Vocal grooming in meerkats: weakly bonded subordinates call more in response to dominants

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ABSTRACT

Physical grooming is often used to maintain social bonds in animal groups but the time available for grooming each group member may be limited. Vocal exchanges have been proposed to serve as a solution for sustaining social bonds without the need for physical proximity. To explore this possible social function of vocal exchanges, we examined the effect of dominance and dyadic bond strength of the interacting partners on the intensity of vocal interaction in meerkats (Suricata suricatta). Focusing on "sunning calls", socially facilitated vocalisations produced when meerkats warm themselves in the sun, we conducted experiments, where we played sunning calls to individuals and recorded their responses. Subordinates increased their call rate in response to calls from dominants with whom they had weak associations during sunning periods and to calls from subordinates with whom they had strong associations. These patterns support the notion of meerkat sunning calls having a social regulatory function, potentially as a bonding or appeasing signal. Our results reflect the dichotomy between the subordinate and dominant individuals and underscore the strategic nature of social relationships within a despotic society. Engaging in continuous reciprocal interactions can signify commitment, promoting tolerance and cooperation. Investing in such interaction with influential dominants could lower the chances of aggression and would fit the "vocal grooming" functionality of such call exchanges. Accumulation of evidence of vocal exchanges reflecting social relationships, together with establishing a causal link between them, would demonstrate that remote "vocal grooming" is a fundamental mechanism for maintaining social affinity in nature.

***Keywords**: remote grooming, vocal interactions, social ties*

INTRODUCTION

Robin Dunbar's (1998) vocal bonding hypothesis suggests that as group size increases, the time available to physically groom each individual may become limited and that vocal interactions among group members can complement and perhaps even replace the social function of physical grooming. Frequently, the tendency to respond to vocal signals of conspecifics can be correlated with social affinity. In many social species, strongly bonded individuals engage in both mutual physical grooming and vocal interactions more frequently than those with weaker social bonds (Arlet et al., 2015; Kulahci et al., 2015), resulting in a positive relationship between physical grooming and vocal interactions. For example, dyads of male chimpanzees (*Pan troglodytes schweinfurthii*) were more likely to engage in other affiliative behaviours such as grooming on days when they participated in pant-hoot displays, suggesting that joint vocal activity might represent bonding (Fedurek et al., 2013). Vocal exchanges can also be negatively correlated with social affinity, when weakly bonded individuals engage more frequently in vocal exchanges, while strongly bonded individuals engage more frequently in physical grooming (Chereskin et al., 2022). These processes could potentially reflect strategies for maintaining existing social ties or improving the strength and stability of weak ties, and both could have fitness implications for group living animals (Lusseau et al., 2006).

Most of the existing evidence linking the social function of grooming and vocal exchange behaviours is derived from studies of primates (Arlet et al., 2015; Kulahci et al., 2015; McComb and Semple, 2005). However, recently the association of primary bonds with affiliative physical interactions and of secondary bonds with vocal exchanges have been reported in bottlenose dolphins (*Tursiops aduncus*) (Chereskin et al., 2022). This raises questions regarding the suggested parallels between the social function of vocal exchanges and physical grooming. How commonly do vocal exchange patterns independently reflect social affiliation across taxa? Under which social conditions could vocal exchanges be beneficial for maintaining already existing strong bonds or for improving weak ones? Do vocal exchanges directly affect the stability of social relationships in animal groups?

We investigated the latter question in meerkats (*Suricatta suricata)*, a cooperatively breeding mongoose species that lives in highly cohesive groups (Clutton-Brock and Manser, 2016). Meerkats show a despotic dominance hierarchy with a dominant breeding pair and subordinate helpers (Clutton-Brock and Manser, 2016). Within the subordinate class, the hierarchy is less obvious: age and weight largely explain the dominance relationships among subordinate females (Thavarajah et al., 2014), however, overall dominance-related associations among subordinates are infrequent (Madden et al., 2011). Intra-group social interaction and cooperative behaviour patterns are also not associated with kinship (Clutton-Brock et al., 2001; Madden et al., 2012) and groups show no sexual segregation during diurnal activities (Gall and Manser, 2018). While conflict among meerkats is most extensive within the same sex, such intra-sex conflicts are low during the non-breeding season (Kutsukake and Clutton-Brock, 2006a). Instead, meerkats cooperate and coordinate their actions with all group members on a day-to-day basis (Gall and Manser, 2017). However, the dominant-subordinate asymmetry has been repeatedly shown to influence social relationships (Kutsukake and Clutton-Brock, 2006a; Kutsukake and Clutton-Brock, 2008a) in both reproductive and non-reproductive contexts (Kutsukake and Clutton-Brock, 2008a; Madden et al., 2009). Physical

