







ORIGINAL RESEARCH

Reproductive females of a cooperatively breeding rodent are in better body condition when living in large groups

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Abstract

Cooperation and group living have been suggested to facilitate survival in varying environments and under challenging conditions. However, group living may also be associated with costs, particularly in species where individuals within groups may compete for limited resources. The costs and benefits of cooperative group living on cooperatively breeding mammals in varying environments remain unclear. Here, we use data collected from wild, cooperatively breeding Natal mole-rats (*Cryptomys hottentotus natalensis*) inhabiting a seasonally varying environment to assess whether body condition changes between seasons and whether these changes are contingent upon group size. We demonstrate that the body condition of reproductive females improved with increasing helper number during both the benign summer and the harsher winter seasons. However, the body condition of other group members showed little dependency on group size or season. Only when including one extremely large group did the body condition of non-breeders weakly, albeit significantly, change depending on group size and seasonality. These results suggest that larger group sizes may yield some benefits for non-breeding group members during winter and may invoke some costs during summer. Group living in Natal mole-rats is likely promoted by a combination of collective foraging, thermoregulatory benefits, and potentially some indirect fitness benefits through improved body condition of the breeding female.

Introduction

Cooperation has been suggested as one of the primary drivers for the evolution of group living (Cornwallis et al., 2017; Downing et al., 2020a; Taborsky et al., 2021). In cooperatively breeding species, increased group size can improve the survival rates and lifespan of breeding individuals (Downing et al. 2020b). However, increasing group size not only comes with the potential for improved survival and cooperation, but also involves increasing competition between individuals for food or mating opportunities (Beltrão et al., 2022). This competition can lead to fitness consequences that may vary between species (or individuals) due to life history or environmental factors (Ebensperger et al., 2012; Emlen, 1982). The impact of these costs and benefits on individuals living in groups of varying sizes and under diverse environmental conditions is poorly understood.

The members of cooperative groups differ in individual characteristics, such as sex, age, competitiveness, and their role

in the breeding process within the group. Depending on these characteristics, the most beneficial group size can vary and may be influenced by the current environmental conditions. For example, cooperatively breeding ostrich (*Struthio camelus*) groups have different optimal group sizes for males and females (Melgar et al., 2022), and environmental conditions determine the optimal group size for greater anis (*Crotophaga major*) (Riehl & Smart, 2022). Group size and the presence of subordinate “helper” group members can mediate the environmental effects on the survival and fecundity of group members (Groenewoud & Clutton-Brock, 2021; Guindre-Parker & Rubenstein, 2020; Wiley & Ridley, 2016). In pied babblers (*Turdoides bicolor*), when the cost of maintaining adequate body condition during heat waves becomes too high, parents shift their focus from offspring investment to personal investment, allowing subordinates to carry the burden of provisioning their offspring (Wiley & Ridley, 2016). This “load-lightening” decreases the provisioning rates of reproductive females, allowing them to maintain a stable body

condition (Crick, 1992; Helstab *et al.*, 2017; Wiley & Ridley, 2016). Thus, dominant group members often benefit more than those of helper individuals, with dominant individuals experiencing a decrease in workload, increased fecundity, decreased interbirth intervals, and increased survival rates directly related to the number of helpers (Downing *et al.* 2020b; Gilchrist *et al.*, 2004; Houslay *et al.*, 2020; Josi *et al.*, 2020; Wiley & Ridley, 2016). Living in larger groups can also lead to improved body condition, faster growth rates, and increased survival rates of other group members (Clutton-Brock *et al.*, 2001; Guindre-Parker & Rubenstein, 2020; McNutt & Silk, 2008). However, the effects of seasonal climate variation and group size on individual body condition remain poorly understood in cooperatively breeding mammals.

