





## Spatial position relative to group members affects weight gain in meerkats, *Suricata suricatta*

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Social animals often face a trade-off between the costs of foraging competition among group members and the benefits of protection from predators offered by group living. The spatial position of an individual in relation to the other group members during foraging can mediate the effects of this trade-off as individuals at the front or edge may have better access to food resources, but also higher predation risk than individuals near the centre of the group. Using meerkats, *Suricata suricatta*, as a model species, we investigated the effect of individual spatial position within a group on foraging success. We determined the spatial position of individuals in a meerkat group by fitting the animals with high-resolution GPS loggers. As a proxy of foraging success, we used meerkats' individual body weight differences between the start and the end of daily data collection over foraging periods (3 h). We found significant individual differences in meerkats' spatial positions within the group. In addition, age-dependent differences in spatial position became obvious, with older meerkats spending less time in the centre of the group and more time in side positions, subordinate females spending less time in the front, and subordinate males spending more time in the back. Younger meerkats who spent more time in the front of the group relative to older meerkats had decreased daily weight gain, indicating less successful foraging. We also found that the dominant females tended to spend more time towards the front of the group, but gained less weight in this position, contrary to the predicted association between front edge of the group and better access to food resources. Our results suggest that the relationship between weight gain and spatial position is highly nuanced and likely to be dependent on more than just trade-offs between foraging success and predation risk.

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Collective movement of animal groups has been described across taxa including herds of mammals, swarms of insects, schools of fish and flocks of birds (Bode et al., 2010; Farine et al., 2014; Giardina, 2008). The advantages of moving collectively largely overlap with the advantages of social living. In many species, individuals benefit from moving with group members because of increased antipredator vigilance and higher success in between-group competition for food resources (Bednekoff & Lima, 1998; Lehmann et al., 2016). For example, blue monkeys, *Cercopithecus mitis*, are more vigilant when

in lower foliage density, which is associated with higher predation risk, but reduce their vigilance in the presence of kin with which they form strong affiliative relationships (Gaynor & Cords, 2012). Further, animals that move collectively can benefit from the sharing of information about the environment. For example, schools of golden shiners, *Notemigonus crysoleucas*, were able to track environmental gradients (gradual changes in an environmental factor over a specific distance or area) better when moving in larger groups (Berdahl et al., 2013). However, collective living also comes with challenges, such as coordinating optimal decisions among all group members (Conradt & Roper, 2005; Petit & Bon, 2010) and facing intragroup competition over resources such as food (Arseneau-Robar et al., 2023; Holekamp & Sawdy, 2019).

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When moving collectively, animals may mitigate some of the trade-offs between competition and predation risk by occupying different relative spatial positions within the group, which may vary in their predation risk and access to resources (Hall & Fedigan, 1997; Hirsch, 2007; Tkaczynski et al., 2014). While individuals positioned at the front or at the edge of the group might be subjected to higher predation risk, they may also gain better access to food resources compared to those at the centre or the back of the group (Rayor & Uetz, 1990; Rowcliffe et al., 2004; Stahl et al., 2001). For instance, foraging success increases towards the edge of the group in fallow deer, *Dama dama* (Focardi & Pecchioli, 2005). These cost–benefit trade-offs may also be influenced by dominance hierarchies as dominant individuals are often found in positions that are associated with lower costs and higher benefits (Hall & Fedigan, 1997; Murray et al., 2007). In particular, when food resources are scarce, individuals that are located towards the edge of the group may have increased foraging success or food intake (Morrell & Romey, 2008). However, the edge positions are not necessarily the preferred positions for all group members, as dominant individuals in the centre of the group can monopolize food patches or employ scrounger tactics to improve their foraging success (Grant et al., 2002; Hirsch, 2007; Murray et al., 2007).

Quantifying foraging success directly is challenging, and most research on these trade-offs uses indirect methods of estimating foraging success such as counting the number of feeding events per minute (Hintz & Lonzarich, 2018). Here, we aimed to investigate the trade-off between spatial position and foraging success, estimated by individual weight gain, during roughly 3 h foraging periods in meerkats, *Suricata suricatta*. We used weight gain as a measure of foraging success because it takes into account the cumulative effect of numerous foraging events over these 3 h periods and, importantly, the quantity of food acquired, which other indirect measures of foraging success may fail to account for.

Meerkats live in groups of up to 50 individuals, and they are a cooperatively breeding species living in arid parts of Southern Africa (Clutton-Brock & Manser, 2016). During the day, they maintain a cohesive group structure and forage together on dispersed subterranean prey while moving through their territory (Doolan & Macdonald, 1996). Meerkat groups consist of a dominant pair that monopolizes breeding, and subordinate individuals, mostly offspring of the dominant pair, that help raise the young (Russell et al., 2003). Previous research has found that dominant meerkats were frequently located towards the front of the group, presumably due to higher foraging success in the front (Averly et al., 2022; Gall & Manser, 2018). However, the link between spatial position and foraging success has never been tested in meerkats. Here, we investigated the potential link between spatial position and foraging success during cooler and drier winter months (June–September 2023), when prey availability is lower (Doolan & Macdonald, 1996) and any trade-offs between predation risk and foraging success are likely to be most apparent.

We predicted that meerkats at the front of the group, which potentially encounter food resources first, would have increased weight gain at the end of each foraging session. We also predicted that, since the front position might be associated with better assessment of the resource distribution (Focardi & Pecchioli, 2005; Gall & Manser, 2018), more experienced older or higher-ranking meerkats would occupy this position more frequently. In addition, we expected younger individual meerkats, which are potentially more at risk from predation because they are less experienced in responding to predatory threats (Hollén et al., 2008), would spend less time at the front edge of the group, as this position is particularly exposed, especially to sit-and-wait predators (Hirsch, 2007).

## METHODS

### *Study Site and Population*

We conducted the study at the Kalahari Research Centre (KRC), Kuruman River Reserve (28°58' S, 21°49' E), in the Northern Cape, South Africa. The meerkat population on site has been studied since 1993. Meerkats are habituated to human presence and marked with unique dye marks making them easily identifiable at the individual level (Manser, 2018). Individual weights are routinely collected, up to three times per day on 3–5 days per week, by luring meerkats onto electronic scales using a small piece of hardboiled egg or a few drops of water (Manser, 2018). Over 12 h foraging periods meerkats gain an average of  $36.2 \pm 22.5$  g (5.9% of body weight) so there is both substantial gain in body mass over the day on average and also substantial variation in how much weight meerkats gain or lose each day (Clutton-Brock et al., 1998). Weight gain (within 2–12 h daily foraging periods) is frequently used as a proxy for foraging success in this population (Clutton-Brock et al., 1999, 2001; Russell et al., 2003; Thornton, 2008; Thornton & Samson, 2012; Townsend & Manser, 2011) and correlates with meerkat behaviour in a manner that suggests it is a valid proxy; for example, weight gain is reduced in males when they spend more time participating in territorial defence against intruding males (Mares et al., 2012), subordinates that have greater weight gain contribute more to cooperative behaviours such as digging and sentinel guarding (Duncan et al., 2019) and the weight gain of dominant females correlates strongly with the choice of sleeping burrow location, while the weight gain of subordinates correlates with the timing of return to the sleeping burrow (Strandburg-Peshkin et al., 2019).