grooming is one of multiple aspects of meerkat behaviour where a dominance dichotomy is evident (Madden et al., 2009). Adult subordinates were more likely to groom the dominant female than vice versa (Kutsukake and Clutton-Brock, 2006b) and dominant males received more grooming from other group members while providing less (Kutsukake and Clutton-Brock, 2010). The only fully reciprocal grooming relationship among adult individuals exists between the dominant male and female. As group size increases, grooming networks become sparser, suggesting that individuals are limited in the number of grooming partners (Madden et al., 2009). The duration of grooming by a dominant male decreases in larger groups (Kutsukake and Clutton-Brock, 2010), in agreement with Dunbar's hypothesis (Dunbar, 1998). However, subordinates spend more time grooming the dominant male in larger groups, suggesting a higher investment in bond maintenance, perhaps due to stronger competition (Kutsukake and Clutton-Brock, 2010).

Thus, allogrooming in meerkats is linked to the regulation of social relationships via appeasement of the dominant individuals (Kutsukake and Clutton-Brock, 2006b; Madden and Clutton-Brock, 2009). Given the social organisation of meerkat groups (Madden et al., 2009) and their reliance on vocalizations for social monitoring (Demartsev et al., 2024; Reber et al., 2013) we hypothesised that meerkats' vocal exchange patterns would reflect their social relationships and could serve as prosocial behaviour (behavior that produce benefits to others, Burkart et al., 2009), similarly to allogrooming. A candidate vocalization that we explored in this regard is the "sunning call"; a short and tonal call produced mostly in the morning after a group has emerged from its sleeping burrow and spends up to an hour warming up in the sun (Demartsev et al., 2018). Sunning calls are socially facilitated and only produced when other individuals are present or have been heard calling. Additionally, individuals avoid overlapping the calls of their group mates and call in a turn-taking pattern (Demartsev et al., 2018) suggesting a call-and-response interaction rather than a group chorusing behaviour. During the morning sunning period, there are relatively few physical social interactions between the individuals. However, on cloudy or windy mornings, when meerkats are unable to sun effectively, they often engage in grooming and play behaviour (VD, GG, ASP, MM personal observations), potentially indicating the time after emergence from the sleeping burrows as a "social time" aimed at reaffirming bonds before initiation of group travel and foraging. Acoustically, sunning calls resemble sentinel calls (Rauber and Manser, 2017), short note calls produced while running (Demartsev et al., 2024; Manser, 1998) and submission calls (Manser, 1998) calls. However, while running short notes and submission calls are produced in long and rapid sequences, sunning calls are emitted either as single note or in short (mostly double or triple note) bursts (Demartsev et al., 2018).

The production of sunning calls during the low conflict, stationary and passive sunning behaviour and the structural similarity to submission calls, have led us to predict that sunning call exchanges may be a form of social regulatory activity functioning as appeasement and affected by the social relationships between the interacting individuals. As individuals often groom other group members selectively, dependent on the strengths of their social relationships, we expected a higher rate of sunning call exchanges between strongly bonded individuals. Given the dominance-related asymmetry of physical grooming in meerkats, we expected to find a similar asymmetry in sunning call exchanges as an indication of their function in maintaining bonds with influential individuals in the group. To test these predictions, we estimated the context-dependent social association between group members by performing a social network analysis based on physical proximity in the sunning period. In parallel, we conducted a series of playback experiments in which we recorded the calls of individual meerkats while also transmitting to them the sunning calls of different group members.

METHODS

We collected the data for this study at the Kalahari Research Centre (KRC), Northern Cape, South Africa (Clutton-Brock et al., 1998a) in June-August of 2019 and 2021. The individually marked meerkat population of the Kalahari Meerkat Project (KMP) on site is fully habituated to human presence, including behavioural observations and audio recordings from < 1m. All field procedures were performed according to existing protocols and were subject to the ethical regulations of the University of Pretoria, South Africa (permit: EC047-16) and the Northern Cape Department of Environment and Nature Conservation (permit: FAUNA 1020/2016).

Social association

As a part of long-term data collection at the KMP, meerkat groups were continuously monitored with individual and behavioural data collected by a team of trained volunteer researchers. Through this dataset, we had access to information on age, sex and dominance status of all animals included in the study. To estimate social association within meerkat groups, we collected data on the physical proximity of individuals during sunning behaviour. Each morning, we observed the selected group of meerkats during their emergence from the sleeping burrow. In 2019 we observed four groups on average 7.25 (range 5-9) mornings and in 2021 we observed three groups for 9.3 (range 8-12) mornings (see Table S1 for detailed group composition). To avoid unbalanced sampling due to the variable duration of the daily sunning period, we performed one full group scan per day. As soon as all group members emerged from the sleeping burrow and started sunning, we documented the identity and association of all individuals using the gambit of the group (Whitehead and Dufault, 1999). Specifically, we considered all individuals observed within 1 m of each other as being together. At the start of the sunning session, the animals are usually static and there is little rearrangement. We did not record subsequent movements and changes of positions that mostly occur shortly before groups depart from the burrow area and start foraging.

