Vocal turn-taking in meerkat group calling sessions

Vlad Demartsev[#][*][1,2], Ariana Strandburg-Peshkin[*][1,2],
Michaela Ruffner[1,2], Marta Manser[1,2,3].

[1]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich

8057, Switzerland

[2]Kalahari Meerkat Project, Kuruman River Reserve, Northern Cape, South Africa

[3]Mammal Research Institute, University of Pretoria, 0002 Pretoria, South Africa

[*]These authors contributed equally to the study

[#]Corresponding author

Corresponding author and lead contact: Vlad Demartsev, demartsev@gmail.com

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SUMMARY

Coordination is a fundamental aspect of social living, underlying processes ranging from the maintenance of group cohesion to the avoidance of competition. Coordination can manifest as synchronisation, where individuals perform the same action at the same time, but can also take the form of anti-synchronisation or turn-taking. Turn-taking has mainly been studied in the context of the development of language [1], due to the fact that it is a universal feature in all languages and has been found to appear early in infancy [2,3]. Recently, turn-taking has received attention in animal communication research [4-7] as a potential foundation on which social communication was formed [1,3]. In this study we describe turn-taking in group-wide vocal interactions of meerkats (*Suricata suricatta)* during low-conflict, sunning behaviour, which is accompanied by the production of specific "sunning" calls. We show that sunning call production is socially stimulated, and that at the group level, meerkats avoid overlap, thus fulfilling a key principle of turn-taking [8]. Through observational data and playback experiments, we show that these group-level patterns arise from two, individual-level rules: call inhibition over short time scales which prevents mutual interference, and call excitation over longer time scales which stimulates further group calling. These simple rules suggest that hierarchy formation and turn allocation are not required for achieving group-wide coordination of communication. We also suggest that the potential bonding function of turn-taking shown in humans might have similar effects in animal interactions.

RESULTS

The majority of research on turn-taking in animals and humans has focused on dyadic, or in some cases triadic [5,9,10] interactions. However, as vocal interactions in nature often occur in multi-participant settings, it remains unclear to what extent turn-taking patterns can persist in larger groups [10,11], and what mechanisms underlie such coordination. Multi-participant turn-taking might rely on pre-set order, creating a rigid participation framework. An alternative mechanism is opportunistic turn usurping, while maintaining the fundamental turn-taking rules, it allows a free reshuffling of participation roles [12]. Examining the mechanism of turn-taking in animal groups will allow us to determining whether the maintenance of multi-participant turn-taking can be a result of a spontaneous and cognitively simple process of self-assembly. To address this, we examined call dynamics in intra-group interactions among free ranging meerkats, a social mongoose species [13] with a complex vocal communication system [14]. Since calls produced in non-competitive interactions are more likely to show a turn-taking pattern than those produced in conflict situations [15], we investigated the temporal organisation of meerkat calls during low-conflict "sunning" behaviour. During our data collection period, meerkats spent on average 44 ± 2 min (n = 91) sunning (sitting or standing on hind legs facing the sun with the ventral side of the body, after emerging from their sleeping burrow). The time spent sunning was negatively correlated with minimum overnight temperature (GLMM: F=18.944, n=97, p<0.0001, Tab.S1, Fig.S1).

While sunning, meerkats frequently produced "sunning-calls" (Fig.S2). These vocalisations were almost exclusively produced while sunning (92%) and very seldom while engaging in other activities (e.g. moving, grooming, foraging) during the sunning period (Tab.S2). Calling behaviour during sunning was strongly associated with the presence of other

group members. Only in 7.7% out of 39 group scans (5 min intervals throughout each observation [16]) in which only one individual was out sunning, did a focal subject produce sunning calls, whereas when others were present (340 group scans), individual sunning-call probability was significantly higher at 35.7% (Binomial test: $p<0.0001$). Adult (>1 year) individuals were more likely to produce sunning calls than juveniles (3-6 months) and pups (>3 months) (GLMM, F=1.216, $p<0.001$), whereas dominance and sex of a focal individual had no significant effect on its probability of emitting sunning-calls. When other group members were present, the probability of a meerkat emitting sunning-calls depended on the proportion of them calling (GLMM, F=388.854, $p<0.001$, Tab.S3a, Fig.S3a), suggesting that calls are socially stimulated. Additionally, when the dominant female was vocalising, individuals were less likely to call (GLMM, F=65.011, $P<0.001$, Tab.S3b).

Overlap avoidance in group calling sessions

To assess whether a turn-taking pattern exists in meerkat group sunning-call sessions, we analysed individual recordings of 41 meerkats from 8 different social groups (a total of 23180 calls). In the recordings, both the *focal* individual being recorded and other *background* meerkats nearby could be heard (Fig.1a). Focal calls were clearly distinguishable from sunning-calls in the background. For each recording, we calculated the *group-wide call rate* (number of calls per sec) and the *overlap rate*. *Overlap rate* was calculated by summing the total amount of overlap time between focal individual sunning calls and background sunning calls, and then dividing this number by the maximum possible focal/background overlap time (i.e. the total amount of time vocalising for either the focal or the background callers, whichever had the smaller total). This yielded a value between 0 and 1, with lower values of the overlap representing less overlap and hence more turn-taking (Fig.S4a). Natural overlap rate was well below randomised null overlap

rates generated by pairing each focal track with a random background track from a different day (Fig.1b; p<0.01). This indicates that during group calling sessions, individuals avoid overlapping with conspecific signals, resulting in a turn-taking call pattern. Moreover, our data suggest that the temporal organisation of meerkat calls is finely tuned to a pattern of overlap avoidance. We computed the overlap rate for "time-shifted" data in which the background calls are shifted by a fixed time interval relative to the focal calls for a given recording. The overlap rate was minimized at a time shift of 0 (i.e. natural calling data) and substantially increased even for small time shifts (Fig.2). Additionally, the number of individuals that had a likely visual contact, within a 2m radius of the focal (Median=3, Range=[1,12]), the total number of visible individuals (Median=7, Range=[1,23]) and the group-wide call rate (Median=0.05 call/sec, Range=[0.009, 0.17]) showed no effect on the overlap rate (Tab.S4). These findings suggest that overlap avoidance is a robust phenomenon that is maintained in multi-participant vocal interactions, as indicated by its insensitivity to more than 3 fold increase in both median group size and group call intensity. A general overview of the focal inter-call interval as a function of visible group size also did not show any relationship (Fig.S3b).

Individual-level calling rules: A scale-dependent pattern of call inhibition and enhancement

To tease apart the individual-level mechanisms giving rise to overlap avoidance at the group level, we examined in detail the timing of calls given by focal and background individuals. Following Takahashi et al.[5], we first tested whether the pattern of overlap avoidance seen in meerkats is consistent with one of two simple mechanisms. According to the *reset hypothesis*, individuals have a typical distribution of intervals between calls, and hearing the call of another individual resets the clock on this interval distribution. If this hypothesis is true, the distribution of intervals between consecutive focal calls should be the same as the distribution of intervals

between a background call and a focal call heard consecutively. According to the *inhibition hypothesis*, a call heard from another individual inhibits a focal individual's call, but does not affect subsequent calling behavior. Thus, the distribution of intervals between two focal calls should be the same as the distribution of those in a randomized dataset in which focal call tracks are paired randomly with background call tracks drawn from our dataset, with overlapping calls removed to simulate inhibition. We tested the support for both of these hypotheses in meerkat sunning interactions (see Methods). The results show that our data are broadly consistent with the inhibition hypothesis (Fig.3a, compare blue and green lines) and inconsistent with the reset hypothesis (Fig.3a, compare grey and green lines; KS test: D=0.502, P<0.001), supporting the idea that overlap avoidance is driven by meerkats locally inhibiting their calls when they hear others calling. Furthermore, in contrast to what has been found in dyadic interactions in marmosets and humans [5,17] calling behaviour of meerkats did not appear to be periodic (Fig.S3c), suggesting that more complex mechanisms such as phase locking and entrainment are unlikely to be at play.

