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The role of neighbour proximity and context on meerkat close call acoustic structure

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In many animal species, including humans, producer arousal state is considered a key modifier of vocal production and structure. Encoding of affective arousal state in vocalizations provides a rapid means of information transfer about an individual's internal state, potentially reflecting its response to external stimuli. Meerkats, *Suricata suricatta*, are a highly vocal species. They use close calls to maintain group cohesion while foraging. Due to their patchily distributed prey, motivation for neighbour proximity varies; being too close results in competition (increased arousal–aggression), while too far results in risks of losing the group and predation threats (increased arousal–fear). We investigated how neighbour proximity and behavioural, social and environmental context influence the acoustic structure of wild meerkats' close calls. We found little effect of neighbour distance on the majority of the acoustic parameters measured, although close calls were longer and had a higher fundamental frequency when in very close proximity. However, there was a consistent effect of the behavioural context in which the call was given across several acoustic parameters. Overall, meerkat close calls potentially convey information on current behaviour, highlighting a potential mechanism in the diversification of acoustic signals.

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Expression of emotional states was one of the earliest hypotheses for the drivers of vocal production in nonhuman animals (Darwin, 1872). Despite decades of research, there is still a debate over whether animal vocalizations are simple expressions of internal state, or whether they convey meaning-like information (Marler et al., 1992; Rendall et al., 2009; Schamberg et al., 2018; Suzuki, 2016; Townsend & Manser, 2013). While our understanding of animals' use of vocalizations and repertoire diversity has developed considerably, showing context-related and goal-based vocal production (Manser, 2010; Schamberg et al., 2018), the evidence so far suggests that emotions do nevertheless play a primary role in vocal production (Briefer, 2012). In addition to potentially providing the mechanism behind the production of animal vocalizations, emotion-related acoustic variation within call types may also provide a means for call diversification and increased vocal repertoire (Filippi, 2016, 2020).

Morton's motivational–structural rules state that animal vocalizations vary along a spectrum that are similar across species,

from low-pitched, harsh sounds given in antagonistic contexts to high-pitched, tonal sounds produced in fearful or appeasing contexts (Morton, 1977). These rules have been extended, distinguishing between fearful high-frequency, tonal sounds and friendly soft, low-frequency sounds (August & Anderson, 1987). In addition, similarities between species in how emotions affect the structure of vocalizations have also been highlighted (Briefer, 2020). Animal emotions are typically described according to their two main dimensions, valence (positive–negative) and arousal (high–low; bodily activation) (Mendl et al., 2010), and, in particular, increases in arousal have been shown to lead to longer, louder and higher-frequency vocalizations across most vertebrates. Similarities between species in how valences are expressed are less clear, but vocalizations associated with positive valence often tend to be shorter and lower in fundamental frequency compared to those produced in negative contexts (Briefer, 2020). Motivation, while distinct from emotion in that it is related to physiological needs and 'wanting' states, varies along the same dimensions of arousal and valence as emotion in core-affect space (Mendl et al., 2010). The two states are therefore often inextricably linked, with vocalizations produced in a hostile context likely associated with a negative emotional state (Briefer, 2012). However, some

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vocalizations, such as distress calls, can have a negative emotional state but reflect the motivation to induce an approach reaction in listeners, making the integration of social and contextual information necessary to better understand the underlying internal state driving acoustic variation (Briefer, 2020). The patterns of emotional/motivational acoustic variation, while not entirely ubiquitous, are common in animal vocal production (Briefer, 2012). The encoding of emotions in animal vocalizations can, in turn, provide conspecifics with valuable information used to inform behavioural decisions (Rendall & Owren, 2010).

Maintaining proximity and cohesion as a foraging group is necessary to benefit from the advantages of group living, particularly in relation to reduced predation risk (Lehtonen & Jaatinen, 2016). Straying too far from the group may induce risks of separation from the group, but foraging too close to group members may result in competition and aggressive interactions (Hirsch, 2007). The spacing and movement of groups has been demonstrated to be governed by simple rules. Individual movement within a group is influenced by repulsion and attraction rules related to the spatial arrangement of group members (Couzin et al., 2002). First, individuals try to maintain a minimum distance between themselves and others, and second, if they are not too close, they are attracted towards other individuals, aligning their orientation with neighbours (Couzin et al., 2002). These rules are simple to follow when group members are clearly visible. However, when group members are not in sight, individuals have to use other cues (e.g. acoustic or olfactory) to assess distances and hence maintain group cohesion.

Vocalizations are a great means through which animals can signal and assess the location of conspecifics. They transmit through vegetated or nocturnal environments, where visual contact may be limited. Close calls, or contact calls, are commonly used vocalizations in group coordination across the animal kingdom (Kondo & Watanabe, 2009). Both the rate of contact calls and the acoustic structure of the vocalizations can be used in maintaining cohesion and minimum distances between group members. For example, nocturnal New Zealand bigeyes, *Pempheris adspersa*, increase their group cohesion and 'pop' vocalizations in response to playbacks of conspecific calls (Van Oosterom et al., 2016). Pied babblers, *Turdoides bicolor*, by contrast, increase their calling rate when foraging neighbours are closer, in order to maintain distance and reduce foraging competition (Radford & Ridley, 2008). The structure of red-tailed monkeys, *Cercopithecus ascanius*, contact calls changes depending on nearest-neighbour proximity, with decreasing mean entropy and fundamental frequency as neighbour distance increases (McLester, 2022). Contact calls advertise not only an individual's spatial location, but also individual identity (Carter & Wilkinson, 2016; Gillam & Chaverri, 2012; Sharpe et al., 2013), and current context (Koda et al., 2008; Ordóñez-Gómez et al., 2018; Rendall et al., 2000).

Meerkats, *Suricata suricatta*, produce close calls frequently while foraging, calling on average five to six times per minute, and up to 20 or more (Mausbach et al., 2017; Wyman et al., 2017). The use of close calls in maintaining cohesion are particularly valuable, as meerkats spend much of their time digging for food with their heads down (Doolan & Macdonald, 1996). The resulting limited vision during foraging, paired with seasonal bursts of high-density vegetation growth, reduces the ability of meerkats to assess group proximity visually (Doolan & Macdonald, 1996). Their contact calls convey information on individual identity, which receivers perceive and use to adjust their behaviour accordingly (Mausbach et al., 2017; Reber et al., 2013; Townsend, Allen, et al., 2011). Meerkats also adjust their close call production in relation to environmental conditions, increasing call rate during periods of drought (Toni et al., 2020), and depending on social conditions, reducing call rate when pups are

present (Wyman et al., 2017). Furthermore, meerkats use close calls to regulate spacing, as the rate of close call production is related to neighbour proximity, with higher calling rates when foraging closer to a neighbour (Engesser & Manser, 2022), and more movement towards locations of higher calling activity, so called 'vocal hot spots' (Gall & Manser, 2017). Together, these findings highlight meerkats' abilities to use acoustic assessment of proximity and identity, and their ability to communicate various levels of information within a single call type. However, previous work did not investigate whether the spectral and temporal features of the calls also varied in relation to neighbour proximity.

In this study, we investigated whether and how close call acoustic structure varies in relation to nearest-neighbour distance. We recorded meerkats vocalizations during foraging, their proximity to their nearest neighbour as well as the behavioural context. During foraging, meerkats produce close calls while performing a range of different behaviours including, scrabbling, digging, foraging, eating, moving and postvigilance (Fig. 1; for detailed descriptions see Table 1). Previous work has not considered such fine-scale categories between close calls' behavioural context. We predicted that close call acoustic structure would vary in line with Morton's motivational–structural rules (Morton, 1977); accordingly, calls given in close proximity should be lower in pitch (F0) and harsher due to increased aggressiveness related to risks of foraging competition, and calls given at intermediate or further distances should be slightly higher in pitch (F0), but more harmonic, acting affiliatively to maintain cohesion. In addition, we recorded nearest-neighbour identity to determine whether neighbour age or dominance status influenced the acoustic structure of close calls. We also recorded vegetation density to determine whether habitat visibility and transmission properties had an effect of vocal production, particularly as recent work has shown that meerkat vocalizations transmit with greater degradation in dense habitats (García Arasco et al., 2022).

