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Social monitoring via close calls in meerkats

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Social monitoring of the actions of group members is thought to be a key development associated with group living. Humans constantly monitor the behaviour of others and respond to them in a flexible way depending on past interactions and the current social context. While other primates have also been reported to change their behaviour towards other group members flexibly based on the current state of their relationship, empirical evidence is typically linked to contextually specific events such as aggressive or reproductive interactions. In the cooperatively breeding meerkat (*Suricata suricatta*), we investigated whether subordinate females use frequently emitted, non-agonistic close calls to monitor the location of the dominant female and whether they subsequently adjust their response based on recent social interactions during conflict and non-conflict periods. Subjects discriminated between the close calls of the dominant female and control playbacks, responding by approaching the loudspeaker and displaying submissive behaviour only if they were currently threatened by eviction. Our results suggest that meerkats assess the risk for aggressive interactions with close associates depending on social circumstances, and respond accordingly. We argue that social monitoring based on non-agonistic cues is probably a common mechanism in group-living species that allows the adjustment of behaviour depending on variation in relationships.

1. Introduction

Monitoring the actions of group members in social-living species is regarded as a crucial evolutionary step in the emergence of socio-cognitive skills [1]. Knowledge about the behaviour or even the mental states of others may help to minimize the costs associated with group-living [2]. Humans frequently take past interactions with others into account, whether cooperative or agonistic, when deciding how to socially interact with each other. Such social monitoring and integration of current relationship status probably requires not only individual recognition of conspecifics [3–5], but also the processing and storage of past interactions with group members [6,7].

Equivalent abilities to monitor social relationships through listening to vocal interactions, and then to adjust subsequent behaviour according to the new information, have so far mainly been demonstrated in primates. Male baboons (*Papio hamadryas ursinus*), for example, have been shown to monitor the current ‘state’ of a reproductive consortship via female copulatory calls and male affiliative grunts [8], approaching receptive females more when playbacks simulate the termination of a consortship. Female baboons, on the other hand, appear to keep track of aggressive interactions with other group members by adjusting their responses to aggressive or affiliative grunts according to recent experiences [9]. While these experimental studies indicate a sophisticated capacity for social monitoring, they rely heavily on the occurrence of very context-specific vocalizations that are not frequently emitted. If relationships between individuals are hostile, waiting to hear the approach grunts of a competitor may already be too late for evasive behaviour. However, a constant monitoring of conspecifics via more frequently available socially neutral cues, such as contact calls, would be advantageous in allowing a continuous, adaptive fine-tuning of behaviour towards specific group members with respect to the qualitative nature of recent interactions

with this individual. Such monitoring of conspecifics and flexible modification of behaviour are particularly relevant in elucidating how attentive individuals in social groups are to each others' behaviour and signal traits [8].

We addressed the topic of social monitoring and flexible responses in wild cooperative breeding meerkats (*Suricata suricatta*). Meerkats, a socially obligate mongoose species inhabiting semidesert areas in southern Africa, live in groups of up to 50 individuals [10] consisting of a dominant pair, which monopolizes the breeding, and mainly related helpers [11]. Meerkats show a high number of cooperative behaviours [12] and rely heavily on vocal communication to coordinate their activities [13], such as anti-predator behaviours mediated by sentinel calls [14] and alarm calls [15,16], or maintaining group cohesion while foraging by producing 'close calls' [17,18]. The highly cooperative nature of their breeding system and the accompanying reproductive skew of dominant females leads to predictable, transient periods of social rivalry between individual group members [19].

