Fitness of breeders in social Damaraland mole-rats is independent of group size

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ABSTRACT

Damaraland mole-rats (*Fukomys damarensis)* are usually viewed as an obligatorily group living eusocial species in which successful reproduction is dependent on reproductive altruism of closely related group members. However, the reproductive ecology of social mole-rats in their natural environment remains poorly understood and it is unclear to what extent successful reproduction is dependent on assistance from other group members. Using data from a 7-year field study of marked individuals, we show that, after dispersal from their natal group, individuals typically settled alone in new burrow systems where they enjoyed high survival rates, and often remained in good body condition for several years before finding a mate. Unlike most other eusocial or singular cooperative breeders, we found that Damaraland mole-rats reproduced successfully in pairs without helpers and experimentally formed pairs had the same reproductive success as larger established groups. Overall there was only a weak increase in reproductive success with increasing group size and no effect of group size on adult survival rates across the population. Juveniles in large groups grew faster early in life but their growth rates declined subsequently so that they eventually plateaued at a lower maximum body mass than juveniles from small groups. Taken together, our data suggest that the fitness benefits of group living to breeders are small and we suggest that extended philopatry in Damaraland mole-rats has evolved because of the high costs and constraints of dispersal rather than because of strong indirect benefits accrued through cooperative behaviour.

Keywords: sociality, cooperative breeding, inclusive fitness, philopatry, family living, Bathyergidae

INTRODUCTION

Naked (*Heterocephalus glaber*) and Damaraland mole-rats (*Fukomys damarensis*) are often referred to as the only eusocial mammals on the grounds that there is a single breeding female, that multiple generations overlap, that non-breeders may be allocated to discrete, specialised castes, and that some individuals remain as members of small-bodied worker castes for their entire lives (Jarvis, 1981; Jarvis *et al.*, 1994; Burda *et al.*, 2000; Scantlebury *et al.*, 2006; Faulkes & Bennett, 2021). It has also been suggested that naked mole-rat groups include a specialised disperser morph similar to the alates of the termites that promotes dispersal and outbreeding (O'Riain, Jarvis & Faulkes, 1996; Braude, 2000; Toor *et al.*, 2020), and that breeders and non-breeders in both species are morphologically different from one another (O'Riain *et al.*, 2000; Young & Bennett, 2010; Thorley *et al.*, 2018a). Studies of other social mole-rats of the family *Bathyergidae* (including Common (*Cryptomys hottentotus*), Ansell's (*Fukomys anselli*) and giant mole-rats (*Fukomys mechowi*)) have shown that groups in these species are generally smaller than those seen in naked and Damaraland mole-rats, but also emphasize strong structural similarities, being comprised of a nuclear family with a single breeding female and limited out-of-group paternity (Bennett & Faulkes, 2000; Spinks, Bennett & Jarvis, 2000; Bishop *et al.*, 2004; Patzenhauerová *et al.*, 2013; Caspar, Müller & Begall, 2021; Caspar, Burda & Begall, 2001). Although there is some uncertainty about how to categorise the various mole-rat species according to their social organisation (Buffenstein *et al.*, 2021), most reviews consider both Damaraland and naked mole-rats as eusocial (Jarvis *et al.*, 1994; Faulkes & Bennett, 2016, 2021), or all social mole-rats as eusocial (Burda *et al.*, 2000; Braude *et al.*, 2021).

Though social mole-rats do share some important characteristics with eusocial and singular cooperatively breeding species, their societies also show some important differences. In groups of social mole-rats, the principal cooperative activity of non-breeding individuals is