In this study, we used field data collected from cooperatively breeding Natal mole-rats (*Cryptomys hottentotus natalensis*) to determine if variation in group size predicts changes in body condition, and if body condition differs between summer and winter. At our high-elevation study site, mole-rats may experience large daily and seasonal fluctuations in burrow temperature due to their shallow tunnels (Finn *et al.*, 2022). Foraging during winter exposes mole-rats to burrow temperatures below their thermal neutral zone, and may require higher energy expenditure (Bennett *et al.*, 1993; Zelová *et al.*, 2010). Living in larger groups may decrease individual energy expenditure due to cooperative foraging and thermoregulatory benefits from huddling (Kotze *et al.*, 2008; Lovegrove & Wissel, 1988; Spinks & Plagányi, 1999; Vavrušková *et al.*, 2022). While large groups may be more efficient at foraging (Jarvis *et al.*, 1998; Lihoreau *et al.*, 2017), there may be individual costs associated with living in large groups. Growth rates of juvenile mole-rats decrease with increasing group size, and intra-sexual competition may further decrease growth rates (Bensch *et al.*, 2024; Thorley *et al.*, 2023; Young *et al.*, 2015). Thus, the benefits of collective foraging may vary with group size and between seasons. If the collective foraging benefits of living in a group prevail, we expect body condition to improve with group size, regardless of the season. Yet, if competition among group members prevails, we expect changes in body condition to occur with group size and across seasons. Lastly, we expect the presence of non-reproductive individuals may coincide with better condition in reproductive females, either because females in better body condition have higher reproductive success or because the presence of helpers may provide load-lightening benefits to the breeders.

Materials and methods

The study species

The Natal mole-rat is a social-dwelling mole-rat endemic to the mesic grasslands of eastern South Africa. They occur from sea level to over 3000 m above sea level, and as a result, some populations may experience environmental seasonality in climate and rainfall patterns. Their group size is small compared to other social mole-rats (mean group size 6, maximum 18)

(this study, Luterman *et al.*, 2013, Oosthuizen *et al.*, 2008, Süess *et al.*, 2024). Like other social mole-rats, they exhibit high reproductive skew with a single reproductive female, delayed dispersal, and an overlap of generations (Oosthuizen *et al.*, 2008). Unlike many other social mole-rats, they lack physiological reproductive suppression (van Janse Vuuren, 2022). Instead, subordinate males and females are reproductively active year-round, and inbreeding avoidance or a lack of unrelated immigrant mates prevents breeding while in the natal group (Oosthuizen *et al.*, 2008; van Janse Vuuren, 2022).

Animal capture

This study was undertaken at Glangarry Holiday Farm (−29.322°, 29.713°, elevation 1600 m), a recreational destination located in the Kamberg Valley in the central Drakensberg Mountains of the KwaZulu-Natal province, South Africa. It encompasses 48.5 hectares of human-altered montane grassland with a golf course, camping grounds, and guest chalets, interspersed with patches of natural grassland. The montane grasslands of the Drakensberg are dominated by perennial grasses and include over 50 species of primarily small variety geophytes (Jewitt *et al.*, 2023), their primary food resource. However, the geophyte diversity at the study site remains unknown.

The study site experiences mild summers (December – March; mean monthly \pm SD: 15.5 \pm 1.5°C, mean daily range 10.3°C–24.8°C) and cold winters (June – September; mean monthly \pm SD: 9.3 \pm 2.7°C, mean daily range 0.8°C–20.7°C). Annual rainfall is relatively predictable, occurring predominantly during summer (mean \pm SD = 1260.9 \pm 181.1 mm), with some rainfall during winter (mean \pm SD = 316.5 \pm 104.0 mm; Fig. S1a). The soil temperatures experienced by mole-rats may be slightly warmer than air temperatures (Fig. S1b).

We captured Natal mole-rats twice a year from January 2020 to July 2021, during the wet summer season (January–March) and the dry winter season (July–September), using Hickman live traps baited with sweet potatoes and checked every 1–2 h. Groups of mole-rats were recaptured at six-month intervals. To identify individuals, we implanted each with a subcutaneous passive integrated transponder (PIT) tag (Trovan Unique, DorsetID, Netherlands). At capture, we checked all animals for a PIT tag, sexed them, weighed them, and measured the upper tooth width across both incisors using digital callipers (accurate to \pm 0.01 mm). Two observers measured tooth width, and the mean value was used for analysis. During capture, individuals were housed with group members in plastic boxes and provided with wood shavings and sweet potatoes *ad libitum* (mean \pm SD = 6.3 \pm 2.2 days in captivity). We returned the groups to their burrows after all the animals in the group were captured.

We captured 402 individual mole-rats (males, $n = 203$; females, $n = 199$) from 51 groups during the study, across 652 total animal captures in 95 unique group capture events. All protocols were approved by the University of Pretoria ethics committee (permit EC001-19). All statistical analyses were performed in R 4.3.0 (R Core Team, 2023).