Most conflicts arise during late pregnancy when the dominant female is close to giving birth and when subordinates also attempt to breed [20,21]. Such interactions can culminate in the eviction of subordinate females from the group [22,23]. Often, a few days before such an event, the dominant female becomes highly aggressive towards specific subordinate females, attacking them and expelling them, until after the dominant has given birth when they are allowed to rejoin the group [23]. Meerkats are highly dependent on their group and evicted females face a high mortality rate [24]. Given the substantial threat posed by dominant females to subordinate females, we investigated whether subordinates monitor the spatial position of the dominant female during foraging and adjust their behaviour differently during conflict and non-conflict periods. Because such agonistic interactions between individual meerkats are typically transient in duration, they subsequently provide an ideal opportunity to identify if and how meerkats monitor conspecifics relative to current relationship status.

As meerkats spend the majority of their time foraging with their head down, digging in the soil, they cannot always monitor actions of others visually. Hence, the acoustic medium probably plays an important role. We specifically focused on close calls, which meerkats frequently emit while foraging (on average one call every 15 s [13]). Close calls are highly stereotyped, individually distinct vocalizations [17], which meerkats use to discriminate between group members [5]. To test whether subordinate females use close calls to monitor the spatial location of the dominant female, we conducted playback experiments during two different contexts: (i) during a period of social aggression; and (ii) when there was no aggression occurring. For (i), we played back the dominant female's close calls to subordinate females, who were threatened with eviction at the time of the experiment. To rule out more parsimonious explanations, we implemented additional control playbacks to investigate if subjects merely responded to any known dominant individual, to any known female conspecific or to any pregnant dominant female meerkat. For (ii), we repeated the experiments outside of a conflict period on the same subordinate females to confirm that their reactions were due to the temporary social circumstance and not due to a potential aggressive signature in the dominant female's close calls, caused by physiological changes during pregnancy. We predicted that if meerkats do monitor the location of the dominant female and respond differently based on the current state

of their relationship with her, subordinate females threatened with eviction should show a distinctive response to close calls of the dominant female during a period of strong social conflict, but not in non-conflict periods. We did not expect to see any obvious response to the playback of control close calls from other social categories.

2. Material and methods

(a) Study site and study population

The study was conducted on a population of wild meerkats at the Kalahari Meerkat Project, Kuruman River Reserve, located 30 km west from Van Zylsrus (26°58' S, 21°49' E) in the South African Kalahari Desert [20] from September 2009 to April 2010. This population has been monitored since 1993, and the animals are habituated to human presence. They are used to handling and can be visually identified by individually distinctive dye-marks. Long-term behavioural data and life histories including genetic relationships exist for almost all of the individuals. All meerkats in habituated groups have an implanted transponder chip, which allows for lifelong individual identification. At least one (dominant) animal per group is tagged with a radio collar enabling group localization [25].

(b) Recording and processing of close calls

Meerkats' 'foraging close calls' [26] were recorded in a total of 10 different groups. Only adult individuals (12 months of age or older) were followed. Recordings were taken in the morning and evening hours, when at least half of all group members were foraging, using a Sennheiser directional microphone (ME66/K6) connected to a Marantz solid-state recorder (PMD660) at a distance of approximately 0.3–1 m from the chosen individual's head. Foraging close calls were extracted from the recordings using the software 'COOL EDIT 2000' (Syntrillium Software Corporation, Phoenix, AZ, USA). To reduce background noises (different from the target vocalization's frequency range, e.g. cicada stridulation), the audio files were filtered with a band reject filter if necessary (less than 5% of all recordings). Collection of close calls for a group was restarted after the dominant female had given birth to a new litter, and the conflict in a group ceased to exist.