to maintain the extensive network of tunnels that provide access to underground plant tubers and to bring food to food stores that are accessible to all group members (Brett, 1991; Bennett & Faulkes, 2000). This extensive involvement of many non-breeders in cooperative foraging has led to the suggestion that there are strong positive effects of group size on breeding success and survival in groups of social mole-rats, particularly in arid environments (Jarvis *et al.*, 1994; Jarvis, Bennett & Spinks, 1998). However, direct alloparental care by non-breeders is limited to rare occasions when young offspring wander out of the nest and are retrieved by helpers (Zöttl *et al.*, 2016b, 2018), and unlike in most cooperative breeders (Solomon & French, 1997; Koenig & Dickinson, 2016) non-breeders do not provision offspring or the breeding female directly (Bennett & Faulkes, 2000; Zöttl *et al.*, 2016b). Experiments in captivity have also indicated that territory defence against conspecific intruders in Damaraland mole-rats is predominantly carried out by the breeding individuals (Cooney, 2002), which also contrasts with many other cooperative societies where most group members participate in group defence (Radford & du Plessis, 2004; Mares, Young & Clutton-Brock, 2012; Cassidy *et al.*, 2015). Together these studies raise the question of whether most or all of the activities of non-breeders should be regarded as selfish and mutually beneficial to all group members rather than as altruistic behaviours. Currently, there is little evidence of clear, altruistic behaviour of non-breeders directed towards collateral kin and it remains unclear whether non-breeding helpers in mole-rats enhance breeding success or survival of the breeding individuals.

To assess to what extent the societies of social mole-rats share characteristics of eusocial breeders and to what extent they resemble those of group living species without substantial altruistic behaviour we need to understand the fitness consequences of group living and cooperative behaviour in natural populations of mole-rats. Longitudinal studies of wild mole-rat populations are particularly uncommon (Faulkes & Bennett, 2021), but one rare study that explored the effects of group size on various demographic parameters was conducted on a

Damaraland mole-rat population in central Namibia, where Young et al. (2015) found that larger groups recruited more offspring. At the same time, juvenile survival was largely unaffected by group size, and juvenile growth rate was suppressed in large groups; possibly due to competition between non-breeders, and perhaps implying that large groups may also impose costs on the development of offspring (Young *et al.*, 2015). Breeding females have also been shown to have lower workloads than breeders in a separate population of Damaraland mole-rats (Francioli *et al.*, 2020), and in captivity, the workload of breeding females was also reduced in larger groups (Houslay *et al.*, 2020), alluding to helper effects in this setting. However, it is still unclear whether single individuals and small groups in natural populations of social mole-rats experience high mortality, whether nascent groups consisting only of a pair habitually fail with reproduction, whether the presence of non-breeders increases breeder survival and whether group size affects the growth trajectories of juveniles. Different populations of mole-rats will also vary in the environmental conditions they experience and in their demography and this may in turn affect the expression of social traits and the effects of group size at both temporal and spatial scales (Spinks *et al.*, 2000; Finn *et al.*, 2018); as seen for many other social mammals (Silk, 2007; Schradin, König & Pillay, 2010; Ebensperger, Rivera & Hayes, 2012; Clutton-Brock, 2016). For any given species the contributions of group members to the various components of fitness cannot therefore be assumed to be consistent across all populations.

In this study we investigate the effects of non-breeders on fitness correlates in a wild population of Damaraland mole-rats located in the southern Kalahari Desert. We first ask whether individuals living in groups experience higher survivorship than individuals that have dispersed and settled solitarily. Second, by experimentally creating breeding pairs in the field, we examine whether the reproductive output of breeders lacking non-breeding group members is lower than that of established groups which have access to a potential workforce. Lastly, we

leverage demographic information collected across 7 years of field study to analyse the associations of group size with (i) reproductive success, (ii) adult survival, and (iii) growth of recruited offspring, testing the prediction that large group size generates reproductive and survival benefits and enhances growth among young individuals.

MATERIALS AND METHODS

a) General methods

Damaraland mole-rats were captured in the area surrounding the Kuruman River Reserve (-26.978560, 21.832459) in the Kalahari Desert of South Africa between September 2013 and May 2020. Field work was carried out at two neighbouring localities, the Kuruman River Reserve ("Kuruman"), and the Lonely farm ("Lonely", Figures S1 & S2). The two locations form a continuous population but because of the time intensive nature of mole-rat trapping they tended to be trapped in discrete periods (Figures S3 & S4), hereafter referred to as "trapping windows". For logistical reasons, trapping stopped at Lonely in July 2017.