Demographic effects on body condition

To estimate individual body condition, we used the scaled mass index (SMI), a relationship between body length and body mass. SMI is a reliable proxy to estimate the energy reserves available to an individual when absolute measures (e.g., body fat) are unavailable (Peig & Green, 2010). We used upper tooth width as a measure for body length because it is an accurate and easily measured (and remeasured) feature in mole-rats without the need for anaesthesia (Thorley & Clutton-Brock, 2019; Young & Bennett, 2013). Calculating SMI is a two-step process using major axis regression of body mass (M_i) against upper tooth width (L_i), and then scales body size using the mean population body size (L_o) and slope of the regression line of body mass against body size (b_{SMA}):

$$SMI = M_i \left(\frac{L_o}{L_i} \right)^{b_{SMA}}$$

We performed a major axis regression of body mass against upper tooth width (Fig. S2) using *smatr* in R (Warton *et al.*, 2012). To eliminate any potential influence of juvenile growth on body condition calculations, we excluded individuals weighing less than 40 g, as these individuals are sexually immature (Hart *et al.*, 2021; Spinks *et al.*, 1997; Spinks & Plagányi, 1999). This threshold has often been used in mole-rats of the genus *Cryptomys* to distinguish between juveniles and adults (Hart *et al.*, 2021; Luterman *et al.*, 2013; Süess *et al.*, 2024). Reproductive females were also removed and analysed separately (see below). Including reproductive females caused the slopes of the regression to significantly differ between the sexes ($\chi^2_1 = 19.37$, P -value > 0.001). When reproductive females were removed, there was not a significant difference in the slopes of the regression line between sexes ($\chi^2_1 = 0.18$, P -value = 0.28), or reproductive status ($\chi^2_1 = 1.46$, P -value = 0.48) in the remaining individuals. Our dataset included 496 SMI values from 354 individuals (161 females, 193 males).

To determine if body condition differed between seasons (summer and winter), or was affected by group size, we used a generalized linear mixed model (GLMM) in *glmmTMB* (Brooks *et al.*, 2017). SMI was selected as the response, and the predictors were sex, group size, season, and the interaction between season and group size. The group size included juvenile (body mass < 40 g) and adult individuals.

Reproductive females were analysed separately because body mass gain could be related to pregnancies instead of food availability. However, any increase in body condition could be related to helper effects regardless of whether the female was pregnant or not. To assess how the body condition of reproductive females fluctuated between seasons or due to helping effects of group members, we ran a separate GLMM with the same predictors. However, instead of group size, we used the number of non-juvenile individuals (mass > 40 g) because juveniles are unlikely to contribute significantly to cooperative behaviours. This method allowed us to separate the effects of helper contributions from general group size effects. We calculated SMI scores for reproductive females ($n = 31$) across all captures ($n = 46$ SMI values). Individual and group identity were included as random

factors in both models to control for repeated measurements. Scaling group size did not improve the model fit.

Results

The body condition of the reproductive females improved in larger groups during both seasons (Table 1, Fig. 1a). This relationship remained even when excluding the largest group in which a reproductive female was captured (Table 1).

Body condition in all other group members was weakly predicted by the interaction between group size and seasonality (Table 2). During winter, body condition improved with increasing group size, whereas it declined with group size in summer (Fig. 1b). However, these effects were only apparent as a significant interaction effect. Only during summer did body condition significantly decrease with group size (winter: est. = 0.38, SE = 1.22, P -value = 0.223; summer: est. = -0.51, SE = 0.25, P -value = 0.047). Additionally, the significant interaction was dependent on the inclusion of the largest group of 18 individuals because after removing this group from the data, the effects of group size and season on body condition were no longer apparent (Table 2).

Table 1 Effects of group size and season on body condition of reproductive females in Natal mole-rats

Predictor	Estimate	SE	P -value
<i>Including the largest group</i>			
Fixed effects			
Intercept	84.54	5.31	<0.001*
Number of helpers	1.79	0.86	0.038*
Season: winter	-0.75	5.41	0.890
Number of helpers x season	0.16	0.86	0.856
Random effects		Variance	Std Dev
Group ID:Animal ID	<0.01	<0.01	
Group ID	116.9	10.81	
Residual	38.4	6.20	
<i>Excluding the largest group</i>			
Fixed effects			
Intercept	85.56	4.95	<0.001*
Number of helpers	1.66	0.78	0.033*
Season: winter	1.48	4.39	0.736
Number of helpers x season	-0.50	0.70	0.476
Random effects		Variance	Std Dev
Group ID:Animal ID	0.02	0.14	
Group ID	141.6	11.90	
Residual	20.6	4.54	