(c) Playback experiments

Each playback track contained the close calls of one individual only. At least six different close calls of the individual were used. If enough recordings were available, a playback consisted entirely of different close calls, otherwise the same call was repeatedly used (max. three times within a sound file). The peak amplitude of all calls within a track was equalized to an average level of -12 dB SPL (in COOL EDIT 2000 wave display) to prevent the subject reacting purely to abrupt changes in loudness. The chosen close calls were all recorded within four weeks prior to the experiment. Playback details, such as number of calls and inter-call spacing, differed between the two experimental contexts and are specified in the corresponding sections (§2*d,e*). The calls were played back using the Marantz solid-state recorder connected to a loudspeaker (JBL power supply model nos. MU12-2060100). Before each playback, the volume of the sound was adjusted by ear to match that of naturally occurring close calls according to the current wind conditions [18]. The person conducting the experiment attached the loudspeaker to his leg and followed the subject at a distance of 1–3 m. The subject's behaviour was videotaped with a Canon HD camcorder (CANON HD CMOS Camcorder LEGRIA HF200 (E) 15× optical zoom). The baseline behaviour was filmed prior to each trial. The duration of this pre-exposure focal sample matched the length of

the playback track. For consistency between the trials, the subject had to be foraging (sniffing and scratching the soil) together with at least half of the group. When the calls of group members were presented, the call provider had to be outside of the subject's hearing range (out of the experimenter's sight or at least 10 m away). In addition, every time the individual was digging (head completely below ground level), went on raised guard (guarding on a rock or a bush), was out of sight due to obstacles like vegetation, was too close to the call provider or physically interacted with another group member (food competition, submission and grooming), the playback was paused and restarted after the meerkat had resumed foraging. In cases when predator or group encounters interrupted the experiment, a break of 30 min was given to the subject before carrying on, and again half of the group had to be foraging. Subjects were exposed to four (during the period with conflict) or five (during the period without conflict) conditions per session. To avoid order effects, the presentations of the test playback and the controls were selectively randomized across the experimental series. Only one experimental series was conducted in a given group per day. None of the sound files was used twice in the same group, but some served as controls in other groups.

(d) Period of social conflict

Playbacks during periods of social conflict were 5 min in duration and included 21 close calls separated by 15 s of silence. The subject was filmed during and 5 min prior to the playbacks. The inter-playback interval was approximately 15 min. Groups with a pregnant dominant female and subordinates who were close to being evicted provided opportunities for the experiment. The subject had to be a subordinate adult female, which had been subjected to dominance assertion behaviours such as anal marking or chinning [21], and had been seen to submit on numerous occasions to the dominant female. The test playback consisted of close calls of the within-group dominant female. Close calls of the dominant male controlled for dominance status and the calls of a within-group subordinate female for sex. As a control for female dominance and reproductive state, the subject was also presented with the calls of a pregnant out-group dominant female. In one group, we were not able to record the close calls of the dominant male because it was an immigrant from a non-habituated group and could not be approached with a microphone. In another instance, we had to conduct an experiment without a subordinate female control, as we did not have the recordings of the required close calls at the time when the subject was threatened with eviction. In total, 10 subordinate females from six different groups were tested (between one and four animals per group). Maximally, two experimental series per group per breeding cycle were conducted. All experiments in a group were separated by at least 14 days, except in one group, where we conducted the experiments on two consecutive days on two subordinate females being threatened by the dominant female at the same time. This was due to the fact that the subjects in our experiments experienced aggression for only 2–4 days before evictions.

(e) Period without social conflict

During the period without social conflict, each playback was 2-min long and included nine close calls separated by 15 s of silence. We shortened the playback track length in comparison with the experiments in the conflict period to allow the completion of one experiment (test condition plus all controls) per active foraging session. Furthermore, analyses of the 5-min experimental period had indicated that the effect of the playback was obvious within the first 2 min. The sequences of filming during and before the playbacks were each 2-min long, and the inter-playback interval was approximately 9 min. The same

individuals investigated in the experiments during the conflict period were meant to be the subjects of this experimental series. However, in one group, the former subordinate subject became dominant, another female had died and one had disappeared. Therefore, only seven individuals from four groups could be tested. These experiments were conducted during a period when the dominant female did not show signs of pregnancy, and when subordinates were not threatened with eviction, or aggressed against by the dominant female. In total, five playback conditions were used. Two consisted of the close calls of the within-group dominant female. In one case, the calls were recorded during the same conflict period as the ones used for the earlier experiment. The calls of the second playback were recorded a few days prior to the non-conflict period experiments. Another two of the five playbacks contained calls of the same out-group dominant female previously used in the conflict situation. The recordings for these tracks again dated from the two previously mentioned periods, one with and one without the threat of being evicted. Finally, one playback was made of close calls of an out-group subordinate female as an additional control for familiarity.