Groups of mole-rats in the wild are revealed by the lines of mounds that they extrude when excavating their tunnel systems (Figure 1). Groups were trapped periodically at 6 to 12-month intervals using modified Hickman traps that were baited with sweet potato and positioned into tunnel systems once accessed by digging. After trap setting, traps were checked every 2-3 hours throughout the day and night. On capture, animals were placed into a closed box and provided with food and shelter. Intermittently, individuals were transported back to the laboratory where they were sexes, weighed to the nearest gram and measured for various morphometrics. Breeding females are commonly the largest female in their group and can be easily identified from their perforated vagina and prominent teats. All captured individuals were marked with passive integrated transponder (PIT) tags on first capture to allow for individual recognition on recapture. After sampling, groups were housed temporarily in semi-

natural tunnel systems in the laboratory and provided with food, nesting material and sand. The complete group was assumed to have been captured after an absence of activity at the trap sites for 24hrs, after which point the animals were returned to their tunnel system.

Between September 2013 and May 2020, 752 unique individuals (368 females, 384 males) were trapped at the two sites (N = 1941 individual captures). The mean recapture-rate of individuals across successive trapping windows was 73.1% at Kuruman and 54.8% at Lonely (Table S1). In total, analyses used data from 328 group captures that were carried out at 84 groups with mean of 4.0 (1SD = 3.07) captures per group (Figure S2). Groups were defined as individuals repeatedly found at the same trapping location, and in the majority of recapture events the same breeding female remained at a group for their duration. Thus, as long as the majority of individuals trapped within the same area were known to originate from the same group, the group continued to be defined as such. On several occasions a new group had moved into the tunnel system previously occupied by another group. The initial group were then either found elsewhere or never recaptured and likely extinct. Single individuals, either new unknown individuals or known individuals that had dispersed from an established group were assigned their own unique group ID, which was retained if they were later joined by an immigrant partner and started breeding in the same area.

In 15.2% of group captures, continued activity at trapping sites indicated that the complete group had not been captured by the end of the week of trapping. The decision to include or exclude these incomplete captures depended on the analysis: group-level analyses excluded incomplete captures whereas individual-level analyses included them (a summary of the data and models used for the various analyses is provided in Table S2.). Analyses were conducted in R version 3.6.3 (R Core Team, 2021), and all code is provided online (Github, to be made public on acceptance).

b) Status-related survivorship among females

To estimate the survivorship of females in different states we fitted a multi-state Markov model. Such models are typically used in a medical setting for 'panel data', where a continuously observed process - like disease progression - is measured only at discrete time points - when people choose to visit the hospital. The timing of transitions between states can then be estimated indirectly under the assumption that the next state in a sequence of states depends only on the current state, and not on the history of transitions or on the time spent in the prior state (Jackson, 2011). Our longitudinal data bears a panel-like structure, with individuals and groups being periodically captured (or not) in different life history stages or 'states'. The model then estimates the probability that individual mole-rats transition between different states. Here, we present information on survival probability from each state.

Information on individual capture histories was used to assign individuals to one of four states relative to the time since their first capture: *i- non-breeder* in their natal group, ii- *single individual*, *iii- breeding individual* out of their natal group, *iv- disappeared*/*dead* (Figure S5). For model fitting purposes, in the small number of cases where females inherited a breeding position within their natal group (n = 7), these females were categorised in the same state as females that acquired a breeding position out of their natal group (*iii*). To define state *iv* (disappeared/died), we incorporated information from the trapping windows at "Kuruman" and "Lonely". If an individual had not been recaptured for at least two consecutive trapping windows, it was assumed to have dispersed or died at some point between its last live capture and the start of the subsequent trapping window, and given an extra row of data reflecting this; the model is then parameterised so that the timing of disappearance or death is not exact. Similarly, if individuals were captured within the last trapping window at each location, we assumed that they were still alive at the end of that trapping window (i.e. the end of the study). They were then given an extra row of data reflecting this assumption and were censored at this

point, which in the most extreme case assumes that individuals remained in their last captured state for a further 80 days (Figure S5). To explore whether group size affected the likelihood that non-breeding females or breeding females died/disappeared, we fitted an additional model that included a group size covariate for each of these transitions. The multi-state models were fitted in the *msm* package (Jackson, 2011; Figure S6 for multi-state diagram). When reporting hazard ratios and relative likelihoods from the multi-state models we class cases where the 95% confidence intervals do not overlap one as indicating a biologically important effect, and otherwise emphasize effect sizes.