METHODS

Ethical Note

The recordings were carried out following methodology approved by the ethical committee of University of Pretoria (NAS003/2022) and the Northern Cape Conservation Service, South Africa (FAUNA 0930/2022). Due to the long-term habituation of the meerkat population to recording, our observations had no impact on the meerkats' welfare or environment. We did not handle or trap any individuals as part of the study.

Study Site and Population

We collected data at the Kalahari Meerkat Project, Kuruman River Reserve, (26°59'S, 21°50'E) in South Africa (Clutton-Brock et al., 1998) between February and May 2022. For detailed description of the study site habitat and climate see Russell et al. (2002). All individuals in the study population were habituated to being followed and recorded at <1 m, and each individual was uniquely identifiable from RFID chips and dye mark combinations on their backs (Jordan et al., 2007). Detailed life history information was recorded for all individuals from the moment they entered the population, primarily at birth or at immigration. We recorded a total of 24 individuals from eight groups.

Data Collection

We recorded acoustic and behavioural data of subordinate adult (>1 year) meerkats during foraging, noting every time the focal

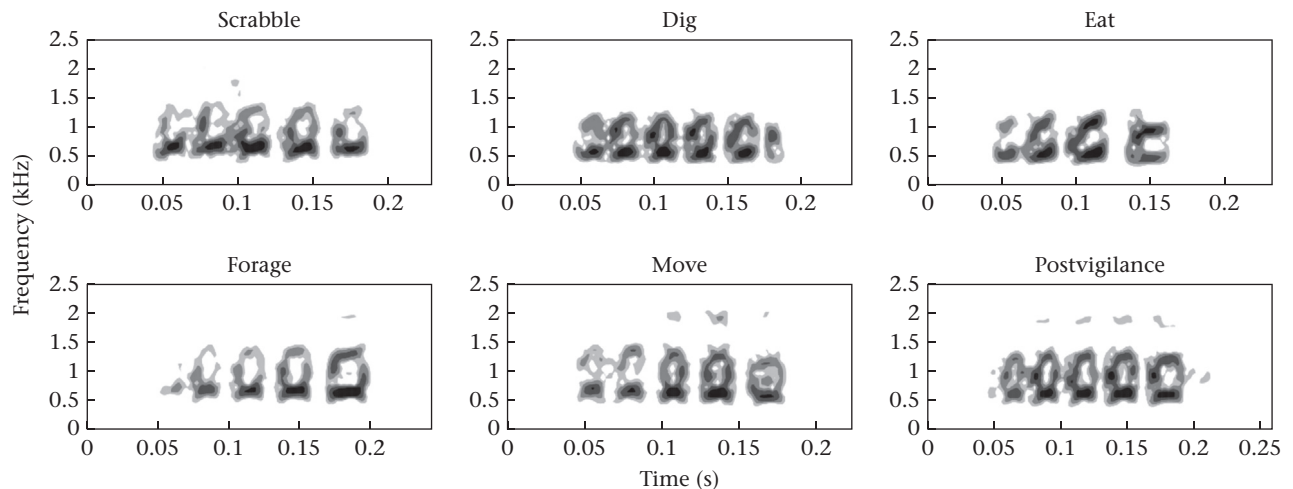


Figure 1. Spectrogram examples of close calls produced under different contexts.

Table 1
Detailed description of behavioural contexts

Behavioural context	Description
Digging	Digging, using both paws, with head and shoulders below the surface
Eating	Consuming a prey item
Foraging	Focused surface digging on a single patch for more than 2 s
Scrabbling	Walking and searching, periodically scratching the surface and with head moving from left to right
Moving	Walking while not scrabbling or displaying any foraging behaviour
Postvigilance	Given after a period of quadrupedal or bipedal vigilance, within 2 s of the end of vigilance

individual produced a close call, the context in which the call was given (see [Table 1](#) for detailed description), the distance to the nearest neighbour and the neighbour identity. Recordings were conducted during continuous periods of approximately 20 min (19.3 ± 4.3 min) per individual in a randomized order, with a minimum interval of 20 min between recordings of the same individual. Per morning foraging session, one to two recordings were collected per individual, over a total of 41 sessions. Individuals were recorded with a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.; sampling frequency 48 kHz, 16 bits accuracy). A wind-shield (Rainhardt, W200) was attached to the microphone to ensure good-quality recordings under variable wind conditions. We only recorded when wind conditions were good (low wind), which we assessed acoustically in the field by listening to recording quality, and aimed to have the microphone angle away from the wind and towards the focal meerkat to minimize wind effects on the recordings. To avoid disturbing the meerkats, the microphone was attached to a 1.5 m telescopic pole ensuring a distance of ca. 1 m between meerkat and observer but allowing for a recording distance of 0.3–1 m for a high signal-to-background ratio. Nearest-neighbour distance was determined by eye at 0.5 m intervals up to 2.5 m and if more than this at 1 m intervals up to 10 m. Prior to starting the study, observer distance training with a rangefinder was performed on static objects to ensure accuracy of distance measurement. It was not possible to use the rangefinder during the recordings due to the density of vegetation and rapid changes in position of the meerkats. The vegetation density (none, low, medium or dense) was recorded for the 3 m radius around the focal

individual, as an indicator of visibility and potential reduction in sound transmission. We also noted the distance between the microphone and the focal meerkat (0.3–1 m) and whether recordings took place from the front or back of the individual, to later adjust call amplitude based on microphone location. At the start and end of each recording, a calibration beep of 500 Hz was played at a distance of 1 m on the ground and the decibels recorded using a digital sound level meter (Voltcraft SL-100; Hirschau, Germany; accuracy: ± 2 dB, frequency measurement range 31.5 Hz–8 kHz) to control for differences in amplitude recorded related to environmental wind and background noise conditions between each recording.

Acoustic Analysis

Vocalizations were imported at a sampling rate of 48 kHz and saved in WAV format at 16-bit amplitude resolution. Each recording was manually annotated in Adobe Audition (Adobe Systems Inc., San Jose, CA, U.S.A.) for close calls and corresponding contextual information. Close calls were verbally indicated by the recording observer and confirmed visually by the spectrograms during annotation. Close calls were primarily given during scrabbling, foraging, digging, eating, postvigilance and moving (for detailed descriptions see [Table 1](#)). Each annotated close call was extracted from the recordings and Hann band-pass filtered between 0.05 and 12 kHz for analysis. We only included calls confirmed to be from the focal individual, as indicated verbally during data collection by the recording observer, and only calls with no overlap with other meerkat or bird calls. We extracted and analysed 2399 calls produced by 24 individuals (65–118 per individual) over 1893 min of recordings. We then extracted acoustic parameters in PRAAT ([Boersma & Weenink, 2023](#)) using a custom script for spectral and temporal analysis (adapted from [Briefer et al., 2019](#); [Charlton et al., 2009](#); [Reby & McComb, 2003](#); [Wyman et al. n.d.](#)); see [Table 2](#) for detailed description of variables analysed.