The finding that an individual's calls are inhibited by the calls of others could be seen as contradictory to the result that calls are socially stimulated, however, these effects could in fact coexist if they operate over different time scales. To investigate this idea, we measured the focal individual's call rate over a range of different time windows immediately following each background call, or at random times as a control. Meerkats showed a time scale-dependent pattern of call rate following conspecific calls. Over short time scales (<0.2sec) following a background call, a focal's call rate fell below the control rate, indicating a local inhibition by the incoming vocal signals. However, over longer time scales after a background call, the focal call

rate increased beyond the control baseline, in agreement with the results of a positive social stimulation (Fig.4a).

Although our analysis of natural sunning interactions suggest that short-term inhibition and long-term social stimulation underlie the observed calling dynamics, observational data alone cannot demonstrate a causal relationship between the calls of conspecifics and the call timing of focals. Moreover, vocal behaviour can often be affected by conspecific signals and cues in non-acoustic modalities as well as by environmental events. To experimentally test our proposed mechanism of overlap avoidance, we performed a series of playback experiments. Sunning calls were played back to focal meerkats standing at least one meter away from a closest neighbour, thus making the played back calls as the closest and potentially strongest acoustic effector of focal calling behaviour. We assessed the timing of calls from the focal individual with respect to the timing of calls from the playback stimulus. As a control, the same individuals were also recorded in the absence of a playback stimulus, and the timing of their calls was assessed relative to the same time points in which playback calls occurred in the experimental condition. In agreement with the patterns seen in natural sunning data, results from these playbacks also showed consistency with the inhibition hypothesis (Fig.3b). Moreover, playback results confirmed the same time-scale dependent pattern as seen in natural observations, with focal individuals reducing their call rates relative to the control over short time windows after a playback call, and increasing them over long time scales (Fig.4b). The results of this manipulation demonstrate a causal relationship between conspecific calls and the focal call timing. This also confirms that turn-taking in meerkats can be efficiently driven by audible signals only, and is not a by-product of unobserved factors, such as visual or olfactory cues.

DISCUSSION

Our results demonstrate a robust pattern of turn-taking in meerkat vocal interactions in the context of sunning sessions. Group calling sessions are characterised by a below chance rate of call overlap indicative of turn-taking, which is maintained over a range of interaction intensities (call rates). Although we could not control for the number of vocalising individuals in the recorded interactions, overall background call rate and the number of individuals present are a good proxy for interaction intensity. These variables showed no effect on the overlap rate, despite being dispersed on a ~20 fold range (Tab.S4) and hence turn-taking coordination was retained even at high call densities likely representing more than 3 active participants.

By considering the detailed individual-level calling dynamics, we show that the calls of other individuals both inhibit and stimulate individuals to call. These effects operate over different time scales, with call inhibition (i.e. a lower call rate per individual) immediately after the calls of others and call stimulation (i.e. a higher call rate per individual) over longer time scales. This multi-scale mechanism allows prolongation of group calling sessions while simultaneously facilitating avoidance of overlap among callers.

Individuals typically need to process incoming signals before emitting a response [5]. Typical response time for human conversation is 200ms [1], and a matching temporal relation between gestural exchange turns was recently found in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) [18]. Additionally, simultaneous transmission and reception of signals of the same modality can create jamming [19], impeding information transfer. Avoiding these two communicational problems may therefore require coordination among communicating parties. Similar to other types of coordinated display, turn-taking has been suggested to be a fundamentally cooperative behaviour indicating shared interest among signallers for an effective exchange of information [18], although see [20]. Violations of turn-taking rules are often

negatively perceived, as they can indicate lack of attention, lack of experience [6] or aggression [21,22]. Although the specific function and the informational content of meerkat sunning calls remain unclear, their apparent non-competitive context and the turn-taking pattern uncovered here suggest that they are a cooperative signal. Potentially these calls might have a calming effect (as has been shown for acoustically similar sentinel calls [23,24]) and may play a role in maintaining group bond.

Early models developed to explain turn-taking in human conversation suggested that speaker transition is regulated by attending to turn termination cues produced by the current speaker [1]. More recent models add that signaller transition is achieved by an early turn planning, before the occurrence of turn termination cues [25]. Parallels for these two principles can potentially be found in animal communication. Early turn planning in human conversation is indicative of the intention to communicate, stimulated by the incoming signals [26-28]. It is possibly parallel to the increase in signalling motivation stimulated by conspecific calls as demonstrated here by an overall increase in the probability to call when others do so. The use of turn termination cues and avoidance of overlapping talk in humans is similar to the observed transient call suppression, possibly until a silent gap is perceived as a cue for the end of a turn. Another potential parallel between human and animal turn-taking organisation is the similarity in the response time of approximately 200ms found in humans [1] and apes [18] which also approximates the suppression time we find here in meerkats (Figures 2 and 3).

As few previous studies have attempted to examine anti-synchronised calling within a group [9,11], it is unclear if there is an upper limit on the number of active participants in a vocal interaction governed by the principles discussed above. In humans, turn-taking in unsupervised group-discussions was found to be challenging [10]. Additionally, in humans, factors such as

turn allocation, gestures and seniority [10,29] likely play a central role. It has been stated that the basic organisational rules for spontaneous turn-taking "favour" only small groups of three or fewer participants and that larger groups require sequence organisation [8] or segmentation [30]. In contrast to this assertion, our results suggest that such patterns can be driven by a simple individual-level mechanism, and can be efficiently maintained in unrestricted sender/receiver vocal interaction with well above three participants. Our results demonstrate that turn-taking in meerkats is not driven by simple neural resetting, as have been suggested for insect choruses [31]. It is also different from the coupled oscillator dynamics shown in common marmoset (*Callithrix jacchus*) and human turn-taking interactions [32]. The innate foundation of turn-taking [32] as well as the suggested effects of social feedback and learning [33] are important areas for future investigation.

The connection between sociality and communication has been repeatedly suggested in the past [34,35] and human language is considered to be the driving force behind our social and cooperative organisation [36]. Turn-taking is a universal feature, present in all human languages [2] including non-spoken sign language [1] and it manifests well before the appearance of coherent words [3]. Although such defining characteristics of language as syntax and phonology [7] have both been shown to be present in animal vocal communication systems [37,38], turn-taking likely precedes them. It has been suggested that the importance of turn-taking in human communication is not limited to the regulation of informational transfer, but that turn-taking potentially also serves as an "interaction engine" [39], relating to the aspects of creating bond through synchronisation [1]. In terms of mathematical measures of coordination, synchrony and anti-synchrony are extremely close [40] so, as coordinated displays are known to express pertinence and bond [41,42], it is not unlikely that coordinated turn-taking has a similar function.

Differences in cognitive abilities between species do not necessarily negate convergence of cooperative communication [15] so it is only natural to create a parallel between signalling exchange regulation in animal and human cooperative interactions.

Author contribution: Conceptualisation MM, VD; Investigation MR under MM supervision, Formal Analysis ASP, VD, MR; Writing - Original draft VD, ASP; Writing – Review & Editing VD, ASP, MM; Visualisation ASP, VD; Supervision MM

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FIGURE LEGENDS

Figure 1: **Meerkats avoid overlapping their conspecifics during group sunning call interactions (see also Figure S2)**

A: Sample spectrogram of sunning call interaction between an identified focal individual (F) and unidentified background callers (B).

Overlap rate of natural sunning calls is significantly smaller than overlap rates for a randomised null model in which background tracks are permuted across recordings, both on the level of single notes - B and on the level of bouts - C. The grey bars show a histogram of the distribution of overlap scores calculated from 100 different permutations (y-axis represents probability of a given overlap score in this null model). The dashed line shows the overlap rate of the observed data.

Figure 2: **Overlap rate of natural sunning calls is minimised at time shift of 0 sec, indicating strong overlap avoidance**.

Overlap rate of natural sunning calls as a function of the time shift between focal and background calls on the level of: A- single notes; and B - bouts. A time shift of 0 sec is indicated by the dashed line and steeply increases with small time shifts.

Figure 3: **Observed inter-bout interval distributions of sunning calls are consistent with expected distributions for the inhibition hypothesis.**
Observed inter-bout interval distributions of sunning calls (green) are consistent with expected distributions for the inhibition hypothesis (blue) but not for the reset hypothesis (grey) in both natural observations - panel A, and playback experiments - panel B. Shaded areas represent 95% confidence intervals generated either by 100 different permutations of the background tracks used (in the case of inhibition hypothesis (panel A), or from boostrapping the interval data used to generate the distribution (1000 draws with replacement).