(f) Video analysis

Videos were analysed frame-by-frame using OBSERVER XT v. 7.0 (Noldus Information Technology). We specifically focused on the amount of time the animals spent approaching the loudspeaker. This immediate response was only recorded if it occurred within 5 s after the most recent call. The emission of submission calls was recorded at any time in the video. A change in call frequency might indicate a temporary modification of the subject's overall behaviour induced by the playback. Submission calls elicited due to the vicinity of a more dominant animal were not taken into account (playback was paused immediately at the onset of such encounters and only continued after subject resumed foraging more than 5 m away from that individual). To assess changes in the baseline behaviour, the duration of 'head ups' (vigilant scanning of the surroundings on four legs) were included in the analysis. For confirmation of unbiased analyses of the responses, an assistant who was unfamiliar with the questions of this study blind coded half of the videos recorded during the conflict period. Analyses suggest a strong inter-observer reliability (Spearman's ρ : $r \geq 0.83$, $p < 0.001$ for all three response variables).

(g) Statistical analysis

Analyses were conducted using SPSS (v. 17 and 19). Only exact non-parametric tests were used due to the small sample size [27]. For each set of experiments, an overall analysis of the different treatments was performed using a Friedman's test. In a post hoc analysis, the test trials were compared with each control trial using an exact Wilcoxon signed-ranks test. When experiments from periods with different social context were contrasted, the period of social conflict was denominated as the test treatment. In such instances, only the first 2 min of each playback were taken into account, and it was also verified that different results in the two experimental series were not caused by the variation in sample size (see the electronic supplementary material, table S2 for further information). For the experiment during the conflict period, the videotaped sequence prior to the playback was compared with the actual playback film record (exact Wilcoxon signed-ranks test) to ensure that differential reactions of the subject were induced by the playback and not just by being followed or due to a current heightened behavioural state. For post hoc tests, we used a sequential Bonferroni correction for small sample sizes [28] because of repeated pairwise comparisons. Given the relatively small sample sizes, we also computed 95% CIs for effect sizes using a bootstrapping method with 10 000 repetitions

to verify the statistical power of our sample using R v. 2.12 (see the electronic supplementary material).

3. Results

(a) Period of social conflict

Subordinate female subjects responded distinctively to the playback of close calls from the dominant female but not to any other class of subjects controlling for sex, status or female dominance and reproductive state of the caller. We found that during periods of social conflict, subjects responded significantly differently to close calls of the dominant female compared with all other control playbacks (Friedman, d.f. = 3, $n = 8$; approaching loudspeaker $\chi = 18.43$, $p \leq 0.001$; emitting submission calls $\chi = 14.63$, $p \leq 0.001$). Post hoc analyses revealed that the subjects spent more time approaching the loudspeaker and emitting submission calls in the test treatment than in any of the controls (figure 1 and table 1; electronic supplementary material, videos S1 and S2). The 5-min focal recordings before each playback did not differ in submissive behaviour and vigilance between the four treatments (d.f. = 3, $n = 8$; emitting submission calls $\chi = 2.83$, $p = 0.42$; heads up: $\chi = 1.95$, $p = 0.63$). The duration of approaching the loudspeaker was not recorded, as by definition, it had to occur within 5 s after a call had been played back. However, when comparing the 5 min before and during the test playback, we found that the subjects always emitted more submission calls (exact Wilcoxon test: $Z = -2.67$, $p = 0.004$, $n = 10$) and showed more head ups ($Z = -2.29$, $p = 0.020$, $n = 10$) during the playback than before. The comparison of the 5 min before and during the control playbacks showed no significant differences ('emitting submission calls': dominant male $Z = -1.60$, $p = 0.25$, $n = 9$; out-group dominant female $Z < 0.001$, $p = 1.00$, $n = 10$; subordinate female $Z = -1.60$, $p = 0.25$, $n = 9$. 'Head ups': dominant male $Z = -1.13$, $p = 0.30$, $n = 9$; out-group dominant female $Z = -1.17$, $p = 0.28$, $n = 10$; subordinate female $Z = -1.48$, $p = 0.16$, $n = 9$).