Before the beginning of the recording period, we collected additional close call recordings ($N = 360$) from other individuals ($N = 7$) with various microphone directions and distances. These recordings were used to calculate the average close call amplitude variation as a function of the microphone distance and direction. We then used the variation between these average values to adjust the calls used in the main analysis for microphone distance and direction. We also adjusted the analysed calls' amplitudes in relation to the recording conditions, using the amplitude difference

Table 2
Definitions of the acoustic parameters extracted

Extracted parameter	Units	Definition
sound_duration	(s)	Duration of a single call
f0_frames		Number of frames with F0
Mean_F0	(Hz)	Mean F0
SD_F0	(Hz)	Standard deviation of F0 points
F0_start	(Hz)	First F0 point (at the start of the call)
F0_end	(Hz)	Last F0 point (at the end of the call)
F0_tips	(Hz)	Difference between F0 at the start and end of the call (F0_Start – F0_End)
Max_F0	(Hz)	Maximum F0
Time_MaxF0	(s)	Time when Max_F0 occurs
RelDistMaxF0	%	Percentage of time through the call duration when Max_F0 occurs
Min_F0	(Hz)	Minimum F0
F0_Diff	(Hz)	Difference between maximum and minimum F0 (Max_F0 – Min_F0)
F0_abs_slope	(Hz/s)	Mean absolute slope of F0. Measure of average local variability of F0, i.e. frequency difference between F0 points; higher values indicate higher average frequency difference between points
F0_CV		Coefficients of F0 variation (F0_SD/F0_Mean)
infl_asc	(inflections/s)	Number of ascending inflection F0 points
infl_desc	(inflections/s)	Number of descending inflection F0 points
inflex		Number of ascending and descending F0 points divided by call duration ((infl_asc+infl_desc)/sound_duration); larger values indicate larger F0 variation across the call
sumvar	(Hz/s)	Absolute value of the sum of the difference between consecutive F0 points
variationtot	(Hz/s)	Sum of absolute difference in consecutive F0 points
Time_of_max_intensity	(s)	Time when maximum amplitude occurs
Time_of_max_intensity%	%	Percentage of time in call duration when maximum amplitude occurs
Q25_all	(Hz)	25% quantile of energy over the whole call. Measured from power spectrum, i.e. frequency below which 25% of energy found below this frequency point
Q50_all	(Hz)	Same as above, but for 50%
Fpeak_all	(Hz)	Peak frequency (frequency with the strongest amplitude) over the whole call, i.e. dominant frequency
Q25_maxAMP	(Hz)	25% quantile of energy at the point of maximum amplitude (0.01 s slice around maxAmp point)
Q50_maxAMP	(Hz)	Same as above but for 50%
harm	(dB)	Degree of acoustic periodicity, i.e. Harmonics to Noise Ratio; higher values indicate more harmonic (tonal), less noisy calls
jitter	%	Average absolute difference between the frequency of consecutive periods, divided by the average period, i.e. cycle to cycle variation in the frequency of F0
shimmer	%	Average absolute difference between the amplitude of consecutive periods, divided by average period, i.e. cycle to cycle variation in the amplitude of F0
AdjMinAmp	(dB)	Minimum amplitude of the call (adjusted for recording conditions and mic direction)
AdjMaxAmp	(dB)	Maximum amplitude of the call (adjusted for recording conditions and mic direction)
AdjMeanAmp	(dB)	Mean amplitude of the call (adjusted for recording conditions and mic direction)

calculated between the amplitude of the calibration beep in the recording and that detected by the digital sound level meter, to control for recording-level differences.

Statistical Analysis

We conducted a statistical analysis in RStudio (version 2022.07.1; R Core Team, 2023). We began by running a principal component analysis (PCA) to eliminate redundancy within our set of variables and determine which parameters accounted the most for the differences observed between calls (prcomp function, stats library; R Core Team, 2023). To check the prerequisites for a PCA, we ran a Kaiser–Meyer–Olkin test to determine sampling adequacy of the data (kmo_optimal_solution function, FactorAssumptions library; Storopoli, 2022), and removed highly correlated variables (>0.8; see Table A1 for retained variables). For the PCA, we scaled the variables and used an orthogonal rotation transformation. We used the ‘broken stick’ to determine the number of retained principal components (PC). The broken stick method selects PCs with observed variance (eigenvalue) greater than that of the total variance (sum of eigenvalues) when divided randomly among components, following a ‘broken stick distribution’ (King & Jackson, 1999; Peres-Neto et al., 2005). For those PCs with eigenvalues greater than that of the broken stick distribution, we built linear mixed models (LMMs; lmer function, lme4 library; Kuznetsova et al., 2016) with the PC scores as a response variable and the following fixed effects: nearest-neighbour distance (0–0.5, 1–2,

2–5, 6–9, 10+), behavioural context (scrabble, forage, dig, eat, move, postvigilance), nearest-neighbour age category (pup, juvenile, subadult, adult), nearest-neighbour dominance status (subordinate or dominant) and sex (male or female), group size and vegetation density (none, low, medium, dense). All fixed effects were categorical, except for group size which was continuous. Interactions were not included as they were causing the models to fail due to rank deficiency. Models contained individual ID nested within group ID as random effects, as previous work has confirmed individual and group signatures in meerkat close calls (Townsend, Allen, et al., 2011; Townsend et al., 2010). We checked model assumptions for normality and heteroscedasticity, by testing model residuals distribution (KS test), dispersion and outliers (testResiduals function, DHARMA library; Hartig, 2022). All models’ residuals best fitted a normal distribution and thus no transformation was necessary. An information theoretic (IT) approach was applied for model selection, using Akaike’s information criterion (AICc) to rank the models (model.sel function, MUMIn library; Bartoń, 2022) following the approach used by Richards et al. (2011). Models within AICc ≤ 4 of the model with the lowest AICc value formed the ‘top set’. If there was more than one model in the top set, we performed model averaging for parameter estimates (model.avg function, MUMIn library; Bartoń, 2022; Dormann et al., 2018; Grueber et al., 2011). Post hoc analyses were performed using estimated marginal means with Tukey HSD adjustments on the top models, to investigate the significance of the fixed-effects factor levels against zero (emmeans function, emmeans library; Lenth,

2023) and pairwise comparison (contrasts function, emmeans library; Lenth, 2023).

RESULTS

Parameters characterizing the mean and range of the fundamental frequency (F0) of close calls were affected by the context of production. Measures related to F0 mean and F0 range (maximum F0, start and end F0) loaded most highly on PC1, which accounted for 20.7% of variance in the close calls (Table A1). LMM analyses produced two models in the top set, PC1.6 (weight = 0.69) containing call context, and PC1.13 (weight = 0.18), containing call context and neighbour age (Table A2). Model averaging revealed that call context did have a significant effect on parameters related to F0 mean and range (Table A3). According to the loadings of parameters on PC1 (Table A1), this suggests that close call F0 mean and range were lowest for the behavioural contexts eating and digging (Eat: estimated marginal (EM) mean (SE) = -3.19 (0.24), 95% confidence interval, CI $(-3.67, -2.72)$, $P < 0.001$; Dig: EM mean (SE) = -1.33 (0.3), 95% CI $(-1.91, -0.75)$, $P < 0.001$; Table A3, Fig. 2a), and highest for scrabbling, postvigilance and moving contexts (Scrabble: EM mean (SE) = 0.56 (0.21), 95% CI $(0.14, 0.98)$,

$P = 0.009$; Postvigilance: EM mean (SE) = 1.57 (0.28), 95% CI $(1.01, 2.13)$, $P < 0.001$; Move: EM mean (SE) = 2.36 (0.43), 95% CI $(1.52, 3.2)$, $P < 0.001$; Table A3, Fig. 2a). The difference in PC1 scores (F0 mean and range) was significant between all but one pairwise comparison of call contexts, moving – postvigilance (Table A4). The age category of the nearest neighbour, however, did not have a significant effect on F0 mean and range (Table A3).

Similarly, parameters characterizing variance in f0 were affected by the call context. F0 variation measures (sum of variation between F0 points, mean absolute slope of F0 points, number of ascending F0 points) loaded most highly on PC2, which accounted for 15.9% of variance in close calls (Table A1). LMM analyses produced one model in the top set, PC2.2 (weight = 0.98), which included call context and neighbour distance (Table A5). The PC2 parameter loadings (Table A1) suggest that close call F0 variation was highest for the moving behavioural context (Move: EM mean (SE) = -1.25 (0.53), 95% CI $(-2.33, -0.17)$, $P = 0.024$; Table A6, Fig. 2b). Post hoc analyses showed significant differences in PC2 (F0 variance) for eight of 15 pairwise comparisons of call contexts, with a significant difference between the moving context and all others, apart from the digging context (Table A7). There was also a significant difference between scrabbling – eating, scrabbling –