From the proximity data collected while sunning, we generated weighted, undirected networks. In these, each group member was represented as a node and the edges between individuals were calculated as the number of times two individuals were observed sunning together, divided by the number of total observation days (all individuals were present in all days). As constructing social networks using small sample sizes can lead to misrepresentation of the weights of individual social relationships (Lusseau et al., 2008), we estimated social tie uncertainty for all constructed networks. Following Lusseau et al. (2008) we designed a bootstrapping procedure in which we resampled (with replacement) the proximity association data collected for each group, thus keeping the sample size (number of observation days) constant but assessing the robustness of the calculated tie weights and their dependence on the sampling effort. We repeated the bootstrapping procedure 1000 times and for each tie, calculated the 95% range as a confidence interval for the tie length (Fig. S1). Examination of the results shows that the collected proximity data is sufficient for representing the

social tie gradient within the studied meerkat groups and that the differences between tie lengths within the group were maintained, even after considering the 95% range of confidence on the calculated values.

To allow pooling of multiple groups, we standardized the network edge values by transforming them into group z-scores. As direct pairwise tie strength (edges) could not be calculated for individuals who were never observed sunning in physical proximity to others within the data collection period, we calculated an additional network metric that allowed us to connect all individuals in a meerkat group, resulting in a non-zero "connectivity strength" metric for all dyads. Dyadic connectivity strength was determined by calculating the weighted "shortest path" (Sosa et al., 2021), while not necessarily a direct connection, between each pair of individuals in a group using the ANTs package (Sosa et al., 2020). For a given pair of nodes, this metric sums up the inverse edge weights of all sequential edges along the shortest path between the two nodes and multiplies this value by the number of edges in the path (ESM, Fig. S2). Low values are associated with strong connections and large values are associated with weaker connections.

Playback experiments

Before the playback trials, we recorded individual sunning vocalizations of all group members older than 6 months. For the audio recordings, we used a Marantz PMD-661 digital recorder (Marantz, Japan) with a sampling rate 44.1 KHz, 16-bit and a directional Sennheiser ME66 microphone with K6 power module (Sennheiser electronic GmbH, Germany) placed on a telescopic boom pole and held at ~30 cm from the focal animal. We examined the recorded files in Avisoft-SASLab Pro (Avisoft Bioacoustics e.K, Germany) and selected 30 to 60-second segments with clearly recognizable sunning calls, low background noise and no additional meerkat vocalizations. We constructed the playback tracks by adding a leading 30-sec background noise segment as a "control phase" and an additional trailing 30-sec segment of background noise as a "recovery phase", resulting in 90 to 120-second tracks (ESM, Audio S1, Fig. S3). We used each track in up to three playback trials, with individual animals exposed to any specific track only once (ESM, Table 1).

We played the tracks using a BRV-1 Bluetooth speaker (Braven, Australia), frequency response 180Hz to 13kHz ± 3dB, positioned on the ground, in an inconspicuous spot behind a shrub or a sand mound and at a 0.5-1 m distance from a focal sunning meerkat. Using an Android mobile device, Nokia 7.1 (Nokia Corporation, Finland) paired to the speaker via Bluetooth we activated the playback. Meerkats targeted by the playback were all > 6 months old and sunning at > 1.5 m distance from their nearest neighbours. On a given morning no more than three trials were performed, and no individual was targeted as focal receiver more than once. We kept a minimal interval of 15 min between consecutive trials and a minimal interval of 48 hours between trial days performed in the same group. Throughout the playback, we recorded the vocalizations of the focal individual and noted all behavioural responses. If during the payback the focal individual moved away or additional meerkats entered the 1.5 m radius, we terminated the trial and omitted it from the analysis.

For each trial, we documented the identities of both the individual whose sunning calls we used in the playback track (sender) and the focal individual (receiver). Given the pervasive role of dominance in meerkat social relationships, we constructed a "dominance_dyad" variable, reflecting the dominance statuses of the sender and the receiver in each trial (e.g., in a Dominant→Subordinate trial the calls of a Dominant individual (Clutton-Brock et al., 1998b) in the group were played to a Subordinate receiver). In 2019 we performed 83 playbacks, targeting 36 meerkats in four groups with an average of 20.7 trials per group (range 12-30). In 2021 we performed 78 trials in three groups, targeting 29 meerkats with an average of 26 trials per group (range 15-35). Our playback dataset sample sizes were: Dominant→Dominant x2, Dominant→Subordinate x30, Subordinate→Dominant x24, Subordinate→Subordinate x114. As the Dominant→Dominant dyad type was strongly underrepresented, we excluded these trials from subsequent analysis.