(b) Period without social conflict

During periods without social conflict, subjects ignored the played-back calls of their dominant female in the same way as they did the control playbacks of calls of other individuals. Neither of the response variables differed significantly between the playback treatments (Friedman, d.f. = 4, $n = 7$; approaching loudspeaker $\chi = 2.48$, $p = 0.76$; emitting submission calls $\chi = 3.76$, $p = 0.44$). When we compared dominant female playbacks during periods with and without social conflict, we found that the subjects spent significantly more time approaching the loudspeaker and emitting submission calls during the conflict period when they were threatened with eviction (figure 2). Whether the played-back calls of the dominant female had been recorded during a period with or without social conflict did not influence the result (for all comparisons, exact Wilcoxon test: $Z = -2.37$, $p = 0.016$, $n = 7$). Bootstrapping of the effect sizes and calculation of 95% CIs verified the reported results from the non-parametric tests and demonstrated that our sample size was robust enough for a high degree of confidence in the observed effects (see the electronic supplementary material, figure S3).

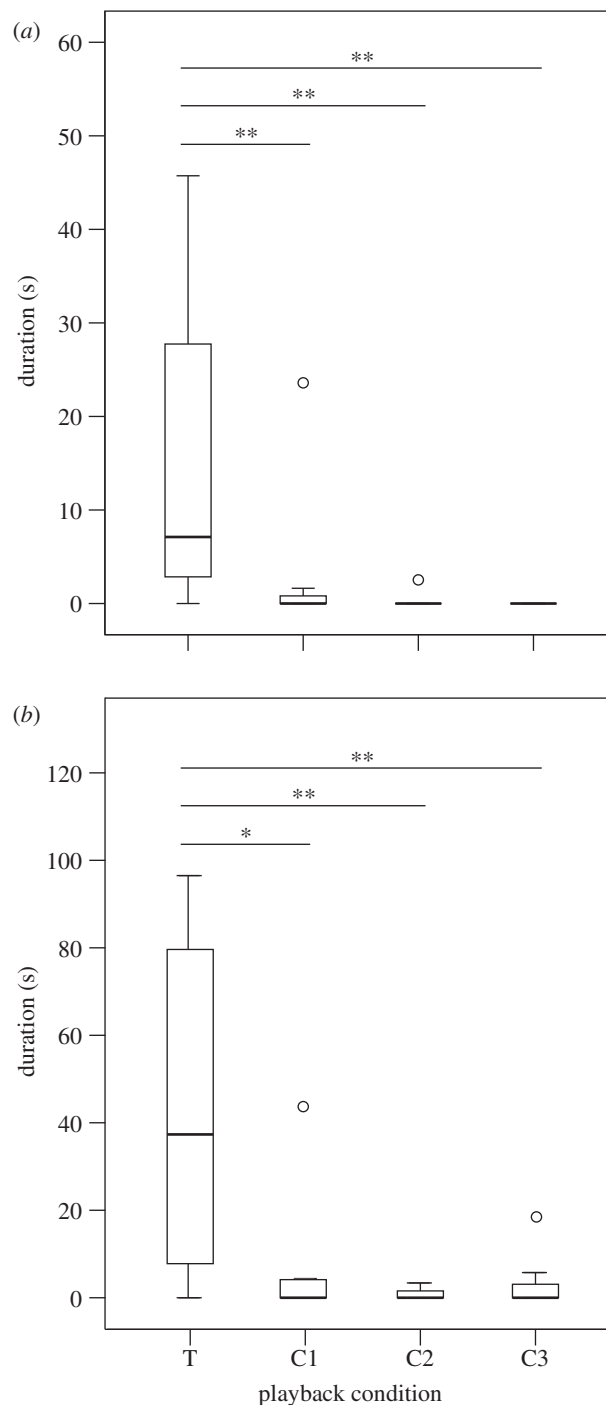


Figure 1. Duration of reactions of subordinate female meerkats in the playback experiment conducted during a period of social conflict: (a) approaching the loudspeaker, and (b) emitting submission calls in the test (T) and in the control (C1–C3) treatments. T, dominant female; C1, dominant male; C2, out-group dominant female; C3, subordinate female ($*p \leq 0.05$; $**p \leq 0.01$).

4. Discussion

Meerkats responded flexibly to the frequently emitted close calls of other foraging group members depending on the current state in their relationship with particular individuals. Subordinate females that experienced repeated, aggressive dominance assertion from their dominant female showed a differential response to her close calls but not to the close calls of any other category of conspecifics. When the subjects were exposed to their dominant female's vocalizations, they approached and looked in the direction of the loudspeaker for a longer period of time than to any of the control

Table 1. Comparisons between the test treatment (close calls of the dominant female) and all the controls during the period of social conflict (exact Wilcoxon signed-rank test, * $p \leq 0.05$; ** $p \leq 0.01$).

playback	<i>n</i>	<i>Z</i>	<i>p</i>
<i>(a) approaching the loudspeaker</i>			
dominant male	9	-2.521	0.008**
subordinate female	9	-2.521	0.008**
out-group dominant female	10	-2.666	0.004**
<i>(b) emitting submission calls</i>			
dominant male	9	-2.38	0.016*
subordinate female	9	-2.521	0.008**