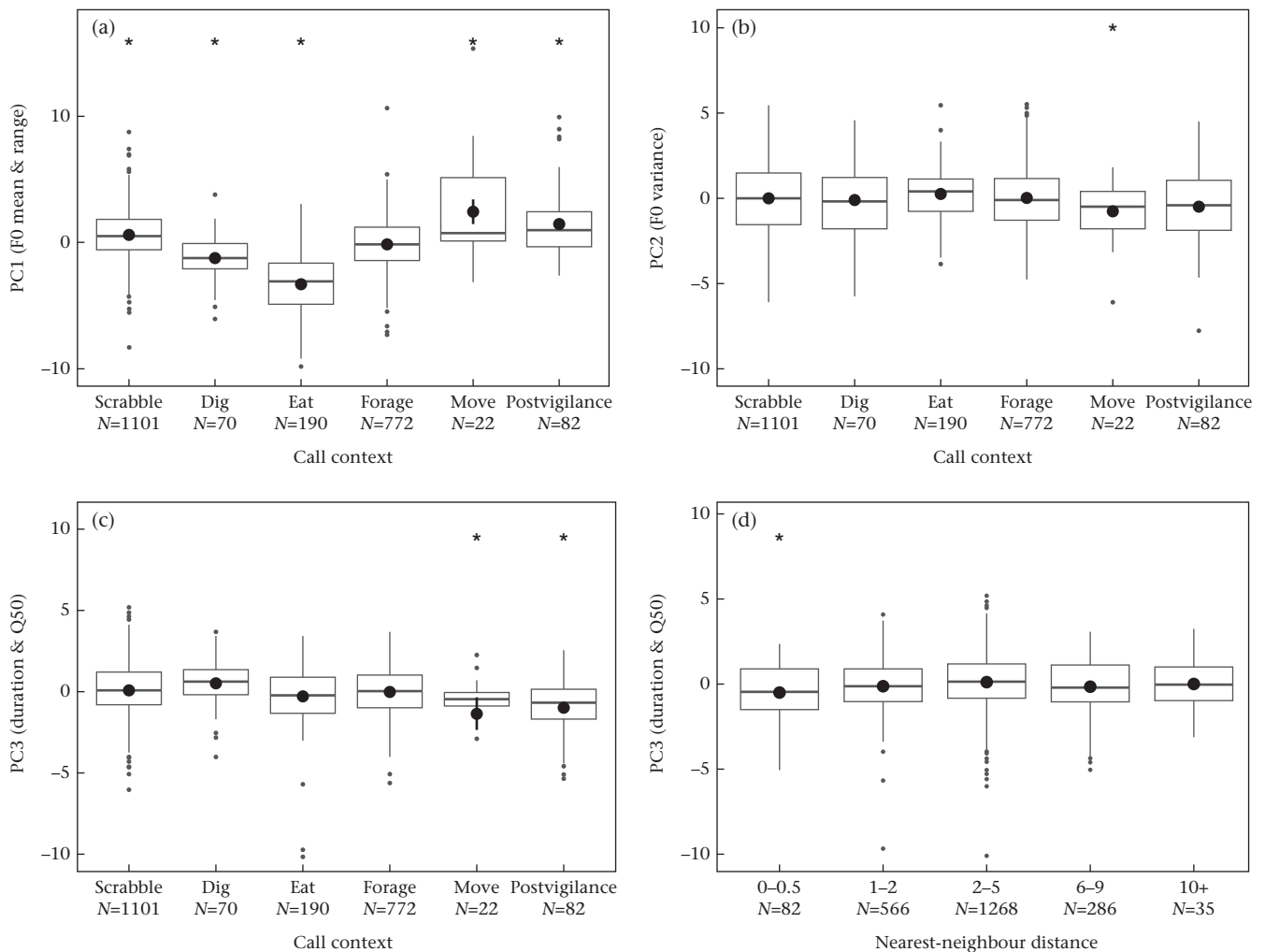


Figure 2. PC scores of close call acoustic parameters for (a) PC1, (b) PC2 and (c) PC3 influenced by call context (scrabble, dig, eat, forage, move and postvigilance) and for (d) PC3 influenced by nearest-neighbour distance. $P < 0.05$. Centre black horizontal line shows the median, boxes represent the interquartile range and whiskers extend to 1.5 times the interquartile range above the upper quartile or below the lower quartile. Small points indicate outliers and large black points show the mean with standard error bars.

postvigilance, eating – foraging and eating – postvigilance (Table A7). Distance to the nearest neighbour did not have a significant effect on F0 variation (Table A6).

Variance in call duration and centre of gravity, i.e. the frequency below which 50% of energy is distributed (Q50), was also mostly explained by the behavioural context and nearest-neighbour distance. Measures related to call duration and centre of gravity (Q50) loaded highly on PC3, which accounted for 10% of acoustic variation in close call structure (Table A1). LMM analyses produced one model in the top set PC3.2 (weight = 0.86), containing call context and neighbour distance (Table A8). Based on the parameter loadings on PC3 (Table A1), this indicates that close calls were longest and with highest centre of gravity in contexts of moving and postvigilance (Move: EM mean (SE) = -0.95 (0.40), 95% CI (-1.76 , -0.14), $P = 0.023$; Postvigilance: EM mean (SE) = 1.06 (0.32), 95% CI (-1.75 , -0.37), $P = 0.005$; Table A9, Fig. 2c), while the other call contexts did not have a significant effect. Pairwise comparisons of call contexts showed significant differences between postvigilance and all other contexts, apart from moving, as well as a significant difference between foraging and moving (Table A10). Additionally, close calls were longest and with highest centre of gravity when the nearest neighbour was within 0–0.5 m (EM mean (SE) = -0.73 (0.32), 95% CI (-1.42 , -0.04), $P = 0.039$; Table A9, Fig. 2d). Pairwise comparisons of neighbour distance categories showed significant differences between 0–0.05 and 1–2, between 1–2 and 6–9 and between 2–5 and 6–9 (Table A10).

There was no significant effect of any of the variables explored on PC4 and PC5 scores (PC4: Tables A11 and A12; PC5: Tables A13 and A14). Measures related to call duration and centre of gravity (Q50) loaded highly on PC4, which accounted for 9% of acoustic variance in close call structure (Table A1). Measures related to start F0, the difference between start and end F0 and time of maximum F0 loaded highly on PC5, which accounted for 7.7% of variation in close call acoustic structure (Table A1).

DISCUSSION

Meerkat close calls are used to maintain group cohesion and acoustically monitor the location of group members during foraging, and also convey information related to individual identity. In this study, we further investigated meerkat close calls' acoustic structure to find out whether it varies with proximity-based hostility, behavioural and social context. The results suggest that the primary driver explaining the observed variance in acoustic structure relates to the behavioural context of vocal production. We also found a limited effect of distance to the nearest neighbour on call duration and centre of gravity. Overall, the results suggest that even within apparent call types, contextual variation can result in consistent acoustic variation.

Most of the variance in meerkat close calls' structure was related to the behavioural context in which the call was given. Three of five PCs retained from the PCA were impacted by call context. Calls varied in measures related to mean F0, F0 variance, call duration and centre of gravity depending on the behavioural context. Close calls produced during digging and eating had lower F0 and less F0 variation, while calls produced when scrabbling had overall higher average F0 and F0 range. Close calls produced postvigilance and when moving had longer durations and a higher centre of gravity. Additionally, close calls given when moving had more F0 variation. Context-related acoustic differences within defined call types have been observed in several other species (Crockford & Boesch, 2003; Fischer et al., 2001; Ordóñez-Gómez et al., 2018; Rendall, 2003). For instance, the acoustic structure of the 'caw' call produced by crows varies between caws given in a food recruitment context and those given as alarm calls or rebuffering begging offspring (Anton Mates

et al., 2015). Contact call acoustic structure has also been shown to vary with valence, resulting in differences in receiver response between calls produced in positive or negative contexts (Baciadonna et al., 2019). However, most studies only report differences between two or three contexts and focus on different general behavioural contexts (e.g. hunting versus alarm; Fischer et al., 2001), rather than behavioural variation within a context category, as we did with foraging. Previous work on meerkats has shown that close calls produced following vigilance vary acoustically from other close calls (Townsend, Zöttl, et al., 2011). However, our study is the first to confirm variation in close call acoustic structure across multiple contexts. There was variation in close calls for six different behavioural contexts. Our findings suggest that context-related variation exists within meerkat close calls, resulting in potential subtypes of calls.