To estimate body condition, we used the scaled mass index (SMI), which scaled body mass for all individuals based on the relationship between body mass and upper incisor width. To assess how helper number (a measure of group size) affected the body condition of reproductive females, we removed juvenile group members (body mass < 40 g) from the group size term because they are not expected to contribute much to helping. Results are from separate generalized linear mixed models, either including the largest group (45 measurements from 31 individuals) or excluding the largest group (44 measurements from 31 individuals).

*Indicates significance.

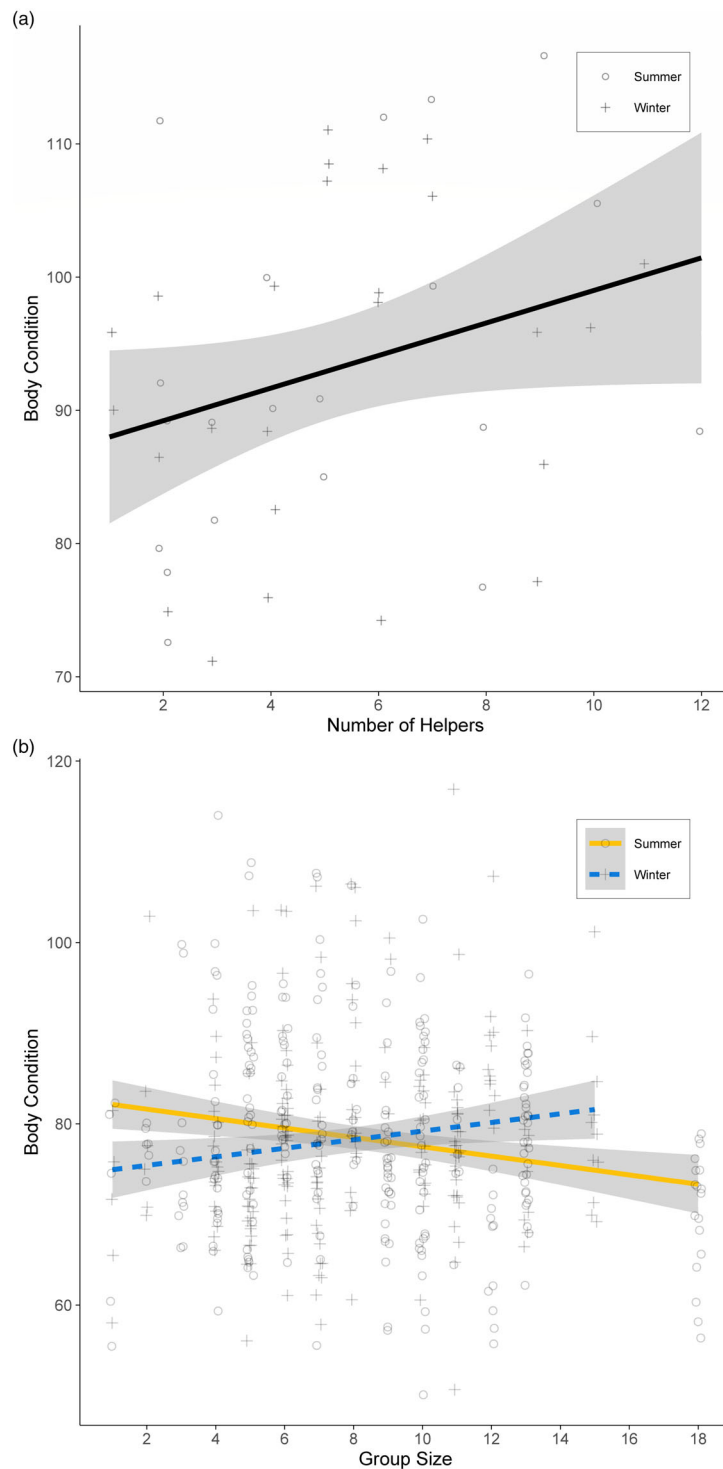


Figure 1 Relationship between body condition, group size, and season among Natal mole-rats. (a) The predicted change in body condition with the number of helpers (a measure of group size) for reproductive females only ($n=45$ measurements from 31 individuals). Juvenile group members (body mass < 40 g) were not included in the group size because they are not expected to contribute much to helping. (b) The predicted change in body condition with group size for all other group members (non-reproductive males and females, reproductive males; $n=496$ measurements from 354 individuals) during summer (solid yellow line) and winter (dashed blue line). In both plots, the 95% confidence intervals of the predictions are shown in the shaded areas, and data points represent one animal capture during summer (circles) and winter (plus sign).