out-group dominant female	10	-2.666	0.004**

categories. In fact, the subjects seemed to actively search for the sound source, as they changed direction several times during the playback to approach the location where they heard the latest call being played back. Furthermore, subjects actively demonstrated submissive behaviour towards the loudspeaker, and in most cases, they did this repeatedly. Such reactions never occurred in the control treatments, when the close calls of the dominant male, another subordinate female or an out-group dominant female were played back, nor during the non-conflict period to the dominant female's calls.

The adjustment of the subjects' own behaviour to the close calls of their dominant females was only obvious during the conflict period. Close calls are the most common meerkat call type, constantly emitted during foraging by almost all individuals [13]. As such vocalizations are generally considered to maintain group cohesion, we can assume that they represent an example of a cooperative signal that directly enhances each group member's fitness. In addition, our experiments indicate that female meerkats have developed the capacity to use the individually distinctive acoustic cues in close calls as a means to monitor their social environment, and flexibly adjust their behaviour. This ability might be adaptive in maintaining a 'safe' distance to their dominant female, or if she is already too close, to appease her with submissive behaviour in periods of conflict.

The submissive behaviour displayed by the subjects, when hearing the dominant female's close calls, could be interpreted as fear conditioning, a fearful response based on simple association learning between a cue or a signal and the immediate consequence of being attacked [29]. However, close calls are only emitted in the foraging context and are therefore not linked with aggressive behaviour. This contradicts fear conditioning being the origin of the observed response. Rather than responding to the acoustic stimulus of the close call alone, the subjects' reactions seemed to indicate that they were responding to the risk of not submitting to the individual with which they associate the calls [5]. Upon hearing the calls, subjects did not just show any submissive behaviour to other meerkats close by but moved towards the loudspeaker and looked out, as if searching for the individual producing those specific calls, the dominant female (see the electronic supplementary material, video S1; M. B. Manser 2002, unpublished data). It is plausible that female meerkats have learned to show the submissive reactions specifically to close calls of an individual who has recently aggressed them. Thereby, observations on females under the threat of eviction indicate that subordinates take not only the