The differences we found in acoustic structure between call contexts may result from physical differences in body position at the time of production. For example, while digging, meerkats' heads are angled down in a hole while they rapidly move their upper body to dig; when scrabbling, meerkats' heads are directed slightly down while they extend their paws to scratch at the surface and search for food; when moving, meerkats' heads are positioned in line with their body as they move without attempting to forage; and when eating, meerkats call with food items in their mouth. The differences in body position and movement may alter the vocal tract shape and respiration rate, thus varying the acoustic structure of the sound produced (Briefer, 2012, 2020; Scherer, 2003; Vorperian et al., 2015). These changes can modify the structure of the signal and, as a result, influence how receivers perceive the information. Therefore, even if the differences in acoustic structure are only the result of posture and activity, and no other cognitive or physiological processes, this variation still provides important information to the receivers. Townsend, Zöttl, et al. (2011) showed that receivers reduce vigilance following playbacks of postvigilance close calls compared to foraging close calls. No effect of other close call variants on receivers have yet been investigated and require further experiments.

Alternatively, the callers' internal state may be what is driving the variation in acoustic structure in different behavioural context, for example excited in anticipation of food when digging. Emotional states are ultimately determined by the response to situations or stimuli that are rewarding and enhance fitness, or punishing and threaten fitness (Mendl et al., 2010). These emotional states may be the proximate mechanism resulting in different call variants being produced in different behavioural contexts (Owren & Rendall, 2001; Rendall et al., 2009; Seyfarth & Cheney, 2003; Wheeler & Fischer, 2012). In big brown bats, *Eptesicus fuscus*, different syllables are produced in different social contexts, corresponding to varying arousal levels measured by heart rate (Gadziola et al., 2012). To investigate whether the variation in acoustic structure is driven by emotion in meerkats, a direct measure of individual arousal, such as heart rate, would need to be taken to test whether arousal level is associated with different call structure.

Contrary to our predictions that the varying hostility levels related to neighbour proximity would influence close call acoustic structure, neighbour proximity only had a limited effect. Meerkat close calls were longer and with a higher frequency below which 50% of energy is found, suggesting higher frequency calls, when neighbours were close (<1 m). This limited effect could be due to vegetation density and wind conditions limiting the acoustic detection of neighbours. However, there was no statistical effect of vegetation density on close call structure, and recordings were only conducted in low wind conditions to ensure high-quality recordings for acoustic analysis. In addition previous work has shown

that meerkats do use close calls for cohesion (Engesser & Manser, 2022; Gall & Manser, 2017) and that meerkat close calls propagate up to 48 m without fully degrading (Garcia Arasco et al., 2022). Instead, the results suggest that there is some influence of proximity-driven arousal on acoustic structure. The findings are not consistent with Morton's hostility rule, that calls have lower F0 in antagonistic contexts (Morton, 1977). Rather, the increase in overall frequency supports the prediction that there is higher underlying emotional arousal when neighbours are nearby (Briefer, 2020), and the increased duration is suggestive of a negatively valenced emotional state (Briefer, 2012, 2020). In other species, proximity to group members was shown to influence call acoustic structure (McLester, 2022; O'Bryan et al., 2019; Ordóñez-Gómez et al., 2018; Sugiura, 2007). For example, female tree shrews, *Tupaia belangeri*, produce calls with a shorter intersyllable rate and increased fundamental frequency onset when close to males (Schehka et al., 2007). In addition, the use of close calls has been hypothesized to have evolved to mitigate foraging conflict by maintaining inter-individual spacing (Radford, 2004; Radford & Ridley, 2008). The limited effect of neighbour proximity on other acoustic parameters of meerkat close calls may be explained by the fact that neighbour proximity may not impact the arousal of the producer enough to be consistently reflected in variation in acoustic structure when taken across fine-scale contextual categories (Doolan & Macdonald, 1996). Direct competition is highest during focused digging for prey, where meerkats respond aggressively first with close calls before escalating to low growls and, in some cases, to physical contact (Flower, 2007). In our study, this context occurred much less frequently than the others, and the effect may not be strong enough to show up (Radford, 2004; Radford & Ridley, 2008). Furthermore, it may be that arousal in meerkat close calls is encoded via call rate. Increases in arousal are commonly associated with increasing call rate (Briefer, 2012; Gaub et al., 2016; Martin et al., 2022). It has already been demonstrated in meerkats that close call rate increases when neighbours are close (Engesser & Manser, 2022). We did not analyse call rate as part of this study as the detailed contextual data recorded meant that not every close call recorded could be confirmed as being produced by the focal meerkat. The time taken to visually identify the neighbouring meerkat meant that not all close calls were verbally annotated when given in close succession, which would thus not have provided an accurate representation of call rate. Encoding of arousal in call rate may hence provide a more reliable signal of proximity than the slight acoustic variation found in this study.

In this study, we were not able to test the specific effects of neighbour identity, affiliation and approach behaviour to the caller due to sample size of calls per neighbour identity and limited visibility of neighbour behaviour due to high seasonal grass. Social relationships between individuals have been shown to influence production and response to calls (Bouchard & Zuberbühler, 2022; Jenikejew et al., 2020; Leighty et al., 2008). For example, Vampire bats, *Desmodus rotundus*, are more attracted to the contact calls from frequent blood donors (Carter & Wilkinson, 2016). Future work could look at whether the affiliation between individuals and the behaviour (approaching or moving away) of the neighbour influences close call acoustic structure as well.

Our findings further expand our understanding of meerkat vocal diversity and complexity. Previous works have shown different receiver responses when played close calls recorded in two different contexts (Engesser & Manser, 2022; Townsend, Zöttl, et al., 2011). However, these are the first results in meerkats, and any other species to our knowledge, of fine-scale coding of so many behavioural variations within an apparent general context category (foraging) and call type. Further work would need to confirm through playback experiments whether receivers use the context-

based information contained in close calls to inform their responses. In addition, the results highlight that there can be predictable variation within a single call type, suggesting that studies that define vocal repertoires based on simple acoustic structure without considering context could result in overinflation of repertoire size. The contextual variation in close call acoustic structure provides the potential for specific information to be communicated between group members based on current activity. This degree of specificity in nonhuman animal communication has rarely been described. How and why animals communicate with such specificity can provide insight into possible selection pressures leading to distinct call categories, via vocal diversification, and increasing repertoire sizes. This additionally improves our understanding of the potential pressures leading to the emergence of precursors to human language. Living and moving in social groups while performing different behaviours may necessitate the communication of current activity to monitor not only group member location but also motivation to stay or move. Only by studying nonhuman animal communication with such fine-scale contextual information can we fully appreciate the complexity of their communication systems.

Author Contributions

I.D.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft. E.B.: Conceptualization, Methodology, Supervision, Writing—review & editing. M.M.: Conceptualization, Methodology, Project administration, Resources, Supervision, Writing—review & editing.

Data Availability

The data set used in this study is available at <https://doi.org/10.5061/dryad.rn8pk0pgs>.

Declaration of Interest

None.

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Appendix

Table A1

Loadings of extracted close call acoustic parameters on the principal components (PC1–PC5)

	PC1	PC2	PC3	PC4	PC5
Mean_F0	0.90	0.27	0.12	0.11	–0.02
Q25_all	0.83	0.10	–0.13	–0.20	0.11
Max_F0	0.82	–0.15	0.18	0.10	–0.07
F0_start	0.73	–0.05	0.01	0.03	–0.58
F0_end	0.66	0.28	0.34	–0.02	0.36
Q25_maxAMP	0.61	0.07	–0.23	–0.39	0.21
Jitter	–0.49	–0.49	–0.16	–0.24	0.08
Min_F0	0.46	0.63	–0.22	0.07	–0.06
Fpeak_all	0.40	–0.01	–0.17	–0.22	0.07
Harm	0.40	0.51	0.24	0.37	–0.01
variationtot	0.40	–0.78	0.11	0.17	0.14
SD_F0	0.36	–0.64	0.41	–0.06	–0.02
infl_asc	0.32	–0.70	–0.27	0.27	0.12
Q50_all	0.31	0.04	–0.52	–0.58	0.07
Q50_maxAMP	0.31	0.04	–0.53	–0.59	0.17
F0_abs_slope	0.30	–0.73	0.44	–0.15	0.12
sound_duration	0.23	–0.22	–0.53	0.61	0.12
shimmer	–0.23	–0.47	–0.15	–0.25	0.02
inflex	0.21	–0.68	0.03	–0.08	0.05
sumvar	–0.17	0.12	0.29	–0.17	0.26
AdjMaxAmp	0.14	–0.02	0.37	0.08	–0.09
F0_tips	0.12	–0.29	–0.28	0.04	–0.84
Time_of_max_intensity	0.11	–0.14	–0.52	0.58	0.06
AdjMinAmp	0.03	0.10	0.48	–0.24	–0.12
Time_MaxF0	0.00	0.01	–0.06	0.35	0.69
SD	2.28	2.00	1.58	1.50	1.39
Percentage of variance	20.7	15.9	10.0	9.0	7.7
Cumulative percentage	20.7	36.7	46.7	55.7	63.4

Top loading acoustic parameters (>0.5) are marked in bold.