Table 2 Effects of group size and season on body condition of non-reproductive Natal mole-rats

Predictor	Estimate	SE	P-value
<i>Including the largest group</i>			
Fixed effects			
Intercept	81.58	1.77	<0.001*
Sex: male	1.12	0.90	0.213
Season: winter	-5.82	2.06	<0.005*
Group size	-0.49	0.18	<0.007*
Group size × season	0.72	0.23	<0.002*
Random effects			
	Variance	Std Dev	
Group ID:Animal ID	25.15	5.02	
Group ID	43.34	6.58	
Residual	49.09	7.01	
<i>Excluding the largest group</i>			
Fixed effects			
Intercept	79.61	1.99	< 0.001*
Sex: male	1.03	0.91	0.258
Season: winter	-3.70	2.31	0.109
Group size	-0.18	0.23	0.437
Group size × season	0.39	0.28	0.169
Random effects			
	Variance	Std Dev	
Group ID:Animal ID	23.40	4.84	
Group ID	42.72	6.54	
Residual	51.10	7.15	

Results are from a generalized linear mixed model using all groups (496 scaled mass index measurements from 354 individuals) and excluding the largest group, which was captured during the summer (478 scaled mass index measurements from 345 individuals). In both models, group size included juvenile individuals.

*Indicates significance.

When we limited our analysis to individuals with at least one capture during each season and excluding the largest group ($n = 180$ measurements from 69 individuals), body condition did not differ between seasons (est. = -2.24 , SE = 2.99 , P -value = 0.454), nor was it affected by group size (GLMM: est. = -0.22 , SE = 0.28 , P -value = 0.433), nor the interaction between season and group size (est. = 0.34 , SE = 0.38 , P -value = 0.375). The body mass of group members did not significantly differ between seasons, nor increase or decrease due to group size (GLMM: P -values > 0.05 , Table S2, Fig. S3).

Discussion

In cooperatively breeding species, such as many social mole-rats, groups include “helper” individuals that can improve the quality of life for group members, especially the reproductive female, by distributing energy expenditure among group members (Clutton-Brock *et al.*, 2001; Crick, 1992; Housley *et al.*, 2020). We found that the body condition of the reproductive female improved with the number of helpers during both seasons; however, the body condition of other group members was likely unaffected by group size and environmental variation between seasons. This relationship suggests that group size effects may have benefits for reproductive Natal

mole-rat females, as observed in other cooperative breeders (Clutton-Brock *et al.*, 2001; Downing *et al.* 2020b; Housley *et al.*, 2020; Josi *et al.*, 2020; Wiley & Ridley, 2016). Alternatively, reproductive females in better body condition may have larger litter sizes or shorter intervals between births (Housley *et al.*, 2020; Thorley *et al.*, 2018). Better body condition (being heavier for a given body length) in larger groups may not be a result of larger group size, but rather the cause of it. Experiments manipulating group size would be required to elucidate the effects of group size on body condition. These experiments could be conducted in a controlled environment, allowing for the manipulation of temperature to further assess the seasonal effects of group size on body condition.

The assistance of helper individuals can mitigate reductions in body condition and survival caused by seasonal fluctuations (Groenewoud & Clutton-Brock, 2021; Wiley & Ridley, 2016). Indeed, theory predicts in social mole-rats that additional group members contribute to digging and foraging efforts, which can greatly reduce the risk of a negative energy balance between energy expended from digging and energy gained from foraging (Spinks & Plagányi, 1999). A previous study on Natal mole-rats supported this hypothesis, showing that overall body condition (measured by body fat content) increased with group size (Luterman *et al.*, 2013). Our results showed some support for the idea that body condition decreases with group size during summer and increases with group size during winter. However, excluding the largest group from the analysis caused this relationship to disappear. Thus, it remains unclear to what extent these correlations are biologically important. Whereas there may be foraging benefits accrued through cooperative foraging, these effects appear to be limited and relatively weak in Natal mole-rats. Yet, for individuals living in large groups, body condition may decrease with increasing group size during the summer compared to the winter season. A decline in body condition with increasing group size in summer could also promote dispersal if current conditions lead to a negative energy balance. Our capture records indicate that dispersal primarily occurs during the rainy summer season (January to May; Finn, unpublished data). As a result, group size in Natal mole-rats may decrease with increasing competition, as observed in other group-living species (Beltrão *et al.*, 2022; Young *et al.*, 2005). This result may indicate an optimal group size for Natal mole-rats, which is why groups of over 10 are relatively uncommon in the wild (Fig. S4).