Figure 4: **Individual call rate is suppressed immediately after a conspecific's call but enhanced over a longer time scale in both natural observations - A, and playback experiments - B (see Methods; see also Figure S3A)**
A: Mean focal individual call rate (percentage of time occupied by vocal signals; y-axis) during natural vocal interactions, computed over increasing lengths of time windows (x-axis) immediately following a conspecific call (circles) or at randomly-positioned start times (triangles). B: Mean focal individual call rate computed over increasing lengths of time windows immediately following a playback call (circles) or at the equivalent time in the control condition (triangles). In both cases, focal individual call rate is suppressed 0 to ~0.2 sec after a call relative to the control, and enhanced over longer time windows. Shaded areas denote 95% confidence intervals, generated by block bootstrapping

STAR Methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for data should be directed to and will be fulfilled by the Lead Contact, Vlad Demartsev (demartsev@gmail.com)

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Research was carried out on the Kalahari Meerkat Project (KMP) on a long-term study population of wild meerkats at the Kuruman River Reserve, South Africa [43]. Since 1993, all meerkats on site have been fitted with transponders and dye-marked for individual recognition, and life histories, genetic lineages and morphometric measures have been documented [44]. Meerkats were habituated to human presence within < 1 m and were routinely observed, recorded, and handled. For this study 13 different meerkat groups, with group sizes ranging from 7 to 34 individuals, were observed between March and August 2007. All procedures were based on well-established protocols and were approved by ethical committees of University of Pretoria, South Africa (permit: EC011-10) and the Northern Cape Department of Environment and Nature Conservation (permit: FAUNA 1020/2016).

Meerkats are cooperative breeders [13] that live in despotic social groups with a dominant breeding pair and subordinate helpers [45]. They have a complex vocal communication system with over 30 different call types [14] and most group activities are mediated through vocal signals, including group movement, foraging and sentinel behaviour, [45-47]. Meerkat groups typically spend the early morning basking in the sun around their burrow entrance, before moving off to forage [48]. During these "sunning" sessions, individuals often emit soft calls (sunning calls, Fig.S2), consisting of one or more short notes.

METHOD DETAILS

Behavioural observations

Data collection was restricted to the "sunning period", a time when meerkats mainly show sunning behaviour, ranging from the time of emergence of the first individual to the last individual's departure for foraging. Scan sampling [16] was conducted at 5-minute intervals throughout each recording session to identify the individuals present and the individuals visible within a 2m radius of a focal meerkat (see below), and to document the following behaviours: sunning (sitting or standing on hind legs facing the sun with the ventral side of the body), sitting (not facing the sun), standing (on hind legs, not facing the sun), moving, and grooming (self or allo-grooming).

For each observation day a set of environmental data were collected including minimum overnight temperature, minimum overnight air-humidity (long-term data available from weather station on site), and maximum wind speed during sunning period (measured with a Windmaster 2; Kaindl electronic, Germany).

Acoustic recordings and measurements

Audio recordings were made using Marantz PMD-660 solid state digital recorder (Marantz, Japan) and a directional Sennheiser ME66 microphone with K6 power module (Sennheiser electronic, Germany), sampling rate 44.1 KHz, 16-bit. The microphone was attached to a telescopic pole and held close (10 to 20 cm) to the focal individual.

Vocalisations of meerkats from eight groups were recorded during 51 daily sunning sessions between March and July 2007. Vocalisations produced by the focal individual were audibly marked by the observer during the recording session. All vocal elements were manually

identified and marked in post-processing, and their start and end times determined, using Avisoft SASLabPro. Sunning calls consisted of *notes* (a single continuous vocal unit) and *bouts* (sequences of one or more notes given by an individual, separated less than 0.25s from its next note). Calls were identified as *Focal* according to the acoustic marks made by observer, and *Background* for all non-focal calls heard in the recordings. Sunning recordings of 41 randomly-selected focal individuals were analysed in detail for overlap patterns with background calls. No pre-selection of individuals for analysis was done. All available recordings were examined for quality and the final dataset was set to adequately represent both sexes and all eight recorded meerkat groups.

Recorded calls were analysed using Avisoft SASLabPro software (Avisoft Bioacoustics, Germany). For each recording, a spectrogram was generated at 512 FFT length, 100% frame, using a Hamming window. Individual notes within each bout were manually marked (Fig.S2), and identified as Focal or Background, for a total of 23180 sunning notes. For each note, start (T_S) and end (T_E) times were taken using the SASLabPro automatic spectrogram parameters function. Sunning calls were sub-divided into four types, characterised by the number of notes: single, double, triple and multiple (>3) notes (Fig. S2, a-d). In addition, two "modulated" sunning calls types are identified. These calls were not included in this study as they were relatively rare (2.4%), possibly a combination of sunning and another call (Fig.S2, e-f) and potentially bear different informational content, such as low-urgency alert similarly to calls elicited during sentinel behaviour [23].

Playback experiments

Playback trials were performed between July and August, 2007. An adult focal individual, sunning at least one meter from the closest group member, was recorded for two

minutes (control period). Afterwards, one of the two previously recorded, 2 min long sunning call tracks was played following previously published protocols [49]. To avoid effects of caller identity on the focal subjects' behavioural response, the recordings used originated from groups not used in the playback trials. The recordings were played using the Marantz PMD-660 digital recorder connected to JBL portable loudspeaker (JBL, USA), fixed to the observers leg at 30 cm height (approximate height of a meerkat in a typical sunning position). Through the whole duration of the control period and the playback trial, the focals` behaviours were documented and vocalisation were recorded with a Marantz PMD-660 digital recorder (Marantz, Japan) and a Sennheiser ME66 microphone with K6 power module (Sennheiser electronic, Germany), *Focal*, *Playback* and *Background* (non-focal sunning vocalisations heard) calls were manually marked using Avisoft SASLabPro. 36 playback trials were performed to 32 individuals from 7 groups, with both stimulus tracks equally represented. Audio recordings of playback trials were analysed similarly to recordings of naturally produced vocalisations with the addition of Playback call category.

QUANTIFICATION AND STATISTICAL ANALYSIS

Social and environmental correlates of sunning calls:

We fitted a generalised linear mixed model (GLMM) to test the effect of environmental factors affecting temperature and group size (as a potential for thermoregulatory behaviour) on meerkat sunning duration. Group was assigned as a random factor. Minimum overnight temperature, wind speed, air humidity and group size were set as fixed effects. To assess the effect of the group members' calling on the probability of a focal individual producing sunning calls, identify sex, dominance and age specific differences in calling rates and examine the effect of dominant female calls on subordinate call rates, a second GLMM was fitted. Focal ID was

assigned as a random factor nested within group. The percentage of group members calling, focal sex, age and focal dominance and whether dominant female was giving sunning calls, were fitted as fixed effects.

Assessing overlap rate in sunning calls:

For each recording, we calculated a *group-wide call rate* and *overlap rate*. *Overlap rate* was calculated by summing the total amount of overlap time between Focal and Background calls, and then dividing this number by the maximum possible Focal/Background overlap time (i.e. the total amount of time vocalising for either the Focal or the Background callers, whichever had the smaller total). This yielded a value between 0 and 1, with lower values of the overlap representing less overlap and hence more turn-taking (Fig.S4a).

We used GEEs to test whether overlap rate was affected by the group-wide call rate. Overlap rate between Focal and Background calls was calculated for 68 recordings of natural sunning interactions. For each recording group-wide call rate (calls/sec) was calculated, and number of Nearest Neighbours (NN) in 2m radius from focal, as well as all Visible Neighbours (VN) was noted. We fitted generalised estimating equations (GEE, an extension of generalised linear models for correlated data) to test whether high overall call density can cause an increase in overlap between the produced calls.

