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Spatial structure of foraging meerkat groups is affected by both social and ecological factors

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Abstract

Group-living animals need to trade off the benefits and the costs of close proximity to conspecifics. Benefits can be increased, and costs reduced by preferentially choosing specific locations within a group best adjusted to an individual's needs or by associating with specific group members and/or avoiding others. We investigated the spatial structure of meerkat (*Suricata suricatta*) groups and whether it was shaped by social factors such as affiliation or aggression among group members, predation risk, foraging success, or a mix of these different factors. Using social network analyses, based on spatial networks, we found associations between the dominant pair, among males and among same aged individuals, and dis-assortment by sex only in one to two of the six groups. In addition, the structure of meerkat groups was highly variable, as individual strength within the calculated networks was not repeatable over time. Meerkats seemed to adjust their location to their physical environment, as dominant individuals were located further toward the front of the group, where foraging success is likely higher and young individuals located further toward the back of the group, where they can benefit most from the vigilance effort of their conspecifics. We conclude that meerkat groups display a dynamic spatial structure depending on both the current social and physical environmental.

Significance

Group-living animals can achieve greater benefits from close association with conspecifics by choosing specific locations within a group or associating with specific group members and/or avoiding others. A considerable body of work has examined how differences in predation risk or foraging success affect the relative location of individuals within a group. Several studies investigated the association between individuals, in order to draw conclusions on the social structure. However, it is important to disentangle the impact of all of these different aspects on the spatial structure of a group. Here, we provide evidence that both the social and physical environment is important for the spatial assortment of meerkats, a social mongoose foraging in cohesive groups.

Keywords Group structure · Meerkat · Social network analysis · Spatial location

Introduction

The costs and benefits of group living are unevenly distributed as a function of individual traits, within-group spatial location,

and the mobility of a group (Krause and Ruxton 2002). However, most studies focus either on the association between individuals, in order to draw conclusions on the social structure, or they focus on the relative location of individuals

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within a group to assess differences in predation risk or foraging success. Theoretical models and empirical studies suggest that in stationary groups, both predation risk (Hamilton 1971; Patterson 1984; Rayor and Uetz 1990; Rayor and Uetz 1993; Di Bitetti and Janson 2001; Teichroeb et al. 2015) and foraging success (Rayor and Uetz 1990; Hirsch 2007; Hansen et al. 2016) increase toward a group's periphery. In mobile groups, not only individuals at the edge of the group, but also especially those at the front or the rear of the group's progression are at higher risk of predation, depending on the mobility of the predator (Bumann et al. 1997; Krause et al. 1998; Krause and Ruxton 2002; Di Blanco and Hirsch 2006). Similarly, foraging success increases toward the front of the group, as the individuals located there are the first to reach a food source (Sterck et al. 1997; Hirsch 2007).

Variation in the costs of close proximity to group members is often dependent on an individual's traits and the traits of its surrounding group members, such as rank, sex, or age, and can vary in time and space, leading to the emergence of non-random spatial distributions of phenotypes within a group (Krause and Ruxton 2002; Croft et al. 2005; Ruckstuhl and Neuhaus 2005; Carter et al. 2015). Through further non-random association or avoidance of particular conspecifics, each individual can increase the benefits of grouping or decrease its costs to an even greater extent. For example, individuals of the same sex or age might associate more often than random (Carter et al. 2009; Hirsch 2011; Kurvers et al. 2013), and subordinate or sub-adult individuals might avoid encounters with dominant or older group members and therefore avoid central positions or they might be actively excluded from these locations (Hall and Fedigan 1997; Asensio et al. 2008; Hirsch 2011). Such processes could drive patterns of assortativity (preference for alike individuals) or disassortativity (preference for different individuals) in the spatial positioning of individuals.

Meerkats (*Suricata suricatta*) provide an ideal study organism to identify how the trade-offs faced by individuals lead to the occupation of their specific spatial locations within a group. Meerkats are a cooperatively breeding mongoose species populating the southern part of Africa and living in groups of 2–50 individuals (Clutton-Brock and Manser 2016). They have a despotic hierarchy, with a dominant breeding pair and subordinate helpers (Clutton-Brock et al. 1999a). Individuals compete for dominance status and reproductive opportunities within a sex (Clutton-Brock et al. 1998) leading to a hierarchy in subordinate individuals (Thavarajah et al. 2014) as well as the temporary expulsion of some individuals from the group (Young et al. 2006). Meerkats face competition early in life, competing for access to helpers that provide them with food as pups (Hodge et al. 2007, 2009; Madden et al. 2009) and adjusting their growth when at risk of being outcompeted by their littermates (Huchard et al. 2016). The dominant female is the most aggressive individual within the