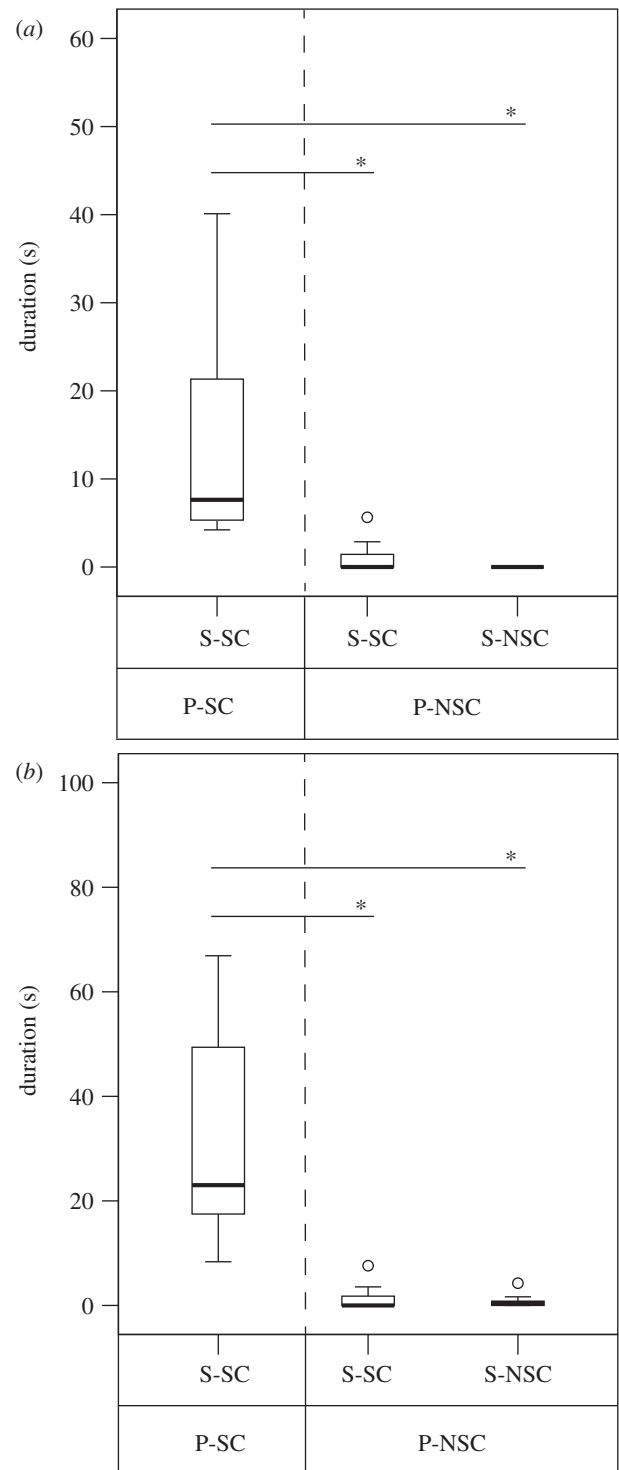


Figure 2. Duration of reactions, (a) approaching the loudspeaker, and (b) emitting submission calls, of subordinate female meerkats to the dominant female's close calls during a period of social conflict (P-SC) and a period without social conflict (P-NSC). The stimuli were recorded during a period of social conflict (S-SC) and a period without social conflict (S-NSC). (* $p \leq 0.05$).

most recent interaction into account, but more likely a series of recent interactions. Prior to two of the experiments in the threatened context, we witnessed how the subject female submitted to the dominant while simultaneously grooming her and receiving grooming back, that is, a positive affiliative interaction. Such close proximity and reciprocity of behaviour suggests that subordinates are not just demonstrating immediate behavioural reactions to specific individuals and their immediate preceding interaction, but that they are continuously assessing and updating their relationship to other group members.