To test whether the overlap rate was lower than expected by chance, a null model was constructed by randomly pairing each track of focal calls with a randomly-selected (without replacement) background track. This procedure was repeated 100 times to generate 100 null overall overlap rates from randomly-permuted datasets. The true overall overlap rate was then compared to this null distribution to determine whether it was lower than expected by chance

(alpha level = 0.05), which would indicate turn-taking (Fig.S4c). The analysis of call overlap

rates yielded similar results both at the level of overlap between individual notes (Fig.1a) and at

the level of overlap between bouts of notes (Fig.1b), with bouts defined as consecutive sequences

of notes less than 0.25 sec apart. We also performed a time shift analysis in which the

background call track was shifted by a given interval relative to the focal call track, and the

overlap rate computed for each time shift (Fig.2). All overlap rate calculations and

randomisations were done in R version 3.3.2 (R Core Team, 2016).

Individual-level calling dynamics – testing reset and inhibition hypotheses

   Following Takahashi et al. [5], we tested two alternative mechanisms that could give

rise to overlap avoidance in meerkat sunning call interactions, using data from both natural

(unmanipulated) sunning sessions and playback experiments. To test the *reset hypothesis* in the

natural sunning data, we compared the distribution of intervals between two consecutive focal

calls (green line) to the distribution of intervals between a consecutive sequence consisting of a

background call and a focal call (gray line). In our dataset, as multiple individuals in the group

were calling, background calls were generally more frequent than focal calls. Thus, we also

tested a second variant in which intervals between background and focal calls were only included

if they were immediately preceded by a focal call (i.e. consecutive sequences consisting of a

focal call, a single background call, and then another focal call), which yielded similar results.

To test the reset hypothesis in the playback data, we compared the distribution of intervals

between consecutive focal calls to those between playback calls and focal calls.

   To test the inhibition hypothesis in the natural sunning data, we compared the

distribution of intervals between two focal calls in the real data to those in a randomized dataset

in which focal call tracks were paired randomly with background call tracks drawn from our

dataset. In these paired samples, overlapping calls were removed to simulate inhibition. Similarly, in the playback data, playback tracks were paired with control conditions within each trial, and overlaps were removed to generate the distributions. In the case of natural sunning data, because there are many ways in which calls could be randomized, we performed the randomization 100 times and computed 95% confidence intervals on the distribution from these different permutations.

To test whether calls from a focal individual were periodic, we computed the distribution of intervals between all bouts across all, natural recordings, including non-consecutive bouts. This distribution did not show a pattern of repeated peaks, suggesting that calls were not periodic in our data.

Individual-level calling dynamics – timescale dependent patterns

To reveal the individual-level rules leading to turn-taking in sunning calls, we investigated individuals' propensity to call in relation to the calls of their conspecifics. We measured the focals` call rate over a range of different time windows immediately following each background call. These time windows ranged from 0.001sec to 32sec, logarithmically spaced (46 windows total). The focal call rate was plotted as a function of the window size. The resulting curve shows how the sunning calls of focal individuals were either suppressed (low values) or enhanced (high values) by preceding conspecific calls, over different time scales. As a control, we constructed a similar curve, however the beginning time points for the windows were set randomly. 95% confidence intervals on the mean for each time interval were generated using a block bootstrapping procedure to account for non-independence of data within each recording. We drew random recordings (with replacement) to create 1000 artificial datasets containing the same number of recordings as in the full dataset, then computed the mean call rate for each of

these artificial datasets. Finally, we calculated the 2.5% and 97.5% quantiles of this distribution to estimate 95% CIs.

A similar analysis was performed on the recordings obtained during playback trials, to rule out the possibility that the observed individual calling dynamics were driven by unmeasured factors, such as visual or olfactory cues and to demonstrate a causal relationship between conspecific calling behaviour and the calling behaviour of focal individuals. Here the beginning of the time windows followed each of the played back calls and the control curve was generated using data from the control condition, in which no playback calls were played. The beginning time points for the time windows over which call rates were assessed were the same in both experimental and control condition, allowing for a direct comparison of the resulting curves.

DATA AND SOFTWARE AVAILABILITY

The unprocessed data is available at http://dx.doi.org/10.17632/t23j4wxtyb.1

KEY RESOURCE TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Suricata suricatta	Kalahari Meerkat Project, Kuruman River Reserve, South Africa	NA
Software and Algorithms		
Avisoft-SASLab Pro	Avisoft Bioacoustics, Germany	5.2.12
SPSS Statistics	IBM, USA	20.0.0
R	R Core Team, 2016	3.3.2
Deposited data		
Sunning call timing	This paper	http://dx.doi.org/10.17632/t23j4wxtyb.1

Figure1

Figure2

A

Probability density vs. Interval (sec)

Legend:
- Data (green)
- Reset (gray)
- Inhibition (blue)