group and also highly competitive for food, especially when her dietary requirements increase, as during the breeding season (Kutsukake and Clutton-Brock 2006). Meerkats forage cohesively and move continuously in search of mainly small prey scattered in the sand (Doolan and Macdonald 1996). During foraging, meerkats are at high risk of predation by terrestrial and aerial predators (Clutton-Brock et al. 1999a) which has led to the evolution of a coordinated sentinel system (Clutton-Brock et al. 1999b) and a sophisticated vocal system (Manser et al. 2014).

Here, we investigated whether the spatial structure of foraging meerkat groups is influenced by social competition, by the potential predation risk or foraging success in different locations, or by several or all of these factors. If social competition among individuals plays the most important role, then we expect to see individuals avoiding their strongest competitors, potentially occupying specific locations, e.g., less rewarding and more risky locations, relative to the whole group (Hirsch 2011). As our data was collected during the breeding season, when the dominant female can be highly aggressive to subordinate group members (Kutsukake and Clutton-Brock 2006), we expect the highest competition between subordinate and dominant individuals and also between individuals of the same sex or age (Thavarajah et al. 2014). However, if foraging meerkat groups are spatially structured based on predation pressure or their nutritional needs, we expect individual differences in their location relative to the front of the group based on dominance status and age (Di Blanco and Hirsch 2006; Hirsch 2007). In particular, as has been previously shown on meerkats (Barnard 2000; Bousquet 2011), we expect older and dominant individuals, as the more experienced and competitive foragers, to be more likely located toward the centre-front of the group, where foraging success is highest. In contrast, we expect younger individuals, lacking knowledge and experience in searching for their own prey, to be located toward the centre-back where they can benefit from the vigilance by their conspecifics, while taking more time to find and extract prey and be less vigilant themselves (Barnard 2000). These different aspects are not exclusive; therefore, if multiple factors are important, we expect to find a combination of these patterns, i.e. an age and dominance related distribution toward the front and rear as well as an avoidance pattern between similar individuals and the avoidance of dominant individuals by subordinates within the same sex.

Methods

Study site and subjects

The study was conducted at the Kalahari Meerkat Project, Kuruman River Reserve, in the Northern Cape of South Africa. Description of the habitat and climate is provided in

(Clutton-Brock et al. 1998). Data were collected between January and March 2015 on six meerkat groups, with group sizes ranging from 9 to 16 individuals and with an age range from 0.2 to 7.1 years, whereby 3 of the 6 groups had dependent pups of less than 3 months old. See Table 1 for detailed information on the number of individuals for each trait-category. The data were collected during 17 afternoon foraging sessions, with two to three sessions per group and at least 3 days between visits to the same group. The afternoon foraging session during this time of the year typically lasted for 1.5 to 2 h, starting when the meerkats resumed foraging after their rest during the hottest hours of the day and ending with the return of the group to their sleeping site. All animals in this study could be individually identified through dye mark combinations (Jordan et al. 2007) and were habituated to human handling and close observation, within a distance of 1 m. The dominance status, i.e. whether an individual was part of the dominant breeding pair or not, sex, and age of each individual in a group as well as the group size were known.

Recordings of location and behaviour

We continuously recorded the location and behaviour (resting, foraging) of four individuals in the same group, with each of four observers simultaneously following one of the focal meerkats (the dominant pair and two adult subordinates, when possible of different sex). The location of each individual was tracked at 1-Hz frequency using a small *GPS unit* (22 g, CDD.ltd, Greece) recording the GPS (global positioning system), carried by each observer. Up to 4 additional adult meerkats (mean \pm SD = 1.6 ± 1.4 individuals per group) were fitted with a *GPS unit* attached on a collar around the neck before the start of a session. We did not attach a collar on meerkats younger than 1 year or those that shied away from a collar during a given session. In addition, we usually avoided collaring the same individuals during the different sessions in the same group, but where possible we collared the same number of males and females. In order to estimate the