### *Long-Term Data and Individual Traits*

All meerkat groups in this study were part of detailed longitudinal monitoring that includes daily records over 3–5 days per week of behaviour, group composition, pregnancy, disease, injuries and life history data (Clutton-Brock et al., 2006; Huchard et al., 2016; Sharpe et al., 2002). We used a binary variable for age that merged several age categories used in other studies with meerkats: meerkats that were older than 1 year were considered 'older' and this category included dominant females, dominant males, yearlings (1–2 years) and adults (2 years and older). Meerkats younger than 1 year were considered 'younger' and this category included subadults and juveniles (see Table 1 for detailed group composition and age classification). We chose 1 year of age as a binary cutoff because this roughly represents the age of sexual maturity in meerkats (English et al., 2013). All meerkats were assigned a date of birth based on physical signs of parturition in the mother; for example, a sudden loss in weight and signs of lactation. The age categories of juvenile, subadult, yearling and adult are based on the typical ages of life history milestones (e.g. foraging independence, sexual maturity, dispersal). Meerkats are sexed as pups based on the anogenital distance and sexes are further confirmed by the later appearance of sexual characteristics (e.g. the appearance of the scrotum). Dominance is determined based on aggressive and submissive interactions with other same-sex group members alongside behavioural changes (e.g. anal marking) or physiological changes (e.g. weight; Duncan, 2021).

### *Data Collection Periods*

We obtained data from a series of short-term deployments of meerkat groups between August 2017 and July 2022 (Table 1). The deployments covered nine different groups in total.

**Table 1**  
Summary of group composition and GPS data collection

Group name	Group size	Group composition (recorded/present)		Recording period	Number of recording days
		Older meerkats	Younger meerkats		
HM17	7	1/1 df; 1/1 dm; 0/0 ad; 3/3 ye	2/2 sub; 0/0 juv	06 Aug 2017–08 Sep 2017	13
HM19	18	1/1 df; 1/1 dm; 3/3 ad; 4/4 ye	3/4 sub; 0/5 juv	23 Jun 2019–19 July 2019	12
L19	19	1/1 df; 1/1 dm; 2/2 ad; 4/4 ye	5/5 sub; 0/6 juv	01 Aug 2019–12 Aug 2019	12
ZU21	13	1/1 df; 1/1 dm; 1/1 ad; 7/7 ye	0/0 sub; 0/3 juv	15 May 2021–25 July 2021	16
RW21	12	1/1 df; 1/1 dm; 4/4 ad; 0/0 ye	0/0 sub; 0/6 juv	04 Jun 2021–11 Jun 2021	11
NQ21	11	1/1 df; 1/1 dm; 0/0 ad; 6/6 ye	0/0 sub; 0/3 juv	11 Aug 2021–17 Aug 2021	7
NQ22	11	1/1 df; 1/1 dm; 0/0 ad; 2/3 ye	0/1 sub; 0/4 juv	12 Jun 2022–15 Jun 2022	4
SI22	11	1/1 df; 1/1 dm; 0/0 ad; 2/3 ye	1/2 sub; 0/3 juv	29 Jun 2022–3 Jul 2022	5
RW22	14	1/1 df; 1/1 dm; 0/2 ad; 0/3 ye	2/4 sub; 2/5 juv	12 Jul 2022–19 Jul 2022	8

We report these categories for consistency with other publications, but our analyses use binary variables for sex (male/female), rank (dominant/subordinate) and age (older/younger). The numbers in Group composition column are the ratio between meerkats present in the group and meerkats actually recorded. df = dominant female; dm = dominant male; ad = adult (>2 years); ye = yearlings (1–2 years); sub = subadult (6–12 months); juv = juveniles (3–6 months).

### Spatial Positioning: Collar Deployment

We deployed custom-built collars on as many meerkats in a group as was possible, without the need for anaesthetization. We lured meerkats to stand up bipedally using a water bottle, then secured the collars using a custom designed magnetic clasp. The closing system of the collar included two magnets (measuring 1 mm × 5 mm × 5 mm) affixed to 3D-printed plastic clasps positioned at both ends of the leather band. This design aimed for effortless closure while necessitating human action to open it.

We constructed each collar according to the neck size and weight of the individual meerkat, with the collar weight (22–26 g) not exceeding 5% of the animals' body weight, in accordance with Golabek et al. (2008). Attached to the collar was a GPS tag (Gipsy 5 in 2017 and 2019, Axy Trek Mini in 2021; Technosmart, Colleverde, Italy, <https://www.technosmart.eu>) that recorded the animal's coordinates at 1 fix/s. Only meerkats over 500 g (i.e. most meerkats other than juveniles) were collared with GPS tags. We programmed all units to activate daily, for 3 h consecutively, during times when meerkats engaged in group foraging. At the end of data collection, we removed the collars by snipping the leather straps with a mini diagonal cutter.

### Spatial Positioning: Focal Recording

For meerkats that were already equipped with a long-term radio collar or could not otherwise be collared, we performed focal data collection by following the individual with a telescopic pole with a GPS tag attached to it. Here, the observer kept within 1 m of the foraging meerkat for the 3 h duration of each daily session. At the same time, the observer recorded voice notes of the focal meerkat's behaviour (e.g. eating, calling, grooming) including noting occasional moments when the meerkat moved more than 2 m away from the GPS tag (these time segments were then removed from the recorded trajectories).

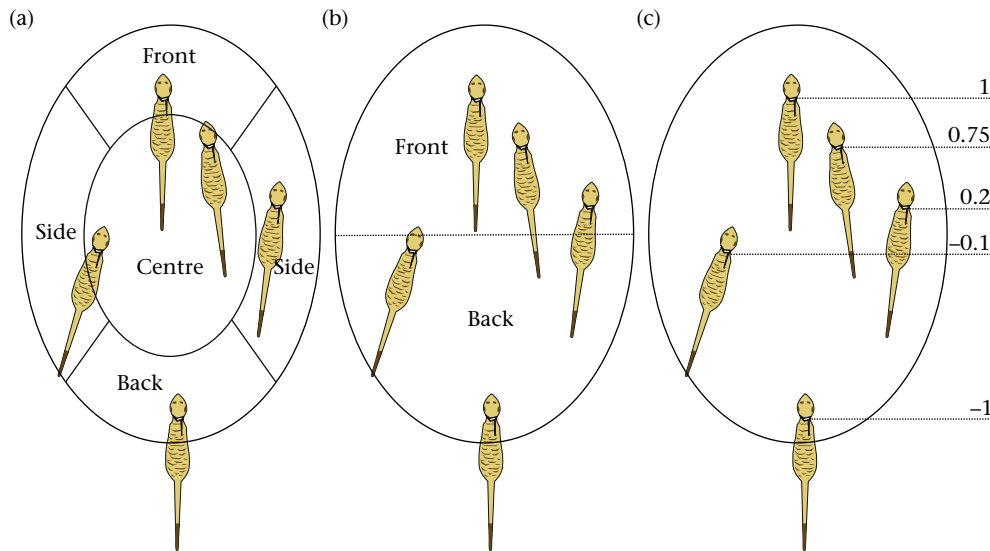
### Spatial Categories Calculation

From the recorded individual GPS coordinates we calculated the group 'centroid' by averaging all meerkats' GPS locations each second. We used a 10 m spatial discretization to calculate the heading of the group based on previously established methodology (Averly et al., 2022). Briefly, the heading at a given time was defined as the vector pointing from the centroid's past location after the group has moved a distance of 10 m to its present location at the given time. We then calculated each individual's location relative to the group centroid and heading at every second. We then summarized information about spatial position over the 3 h data