B

Probability density vs. Interval (sec)
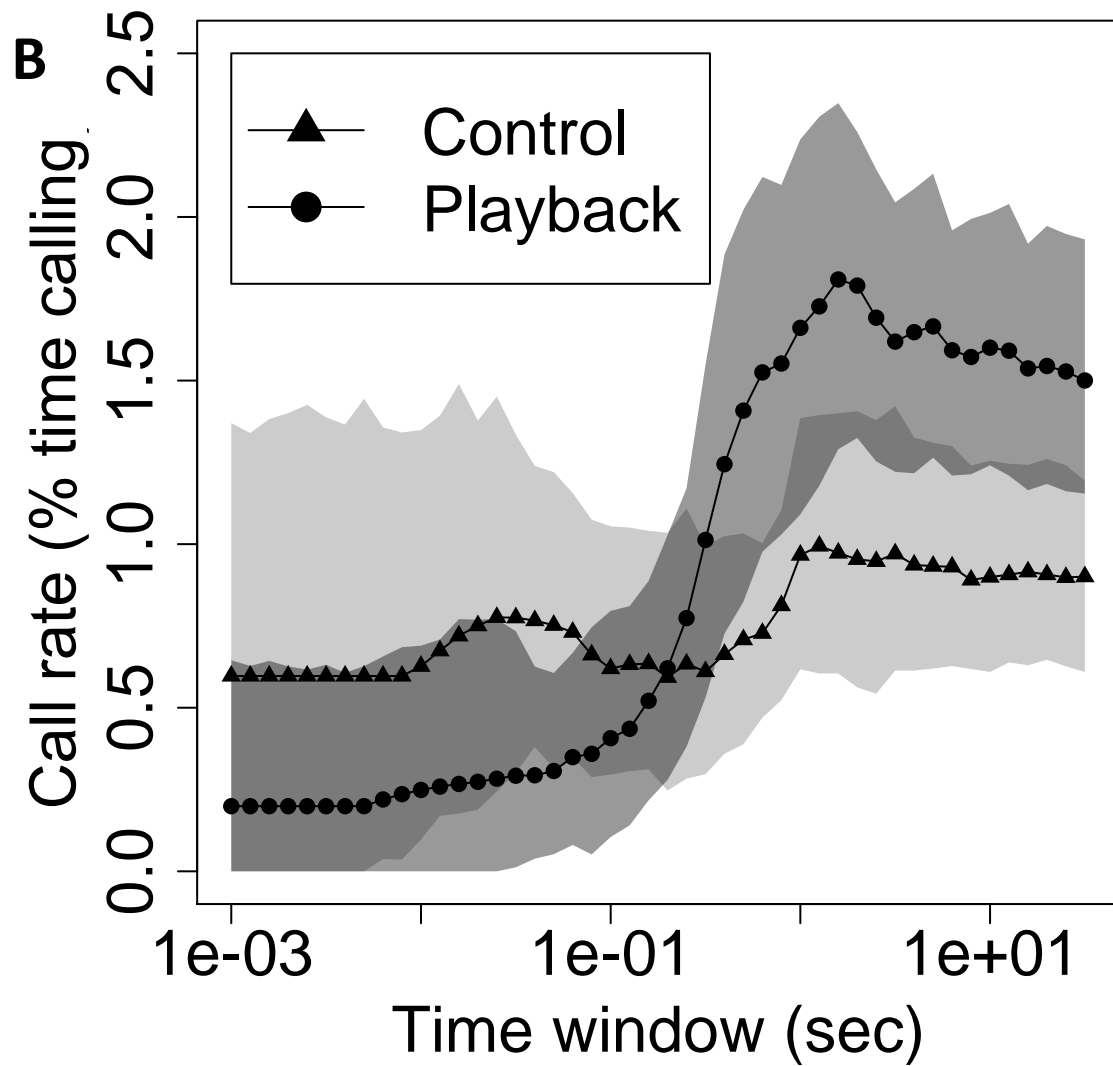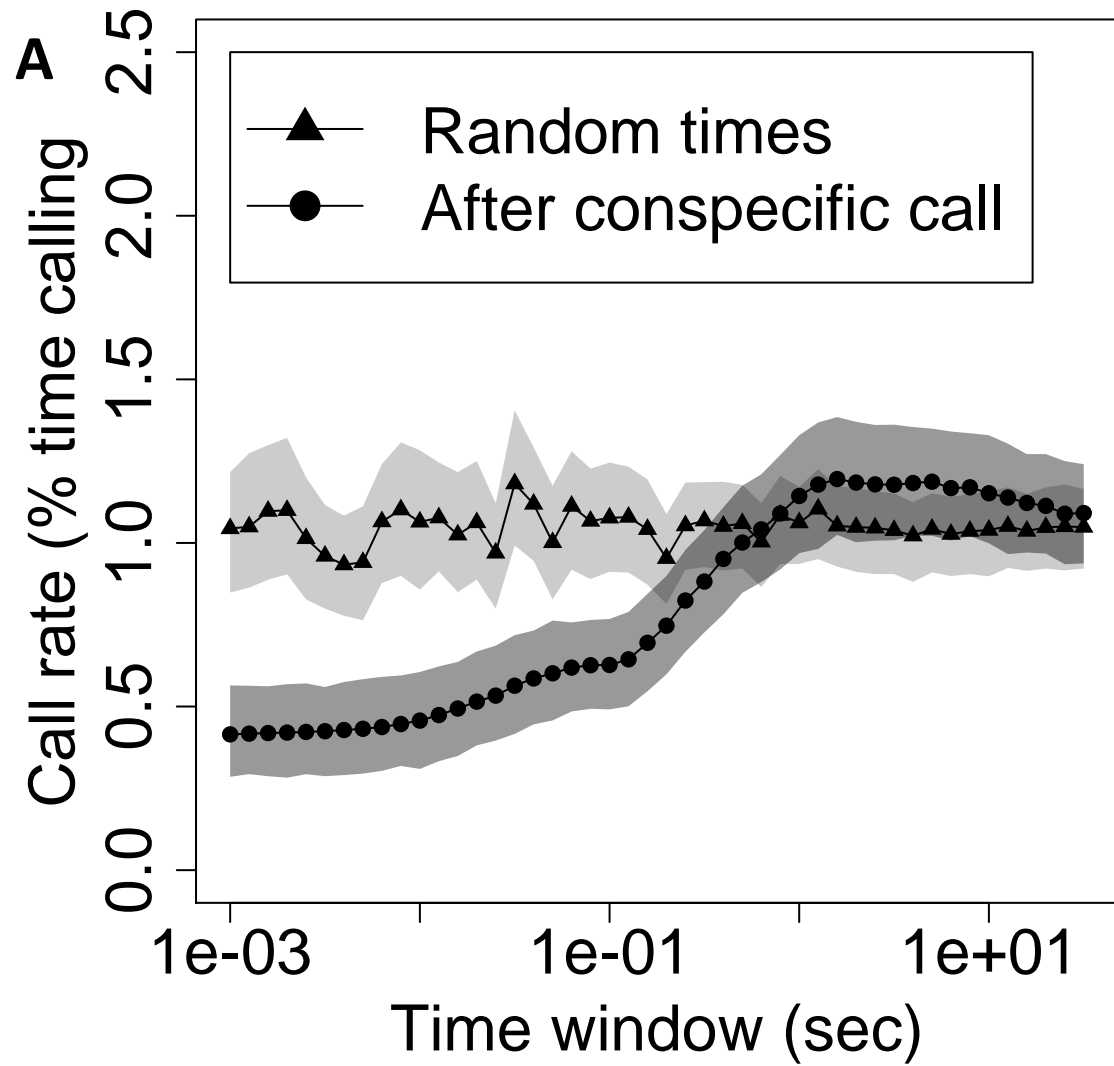
Legend:
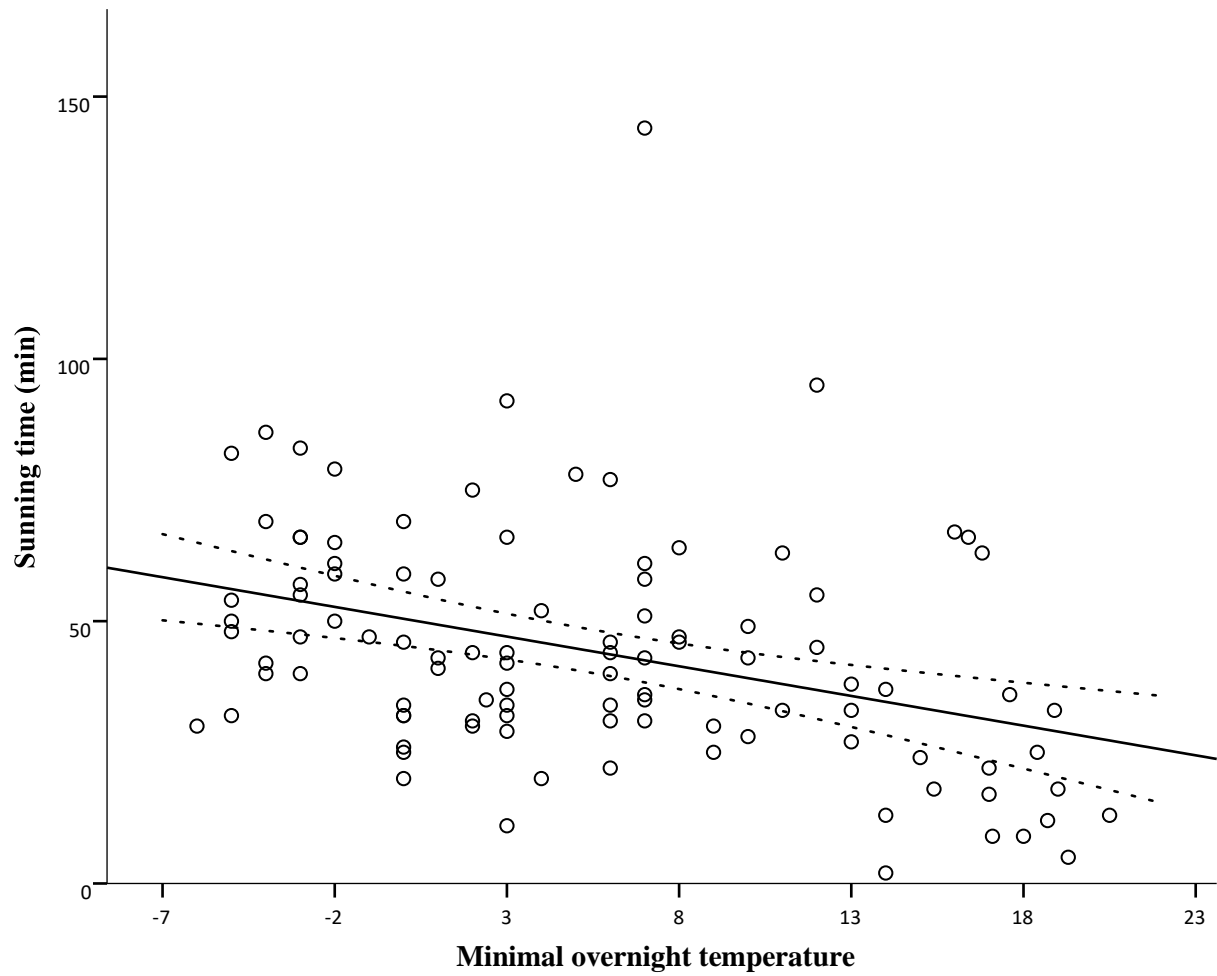- Data (green)
- Reset (gray)
- Inhibition (blue)