accuracy of the GPS data, we left the tags hanging in a bush with known location for up to 24 h. From these recorded locations, we calculated the accuracy, whereby 99% of fixes were within 5 m, 82% of fixes were within 2 m, and 60% of fixes were within 1 m. The GPS data on the focals' movements were filtered using the speed between points, thus excluding locations within unrealistic speeds. In addition, we used visual inspection for outliers. For both methods, we used R statistical software version 3.3.0 (R Core Team 2016) and the packages 'psych' (Revelle 2016), 'mapprotools' (Bivand and Lewin-Koh 2016), and 'move' (Kranstauber and Smolla 2016). To estimate the location of group members which did not carry a *GPS unit* or were followed by an observer, we conducted 'scans' at 2-min intervals. During these scans, each of the four observers estimated the distance and direction of each visible meerkat in relation to his or her own location. From this distance and direction estimates as well as the known location of each observer at each 'scan' given by the carried *GPS unit*, we calculated the coordinates of each seen meerkat in the group, using R and the packages 'mapprotools' (Bivand and Lewin-Koh 2016), 'geosphere' (Hijmans 2015), 'move' (Kranstauber and Smolla 2016), and 'NISTunits' (Gama 2014). For all following calculations and analyses, these data were projected in a longitude/latitude coordinate system with the WGS 84 datum. For individuals seen by multiple observers, we took the mean of each of the individually estimated locations. This also allowed for a detailed assessment of the estimation error by each observer (see Supplement A). To maintain a similar temporal resolution for all tracked group members, we subsampled the GPS data of these individuals by sampling coordinates from the start time of the scan. We removed dependent pups from the following analysis to avoid confounding effects, as dependent pups tend to follow adults in very close proximity making the analysis of associations between some adult group members impossible. Thus, the final dataset comprised the location data of an average of $85 \pm 24\%$ (mean \pm SD) of each group (excluding pups) at 2-min intervals.

Table 1 Number of individuals per group with each of the different traits of interest, i.e. dominance status, age category, and sex. Pups were excluded in the analysis, and subadults and juveniles were clumped together in the category "subadult" for the analysis

Group	Sessions observed	Dominance status		Age category				Sex		Total	Total (pups excluded)
		Dominant	Subordinate	Adult > 1 year	Subadult 7-12 months	Juvenile 4-6 months	Pups 0-3 months	Female	Male		
A	3	2	13	11	1	3	1	8	7	16	15
B	2	2	8	3	4	3	0	4	6	10	10
C	3	2	10	8	4	0	0	6	6	12	12
D	3	2	8	7	2	1	0	6	4	10	10
E	3	2	11	10	3	0	2	3	10	15	13
F	3	2	5	7	0	0	2	2	5	9	7

Meerkats behave differently when resting compared to foraging and hence the association patterns are likely to differ between contexts. Thus, we excluded scans where at least two individuals were resting at the start of the scan, i.e. the sampling time for all locations. Consequently, we calculated the time each individual spent resting during the time from the start of each scan (scan time) to 60 s after the scan time from the behavioural data of the four followed meerkats and excluded scans with two or more individuals resting for at least 30 s. Thus, we excluded 162 of the 816 scans performed during the 17 sessions.

Statistical analysis

Association patterns

For all analyses, we used R version 3.3.0. Specifically, we used the packages ‘sna’ (Butts 2014) to calculate networks, ‘asnipe’ (Farine 2016a) and ‘assortnet’ (Farine 2016b) for the social network analysis and data stream permutations, and ‘psych’ (Revelle 2017) for the statistical analysis. As the data was collected and analysed by the same person, it was not possible to conduct this study in a ‘double-blind’ or ‘blind’ way. To investigate whether meerkats associate preferentially with similar individuals based on their dominance status, sex, or age class, we generated directed networks for each session. Rather than calculating a proximity network, we calculated ‘nearest neighbour networks’, as the latter type of network is better in accounting for differences in group dispersion between the different days of data collection. Thus, in each of these networks, the edge weights were defined as the number of scans where an individual was the nearest neighbour of another individual, divided by the total number of scans in which at least one of the two individuals were observed. From the GPS data, we first calculated the distance between all observed individuals during a given scan and defined the nearest neighbour as the closest individual by distance. We included a threshold of 15 m whereby the closest individual was not considered as a nearest neighbour if the distance was greater than 15 m. We used 15 m as individuals should still be within audible distance of each other. To assess how individuals of different traits associate with each other, we calculated the weighted assortativity coefficient using the package ‘assortnet’ (Farine 2016b) for each group separately, while collapsing all sessions for a group. We performed 1000 data stream permutations where we only allowed swaps between individuals of the same group, within the same session and scan, thus changing the total proportion of scans where individuals were the nearest neighbour of some other individual. Using this randomisation method, we also accounted for missing individuals in the data as well as the data structure, i.e. different numbers of individuals in each trait category. We then compared the observed assortment value with those of the 1000 random networks and calculated significance as the proportion

of randomised values that were larger than the observed value for assortment (P_A) and smaller than the observed values for dis-assortment (P_D) (Farine 2014; Farine and Whitehead 2015). We excluded one group (group F) for the age comparison as it consisted only of adult group members.