collection session using three different approaches. (1) Relative position: we first classified meerkats as either 'centre' or 'edge' based on whether they were closer or farther than the median meerkat's distance to the centroid at each second, such that half of meerkats in the group were categorized as centre and half as edge each second. Within the edge category, we classified meerkats that were in the front quarter (between  $-\pi/4$  and  $\pi/4$  radians) as 'front'. We classified those that were behind the centroid (greater than  $\pm 3\pi/4$  radians) as 'back', and those that were between  $\pi/4$  and  $3\pi/4$  or  $-\pi/4$  and  $-3\pi/4$  as 'side' (Fig. 1). We then calculated the proportion of time each meerkat spent in these four positions (front, side, centre and back) in each of the 3 h daily data collection sessions. We developed this measure of position in order to distinguish both centre from edge positions and, within edge, to distinguish front, back and side positions, in line with other research on spatial positioning outside of meerkats (e.g. Focardi & Pecchioli, 2005; Morrell & Romey, 2008). (2) Binary position: we calculated the proportion of time spent in the front half (binary position) of the group, to replicate results from Averly et al. (2022). (3) Ranked position: we ranked individual meerkats based on their front–back distance at each second and took the mean rank over the 3 h data collection session ('ranked position'), to replicate results from Gall and Manser (2018). Rank was scaled from  $-1$  to  $1$  where a rank of  $1$  indicated that a meerkat was the furthest towards the front of the group and a rank of  $-1$  indicated that a meerkat was the furthest towards the back of the group. Rank thus reveals which meerkats were, on average, far ahead or far behind other group members across a continuous scale, whereas relative position and binary position are categorical.

### Foraging Success: Change in Body Weight Gain

To determine individual daily weight change, we followed the standard weighing procedure at the study site and weighed meerkats every morning, before they began foraging, and at the end of the daily 3 h data collection session. Only individuals that had two weight sessions (morning and lunch) were used for the analysis. We used the change in body weight ( $\Delta$ weight) between the two daily weighing sessions as a proxy for individual foraging success. To control for average weight of meerkats of different age and sex classes, we standardized each individual's daily  $\Delta$ weight (calculated Z score of  $\Delta$ weight) against the average  $\Delta$ weight values, which were determined by calculating the mean for individual weight over 11 weight sessions, including the previous and following five sessions and the current one ( $\Delta$ weight-Z). The Z scores for both  $\Delta$ weight-Z were calculated using the formula: Z score =  $(x - \mu)/\sigma$  where  $\mu$  and  $\sigma$  are the average and standard deviation for an individual meerkat's  $\Delta$ weight over 11 weights.



**Figure 1.** Diagram visualizing the three different measures of spatial position with boundaries determined by the location of the GPS collar: (a) Relative position, (b) Binary position and (c) Ranked position. Numbers roughly correspond to the values these meerkats would be assigned based on their front-back position for Ranked position.

### Statistical Analyses

To test our predictions, we first determined how consistently individual meerkats occupy certain spatial positions while foraging. We also tested if the spatial preferences were affected by age, sex or dominance rank. Second, we also investigated whether weight gain was affected by the proportion of time spent in different positions and whether the effect of spatial position on weight gain is moderated by age, sex or dominance rank.

We created generalized linear mixed models with the R package *glmmTMB* (Brooks et al., 2017; R Core Team, 2023) to determine whether meerkats showed consistency in within-group spatial positioning. In these models ( $N = 6$ ), we used position as the response variable (front, back, side, centre, binary position or ranked position) and age (older versus younger meerkats), dominance rank (dominant versus subordinate) and sex (female versus male) as predictor variables with random effects of individual ID, group ID and date. Because the dominant female fills a critically different social role from the dominant male in meerkats (Averly et al., 2022), we also included a rank by sex interaction. After confirming model fit from *glmmTMB*, we calculated R values for individual ID using the R package *rptR* (Stoffel et al., 2017) for models with and without fixed effects. We used the R package *emmeans* to calculate the estimated marginal means for age, rank and sex (Lenth, 2022).

Next, we investigated whether within-group position predicted weight gain. In these models ( $N = 6$ ) we used standardized weight gain as the response variable and position (front, back, side, centre, binary position or ranked position) as the main predictor variable. Other factors such as sex (male or female), rank (dominants or subordinates) and age (older meerkats or younger meerkats) were also included as fixed effects and individual ID, group ID and date were included as random effects so that their effects could be controlled for. Date was included specifically to control for the fact that the entire group sometimes has better or worse foraging success on some days compared to others. Age, sex and dominance rank were included as moderators of the position–weight gain relationships (i.e. they were included as interactions with position). We also included an interaction between rank and sex for the same reasons specified above. We used the R package *modelbased* to estimate marginal slopes from models (Makowski et al., 2020) for age, rank and sex.

We fitted models based on a priori hypotheses (confirmatory analysis) and did not use model exploration (exploratory analysis). Model fit was checked using the R package *DHARMA* to examine residuals (Hartig, 2022).

### Ethical Note

The study was approved by the University of Pretoria Ethical Committee (EC031-1, NAS003/2022) and the Northern Cape Department of Environment (NAS033/2022, EC031-17, EC047-16) and Northern Cape Province Department of Environment and Nature Conservation (FAUNA 1020/2016, FAUNA 0996/2022). We certify that our study complies with all applicable institutional norms as well as with the ASAB/ABS guidelines for the use of animals in research and with the laws of South Africa, the country in which the study was conducted. All field procedures including collaring, focal follows and weight collection are based on previously established protocols. Because meerkats are highly habituated to humans, weighing scales and accepting water from water bottles, we were able to both measure neck sizes and deploy custom-fitted collars without the need for anaesthetization while meerkats took a few sips from a water bottle (Fig. A1; also see Spatial Positioning: Collar Deployment, above). While most meerkats showed no reaction to the attachment of a collar, some meerkats showed momentary confusion (e.g. rolling in the sand immediately after a collar was attached). However, all meerkats resumed their previous behaviour less than 1 min after deploying the collar. We observed no behavioural changes in meerkats as a result of wearing collars or changes in their habituation towards human observers. If meerkats showed any signs of ongoing discomfort (e.g. persistent scratching or rolling), or if we observed the collar was fitted too loosely, it was removed immediately ( $N = 1$  and 4 instances respectively out of 71 collared meerkats). All collars were removed within 24 h of the end of the data collection period (Fig. A1). For detailed information on collar deployment see the Supplementary Information from Averly et al. (2022), which followed an identical protocol. Previous research on the effects of radio collaring in meerkats have likewise found no effect of collars on predation rates or foraging efficiency (Golabek et al., 2008).