Indirect fitness benefits alone may not be enough to facilitate the evolution of cooperative behaviours without direct survival benefits because per capita reproductive benefits decrease as group size increases (Downing, 2024; García Ruiz *et al.*, 2022). In other social mole-rats, such as Damaraland (*Fukomys damarensis*) and naked mole-rats (*Heterocephalus glaber*), indirect fitness benefits have been assumed to facilitate group living (Faulkes & Bennett, 2021; Jarvis *et al.*, 1994). However, group living in Natal mole-rats may be promoted by direct benefits (e.g., cooperative foraging or social thermoregulation) instead of indirect fitness benefits. Natal mole-rats at our study site live in a temperate region with high rainfall and evenly distributed food resources (Spinks & Plagányi, 1999). Due to these relatively benign conditions, they may not

necessarily need to live in large groups. However, cold winter temperatures may require social thermoregulation for survival. For cooperative foraging to function successfully, individuals must share their finds with other group members (Schloesser *et al.*, 2019). Social cohesion and cooperation may break down due to within-group competition when food resources become scarce (Beltrão *et al.*, 2022), causing contributions to helping behaviour to vary between individuals based on body condition, relatedness, or group size (Barclay & Reeve, 2012; Leedale *et al.*, 2017; Rotics & Clutton-Brock, 2021). For example, group members of lower body condition may contribute less to offspring care or other cooperative behaviours (Barclay & Reeve, 2012; Young *et al.*, 2005). We speculate that as group size increases, competition among individuals increases, causing a decline in body condition and, as a result, individual contributions to cooperative behaviours may decrease, and ultimately, group members may disperse. Miniaturized accelerometers could be utilized to quantify fine-scale movements and behaviours (Brown *et al.*, 2013; Finn *et al.*, 2024), and test how helping contributions change with body condition, group size, and across seasons in wild mole-rats.

The temperate environmental conditions of our study site are not experienced by other social mole-rat species living in harsh, arid conditions with high summer temperatures and low annual rainfall (e.g., Damaraland mole-rats, naked mole-rats, Mahali mole-rat (*Cryptomys hottentotus mahali*)). Group living in arid-dwelling mole-rats is most likely driven by ecological constraints (Emlen, 1982; Jarvis *et al.*, 1994). Yet, theory predicts that group living in less arid environments is promoted by density-dependent (habitat saturation) or social constraints (sexual maturation, lack of mates), which prevent the independent reproduction of subordinates (Emlen, 1982). The Natal mole-rat provides us with a rare glimpse into how cooperative breeding can evolve in mammals living in variable, temperate environments with predictable rainfall, as previously shown in birds (Cornwallis *et al.*, 2017). The evolution of cooperative breeding in ancestral bathyergids living in temperate environments may have allowed more recently evolved species (e.g., Damaraland mole-rats and other members of the genus *Fukomys*) to better colonize and adapt to harsher environments. Indeed, it has been suggested that the ancestor of the social bathyergids (i.e., members of the genera *Cryptomys* and *Fukomys*) first colonized mesic eastern Southern Africa, then expanded west and north into the arid regions of Botswana and Zambia (Faulkes *et al.*, 2004).

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Conflict of interest

The authors have no conflict of interest to declare.

Author contributions

KF, NB, and MZ conceived and designed the study. KF, AJvV, and TS collected data. KF analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

Data availability statement

Research data and R code supporting this work are available on Figshare: <https://doi.org/10.6084/m9.figshare.26488255.v4>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Climate conditions at the study site.

Figure S2. The major axis regression of tooth width on body mass.

Figure S3. Group size has limited effect on body mass between seasons.

Figure S4. Histogram of group sizes of Natal mole-rats across all captures.

Table S1. Effects of group size and season on body mass in Natal mole-rats.