Network strength and individual repeatability

To test whether the strength of individuals, i.e. the total proportion of time an individual was the nearest neighbour of other individuals (calculated as the sum of edge weights; a measure of local social density) depended on the dominance status, sex, or age class of an individual, we calculated the difference between the mean strength of dominants and subordinates, males and females as well as adults and subadults. The differences in mean strength were calculated over all the sessions for each group for the observed data and were compared to the difference in mean strength for each of these traits calculated from data randomised with 1000 data stream permutations. For the age comparison, we again only included five of the six groups, as all individuals in group F were adults. In order to investigate whether individual strength was repeatable over multiple different sessions, we calculated the intraclass correlations (ICC2k) (Shrout and Fleiss 1979) for each group for the observed data as well as for each of 1000 data-stream permutations. We then compared the observed vs. the random ICC for each group separately. For this analysis, we only included five of the six groups, as the last group (group A) had different individuals missing each session as they were babysitting the pups.

Location of individuals within the group

To examine whether individuals preferentially use specific locations within the group, we first calculated the group’s centroid (mean x, y position across all individuals) for each scan and then the distances to the centroid for each individual. To account for differences in group spread between sessions and groups, we normalised the distances within each session by dividing the distance to the centroid of each individual during each scan by the maximum distance calculated for a given session. To assess whether the pattern of spatial locations of individuals with specific characteristics (dominance status, age class) differed from a random pattern, we randomised the data 1000 times, by randomly changing the identity of each individual for each session. For the observed data and each randomisation, we calculated the mean normalised distance to the centroid for each trait and compared the overall variance within a trait, by calculating whether the observed variance was within the 95% quantile of the random data distribution. Furthermore, we calculated the order of individuals within the group in the direction of group movement (front to back). We projected the coordinates of each individual by the turning angle of the group, thus aligning the direction of

group movement with the y-axis and then ranking each individual by its y-coordinate. To compare individuals of all groups, we normalised the order within the group by dividing the rank of an individual within the group progression by group size, thus getting the normalised order with values between 0 and 1. We randomised the data 1000 times by randomly assigning an individual a new identity and the according traits for each session. We calculated the mean normalised order for each trait category for the collected and the randomised data and compared the variance in the means for dominance status and age class between the randomised and the collected data to assess whether the pattern in the collected data differed significantly from random.

Data availability The datasets during and/or analysed during the current study are available from the corresponding author on reasonable request.

Results

Association patterns

Examining the distribution of edge weights in the mixing matrices for dominance shows that between 40 and 60% of all edges occurred between subordinates, roughly 40% between dominant and subordinates and only 2–5% between dominant individuals (Table S1). Using the weighted assortativity coefficient, we found significant assortment for dominance in only one of the six groups (group D) (Table 2, supplementary Fig. S2a). The mixing matrix of this group suggests that the significant assortment might be due to higher assortment between the dominant pair. This is because the edge weights for subordinate-subordinate interactions, although high for this group, were not the highest overall, but the edge weights for dominant-dominant interactions were the highest (together with group F, which however had lower subordinate-to-subordinate values, supplementary Table S1).

The mixing matrices by sex suggest more random assortment and differences between groups, with 4–50% of all edges occurring between males, 43–56% of edges between males and females, and 6–53% of all edges between females (supplementary Table S2). In line with this, we found both assortment (Group F) as well as dis-assortment (group E) by sex (Table 2, supplementary Fig. S2b). Both of these groups had a skewed sex ratio at the time of data collection (Table 1), with many males and few females. While in group F males associated more with each other than in other groups, in group e, only 4% of edge weights were distributed between males, while 50% of edge weights were distributed between the females. Thus, in the group E, the close association of females and low association between males seemed to drive the pattern of dis-assortativity found.