**RESULTS**

Our combined spatial and weight gain data sets resulted in data for 55 different meerkats over 40 days for a total of 19 observations across nine groups used in our analyses. On average, this data set includes 3.5 days of data per meerkat and an average of five meerkats per day.

*The Effect of Age, Sex and Dominance on Within-Group Spatial Position*

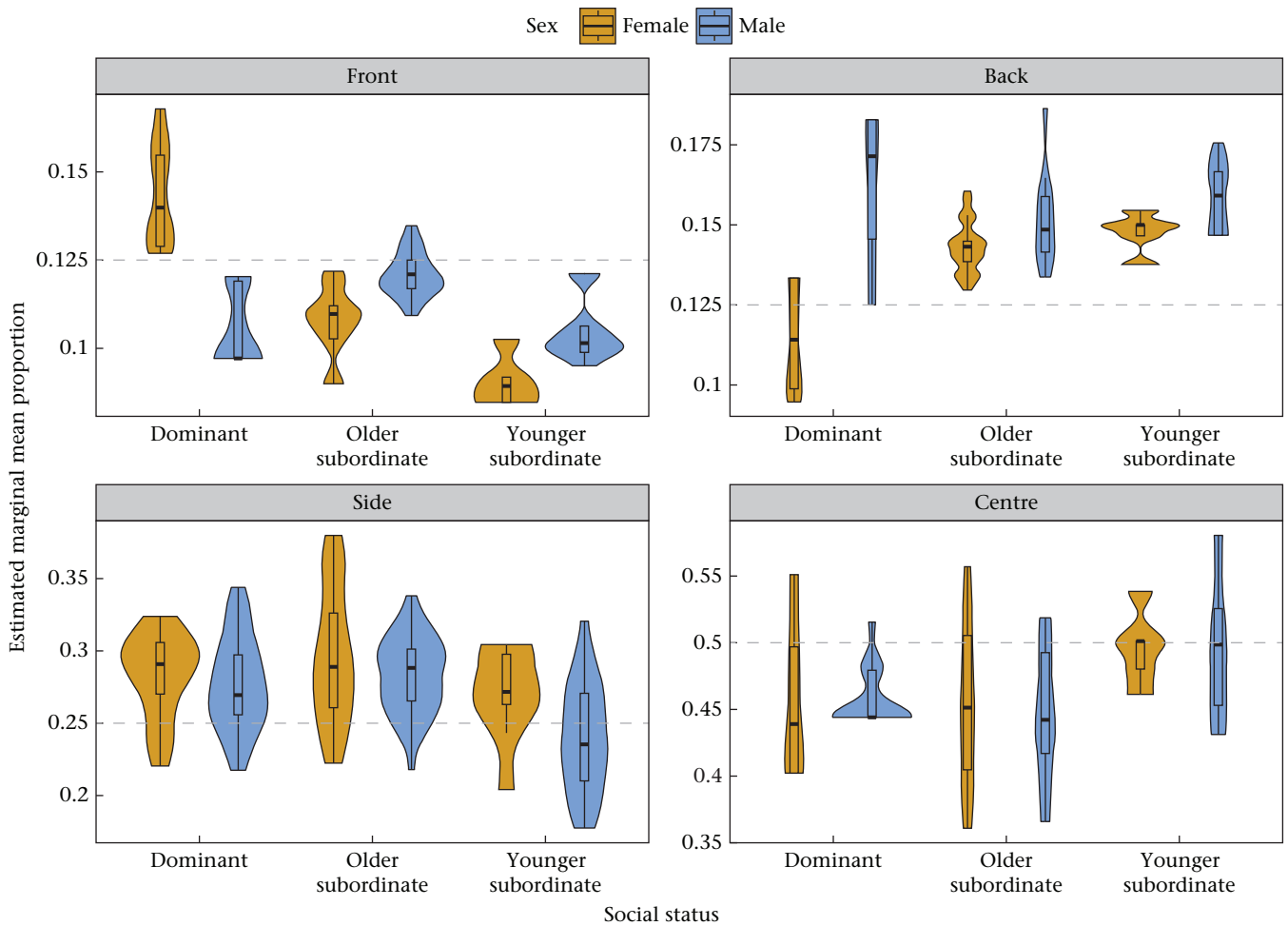
Using Relative position (front, back, side or centre), we found that most meerkats spent roughly half of their time in the centre of the group (Fig. 2), which was expected from our definition of the group centre as the median meerkat distance from the group's centroid. We also found significantly repeatable effects of individual ID for all relative positions (Table A1:  $R = 0.09-0.29, P < 0.05$ ), although time spent in the back was not significant when accounting for the variation explained by fixed effects ( $R = 0.09, P = 0.08$ ). These results suggest that individual meerkats tend to spend a somewhat consistent amount of time in these relative positions across days that is not generally explained by age, sex or rank. In our post hoc analysis we also observed some significant deviation from expected proportions based on chance; older meerkats (>1 year) spent less time in the centre and more time on

the side of the group than expected by chance (Fig. 2, Table A2). In addition, subordinate females spent less time in the front and subordinate males spent more time in the back than expected by chance (Fig. 2; Table A2).

