		

Focal/test subject's group and identity codes and its social category are shown. In each of experiment A and B, treatments were conducted on the same individual per group.

Table A3

The 95% confidence intervals of the difference (CI) investigating differences in close call counts per observation time when focal individuals foraged at different closest-neighbour distances in the behavioural observations

Contrast	2.5% CI	97.5% CI
Behavioural observations: close call count (GLMM, Poisson distribution with offset term)		
Closest neighbour distance 0–1 m	–2.707	–1.952
Closest neighbour distance 0–1 m versus 1–2 m	–0.386	–0.008
Closest neighbour distance 0–1 m versus 2–5 m	–0.573	–0.175
Closest neighbour distance 0–1 m versus 5–10 m	–0.964	–0.283
Closest neighbour distance 0–1 m versus > 10 m	–0.814	0.050
Closest neighbour distance 1–2 m	–2.873	–2.162
Closest neighbour distance 1–2 m versus 0–1 m	0.007	0.391
Closest neighbour distance 1–2 m versus 2–5 m	–0.386	0.019
Closest neighbour distance 1–2 m versus 5–10 m	–0.741	–0.109
Closest neighbour distance 1–2 m versus > 10 m	–0.613	0.237
Closest neighbour distance 2–5 m	–3.015	–2.337
Closest neighbour distance 2–5 m versus 0–1 m	0.177	0.598
Closest neighbour distance 2–5 m versus 1–2 m	–0.010	0.375
Closest neighbour distance 2–5 m versus 5–10 m	–0.548	–0.009
Closest neighbour distance 2–5 m versus > 10 m	–0.413	0.447
Closest neighbour distance 5–10 m	–3.372	–2.573
Closest neighbour distance 5–10 m versus 0–1 m	0.323	0.940
Closest neighbour distance 5–10 m versus 1–2 m	0.142	0.769
Closest neighbour distance 5–10 m versus 2–5 m	0.007	0.570
Closest neighbour distance 5–10 m versus > 10 m	–0.221	0.769
Closest neighbour distance > 10 m	–3.213	–2.158
Closest neighbour distance > 10 m versus 0–1 m	–0.064	0.797
Closest neighbour distance > 10 m versus 1–2 m	–0.252	0.598
Closest neighbour distance > 10 m versus 2–5 m	–0.415	0.424
Closest neighbour distance > 10 m versus 5–10 m	–0.759	0.139

Each closest-neighbour distance category was levelled once and then compared with the remaining categories. CIs not crossing zero were classified as a significant contrast, with values in bold indicating significant differences between categories.

Table A4

The 95% confidence intervals of the difference (CI) investigating differences between the playback treatments in experiments A–C

Contrast	2.5% CI	97.5% CI
Experiment A: close calls/min (LMM, square-root transformed)		
Background noise	0.673	1.890
Background noise versus low rate	0.320	1.553
Background noise versus high rate	0.496	1.830
Background noise versus two individuals	0.719	1.862
Low rate	1.601	2.936
Low rate versus background noise	–1.548	–0.295
Low rate versus high rate	–0.329	0.834
Low rate versus two individuals	–0.256	0.995
High rate	1.881	3.051
High rate versus background noise	–1.799	–0.654
High rate versus low rate	–0.883	0.333
High rate versus two individuals	–0.446	0.716
Two individuals	1.994	3.190
Two individuals versus background noise	–1.872	–0.657
Two individuals versus low rate	–1.038	0.187
Two individuals versus high rate	–0.779	0.464
Experiment B: close calls/min (LMM, square-root transformed)		
Same side	0.979	2.654
Same side versus opposite sides	0.378	1.717
Opposite sides	1.983	3.714
Opposite sides versus same side	–1.696	–0.407
Experiment C: time proportion within 2 m (LMM, square-root transformed)		
Foraging close calls	0.291	0.557
Foraging close calls versus background noise calls	–0.448	–0.221
Foraging close calls versus aggression close calls	–0.434	–0.221
Aggression close calls	–0.043	0.227
Aggression close calls versus background noise calls	–0.115	0.107
Aggression close calls versus foraging close calls	0.219	0.447
Background noise	–0.038	0.234
Background noise versus foraging close calls	0.235	0.457
Background noise versus aggression close calls	–0.101	0.127

Each treatment was levelled once and then compared with the remaining treatments. CIs not crossing zero were classified as a significant contrast, with values in bold indicating significant differences between playback treatments.