The experiment performed during the non-conflict period without the threat of eviction served to rule out a potentially confounding variable concerning the results of the first experimental series. In meerkats, there is a strong increase in aggressive behaviour shown by the dominant female towards her subordinates in the second half of her own pregnancy [22,23]. The close calls used for the experiment in the conflict context were recorded shortly before the playbacks were conducted. As the dominant females showed clear signs of pregnancy during this time period, it could not be excluded that the foraging close calls contained some sort of an aggressive cue caused by a change in their physiology (e.g. hormones related to pregnancy). However, in the experiment where the threat of being evicted was absent, when we played back calls recorded during both periods with or without signs of pregnancy, none evoked a response. This therefore suggests that during the conflict period, identity cues were responsible for the reactions we observed, and these are only of importance in eliciting a response during the critical eviction period, and not during a period without conflict. Hence, threatened females appeared to make an association between a specific close call, the individual that produced it, and the behaviours they have experienced in the recent past from this producer.

During periods without social conflict, we could not accurately predict which subordinates would experience aggression from the dominant female during the late stage of her pregnancy. Hence, all experiments during periods without conflict were conducted after those performed during a period with social conflict. However, we think that there were no carry-over effects or habituation affecting the outcome of our second experimental series. There was a break of at least 40 days between the two experiments, and as a single meerkat produces on average four close calls per minute [13], it is safe to assume that each subject was in the meantime exposed to a large number of close calls all around itself. Owing to this high frequency, we are confident that the different inter-playback intervals in the two series had no effect on the results.

This particular sensitivity to the dominant female's vocalizations and an adjusted response based on the current state of their relationship have major fitness advantages for subordinate meerkats. It is very costly for a meerkat to be evicted from her group, since she is unlikely to survive for long periods by herself [23,24]. Therefore, typically threatened subordinate females try to secure their acceptance within the group by submitting to the dominant female when she is close by or by avoiding her spatially [21]. Similarly, in other animal societies, non-agonistic cues including, for example, body posture, are used to monitor the location or behaviour of group members or conspecifics and thus play a crucial role in mediating social interactions. Our

experiments also show that although social monitoring seems a constant process, also in non-conflict periods [5], the responses to these non-agonistic cues only become obvious when of clear advantage. The same individuals reacted very differently to the same stimulus in the two experiments. Understanding the complexity of the study organism's social ecology is therefore absolutely critical when attempting to design and interpret experimental manipulations, especially when negative results are obtained.

Social monitoring based on constantly available cues, such as contact calls, is probably a common feature used by social animals to strategically adjust their behaviour towards other group members based on the current state of their relationship. This experiment, together with previous work in meerkats [5], shows that subordinates monitor the spatial position of other group members and strategically adjust their behaviour to maintain a positive relation with the dominant female. The cognitive mechanisms underlying these skills do not seem to reflect stereotyped responses to cues or signals based on simple associative learning, but rather indicate information processing and a simultaneous integration of subtle temporally variable assessments of the state of relationship to other group members. The capacity for individual recognition, the assessment of the current social context (via a representation of the state of the relationship) and demonstrating the according strategic response to reduce risk of impending conflict, seem to be determining features not only in humans, but also in non-human animal societies. Whether social monitoring and strategically adjusted responses to ever-changing social contexts are also common in individualized group-living species of other vertebrate and potentially even invertebrate taxa still needs to be tested. This ability might represent the evolutionary precursor to more advanced socio-cognitive skills in other non-human animal taxa, and ultimately humans.

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Data accessibility. The electronic supplementary material contains two tables (tables S3 and S4) with the raw data used for this study.

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