Audio processing and statistical analysis

We inspected the recorded files in Avisoft-SASLab Pro and manually labelled both the recorded playback calls and the calls emitted by the receiver in the three phases of the trial (control, stimulus, recovery) using Avisoft cursors. For each of the playback phases, we calculated the call rate by dividing the number of calls emitted by the receiver by the duration of the playback phase. To control for contextual and individual variation in basal call rates, for each trial we subtracted the call rate in the stimulus and recovery phases from the call rate in the control phase. The resulting Δ call rate values represent an individual change in calling behaviour between the phases of a given playback trial, thus accounting for unobserved effects that could affect individuals' basal call rate (e.g. calls of remote neighbours).

To test for differences in age and dominance-dependent association while sunning we fit a lognormal generalized linear mixed model (GLMM) with the adjusted tie lengths as the response variable and paired age-dominance relationship as an explanatory variable. Group identity was fitted as a random effect. To test whether the sunning call playbacks affected individual call rates and thus whether call rate changed in different phases of the playback experiments, we fit pairwise Wilcoxon tests and controlled for multiple testing using a Benjamini and Hochberg (1995) correction. This was done, as the data did violate multiple assumptions of GLMMs and we thus decided to use a non-parametric test. To test for the effect of the senders and receiver dominance (dominance dyad) and social (adjusted tie length) relationships on receiver call rate during the stimulus phase of the playback, we fit an LMM with the Δ call rate as a response variable and an interaction between the explanatory variables (adjusted tie length and dominance pair). We controlled for individuals tested during multiple trials by adding focal individual identity as a random effect and used the Tukey method for post hoc p-value adjustment.

All statistical analyses were conducted in R 4.0.3 and 4.3.1 (R Development Core Team, 2020). We used mixed-effects models (Bates et al., 2015) to account for repeated testing of the same receivers. Tests were two-tailed and considered significant at $P < 0.05$. For the linear model analyses, we checked that the model assumptions (normality of error, homogeneity of variance and absence of multicollinearity) were satisfied, using DHARMa (Hartig, 2017). We used the "phia" (De Rosario-Martinez et al., 2015) and "emmeans" packages (Lenth et al., 2021) for post-hoc analysis and calculation of p-values from the mixed effects models.

RESULTS

We found that during sunning the subordinate adult individuals (> 2 years) in the group had relatively weak associations (longer tie length) with the two other subordinate age classes (yearling and sub-adults). Subordinate adults also had week associations with dominant individuals of the group.

The younger age classes (sub-adults and yearlings), on the other hand, were frequently sunning together with one another, and together with the dominant individuals, resulting in shorter ties (strong association) in the network (Fig.1, Table 1).