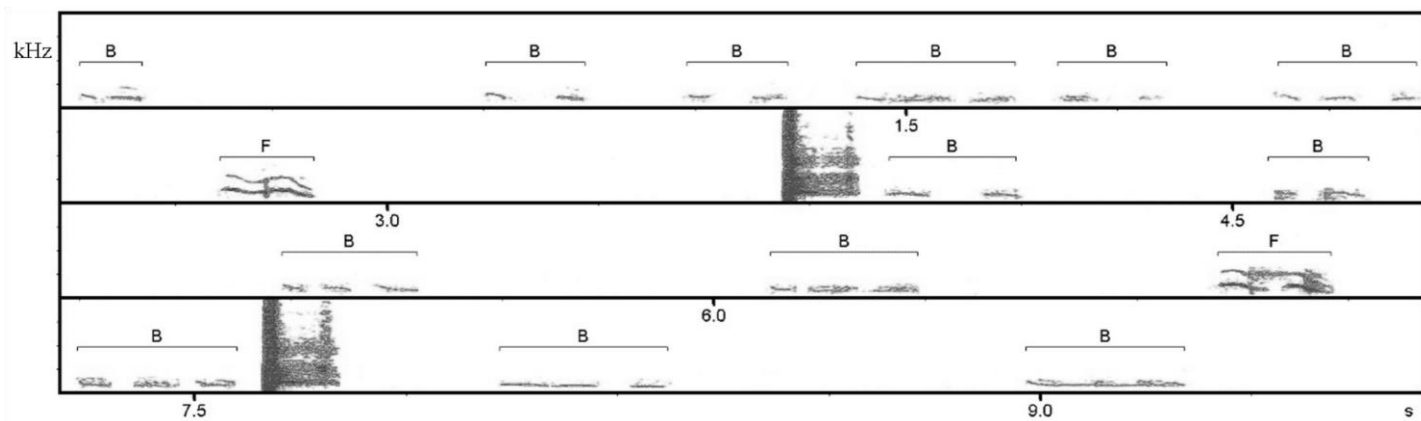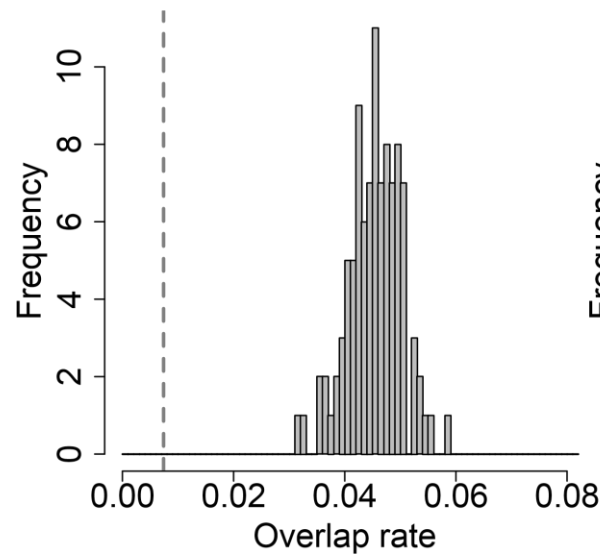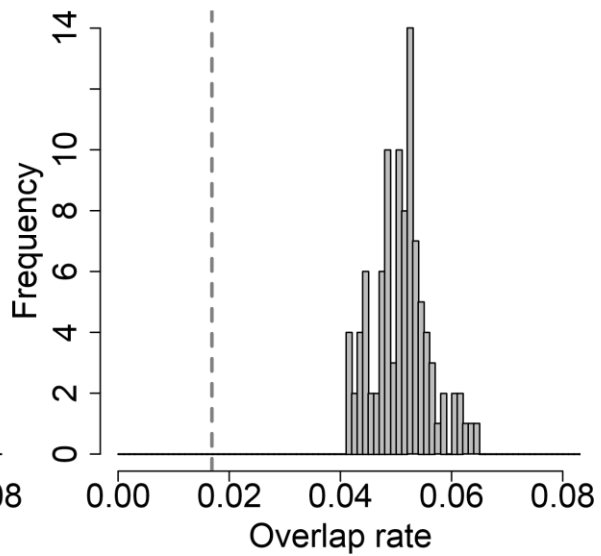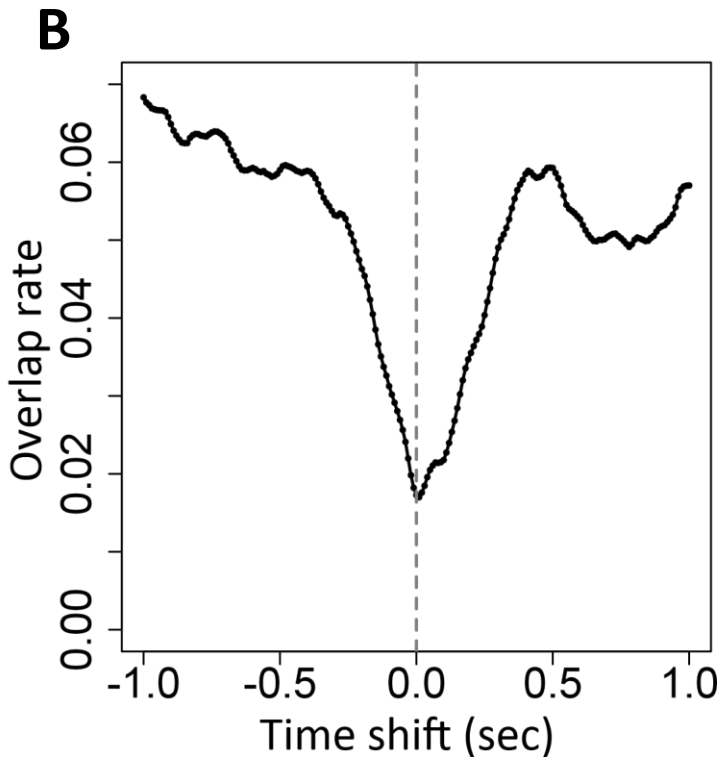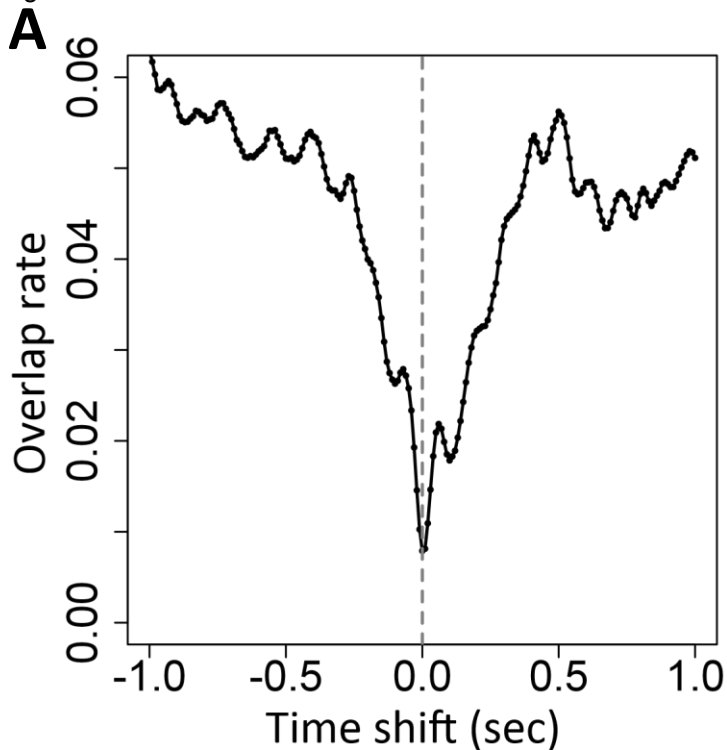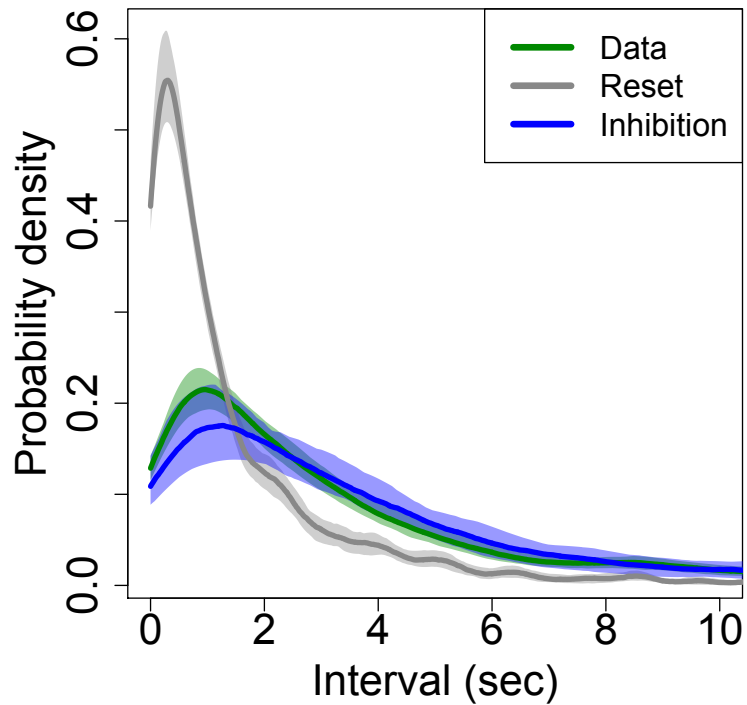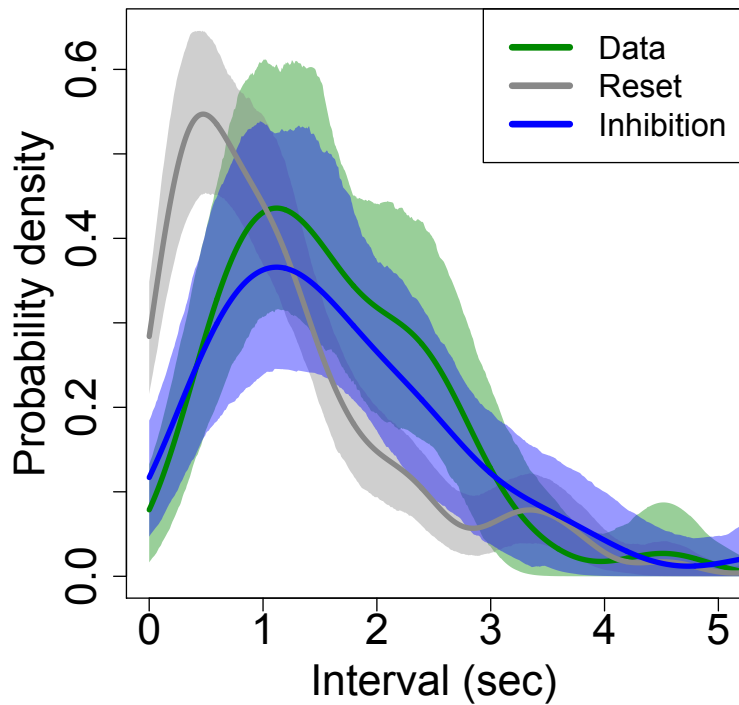
Figure4