Table A2

Model selection for the variables affecting PC1 scores, representing the acoustic variation in meerkat close calls

	(Intercept)	Fixed effects	df	LogLik	AICc	Delta	Weight
PC1.6	0.57	CallContext	9	-4445.53	8909.14	0.00	0.69
PC1.13	0.61	CallContext + NNAgeCat	12	-4443.85	8911.83	2.69	0.18
PC1.2	0.75	CallContext + NNDistCat	13	-4443.51	8913.19	4.05	0.09
PC1.5	0.57	CallContext + NNStatusSex	12	-4445.43	8915.00	5.86	0.04
PC1.12	0.13	Veg	7	-4816.57	9647.20	738.06	0.00
PC1.null	0.04		4	-4819.79	9647.60	738.46	0.00
PC1.11	0.79	NNAgeCat + GroupSize	8	-4816.34	9648.75	739.61	0.00
PC1.8	0.08	NNAgeCat	7	-4817.69	9649.44	740.30	0.00
PC1.10	0.06	NNDistCat + Veg	11	-4814.83	9651.79	742.65	0.00
PC1.7	0.08	NNStatusSex	7	-4819.09	9652.22	743.08	0.00
PC1.1	0.00	NNDistCat	8	-4818.14	9652.35	743.21	0.00
PC1.9	0.51	NNDistCat + GroupSize	9	-4817.40	9652.89	743.75	0.00
PC1.4	0.07	NNDistCat + NNAgeCat	11	-4816.28	9654.67	745.53	0.00
PC1.3	0.04	NNDistCat + NNStatusSex	11	-4817.46	9657.04	747.90	0.00

Variables included in models are nearest-neighbour distance category (NNDistCat), call behavioural context (CallContext), nearest-neighbour dominance status and sex (NNStatus), nearest-neighbour age category (NNAgeCat), group size (GroupSize) and vegetation density (Veg). Rows in bold indicate the models in the top set (delta <4). LogLik: log likelihood; AICc: Akaike information criterion corrected for small sample size; delta: Δ_{IC} ; weight: Akaike weights.

Table A3

Model averaged top set of models estimated marginal means summary for the variables affecting PC1 scores, representing the acoustic variation in meerkat close calls

Variable	Emmean	SE	df	Lower CL	Upper CL	t	P
EA	-3.19	0.24	2225.00	-3.67	-2.72	-13.08	<0.001
DI	-1.33	0.30	2225.00	-1.91	-0.75	-4.50	<0.001
FO	-0.09	0.22	2225.00	-0.51	0.34	-0.41	0.685
SC	0.56	0.21	2225.00	0.14	0.98	2.60	0.009
PV	1.57	0.28	2225.00	1.01	2.13	5.53	<0.001
MO	2.36	0.43	2225.00	1.52	3.20	5.50	<0.001
SA	-0.04	0.24	2225.00	-0.51	0.42	-0.18	0.857
Pup	-0.03	0.24	2225.00	-0.51	0.44	-0.14	0.888
JV	-0.01	0.23	2225.00	-0.45	0.44	-0.03	0.974
AD	0.00	0.22	2225.00	-0.43	0.43	0.00	0.999

Variables included are nearest-neighbour age category (SA: subadult; Pup: adult; JV: juvenile) and behavioural context (EA: eating; DI: digging; FO: foraging; SC: scabbling; PV: postvigilance; MO: moving). Bold *P* values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.

Table A4

Pairwise estimated marginal means comparison for the variables that had a significant effect in the top model for the variables affecting PC1 scores, representing the acoustic variation in meerkat close calls

Contrast	Estimate	SE	df	Lower CL	Upper CL	P
SC-DI	1.89	0.22	2225.00	1.27	2.51	<0.001
SC-EA	3.75	0.14	2225.00	3.36	4.15	<0.001
SC-FO	0.65	0.08	2225.00	0.41	0.88	<0.001
SC-MO	-1.80	0.38	2225.00	-2.88	-0.72	<0.001
SC-PV	-1.01	0.20	2225.00	-1.58	-0.44	<0.001
DI-EA	1.86	0.25	2225.00	1.15	2.57	<0.001
DI-FO	-1.24	0.22	2225.00	-1.88	-0.61	<0.001
DI-MO	-3.69	0.43	2225.00	-4.92	-2.46	<0.001
DI-PV	-2.90	0.29	2225.00	-3.73	-2.08	<0.001
EA-FO	-3.11	0.14	2225.00	-3.51	-2.70	<0.001
EA-MO	-5.55	0.40	2225.00	-6.68	-4.42	<0.001
EA-PV	-4.77	0.23	2225.00	-5.43	-4.11	<0.001
FO-MO	-2.44	0.38	2225.00	-3.53	-1.36	<0.001
FO-PV	-1.66	0.20	2225.00	-2.24	-1.08	<0.001
MO-PV	0.78	0.42	2225.00	-0.41	1.98	0.423

The variable is behavioural context (EA: eating; DI: digging; FO: foraging; SC: scabbling; PV: postvigilance; MO: moving). Bold *P* values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.

Table A5
Model selection for the variables affecting PC2 scores, representing the acoustic variation in meerkat close calls

	(Intercept)	Fixed effects	df	logLik	AICc	Delta	Weight
PC2.2	-0.26	CallContext + NNDistCat	13	-4298.48	8623.13	0.00	0.98
PC2.13	-0.14	CallContext + NNAgeCat	12	-4303.32	8630.78	7.65	0.02
PC2.6	-0.14	CallContext	9	-4309.99	8638.05	14.93	0.00
PC2.4	-0.23	NNDistCat + NNAgeCat	11	-4308.73	8639.57	16.44	0.00
PC2.5	-0.12	CallContext + NNStatusSex	12	-4308.41	8640.96	17.83	0.00
PC2.1	-0.19	NNDistCat	8	-4315.32	8646.70	23.57	0.00
PC2.9	-0.51	NNDistCat + GroupSize	9	-4314.93	8647.94	24.81	0.00
PC2.10	-0.11	NNDistCat + Veg	11	-4313.32	8648.76	25.64	0.00
PC2.3	-0.19	NNDistCat + NNStatusSex	11	-4314.03	8650.17	27.04	0.00
PC2.8	-0.09	NNAgeCat	7	-4321.15	8656.34	33.22	0.00
PC2.11	-0.58	NNAgeCat + GroupSize	8	-4320.28	8656.62	33.50	0.00
PC2.null	-0.09		4	-4328.29	8664.60	41.47	0.00
PC2.12	-0.02	Veg	7	-4325.88	8665.81	42.68	0.00
PC2.7	-0.07	NNStatusSex	7	-4326.63	8667.31	44.18	0.00

Variables included in models are nearest-neighbour distance category (NNDistCat), call behavioural context (CallContext), nearest-neighbour dominance status and sex (NNStatus), nearest-neighbour age category (NNAgeCat), group size (GroupSize) and vegetation density (Veg). Rows in bold indicate the models in the top set (delta <4). LogLik: log likelihood; AICc: Akaike information criterion corrected for small sample size; delta: Δ_{IC} ; weight: Akaike weights.