The mixing matrices for age suggest that for four of the five groups, 40–60% of edges occur between adults, and only in one group 50% of edges occurred between subadults (supplementary Table S3a–e). However, when comparing the weighted assortativity coefficient of the collected to the randomised data, we only found significant assortment by age in one of the six groups (group D), where same aged individuals were more likely to associate with each other than with differently aged individuals (Table 2, supplementary Fig. S2c).

Network strength and individual repeatability

When we compared whether network strength, i.e. the total proportion of time an individual was the nearest neighbour of other individuals, differed between individuals based on traits such as dominance status, sex, or age class, we found no differences in network strength for any of these individual traits (dominance status $t = 0.51$, $P = 0.75$; sex $t = -1.37$, $P = 0.13$, age category $t = -0.70$, $P = 0.73$). When comparing whether strength of individuals was repeatable over several foraging sessions, we found no repeatability of network strength for any of the groups ($ICC_B = 0.17$, $P_B = 0.46$,

Table 2 Weighted assortment by dominance, sex, and age for each of the different group. Weighted assortativity coefficient (r), standard error (SE), and significance from data stream permutations (P_A : assortment, $P_D = 1 - P_A$: dis-assortment) are given. Italicized values indicate significance

Group	Dominance				Sex				Age			
	r	SE	P_A	P_D	r	SE	P_A	P_D	r	SE	P_A	P_D
A	−0.086	0.082	0.714	0.286	−0.046	0.085	0.210	0.790	−0.041	0.068	0.147	0.853
B	−0.148	0.077	0.826	0.174	−0.056	0.117	0.133	0.867	−0.083	0.111	0.249	0.751
C	−0.079	0.127	0.327	0.673	−0.092	0.101	0.518	0.482	−0.085	0.096	0.446	0.554
D	−0.056	0.151	<i>0.041</i>	0.959	−0.138	0.113	0.762	0.238	0.003	0.110	<i>0.000</i>	1.000
E	−0.108	0.099	0.845	0.155	−0.141	0.079	0.969	<i>0.031</i>	−0.074	0.066	0.382	0.618
F	−0.216	0.157	0.908	0.092	−0.085	0.175	<i>0.019</i>	0.981	NA	NA	NA	NA

$ICC_C = 0.58$, $P_C = 0.74$, $ICC_D = -0.24$, $P_D = 0.75$, $ICC_E = -0.27$, $P_E = 0.65$, $ICC_F = 0.52$, $P_F = 0.31$).

Location of individuals within the group

The distance to the centre of the group did not differ between individuals of different dominance status (mean dominant normalised distance to centroid \pm SD = 0.22 ± 0.16 , mean subordinate normalised distance to centroid \pm SD = 0.23 ± 0.17 , variance = 0.0001, $P = 0.39$). We found no significant difference in the distance to the centre of a group based on sex (mean female normalised distance to centroid \pm SD = 0.22 ± 0.16 , mean male normalised distance to centroid \pm SD = 0.23 ± 0.17 , variance = 0.0002, $P = 0.28$). In addition, we found no significant difference in the distance to the centre of a group based on age (mean subadult normalised distance to centroid \pm SD = 0.21 ± 0.17 , mean adult normalised distance to centroid \pm SD = 0.23 ± 0.17 , variance = 0.0003, $P = 0.39$).

We found a significant difference in the location within the groups' progression for individuals of different dominance status, with dominant individuals located more toward the front of the group than subordinates (mean dominant normalised order \pm SD = 0.44 ± 0.23 , mean subordinate normalised order \pm SD = 0.56 ± 0.30 , variance = 0.007, $P = 0.001$, Fig. 1a). Similarly, we found a significant difference in the location of individuals of different sex, with males located more toward the back of the group than females (mean female normalised order \pm SD = 0.51 ± 0.27 , mean male normalised

order \pm SD = 0.55 ± 0.29 , variance = 0.0009, $P = 0.037$, Fig. 1b). In addition, we found a significant difference in the location of individuals of different age class, with subadult individuals located more toward the back of the group than adult individuals (mean subadult normalised order \pm SD = 0.58 ± 0.31 , mean adult normalised order \pm SD = 0.51 ± 0.27 , variance = 0.003, $P < 0.001$, Fig. 1c).