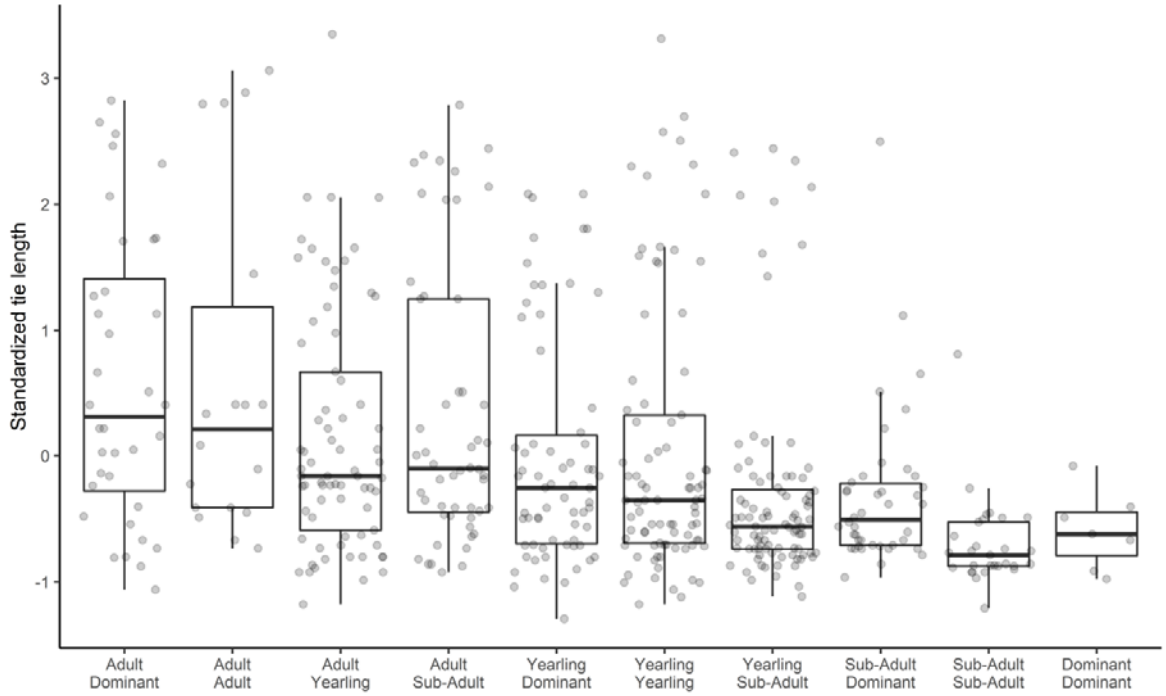

Figure 1: The distribution of standardized tie-lengths (y-axis) within Dominance/Age dyads (x-axis) in meerkat groups during sunning. Each category denotes the tie-length between pairs of individuals of a Dominance/ Age combination according to subordinate age classes: **Adult** > 2 years., 2 > **Yearling** > 1 year, 1 > **Sub-Adult** > 0.5 years, and the dominant male or female individuals: **Dominant**. A shorter tie length indicates stronger social association.

Table 1: Output for loglinear GLMM model. Standardized tie length was the response variable. Dominance/Age dyad was the explanatory variable, with the Dominant-Dominant dyad as the reference category. The subordinate age classes are: **Adult** > 2 years., 2 > **Yearling** > 1 year, 1 > **Sub-Adult** > 0.5 years, the dominant male or female individuals are: **Dominant**. Group was included as a random effect. Significant effects are marked in bold. $\sigma^2 = 1.47$, N Groups = 7, Observations = 499, Marginal $R^2 = 0.016$. All dyads involving subordinate adults showed significantly longer tie-length estimates, indicating weaker social association while sunning.

	Predictors	*Estimates*	*CI*	*p*
	(Intercept)	1.51	1.07 – 2.14	**0.019**
Dominance/Age dyad	Adult_Dominant	1.71	1.18 – 2.47	**0.004**
	Adult_Adult	1.75	1.18 – 2.58	**0.005**
	Adult_Yearling	1.46	1.02 – 2.08	**0.039**
	Adult_Sub-Adult	1.5	1.05 – 2.15	**0.027**
	Yearling_Dominant	1.29	0.90 – 1.84	0.167
	Yearling_Yearling	1.29	0.91 – 1.85	0.154
	Yearling_Sub-Adult	1.13	0.79 – 1.61	0.514
	Sub-Adult_Dominant	1.22	0.85 – 1.76	0.286
	Sub-Adult_Sub-Adult	0.95	0.65 – 1.40	0.808

Examining the overall effect of sunning call playbacks on meerkat vocal behaviour, we found a significantly increased call rate of receivers in the trial phase (Wilcoxon Test: $\chi^2 = 64.79$, df = 2, $P < 0.001$, Figure 2, Table S2). Specifically, receivers increased their call rate during the stimulus phase compared to the control ($P < 0.001$) and the recovery phase ($P = 0.046$). Similarly, the call rate remained higher in the recovery phase compared to the control phase ($P = 0.036$).