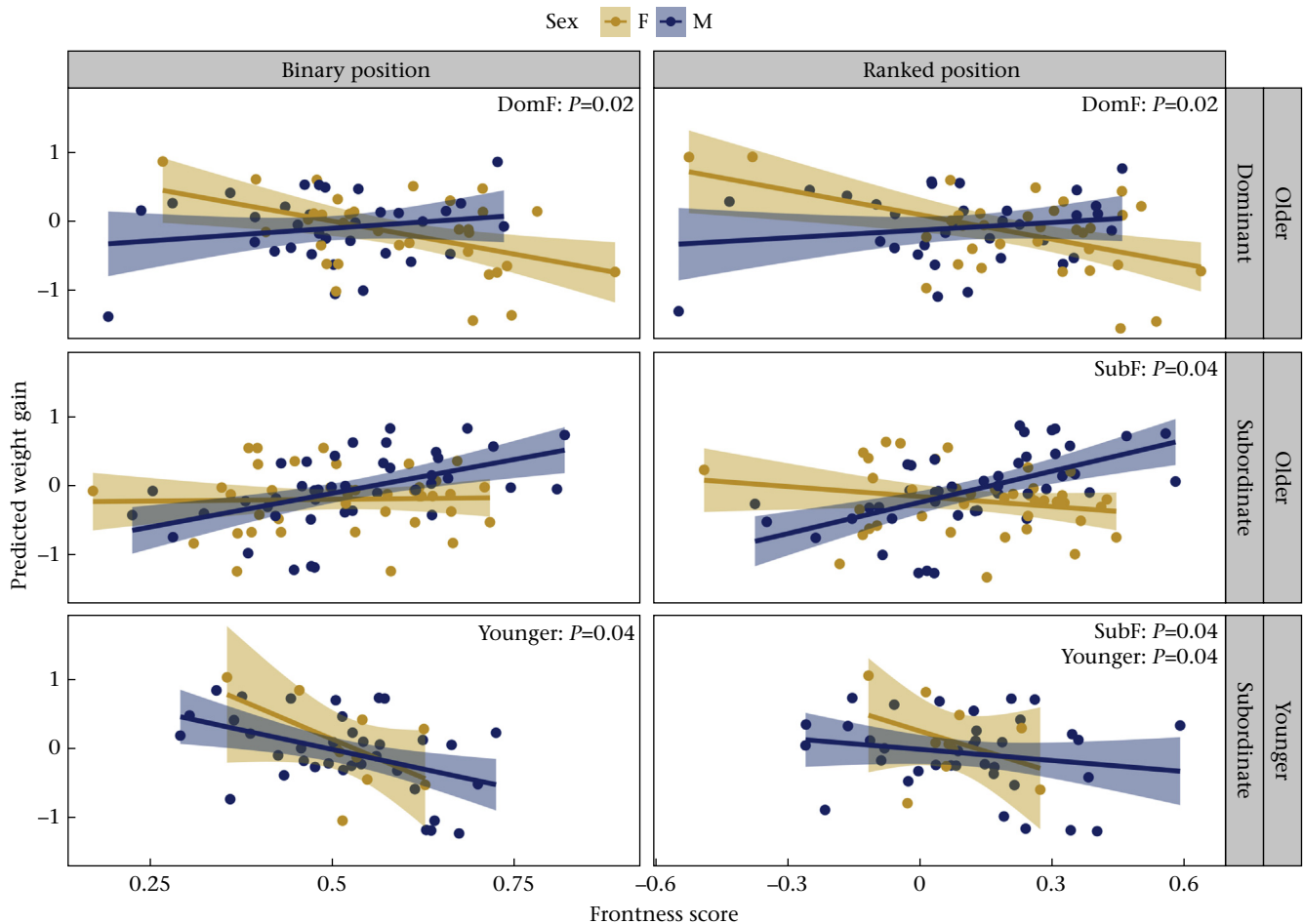
We also looked at meerkat position as a binary variable (Binary position) and a ranked variable (Ranked position) to replicate previous work in meerkats (Averly et al., 2022; Gall & Manser, 2018). We also found significantly repeatable effects of individual ID for both of these variables, but not after controlling for the effects of age, sex and rank (Table A3). For both measures of 'frontness' we found that dominant females spent more time in the front the group (Binary position = 0.59,  $P < 0.01$ ; Ranked position = 0.22,  $P = 0.06$ ) than expected by chance, but this was not quite significant for Ranked position (Table A4).

*Spatial Position and Weight Gain*

For meerkats' Relative position (front, back, centre and side), there was no significant correlation with weight gain despite meerkats' consistency in spending time in these positions (Tables A5, A6). However, both Binary and Ranked position had significant effects on weight gain for dominant females and younger meerkats (Fig. 3, Tables A7, A8). Dominant females, subordinate females and younger meerkats gained significantly less weight towards the front of the group (dominant females: Binary



**Figure 2.** Violin plots with box plots overlaid showing variation in predicted values for the proportion of time spent in different spatial positions by meerkats of different social statuses within the group, estimated from the models reported in Table A1. The horizontal dotted line indicates the proportion of time expected by chance in each position. Boxes extend from the first to third quartile with the middle line showing the median and whiskers showing minimum and maximum values.



**Figure 3.** The effect of meerkats' spatial position on  $\Delta$ weight-Z (standardized to mean individual weight change) including the effect of age, sex and social rank. The X axis is the frontness score for either Binary or Ranked position. The Y axis is the predicted standardized weight gain from models. Text annotations indicate  $P$  values for significant slopes (DomF = dominant female, SubF = subordinate female).

position =  $-2.98$ ,  $P = 0.02$ ; Ranked position =  $-1.72$ ,  $P = 0.02$ ; subordinate females: Ranked position =  $-1.49$ ,  $P = 0.04$ ; younger meerkats: Binary position =  $-2.93$ ,  $P = 0.04$ ; Ranked position =  $-1.75$ ,  $P = 0.04$ ).

## DISCUSSION

We aimed to investigate the relationship between within-group spatial positioning and foraging success in meerkats. We first investigated whether meerkats showed any consistent individual differences in their relative spatial positions within groups because we generally expected that these 'spatial strategies' might reflect variation in the trade-offs between foraging success and perceived risk. We found that individual meerkats did show significant but small differences in the proportion of time spent in different spatial positions. Some of this variation was due to age; older meerkats spent less time in the centre and more time on the side of the group than expected by chance. In addition, subordinate females spent less time in the front and subordinate males spent more time in the back than expected by chance. However, contrary to our expectations we found no effects of time spent in relative spatial position (front, back, centre and side) on foraging success. In addition to relative spatial position, we also used two measures of 'frontness' using a binary metric for time spent in the front versus back, and a ranked metric for metres towards the front versus back, which revealed that dominant females spent more time towards the front

than expected. We found that, in contrast to our prediction that meerkats at the front may gain more weight due to exploiting foraging patches first, dominant female meerkats, subordinate females and younger meerkats that spent more time towards the front gained less weight relative to other positions, suggesting poor foraging success towards the front.

### Differences in Spatial Positioning

Overall, we found significant individual repeatability for the proportion of time meerkats spent in front, back, side and centre relative positions. Indeed, meerkats' choice of spatial position while foraging may be dependent on the complex interaction of several factors including opportunities for information transfer (Goodale et al., 2010), perception of safety (Hirsch & Morrell, 2011; Janson, 1990), familiarity with the area (Wolf et al., 2009), optimal foraging theory (Davis et al., 2022), leadership (Averly et al., 2022) and social status in the group (Stahl et al., 2001). Furthermore, the choice of spatial position may be influenced by animal personality (Jolles et al., 2017; Kurvers et al., 2009; Nakayama et al., 2016; Sasaki et al., 2018; Sumpter et al., 2018); for example, fiddler crabs, *Uca pugilator*, with more active personalities were more likely to be found on the edge of the group and those that were less active were more likely to be located in the centre (Knotts & Griffen, 2016). Additionally, the composition of bold and shy animals in a group can have an influence on collective foraging decisions (Michelena

et al., 2009). Given our significant repeatability results, it appears that individual position in the group is not random but probably governed by socioecological factors that affect individual decision making about relative spatial position.