Discussion

We examined whether the spatial structure of foraging meerkat groups was influenced by social competition, predation risk, or foraging success. When calculating networks based on the frequency of being the nearest neighbour to another individual, we found no difference in strength among individuals in each of the analysed trait categories, including dominance status, sex, and age. In addition, we investigated the assortment among group members and whether it depended on any of the individual traits. Groups differed in their assortment based on the different traits, with significant assortment based on dominance and age in only one of the six groups, where individuals of the same dominance status and age were more likely to associate. Furthermore, we found both assortment as well as disassortment based on sex in one group each. When investigating the use of specific locations within the group, we found that dominant individuals were located more toward the front of the

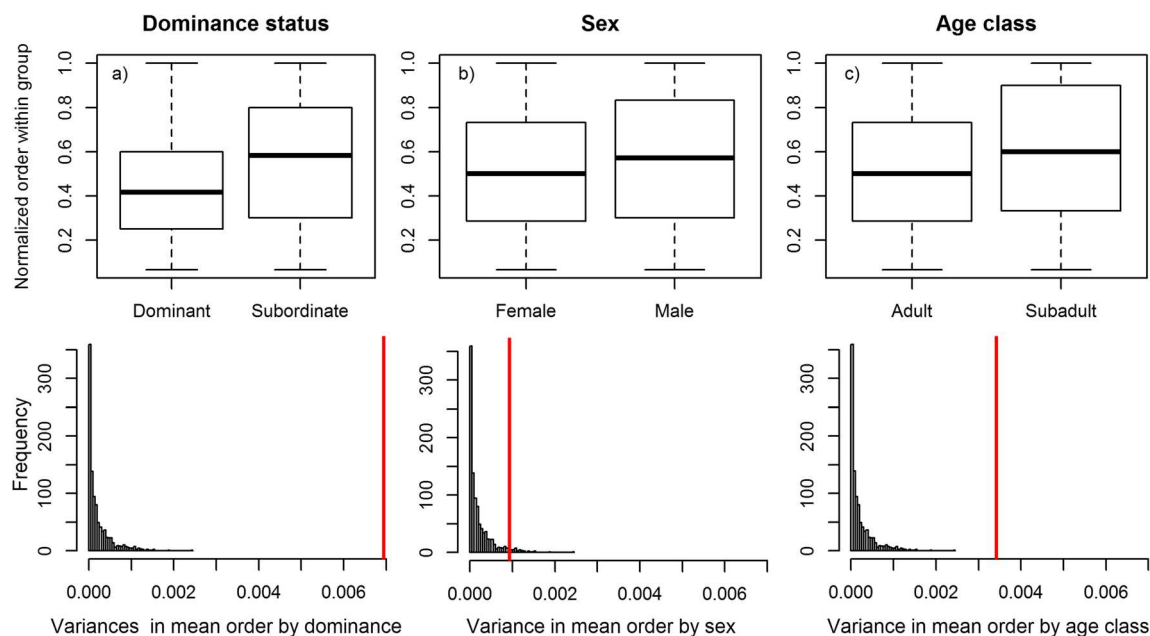


Fig. 1 Mean normalised order of progression within the group in the direction of group movement **a** compared to dominance, **b** compared to sex, and **c** compared to different age classes. Small values indicate being closer toward the front and high values being toward the back. Histograms below the boxplots show the random distribution of

variances within the trait, with the observed variance indicated by the red line. Boxes represent the interquartile range between the first and third quartile of the data; the bold line represents the median and whiskers denote the lowest and highest values

group and younger individuals more toward the back with respect to the direction of group movement.

Our results indicate that the spatial structure of foraging meerkat groups was highly group dependent, influenced by the groups' physical environment and in some groups also by social relationships among individuals. In group D, dominant individuals associated more with each other than in any of the other groups (except group F where association was similar) and more than expected by chance. During the breeding season, and hence the period of data collection, dominant males frequently mate guard, staying close to the dominant female throughout a foraging session (Spong et al. 2008). The group D was the only group where the group did not have dependent pups or the dominant female was already pregnant (as was the case for group B and group C). Thus, it is likely that mate guarding behaviour explains some of the difference in assortativity between the different groups. In group D, individuals associated also more with other individuals of similar age. This pattern might be influenced by the closer association of dominant individuals, which are frequently some of the older individuals. In addition, the three subadults (including the juvenile) in this group associated more closely with each other, as indicated by the mixing matrix (S Table 3D) and it is probably a combination of the two factors explaining the assortment by age for group D. Nevertheless, it is not entirely clear why the younger individuals associated more in this group than in any of the others.