Figure S1: Minimal overnight temperature (ºC) had a negative effect on the duration of meerkat morning sunning session (related to Table S1)

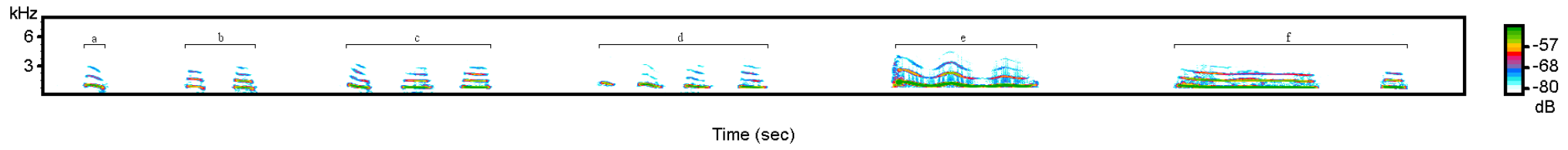Solid line represents a linear fit line; dotted lines are 95% CI.

Figure S2: Sample spectrogram of different sunning call types (related to Figure 1A).

a. single, b. double, c. triple, d. multiple, e. modulated , f. lead/move sunning call
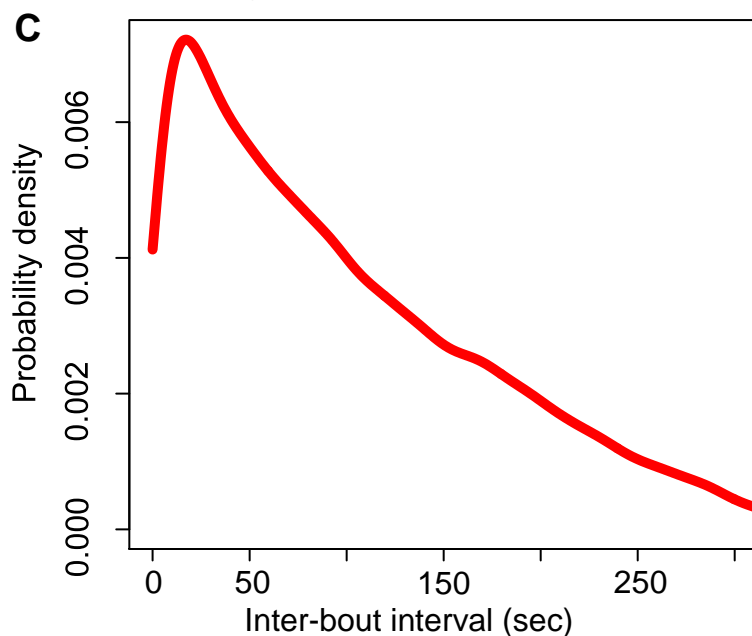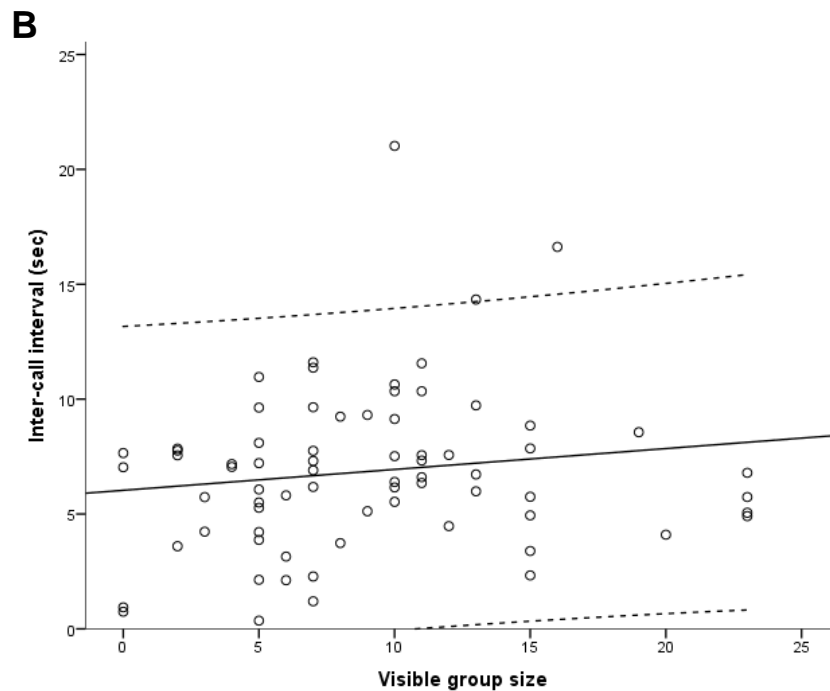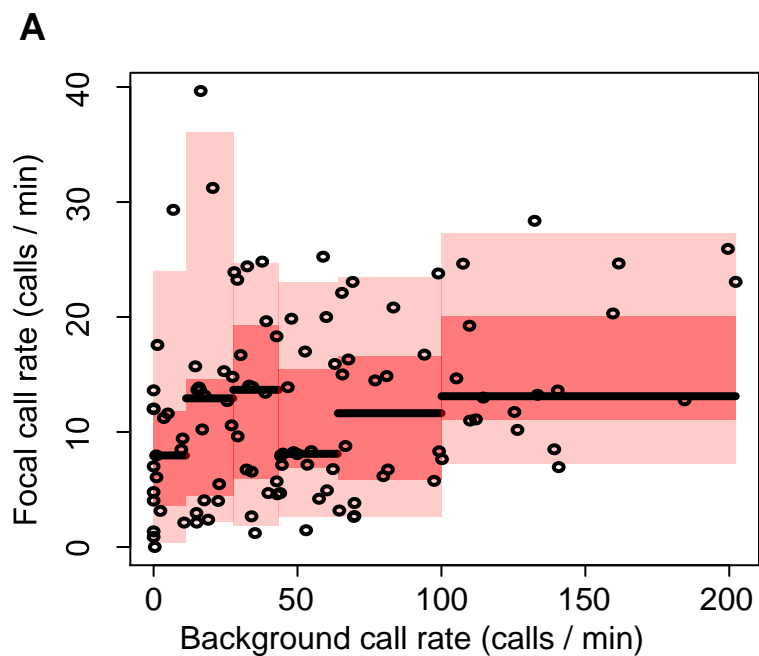
Figure S3: Meerkat sunning call dynamics: **Social affects and individual call rhythm (panels A, B and C are related to Table S3A, Table S4 and Figure 4, respectively)**