Some of the individual variation in time spent in relative spatial positions was due to variation in age, sex and rank classes. We observed that older individuals spent less time at the centre and more time on the side of the group. Older and more experienced individuals are often more confident to occupy risky, peripheral positions and may 'shield' vulnerable group members by keeping them in the centre. For instance, Heesen et al. (2015) found that immature individuals and females with infants in wild Assamese macaques, *Macaca assamensis*, were located in the centre of the group for safety. While the centre of the group is likely to be uniformly shielded from all sides, the edge positions (front, back, sides) could be associated with different cost–benefit balances. The front edge is often the riskiest position as individuals occupying it are advancing into unexplored areas, with a wide angle of exposure to predation and competitive encounters. However, individuals at the front can benefit from wielding higher influence over the group's direction of movement and/or increase their social reputation by investing in risky action. We found that dominant female meerkats consistently spent time towards the front, supporting previous work showing similar results for the dominant class in general (males and females; Gall & Manser, 2018). Dominant female meerkats have been shown to have increased influence over the group in matters such as choosing sleeping burrows (Strandburg-Peskin et al., 2019) as well as direction and speed of movement (Averly et al., 2022). The front position is often associated with leadership in other species (Bumann & Krause, 1993; Couzin et al., 2005; Krause, 1993; Pettit et al., 2015; Zwamborn et al., 2023) and may allow dominant females to assert control over the group's movement direction.

Subordinate females, which spent less time in the front edge position than expected, may have avoided proximity to dominant females who spent more time towards the front. 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 & Clutton-Brock, 2008). Aggression towards subordinate female meerkats tends to increase as they age; adult subordinate females display 'intense' submission behaviour and generally face eventual eviction from the group (Kutsukake & Clutton-Brock, 2006). While most studies on conflict management in meerkats focused on the reproductive conflict between same-sex group members, there are social regulation mechanisms and behaviours that also manifest outside of the breeding season. Similar findings of subordinate females avoiding foraging in the same position as dominant females have been reported in wild female chimpanzees, *Pan troglodytes* (Murray et al., 2007).

The subordinate males' preference to forage in the back of the group could also be driven by avoidance of proximity and interaction with dominant males. Dominant males can benefit from disrupting subordinate males' foraging and interaction with other subordinate males. For instance, dominant white-faced capuchin males, *Cebus capucinus*, constantly interrupted subordinate males' affiliation, to potentially minimize solid relationships between the subordinate males with efforts to reduce the threat to their dominance status in the group or position in the hierarchy (Perry, 1998). When there are many subordinate male meerkats in the group, the dominance tenure of dominant males becomes threatened as the risk of being displaced internally increases (Duncan et al., 2023). Considering that, in this study, we found no significant preference

for dominant males to consistently spend more time in a specific position, it is possible that dominant male meerkats may be flexible in their relative foraging position. However, dominant male meerkats are strongly associated with dominant females, who in our study spent more time in the front. For instance, a previous study in meerkats found higher assortment between dominant individuals during foraging activity (Gall & Manser, 2018). This may have caused the dominant males to explore centre-front and side-front positions more, giving the subordinate males more opportunities at the back of the group.

#### Foraging Success

According to previous studies, dominant individuals spent more time towards the front of their groups compared to other positions within groups, potentially due to the higher foraging potential in this position (Averly et al., 2022; Barnard, 2000; Bousquet et al., 2011; Gall & Manser, 2018). These studies analysed meerkat position as either binary (front versus back half) or a front-to-back ranked position but did not consider centre versus edge effects, as we did here. When determining meerkat position using Binary or Ranked positions, we replicated the results of dominant females spending more time at the front-half. However, in contrast to our expectations and the predictions made in previous studies, we found that dominant females gained significantly less weight the more time they spent towards the front of the group for Binary as well as Ranked positions. This suggests that dominant females probably do not spend more time at the front of a group as a result of higher foraging success in this position. Instead, dominant meerkats may spend more time towards the front because it is associated with a stronger influence on the group heading and speed (Averly et al., 2022). This influence seems to come with predation (described above) and foraging costs. However, for the dominant females to assert influence on the group they are not necessarily required to assume a front position (Averly et al., 2022). Similarly, in our comparison considering more detailed spatial categories (centre, front, side, back), we found that while the dominant females were spending more time in the front half of the group, they were not necessarily occupying the front edge of the group as measured by our Relative position metric.

Our study revealed that centre versus edge preferences in meerkats may not be related to foraging success, and being at the front does not necessarily provide individuals with better foraging opportunities. Indeed, in moving animal groups, front–back gradients may be more ecologically relevant with regards to both predation risk and foraging success than centre versus edge effects. However, using weight gain as a measure of foraging success over a 3 h period fails to elucidate precisely where meerkats were located when they had more successful foraging events. Our data were collected while meerkat groups were foraging, but individual meerkats can engage in other behaviours during these periods. Additionally, when reaching satiation after a successful foraging bout, meerkats might change their relative position to one perceived as less risky or simply divide their time between the different positions evenly (Clutton-Brock et al., 1999). To further understand the effect of spatial position on foraging success and fitness in social animals, future studies will benefit from methods of detecting food intake events in combination with high-resolution GPS data and weight gain. These studies could capture the moment-to-moment location of foraging events rather than looking at relatively longer sections of time, allowing a more direct link between within-group positioning and foraging success to be drawn.

Finally, while we hypothesized that predation pressure is highest towards the front and edge of the group based on research

in other animals (Hirsch & Morrell, 2011; Morrell & Romey, 2008; Rayor & Uetz, 1990; Tkaczynski et al., 2014), we observed no predation events during our data collection periods and therefore it remains to be empirically validated whether meerkats are preyed more or less in these positions. Furthermore, many of the meerkats' predators are aerial and here the position in the group might be less important than for terrestrial predators. To further test hypotheses about the trade-offs related to spatial positioning, more data is needed on the actual or perceived costs of variation in position for meerkats and, ultimately, long-term fitness outcomes (Krause, 1994). Overall, while we found several interactions between position and age/rank/sex classes on weight gain, a great deal of variation in weight gain remained unexplained (model residual variance range 0.84–0.89). This suggests that spatial position is likely to be only one of many other factors that influence foraging success from day to day. It will be necessary for future studies to take into consideration the effect of seasons and habitats in which the study species are found. Similarly, the physical characteristics of environments, affecting movement and potentially shifting the costs of foraging effort must be considered.

### Conclusion

In sum, we found significant individual differences in the proportion of time spent in different relative spatial positions within a group, primarily due to the effects of age, sex and rank. We also found effects of spatial positioning on weight gain for dominant females and younger meerkats, but a large amount of variation in weight gain was unexplained. Future work may benefit from linking our methods to more time-sensitive measures of foraging success, such as by considering individual foraging events or the types of food resources utilized by animals, which may vary in their nutritional content. In addition, future work could investigate the role of personality traits on spatial positioning, in tandem with measures of foraging success and perceived risk. Our results highlight the power of combining high-resolution movement data to gauge spatial positioning with information on foraging success, as well as the benefits of investigating multiple measures of spatial position on foraging success.