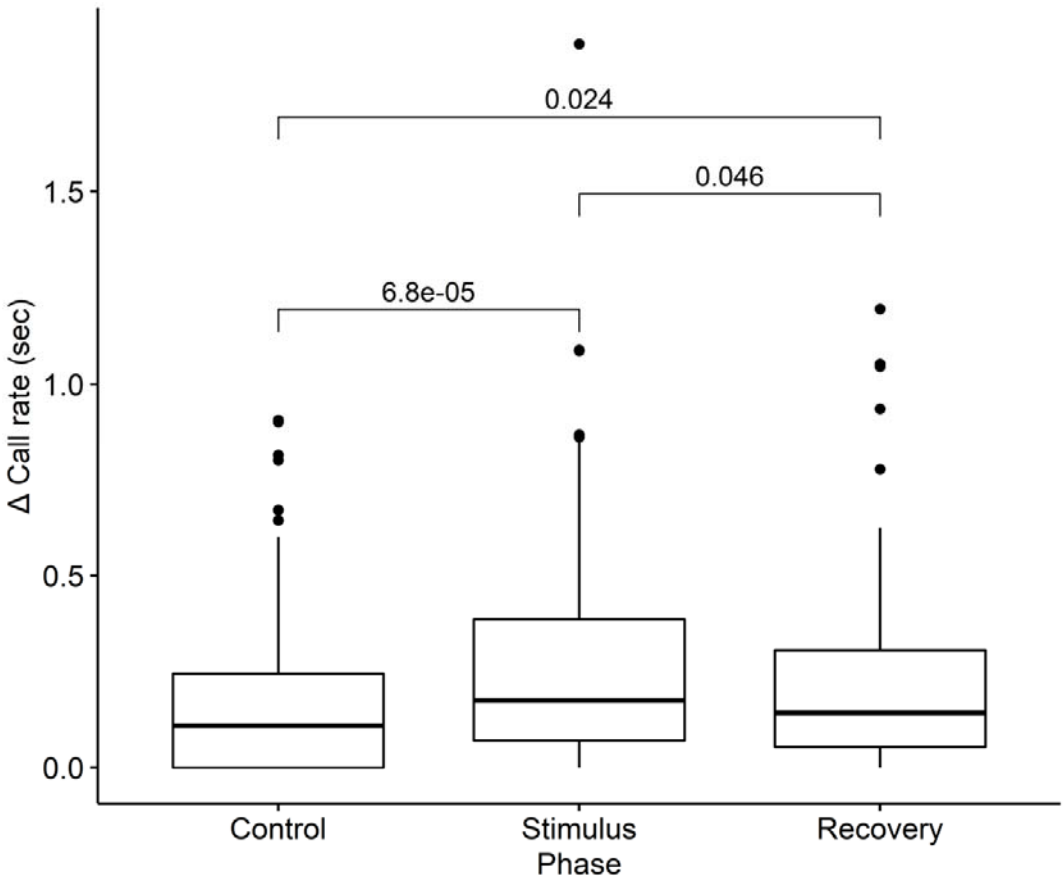

Figure 2: Receiver call rate in the three phases of the playbacks. In comparison with the Control, the call rate is significantly increased during the stimulus phase. The call rate during the Recovery phase is significantly lower in comparison to the Stimulus but significantly higher in comparison to the Control phase (Wilcoxon paired test).

Testing if the receiver's vocal response is affected by the dominance relationships (dominance dyad) and the strength of social ties with the sender, we found a significant interaction between tie-length and dominance dyad (Table 2). Subordinate receivers (> 6 months) showed an increase in call rate when responding to playbacks of closely bonded subordinate senders and when responding to weakly bonded dominant senders (Fig. 3, Table S2).

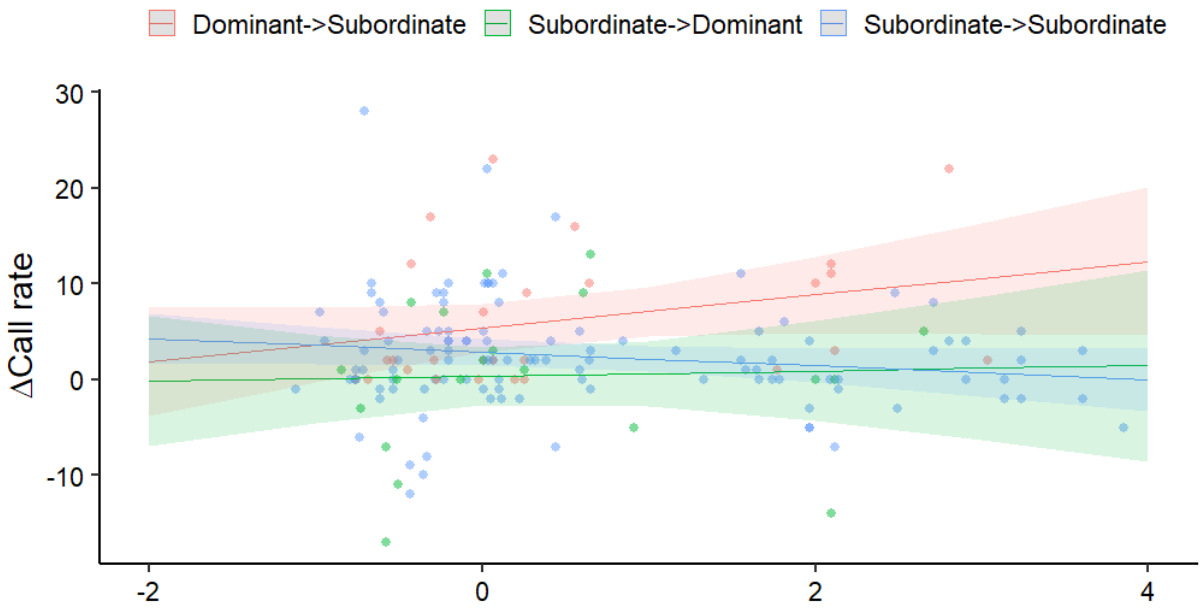

Figure 3: The effect of social tie length on the vocal response to sunning calls playbacks. A change in the call rate between the control and stimulus phases. The curves represent the model prediction regression with a 95% CI as shaded areas of the respective colour. The colours of the curves show the dominance relationship of sender-receiver pairs. Dominant→Subordinate (red) represents cases in which calls of a dominant sender were played to a subordinate receiver. The other two categories follow the same logic.