Table A6
Estimated marginal means model summary for the top model for the variables affecting the PC2 scores, representing the acoustic variation in meerkat close calls

Variable	Emmean	SE	df	Lower CL	Upper CL	t	P
10+	-0.83	0.49	23.52	-1.84	0.17	-1.71	0.100
6–9	-0.61	0.41	10.81	-1.51	0.28	-1.51	0.160
0–0.5	-0.42	0.44	14.64	-1.35	0.51	-0.96	0.355
2–5	-0.28	0.40	9.80	-1.18	0.61	-0.71	0.492
1–2	-0.08	0.40	10.23	-0.97	0.81	-0.20	0.846
MO	-1.25	0.53	34.05	-2.33	-0.17	-2.36	0.024
PV	-0.84	0.44	14.49	-1.77	0.09	-1.93	0.073
DI	-0.29	0.44	15.45	-1.23	0.65	-0.65	0.524
SC	-0.28	0.40	9.75	-1.17	0.61	-0.71	0.492
FO	-0.22	0.40	9.86	-1.11	0.68	-0.54	0.602
EA	0.21	0.41	11.50	-0.70	1.11	0.50	0.627

Variables included are nearest-neighbour distance (m; 0–0.5, 1–2, 2–5, 6–9, 10+) and behavioural context (EA: eating; DI: digging; FO: foraging; SC: scrabbling; PV: postvigilance; MO: moving). Bold *P* values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.

Table A7
Pairwise comparison for the variable that had a significant effect in the top model for the variables affecting the PC2 scores, representing the acoustic variation in meerkat close calls

Contrast	Estimate	SE	df	Lower CL	Upper CL	t
SC–DI	0.00	0.21	2228.64	-0.58	0.59	1.000
SC–EA	-0.49	0.13	2225.26	-0.86	-0.12	0.002
SC–FO	-0.07	0.08	2227.50	-0.29	0.16	0.953
SC–MO	0.97	0.36	2226.35	-0.05	1.98	0.071
SC–PV	0.56	0.19	2225.01	0.02	1.09	0.036
DI–EA	-0.49	0.23	2229.68	-1.16	0.17	0.284
DI–FO	-0.07	0.21	2229.35	-0.67	0.52	0.999
DI–MO	0.96	0.41	2227.31	-0.20	2.12	0.168
DI–PV	0.55	0.27	2227.87	-0.22	1.33	0.322
EA–FO	0.42	0.13	2224.43	0.04	0.80	0.020
EA–MO	1.46	0.37	2227.43	0.39	2.52	0.001
EA–PV	1.05	0.22	2225.07	0.43	1.67	<0.001
FO–MO	1.04	0.36	2226.99	0.02	2.06	0.044
FO–PV	0.63	0.19	2226.81	0.08	1.17	0.014
MO–PV	-0.41	0.40	2226.09	-1.54	0.72	0.905

The variable is behavioural context (EA: eating; DI: digging; FO: foraging; SC: scrabbling; PV: postvigilance; MO: moving). Bold *P* values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.

Table A8

Model selection for the variables affecting PC3 scores, representing the acoustic variation in meerkat close calls

	(Intercept)	Fixed effects	df	logLik	AICc	Delta	Weight
PC3.2	-0.42	CallContext + NNDistCat	13	-3746.42	7519.00	0.00	0.86
PC3.13	0.03	CallContext + NNAgeCat	12	-3749.63	7523.39	4.39	0.10
PC3.5	0.31	CallContext + NNStatusSex	12	-3750.31	7524.77	5.76	0.05
PC3.6	0.01	CallContext	9	-3757.34	7532.75	13.75	0.00
PC3.3	-0.05	NNDistCat + NNStatusSex	11	-3770.43	7562.98	43.98	0.00
PC3.4	-0.30	NNDistCat + NNAgeCat	11	-3771.94	7566.00	46.99	0.00
PC3.9	-1.07	NNDistCat + GroupSize	9	-3774.59	7567.26	48.25	0.00
PC3.7	0.29	NNStatusSex	7	-3778.49	7571.03	52.02	0.00
PC3.1	-0.37	NNDistCat	8	-3777.63	7571.32	52.32	0.00
PC3.11	-0.48	NNAgeCat + GroupSize	8	-3778.33	7572.72	53.72	0.00
PC3.8	-0.01	NNAgeCat	7	-3779.65	7573.35	54.34	0.00
PC3.10	-0.34	NNDistCat + Veg	11	-3776.54	7575.21	56.20	0.00
PC3.null	-0.03		4	-3785.83	7579.67	60.66	0.00
PC3.12	-0.02	Veg	7	-3784.27	7582.58	63.58	0.00

Variables included in models are nearest-neighbour distance category (NNDistCat), call behavioural context (CallContext), nearest-neighbour dominance status and sex (NNStatus), nearest-neighbour age category (NNAgeCat), group size (GroupSize) and vegetation density (Veg). Rows in bold indicate the models in the top set (delta <4). LogLik: log likelihood; AICc: Akaike information criterion corrected for small sample size; delta: Δ_{IC} ; weight: Akaike weights.

Table A9

Estimated marginal means model summary for the top model for the variables affecting the PC3 scores, representing the acoustic variation in meerkat close calls

Variable	Emmean	SE	df	Lower CL	Upper CL	t	P
0–0.5	-0.73	0.32	15.65	-1.42	-0.04	-2.26	0.039
6–9	-0.46	0.30	11.16	-1.12	0.20	-1.52	0.155
1–2	-0.41	0.30	10.49	-1.06	0.25	-1.38	0.197
10+	-0.25	0.37	26.29	-1.00	0.50	-0.68	0.500
2–5	-0.22	0.29	9.98	-0.87	0.43	-0.75	0.473
PV	-1.06	0.32	15.47	-1.75	-0.37	-3.28	0.005
MO	-0.95	0.40	39.11	-1.76	-0.14	-2.37	0.023
EA	-0.31	0.31	11.97	-0.98	0.35	-1.02	0.328
SC	-0.10	0.29	9.93	-0.75	0.55	-0.33	0.745
DI	-0.06	0.33	16.61	-0.75	0.64	-0.17	0.867
FO	-0.01	0.29	10.06	-0.66	0.65	-0.02	0.985

Variables included are nearest-neighbour distance (m; 0–0.5, 1–2, 2–5, 6–9, 10+) and behavioural context (EA: eating; DI: digging; FO: foraging; SC: scrabbling; PV: postvigilance; MO: moving). Bold *P* values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.

Table A10

Pairwise comparison for the variable that had a significant effect in the top model for the variables affecting the PC3 scores, representing the acoustic variation in meerkat close calls

Contrast	Estimate	SE	df	Lower CL	Upper CL	t
SC–DI	-0.04	0.18	3267.22	-0.55	0.46	1.000
SC–EA	0.21	0.11	3261.04	-0.10	0.53	0.394
SC–FO	-0.09	0.07	3265.05	-0.29	0.10	0.752
SC–MO	0.85	0.31	3263.01	-0.02	1.72	0.061
SC–PV	0.96	0.16	3260.63	0.50	1.42	<0.001
DI–EA	0.26	0.20	3269.20	-0.32	0.83	0.804
DI–FO	-0.05	0.18	3268.52	-0.56	0.46	1.000
DI–MO	0.89	0.35	3264.73	-0.11	1.89	0.110
DI–PV	1.00	0.23	3265.73	0.34	1.67	<0.001
EA–FO	-0.31	0.11	3259.62	-0.63	0.02	0.082
EA–MO	0.64	0.32	3264.99	-0.28	1.55	0.350
EA–PV	0.75	0.19	3260.74	0.22	1.28	0.001
FO–MO	0.94	0.31	3264.20	0.07	1.82	0.027
FO–PV	1.05	0.17	3263.87	0.58	1.53	<0.001
MO–PV	0.11	0.34	3262.56	-0.86	1.08	0.999
(0–0.5)–(1–2)	-0.32	0.15	2224.43	-0.74	0.09	0.206
(0–0.5)–(2–5)	-0.51	0.15	2225.78	-0.92	-0.11	0.005
(0–0.5)–(6–9)	-0.27	0.16	2228.33	-0.72	0.17	0.449
(0–0.5)–(10+)	-0.48	0.26	2229.20	-1.20	0.23	0.353
(1–2)–(2–5)	-0.19	0.07	2230.96	-0.37	-0.01	0.036
(1–2)–(6–9)	0.05	0.10	2235.31	-0.21	0.31	0.986
(1–2)–(10+)	-0.16	0.23	2230.97	-0.78	0.46	0.957
(2–5)–(6–9)	0.24	0.08	2230.00	0.01	0.47	0.040
(2–5)–(10+)	0.03	0.22	2230.19	-0.58	0.64	1.000
(6–9)–(10+)	-0.21	0.23	2228.24	-0.84	0.42	0.898

The variables are behavioural context (EA: eating; DI: digging; FO: foraging; SC: scrabbling; PV: postvigilance; MO: moving) and nearest-neighbour distance (m; 0–0.5, 1–2, 2–5, 6–9, 10+). Bold *P* values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.