A: An increase of focal individual call rate (calls/sec) as a function of background conspecific call rate (binned) in natural vocal interactions. Black lines indicate median within each bin of background call rates, shaded areas give IQR and 95% CI respectively. B: Focal inter-call intervals (sec) as a function of number of group members visible in the surrounding area (whose calls potentially could be heard by the focal). Solid line represents a linear fit line; dotted lines are 95% CI.C: Probability distribution of sunning inter-bout intervals derived from naturally recorded sunning interactions. A single peak curve indicates the lack of periodicity in meerkat sunning call production, at least not at the group level
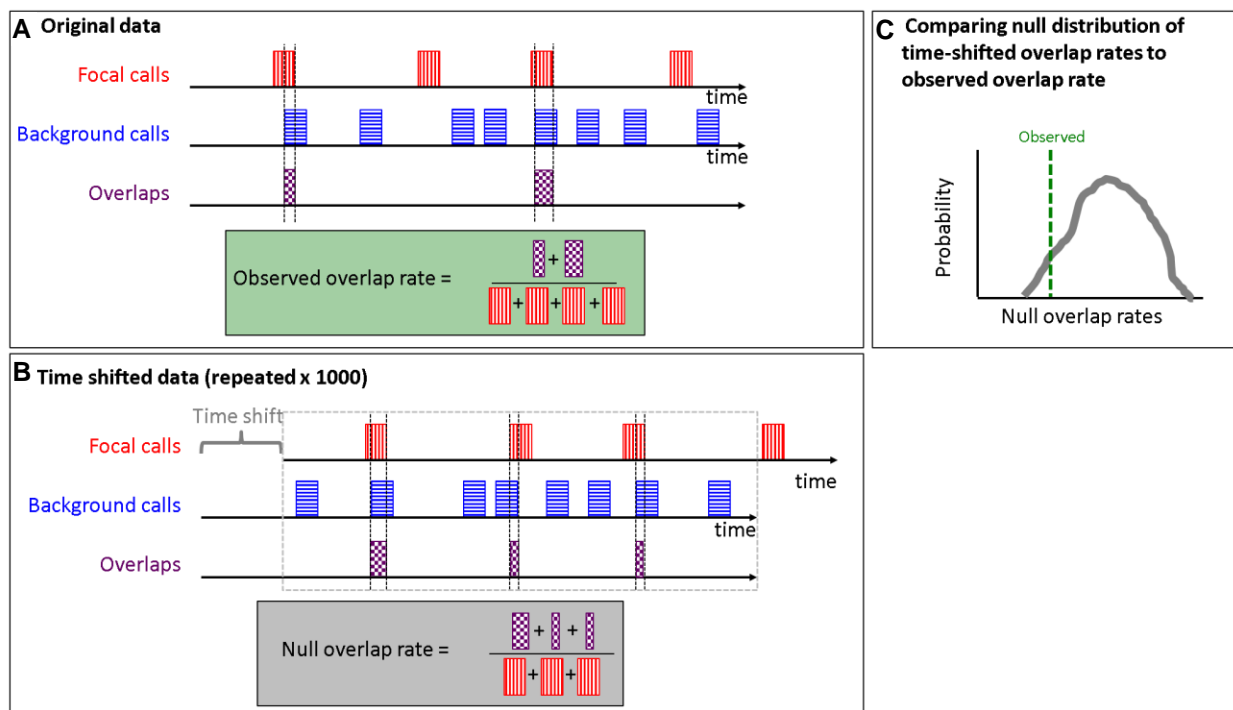
Figure S4: Schematic of the measurement of overlap rates, and the time shift permutation test used to determine whether overlap rates were lower than expected by chance (related to STAR methods).

A: The sequence of calls given by the focal individual and the other (background) individuals in the original (observed) data. Horizontal arrows indicate time, and coloured blocks indicate calls. Top row show calls given by the focal (red boxes with vertical stripes), and second row shows background calls given by the other individuals in the group (blue boxes with horizontal stripes). Third row shows the instances of overlap (checked purple boxes). Green shaded box shows how overlap rate was computed, i.e. by dividing the total amount of time of overlap by the total amount of possible overlap. In this case, since the focal individual calls less often than the background individuals, the maximum amount of possible overlap is equal to the amount of time that the focal individual is calling. B: The same data as in panel A, but with the two tracks shifted relative to one another by a randomly selected time shift (grey text), resulting in a different set of overlaps (purple checked boxes), and a different computed overlap rate (grey box at bottom). Note that the time shift leaves hanging "ends" that by definition cannot result in overlaps, thus these ends are excluded and only the data within the grey dotted line is included in the computations. C: After computing the overlap rate for 1000 randomly selected time shifts, the observed overlap rate can be compared to the distribution of these null overlap rates to determine significance

Measurement	F	*P*
T°C_min	18.944	**<0.001**
RH_min	0.818	0.368
Wind_max	3.611	0.600
Group size	0.049	0.826

Table S1: Effect of environmental factors and group size on the duration of meerkat sunning behaviour (related to Figure S1)

GLMM, n=97, group fitted as random effect. T°C_min (minimal overnight temperature), RH_min (minimal overnight humidity), Wind_max (maximum wind speed) and Group size are fitted as fixed effects.

Activity	Abs. Freq.	Rel. Freq. (%)
sunning	1230	92.00
standing	18	1.35
sitting	46	3.44
moving	20	1.27
grooming	17	1.49
others	6	0.45
Total	1337	100.00

Table S2: Type of activity while producing sunning calls (related to STAR methods).

"Others" category includes behaviours that were observed at a negligible frequency (anal marking, digging, foraging, play-fighting, defecating, renovating sleeping burrow, sleeping, urinating, vomiting). Number of scan units the individuals showed a specific activity (absolute frequency and relative frequency %).

	Measurement	F	df1	df2	P
A	Focal age	10.216	3919	3	**<0.001**
	Focal dominance	1.942	3919	1	0.164
	Focal sex	0.293	3919	1	0.588
	% of neighbours calling	388.854	3919	1	**<0.001**
B	Dominant female calling	65.011	2559	1	**<0.001**

Table S3: Meerkats increase sunning call emission when neighbours are calling and decrease sunning call emission when dominant female is calling (related to Figure S3A)

A. Social effects on focal sunning call probability. GLMM, binomial distribution with logit function, n=3919, Focal ID was fitted as a random effect nested within group. Focal sex, focal dominance, percentage of individuals giving sunning calls fitted as fixed effects. Focals' probability to emit sunning calls increased when a greater percentage of the group was giving sunning calls, the focal age had an effect of sunning call production with adult individuals having higher probability to produce sunning calls.

B. Effect of dominant female vocalization on focal sunning call probability. GLMM, binomial distribution with logit function, n=2561, Focal ID was fitted as a random effect nested within group. Dominant female vocalizations was fitted as a fixed effect. Focals` probability to emit sunning calls decreased when the dominant female was vocalizing.

Variables	Wald χ^2,	P
NN	1.602	0.206
VN	0.018	0.892
Call rate	1.737	0.188

Table S4: No effect of group size on call overlap in meerkat group sunning call interaction (related to Figure S3B)

No effect of number of neighbours within 2 m radius (NN), total number of visible individuals (VN) and total recorded call rate on the overall overlap rate. (GEE, n=68, Group set as random effect, Overlap Rate as dependent variable. NN, VN and Call Rate as covariates)