Table 2: Full output for linear mixed effects model. Δ call rate (difference between the call rate produced in the stimulus and control phase of the playback) is the response variable. The interaction term between adjusted tie length and dominance dyad are explanatory variables. Dominant→Subordinate dominance dyad is the reference category. Receiver identity is included as a random effect. Significant effects are marked in bold.

Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.16	0.09 – 0.24	**<0.001**
Adjusted tie length	0.06	-0.01 – 0.12	0.076
Dominance dyad [Subordinate→Dominant]	-0.10	-0.22 – 0.03	0.121
Dominance dyad [Subordinate→Subordinate]	-0.07	-0.15 – 0.01	0.094
Adjusted tie length * Dominance dyad [Subordinate→Dominant]	-0.08	-0.18 – 0.01	0.094
Adjusted tie length * Dominance dyad [Subordinate→Subordinate]	-0.08	-0.14 – -0.01	**0.020**

DISCUSSION

The younger subordinate age classes (< 2 years) in meerkat groups showed strong within-age class association while sunning and were also strongly associated with the dominant individuals. Adult subordinate meerkats (> 2 years) on the other hand showed overall weaker association within and between the age classes. Both dominance and dyadic bond strength played a significant role in meerkat sunning call exchanges between non-juvenile individuals (> 6 months). Subordinate receivers increased their call rate when responding to dominants with whom they had *weak* bonds, relative to the overall distribution of social bonds in the group. In contrast, when exposed to calls from subordinate individuals, subordinate receivers responded with a slightly elevated call rate when they had *strong* bonds with the sender. Additionally, all categories of meerkats showed an increase in sunning call rate during playbacks, which independently replicates our previous results showing that meerkat sunning calls are socially facilitated as part of vocal interactions with conspecific individuals (Demartsev et al., 2018).

A stronger response to the sunning calls of dominants could indicate a social regulation mechanism and is in line with the social and appeasement functions of sunning calls which we previously proposed (Demartsev et al., 2018). The despotic structure of meerkat groups has strong implications for the social dynamics between subordinate and dominant individuals. Aggressive dominance assertions by dominant females, to the extent of full eviction of subordinate females from the group, are common in the later stages of the dominant female's pregnancy (Kutsukake and Clutton-Brock, 2006a). Evicted and nearly-evicted individuals often attempt to re-integrate into the group by exhibiting submissive behaviour towards the dominants (Clutton-Brock et al., 2010; Reber et al., 2013) or undertaking "pay-to-stay" tactics (e.g. providing alloparental care, MacLeod et al., 2013). Dominance-related aggression has a long-term negative effect on the relationship between opponents in meerkats and only avoidance has been reported to effectively reduce received aggression, as reconciliation behaviour has not been observed and submission did not appear to affect aggression rates (Kutsukake and Clutton-Brock, 2008a). While most studies on conflict management in meerkats focused on the reproductive conflict between same-sex group members, there are likely social regulation mechanisms that also manifest outside of the breeding season.

In Dominant-Subordinate interaction dyads, the receivers' call rate increased when responding to playbacks of individuals with whom they had weak bonds, highlighting the importance of dominance in meerkat groups. The value of having stable bonds with the dominant individuals has been suggested to drive subordinate meerkats to invest in grooming (Kutsukake and Clutton-Brock, 2006b; Kutsukake and Clutton-Brock, 2010) and submission behaviours, especially when more vulnerable (Reber et al., 2013). Sunning call exchange patterns could have similar drivers, as coordinated vocal exchanges are often attributed to a prosocial function, reducing tension and building social relationships (Fedurek et al., 2013; Laporte and Zuberbühler, 2010). Vocal signals towards dominant individuals have been associated with submission (Kutsukake and Clutton-Brock, 2008a), reconciliation (Silk et al., 1996) and willingness to interact (Laporte and Zuberbühler, 2010). Submission behaviour in meerkats is often accompanied by high-pitched vocalizations and a crouching posture (Kutsukake and Clutton-Brock, 2006a) and while sunning calls are similar in acoustic structure to submission calls, sunning individuals do not assume a crouching posture and the calls are produced by most individuals in the group, regardless of their dominance status or sex (Demartsev et al., 2018). Thus, the overall low conflict context of sunning behaviour in meerkats makes it less likely that sunning call exchanges serve as submission interactions. Reconciliation, if defined broadly as improving weakened social bonds (Aureli, 1997), rather than an immediate and specific set of post-conflict behaviours, could potentially fit the observed patterns of subordinates increasing their call rate towards weakly bonded dominant individuals. However, the increase in call rate when responding to strongly bonded subordinates is harder to explain in the context of reconciliation, suggesting rather to function as a confirmation of the strong bond.