### Author Contributions

**Aliza le Roux:** Writing – review & editing, Supervision. **Ariana Strandburg-Peshkin:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Lily Johnson-Ulrich:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marta B. Manser:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Rasekuwane Mosia:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis. **Vlad Demartsev:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

### Data Availability

R code and data sets are available at <https://github.com/ljohnsonulrich/spatialForagingRepo.git>.

### Declaration of Interest

The authors have no conflicts of interest to declare.

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Appendix



Figure A1. (a) V.D. and L.J.U. deploying a collar while the meerkat drinks from a water bottle. (b) V.D. snipping the leather strap of a collar to remove it while the meerkat drinks from a water bottle. Observers always washed their hands and/or used hand sanitizer before and after close contact with meerkats.

Table A1 Model output for the repeatability of individual meerkat ID in each relative position

Model	Predictor	Estimate	SE	P
Front	Intercept	0.142	0.013	<0.001
Front	Rank: Subordinate	-0.032	0.017	0.052
Front	Age: Younger	-0.018	0.013	0.163
Front	Sex: Male	-0.032	0.020	0.106
Front	Rank*Sex: Subordinate, male	0.044	0.024	0.062
Front	Adjusted R	0.131	0.072	<b>0.007</b>
Front	Conditional R	0.114	0.071	<b>0.028</b>
Back	Intercept	0.011	0.017	<0.001
Back	Rank: Subordinate	0.037	0.024	0.119
Back	Age: Younger	-0.002	0.021	0.911
Back	Sex: Male	0.041	0.025	0.105
Back	Rank*Sex: Subordinate, male	-0.033	0.032	0.302
Back	Adjusted R	0.094	0.068	<b>0.035</b>
Back	Conditional R	0.080	0.069	0.080
Centre	Intercept	0.466	0.033	<0.001
Centre	Rank: Subordinate	-0.023	0.040	0.567
Centre	Age: Younger	0.062	0.0029	<b>0.032</b>
Centre	Sex: Male	0.007	0.050	0.887
Centre	Rank*Sex: Subordinate, male	-0.017	0.058	0.762
Centre	Adjusted R	0.243	0.083	<b>&lt;0.001</b>
Centre	Conditional R	0.291	0.086	<b>&lt;0.001</b>
Side	Intercept	0.283	0.023	<0.001
Side	Rank: Subordinate	0.006	0.027	0.816
Side	Age: Younger	-0.025	0.022	0.264
Side	Sex: Male	-0.011	0.032	0.726

**Table A1** (continued)

Model	Predictor	Estimate	SE	P
Side	Rank*Sex: Subordinate, male	0.005	0.038	0.887
Side	Adjusted R	0.206	0.083	<b>&lt;0.001</b>
Side	Conditional R	0.226	0.084	<b>&lt;0.001</b>

Response variable was the proportion of time spent in each position. Each relative position represents a different model ( $N = 4$  models). Fixed effects included age, sex, rank and an interaction between sex and rank. Random effects included meerkat ID, date and group ID. All R values (R total and R with fixed effects) are for the random effect of meerkat ID. Adjusted R shows the total variance explained by random effects. Conditional R shows variance for random effects after controlling for variance explained by fixed effects.  $N$  observations = 195,  $N$  meerkats = 55,  $N$  dates = 40 and  $N$  groups = 9 for all four models. Bold values correspond to  $P$  values significant at  $\alpha = 0.05$ .

**Table A2**

Estimated marginal means for the proportion of time spent in each relative position

Status	Front		Back		Centre		Side	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Rank*Sex: Dominant female	0.13	0.60	0.11	0.48	0.50	0.94	0.27	0.42
Rank*Sex : Dominant male	0.10	0.13	0.15	0.22	0.50	0.92	0.26	0.73
Rank*Sex : Subordinate female	<b>0.10</b>	<b>0.02</b>	0.15	0.13	0.47	0.28	0.28	0.13
Rank*Sex : Subordinate male	0.11	0.13	<b>0.16</b>	<b>0.01</b>	0.46	0.05	0.27	0.16
Age: Older	0.12	0.49	0.14	0.08	<b>0.45</b>	<b>&lt;0.01</b>	<b>0.28</b>	<b>0.01</b>
Age: Younger	0.10	0.07	0.14	0.42	0.52	0.58	0.26	0.75

$P$  values are calculated based on a null value of 0.125 for the front and back positions, 0.25 for the side position, and 0.50 for the centre position. Post hoc values correspond to the four models present in Table A1. Bold values correspond to  $P$  values significant at  $\alpha = 0.05$ .

**Table A3**

Model output for the repeatability of individual meerkat ID in binary and ranked positions

Model	Predictor	Estimate	SE	P
Binary position	Intercept	0.592	0.024	<b>&lt;0.001</b>
Binary position	Rank: Subordinate	-0.075	0.031	<b>0.016</b>
Binary position	Age: Younger	-0.004	0.025	0.879
Binary position	Sex: Male	-0.082	0.036	<b>0.023</b>
Binary position	Rank*Sex: Subordinate, male	0.088	0.044	<b>0.046</b>
Binary position	Adjusted R	0.117	0.071	<b>0.010</b>
Binary position	Conditional R	0.086	0.068	0.065
Ranked position	Intercept	0.232	0.042	<b>&lt;0.001</b>
Ranked position	Rank: Subordinate	-0.115	0.053	<b>0.030</b>
Ranked position	Age: Younger	-0.027	0.042	0.532
Ranked position	Sex: Male	-0.121	0.062	0.052
Ranked position	Rank*Sex: Subordinate, male	0.132	0.075	0.080
Ranked position	Adjusted R	0.106	0.068	<b>0.021</b>
Ranked position	Conditional R	0.082	0.065	0.081

Model results for control consistency models. Response variable was a binary proportion for front versus back (binary position) or a ranked variable from 1 to -1 for front to back (ranked position). Each control position represents a different model ( $N = 2$  models). Fixed effects included age, sex, rank and an interaction between sex and rank. Random effects included meerkat ID, group ID and date. All R values (R total and R with fixed effects) are for the random effect of meerkat ID. Adjusted R shows the total variance explained by random effects. Conditional R shows variance for random effects after controlling for variance explained by fixed effects.  $N$  observations = 195,  $N$  meerkats = 55,  $N$  dates = 40 and  $N$  groups = 9 for all models. Bold values correspond to  $P$  values significant at  $\alpha = 0.05$ .

**Table A4**

Estimated marginal means for the proportion of time spent in front or front-back rank

Status	Binary position		Ranked position	
	Estimate	P	Estimate	P
Rank*Sex: Dominant female	<b>0.59</b>	<b>&lt;0.01</b>	0.22	0.06
Rank*Sex : Dominant male	0.51	0.79	0.10	0.54
Rank*Sex : Subordinate female	0.52	0.43	0.10	0.44
Rank*Sex : Subordinate male	0.52	0.18	0.11	0.55
Age: Older	<b>0.54</b>	<b>&lt;0.01</b>	0.15	0.39
Age: Younger	0.53	0.18	0.12	0.81

$P$  values are calculated based on a null value of 0.50 for front binary and 0.13 (the median rank) for ranked position. Post hoc values correspond to the two models present in Table A3 Bold values correspond to  $P$  values significant at  $\alpha = 0.05$ .