Table A11

Model selection for the variables affecting PC4 scores, representing the acoustic variation in meerkat close calls

	(Intercept)	Fixed effects	df	logLik	AICc	Delta	Weight
PC4.13	0.11	CallContext + NNAgeCat	12	-3679.28	7382.70	0.00	0.97
PC4.6	0.11	CallContext	9	-3686.09	7390.27	7.57	0.02
PC4.5	0.18	CallContext + NNStatusSex	12	-3685.08	7394.31	11.61	0.00
PC4.2	0.09	CallContext + NNDistCat	13	-3685.51	7397.18	14.48	0.00
PC4.11	0.48	NNAgeCat + GroupSize	8	-3725.50	7467.06	84.36	0.00
PC4.8	0.04	NNAgeCat	7	-3726.68	7467.41	84.71	0.00
PC4.4	-0.07	NNDistCat + NNAgeCat	11	-3725.58	7473.27	90.57	0.00
PC4.null	0.04		4	-3732.70	7473.42	90.72	0.00
PC4.12	-0.05	Veg	7	-3729.75	7473.54	90.84	0.00
PC4.7	0.09	NNStatusSex	7	-3732.10	7478.26	95.56	0.00
PC4.1	-0.06	NNDistCat	8	-3731.66	7479.38	96.68	0.00
PC4.10	-0.15	NNDistCat + Veg	11	-3728.74	7479.59	96.89	0.00
PC4.9	0.27	NNDistCat + GroupSize	9	-3730.95	7479.99	97.29	0.00
PC4.3	0.00	NNDistCat + NNStatusSex	11	-3731.09	7484.29	101.59	0.00

Variables included in models are nearest-neighbour distance category (NNDistCat), call behavioural context (CallContext), nearest-neighbour dominance status and sex (NNStatus), nearest-neighbour age category (NNAgeCat), group size (GroupSize) and vegetation density (Veg). Rows in bold indicate the models in the top set (delta <4). LogLik: log likelihood; AICc: Akaike information criterion corrected for small sample size; delta: Δ_{IC} ; weight: Akaike weights.

Table A12

Estimated marginal means model summary for the top model for the variables affecting the PC4 scores, representing the acoustic variation in meerkat close calls

Variable	Emmean	SE	df	Lower CL	Upper CL	t	P
Pup	-0.21	0.29	17.28	-0.83	0.41	-0.72	0.483
JV	0.14	0.27	11.92	-0.45	0.73	0.52	0.615
AD	0.19	0.26	10.12	-0.39	0.77	0.74	0.476
SA	0.38	0.27	12.09	-0.21	0.96	1.40	0.188
FO	-0.34	0.26	9.94	-0.92	0.24	-1.32	0.216
MO	-0.31	0.37	47.15	-1.05	0.43	-0.84	0.407
SC	0.04	0.26	9.76	-0.53	0.62	0.17	0.869
EA	0.35	0.27	12.23	-0.24	0.94	1.30	0.218
PV	0.47	0.29	16.63	-0.14	1.08	1.62	0.125
DI	0.53	0.29	17.89	-0.08	1.15	1.82	0.086

Variables included are nearest-neighbour age category (pup; JV: juvenile; SA: subadult; AD adult) and behavioural context (EA: eating; DI: digging; FO: foraging; SC: scurrying; PV: postvigilance; MO: moving). Bold P values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.

Table A13

Model selection for the variables affecting PC5 scores, representing the acoustic variation in meerkat close calls

	(Intercept)	Fixed effects	df	logLik	AICc	Delta	Weight
PC5.2	-0.60	CallContext + NNDistCat	13	-3828.76	7683.69	0.00	0.49
PC5.4	-0.46	NNDistCat + NNAgeCat	11	-3831.49	7685.10	1.41	0.24
PC5.13	-0.09	CallContext + NNAgeCat	12	-3831.17	7686.48	2.80	0.12
PC5.6	-0.11	CallContext	9	-3835.50	7689.08	5.39	0.03
PC5.1	-0.46	NNDistCat	8	-3836.62	7689.31	5.62	0.03
PC5.8	0.00	NNAgeCat	7	-3837.73	7689.50	5.82	0.03
PC5.9	-0.11	NNDistCat + GroupSize	9	-3835.79	7689.66	5.98	0.02
PC5.11	0.25	NNAgeCat + GroupSize	8	-3837.32	7690.70	7.02	0.01
PC5.3	-0.51	NNDistCat + NNStatusSex	11	-3834.85	7691.82	8.13	0.01
PC5.5	-0.14	CallContext + NNStatusSex	12	-3834.05	7692.23	8.55	0.01
PC5.null	-0.02		4	-3842.15	7692.32	8.64	0.01
PC5.10	-0.43	NNDistCat + Veg	11	-3836.08	7694.27	10.59	0.00
PC5.7	-0.06	NNStatusSex	7	-3840.54	7695.13	11.45	0.00
PC5.12	0.00	Veg	7	-3841.42	7696.89	13.21	0.00

Variables included in models are nearest-neighbour distance category (NNDistCat), call behavioural context (CallContext), nearest-neighbour dominance status and sex (NNStatus), nearest-neighbour age category (NNAgeCat), group size (GroupSize), and vegetation density (Veg). Rows in bold indicate the models in the top set (delta <4). LogLik: log likelihood; AICc: Akaike information criterion corrected for small sample size; delta: Δ_{IC} ; weight: Akaike weights.

Table A14

Model averaged top set of models' estimated marginal means model summary for the variables affecting the PC5 scores, representing the acoustic variation in meerkat close calls

Variable	Emmean	SE	df	Lower CL	Upper CL	t	P
JV	-0.07	0.20	2224.00	-0.46	0.31	-0.37	0.713
SA	0.02	0.15	2224.00	-0.27	0.31	0.13	0.893
AD	0.02	0.14	2224.00	-0.26	0.30	0.14	0.888
Pup	0.14	0.21	2224.00	-0.26	0.54	0.68	0.499
SC	-0.13	0.14	2224.00	-0.41	0.15	-0.94	0.350
PV	-0.12	0.19	2224.00	-0.48	0.25	-0.62	0.533
FO	-0.01	0.13	2224.00	-0.26	0.25	-0.05	0.963
EA	0.03	0.16	2224.00	-0.28	0.34	0.17	0.862
DI	0.08	0.20	2224.00	-0.30	0.47	0.43	0.669
MO	0.30	0.35	2224.00	-0.39	1.00	0.86	0.388
0–0.5	-0.32	0.26	2224.00	-0.83	0.19	-1.23	0.218
1–2	0.04	0.14	2224.00	-0.23	0.32	0.30	0.766
6–9	0.07	0.15	2224.00	-0.22	0.36	0.48	0.629
2–5	0.13	0.13	2224.00	-0.12	0.39	1.00	0.315
10+	0.21	0.25	2224.00	-0.27	0.70	0.85	0.394

Variables included are nearest-neighbour age category (pup; JV: juveniles; SA: subadult; AD adult) and behavioural context (EA: eating; DI: digging; FO: foraging; SC: scurrying; PV: postvigilance; MO: moving) and nearest-neighbour distance (m; 0–0.5, 1–2, 2–5, 6–9, 10+). Bold *P* values indicate significant result. Emmean: estimated marginal mean. CL: confidence limit.