Similarly, it is unclear, why assortment by sex differed strongly between groups, with no assortment in four groups and both assortment (group F) and dis-assortment (group E) in one group each. Both of these groups had a skewed sex ratio at the time of data collection (Table 1), with many males and few females. In group F, males associated more with each other than males and females. In this group, the two females were relatively old and foraged at relatively large distances from the other group members. In addition, this group was marked by continuous fights for dominance between the males throughout the 6 months preceding data collection. Thus, while the males did not fight over dominance at the time of data collection, the dominant male may have stayed close to the other males in order to assert his dominance. In contrast in group E, only 4% of edge weights were distributed between males, while 50% of edge weights were distributed between the females. During the breeding season, especially dominant females can be highly aggressive (Kutsukake and Clutton-Brock 2006). Thus, subordinate females frequently approach and submit to the dominant female during foraging. In group E, the two subordinate females were frequently observed submitting to the dominant female. In addition, the dispersion, as well as nearest neighbour distances were relatively high, and due to our exclusion of nearest neighbours at greater distances, this might explain the low association among the males in this group. The other groups did not show any pattern of assortativity or dis-assortativity along any of the measured traits. This could indicate that in general during foraging, all

group members associate equally and only when competition and conflict arise between some of the group members do individuals start to interact differently. This was also shown in an experimental study on how subordinate females responded to contact calls of the dominant female, depending on the state (aggression or no aggression) of their relationship (Reber et al. 2013).

Theory suggests that foraging success in moving animal groups is higher toward the front of the group as individuals are more likely to encounter prey items (Krause and Ruxton 2002). Thus, we predicted dominant individuals to be preferentially located at these positions. Our results are in line with this prediction and support previous findings by Bousquet (2011) and by Barnard (2000) that dominant individuals in meerkats are more frequently located toward the front of the groups' progression. In addition, literature suggests that predation pressure is highest toward the front of moving animal groups (Bumann et al. 1997; Krause et al. 1998; Krause and Ruxton 2002). We accordingly predicted that young, inexperienced individuals should be located further toward the back of the group, which matches our results. The back likely allows these inexperienced animals to take more time searching for prey, while benefiting from the vigilance of their conspecifics.

While foraging success and predation pressure might be important in shaping the observed spatial structure, dominant individuals might preferentially be located toward the front of the group to influence the direction of group movement. Meerkats have been shown to follow a moving 'vocal hotspot' (Gall and Manser 2017), the area where many contact calls emitted continuously during foraging are heard from. Thus, by locating themselves more toward the front and calling at higher rates, individuals might be able to influence the direction of group movement to a greater extent. However, it is also possible that rather than preferentially locating themselves toward the front, dominant individuals specifically are more likely to be followed than subordinates and thus end up more frequently toward the front of the group's progression. However, we found no differences in the strength for each of the individuals, and also the strength of individuals within the network was not repeatable across multiple different sessions in any of our six groups. This suggests that the spatial structure of meerkat groups during foraging is highly variable, i.e. specific traits are associated to certain preferences for location, but individuals can randomly associate with their group members based on their current personal trade-offs.

Our study shows the difficulties to assess the social factors influencing the spatial structure of wild living groups, where the groups differ greatly in their composition and the associations among their individuals. To investigate these patterns in more detail and to understand whether social competition in its different forms can lead to general patterns found in many different groups in a species, it will be necessary to increase both the sample size in the number of groups as well as in the

time each group is recorded for. In addition, experimental approaches will be necessary to fully disentangle the influence of the physical environment and the impact of social competition on the pattern of spatial association. Yet, by trying to disentangle both of these impacts on the spatial structure of foraging meerkat groups, our results suggest that the spatial pattern of meerkat groups is highly variable and depends both on the physical environment and on social affiliations between group members. Analysing the spatial structure and the associations among individuals together thus provides insight into the dynamic structure of groups, where group members seem to be able to adjust their location within the group to their current perceived trade-offs, such as foraging success or perceived risk as well as to the social dynamic within the group.

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Author's contributions GECG and MBM collected the data with the help of three field assistants and GECG analysed the data. The article was written by both GECG and MBM. Both authors gave final approval for publication.

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Compliance with ethical standards

Ethical approval All data collection adhered to ASAB guidelines. All research was conducted under the permission of the ethical committee of Pretoria University (EC031-13) and the Northern Cape Conservation Service, South Africa (Permit number: FAUNA 192/2014).

Conflict of interest The authors declare that they have no conflict of interest.

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