**Table A5**  
Model output for the effect of relative position on weight gain

Model	Predictor	Estimate	SE	P
Front	Intercept	-0.065	0.277	0.815
Front	Front	-0.608	1.698	0.720
Front	Rank: Subordinate	0.009	0.312	0.978
Front	Age: Younger	0.426	0.376	0.257
Front	Sex: Male	-0.282	0.272	0.300
Front	Front*Rank: Subordinate	-1.745	2.310	0.450
Front	Front*Age: Younger	-2.360	3.225	0.464
Front	Front*Sex: Male	3.083	2.348	0.189
Front	Front*Rank*Sex: Subordinate, male	1.492	2.079	0.473
Back	Intercept	-0.395	0.249	0.113
Back	Front	1.606	1.817	0.377
Back	Rank: Subordinate	0.209	0.281	0.456
Back	Age: Younger	-0.374	0.385	0.331
Back	Sex: Male	0.389	0.263	0.139
Back	Back*Rank: Subordinate	-2.046	2.093	0.328
Back	Back*Age: Younger	3.721	2.137	0.082
Back	Back*Sex: Male	-1.722	1.946	0.376
Back	Back*Rank*Sex: Subordinate, male	0.041	1.674	0.980
Centre	Intercept	0.094	0.517	0.856
Centre	Front	-0.618	1.082	0.568
Centre	Rank: Subordinate	-0.819	0.569	0.150
Centre	Age: Younger	1.153	0.642	0.072
Centre	Sex: Male	0.462	0.503	0.358
Centre	Centre*Rank: Subordinate	1.618	1.220	0.185
Centre	Centre*Age: Younger	-1.954	1.300	0.133
Centre	Centre*Sex: Male	-0.710	1.136	0.532
Centre	Centre*Rank*Sex: Subordinate, male	0.072	0.551	0.896
Side	Intercept	-0.181	0.456	0.692
Side	Front	-0.021	1.550	0.989
Side	Rank: Subordinate	0.094	0.505	0.852
Side	Age: Younger	-0.310	0.561	0.581
Side	Sex: Male	-0.193	0.446	0.666
Side	Side*Rank: Subordinate	-0.626	1.709	0.714
Side	Side*Age: Younger	2.062	1.994	0.301
Side	Side*Sex: Male	1.141	1.629	0.484
Side	Side*Rank*Sex: Subordinate, male	0.177	0.891	0.843

Response variable was weight gain over 3 h (g) standardized against each individual's average weight gain over the previous and following five weight sessions. Each relative position represents a different model ( $N = 4$  models). Fixed effects included proportion of time in each position and the moderating effects of age, sex, rank and an interaction between sex and rank. Random effects included meerkat ID, date and group ID. For all models:  $N$  observations = 195,  $N$  meerkats = 55,  $N$  dates = 40 and  $N$  groups = 9 for all four models.

**Table A6**  
Estimated marginal slopes for the effect of social status and position on weight gain

Status	Front		Back		Centre		Side	
	coefficient	P	coefficient	P	coefficient	P	coefficient	P
Rank*Sex: Dominant female	-1.79	0.47	3.47	0.11	-1.60	0.24	1.01	0.62
Rank*Sex : Dominant male	1.29	0.62	1.74	0.26	-2.31	0.06	2.15	0.21
Rank*Sex : Subordinate female	-3.53	0.12	1.42	0.40	0.02	0.98	0.38	0.76
Rank*Sex : Subordinate male	1.04	0.54	-0.26	0.82	-0.62	0.38	1.70	0.15
Age: Older	0.43	0.70	-0.27	0.76	-0.15	0.80	0.28	0.74
Age: Younger	-1.93	0.52	3.45	0.09	-2.10	0.09	2.34	0.22

Post hoc values correspond to the four models present in Table A5.

**Table A7**  
Model output for the effect of binary and ranked positions on weight gain

Model	Predictor	Estimate	SE	P
Binary position	Intercept	0.617	0.570	0.279
Binary position	Front	-1.331	0.939	0.157
Binary position	Rank: Subordinate	-0.887	0.611	0.146
Binary position	Age: Younger	1.904	0.793	<b>0.016</b>
Binary position	Sex: Male	-0.978	0.582	0.093
Binary position	Front*Rank: Subordinate	1.344	1.090	0.218
Binary position	Front*Age: Younger	-3.295	1.502	<b>0.028</b>
Binary position	Front*Sex: Male	1.914	1.091	0.079
Binary position	Front*Rank*Sex: Subordinate, male	0.257	0.493	0.602
Ranked position	Intercept	0.012	0.181	0.949
Ranked position	Position	-0.812	0.568	0.153

**Table A7** (continued)

Model	Predictor	Estimate	SE	<i>P</i>
Ranked position	Rank: Subordinate	-0.227	0.175	0.195
Ranked position	Age: Younger	0.381	0.200	0.057
Ranked position	Sex: Male	-0.079	0.151	0.603
Ranked position	Position*Rank: Subordinate	0.233	0.798	0.771
Ranked position	Position*Age: Younger	-1.823	0.900	<b>0.043</b>
Ranked position	Position*Sex: Male	0.890	0.835	0.286
Ranked position	Position*Rank*Sex: Subordinate, male	1.279	1.067	0.230

Response variable was weight gain over 3 h (g) standardized against each individual's average weight gain over the previous and following five weight sessions. Each position represents a different model ( $N = 2$  models). Fixed effects include either binary position or ranked position and the moderating effects of age, sex, rank and an interaction between sex and rank. Random effects included meerkat ID, date and group ID. For all models:  $N$  observations = 195,  $N$  meerkats = 55,  $N$  dates = 40 and  $N$  groups = 9 for both models. Bold values correspond to  $P$  values significant at  $\alpha = 0.05$ .

**Table A8**

Estimated marginal slopes for the effect of social status and position on weight gain

Status	Binary position		Ranked position	
	Estimate	<i>P</i>	Estimate	<i>P</i>
Rank*Sex: Dominant female	<b>-2.98</b>	<b>0.02</b>	<b>-1.72</b>	<b>0.02</b>
Rank*Sex : Dominant male	-1.06	0.38	-0.83	0.27
Rank*Sex : Subordinate female	-1.63	0.13	<b>-1.49</b>	<b>0.04</b>
Rank*Sex : Subordinate male	0.54	0.49	0.68	0.16
Age: Older	0.36	0.52	0.07	0.82
Age: Younger	<b>-2.93</b>	<b>0.04</b>	<b>-1.75</b>	<b>0.04</b>

Post hoc values correspond to the two models present in Table A7. Bold values correspond to  $P$  values significant at  $\alpha = 0.05$ .