Increased vocal activity when interacting with dominants could also be related to heightened stress (Lemasson et al., 2010). In red-capped mangabeys (*Cercocebus torquatus*), large hierarchical gaps between

callers have been shown to cause shorter response times in both the high-ranking and low-ranking partners (Meunier et al., 2023). Speaking tempo in humans has been shown to increase under both stressful (Kirchhübel et al., 2011) and joyful (Scherer, 2003) conditions suggesting that arousal rather than valence (Briefer, 2012) might be driving the increase in vocal activity. Similarly, stress response would not generally explain our results of subordinate meerkats increasing call rate when responding to both weakly affiliated dominant and closely affiliated subordinate individuals. The increase in subordinate call rate is likely determined by a more complex motivation when interacting with socially valuable group members.

Engaging in continuous and reciprocal interaction could imply cooperation (Takahashi et al., 2013) and promote tolerance (Smith et al., 2011). For a subordinate meerkat, improving a weak bond with an influential dominant is of general importance and investing in a pro-social interaction with dominant individuals would fit the "vocal grooming" functionality. Within the subordinate class in meerkat groups, the social hierarchy is less steep and aggression events are rare (Kutsukake and Clutton-Brock, 2006a). The cohesive nature of meerkat groups and relatively low variance of ties within the subordinate class may lead to weak drivers towards improving bonds with other subordinates and a general preference for interacting with already closely bonded partners. It is important to acknowledge that our chosen social bond metric (proximity while sunning) offers only a snapshot of the complex social interactions among meerkats and that incorporating a combination of different affiliative behaviours, perhaps via a multilayer network approach, could provide a more nuanced perspective (Finn et al., 2019).

It is possible that the observed response patterns could further diverge across the sexes, especially during the breeding season as the reproductive conflict between the dominant and subordinate meerkats intensifies (Young et al., 2006). Our sample size did not allow us to robustly test the differences between all possible combinations of sex, dominance and bond strengths of both sender and receiver individuals. However, while reproductive conflict clearly affects the social relationships of group members (Kutsukake and Clutton-Brock, 2008b), meerkat groups ultimately comprise a cohesive mixed-sex social unit with individuals of both sexes participating in cooperative activities i.e. sentinel (Rauber and Manser, 2018), babysitting (Clutton-Brock et al., 2000), pup feeding (Carlson et al., 2006), and mobbing (Graw and Manser, 2007). Thus, bond maintenance and conflict prevention are not limited to within-sex mechanisms and are likely to also act more generally to support the social structure and functionality of a group.

The tendency for individuals to interact more with closely (Kulahci et al., 2015) or loosely bonded partners (Chereskin et al., 2022) can have different underlying causes. Maintenance of stable bonds requires effort and vocal grooming may function as an addition to physical grooming (Kulahci et al., 2015). In comparison, the relatively low cost of vocal exchanges could be beneficial for extending individuals` social connectivity and maintaining valuable but loose affiliations (Chereskin et al., 2022). Similarly, vocal exchanges could be used for establishing novel ties, in a process similar to vocally mediated pair formation in songbirds (D'Amelio et al., 2017). Priming (establishing) ties remotely would be especially useful when physical proximity between weakly bonded individuals might result in aggressive interactions, as could be the case between dominant and subordinate meerkats in some cases.

While this work has demonstrated a relationship between vocal exchanges and social bond strength, we have yet to establish a causal link between these variables. In addition, the mechanism by which such a causal relationship might act remains unclear. Given that cooperative activities are often associated with the strengthening of bonds in both animals and humans (Cheney, 2011; Heesen et al., 2020), one possibility is that coordinated signalling exchanges could serve as a ritualized version of joint action, signifying commitment to the partner and the task (Heesen et al., 2020; Wolf et al., 2016). Similar to the pair-bonding function of duetting in birds (Hall, 2004) or gibbons (Geissmann and Orgeldinger, 2000), continuous and repeated call exchanges could imply cooperation (Pougnault et al., 2022) and increase social tolerance (Cheney et al., 1995).

The accumulation of potential examples of vocal grooming beyond the primate lineage suggests that it could be a common phenomenon in nature. Besides the proposed impact on the long-term stability of social units in animals, it has been suggested that vocal grooming provides a plausible scenario for the early stages of language evolution (Dunbar, 1998; Kulahci et al., 2015). Given the broad relevance of this hypothesis to the evolution of sociality, long-term monitoring of both the bond strength and the vocal exchange dynamics would be extremely beneficial in order to causally demonstrate the social function of vocal grooming. It would also be intriguing to explore if the capacity of other communication modalities (e.g. gestural communication, Roberts and Roberts, 2016) for fostering social bonds.

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