c) Within-group recruitment

Two approaches were used to investigate the role of group size on within-group recruitment. In the first, recruitment was analysed longitudinally across the duration of the study. In the second, new groups were experimentally created in the wild through the introduction of unfamiliar adult males to solitary females. The recruitment rate of newly created pairs was then compared to that of established groups that were captured and recaptured within the same time period. The benefit of the second approach is that it allows for a direct test of whether groups in the early stages of group formation were less productive than established groups. Any individuals caught within one year that were lighter than 100g (males) or 80g (females) were assumed to be recruited from within the group, as informed by the growth curves. By contrast, any new individuals heavier than these cut-offs were assumed to represent out-of-group immigrants.

The longitudinal analysis used information from every capture-recapture event where a group was captured and then recaptured within a 100 to 365-day time period; where a resident breeding female was present; and where at least one large male was retained across the two captures. The analysis is therefore restricted to active breeding units. In total, this produced a

dataset of 78 group-level capture-recapture events that took place in 33 groups with a mean trapping interval of 214.2 days (1SD = 52.11). The number of recruits was modelled using a generalised linear mixed effects model with Poisson error in the *glmmTMB* package (Brooks, Mollie *et al.*, 2017). Fixed effects of group size at first capture, the mass of the breeding female at the capture, and rainfall were included. A single random effect of group identity was included, and the logged time interval between capture and recapture was included as an offset term. Rainfall was calculated as the geometric mean monthly rainfall in the year preceding the first capture as this provided the best fit to the data (lowest AIC score) when compared to models fitted to the total rainfall, or the arithmetic mean rainfall. After standardising relative to the trapping duration, the mean 6-monthly recruitment to groups was 2.12 individuals (1SD = 1.82). Continuous variables were z-score transformed prior to model fitting.

For the experimental approach, 8 solitary females were captured between 16th April 2016 and 29th May 2016. Solitary females were brought back into the laboratory and paired with wild males captured concurrently from intact breeding groups. When pairing, males and females were first isolated in their own temporary tunnel system and exposed to the odour of their prospective partner for 24 hours. After this time period, the male was introduced to the female for 24 hours in her lab tunnel system, before they were returned together to the female's tunnel system in the wild. All pairings used large adult males originating from groups > 3km from the focal solitary female, so it is highly unlikely that pairings were conducted between close relatives and/or familiar individuals. The recruitment rate of new pairs was compared to that of established groups captured over the same time period using a Welch's t-test after first standardising recruitment rate to a yearly measure. Groups where a male was removed were not included in the established groups treatment in case the male was a breeder in his original group, which would necessarily reduce the rate of recruitment. The mean trapping interval did

not differ between new pairs (249.89 days ± 94.34) and established groups (306.88 days ± 64.39; Welch's t-test: t = -1.47, df = 14.14, p = 0.16).

d) Early-life growth

As the age of wild-caught individuals was unknown, we modelled growth using interval equations that estimated the change in body mass and upper incisor width of individuals across successive capture events. The upper incisors are a reliable measure of skeletal size in Damaraland mole-rats and are the main apparatus of digging (Young & Bennett, 2010). Incisor width was measured at the widest point using digital callipers (± 0.01mm). All measurements were taken in duplicate by two observers and the mean of these two measurements was used. Previous studies show that the shape of growth in captive mole-rats is concave and can be approximated by a monomolecular curve (Thorley, 2018). To allow for a similar shape of growth in the wild, the interval equation was parameterised as a von Bertalanffy growth curve (Thorley & Clutton-Brock, 2019) and fitted as a non-linear mixed effect model (NLMM) in the *nlme* package (Pinheiro *et al.*, 2019). The body mass or incisor width of an individual at each recapture was estimated as:

$$S2_i = A - (A - S1_i)e^{-k.D_i} + \varepsilon_i$$

where $S1_i$ and $S2_i$ are the size at capture and recapture, respectively, for individual *i*. A is the estimated population-level asymptotic size, *k* is the growth rate constant, D_i is the time difference between capture and recapture (hereafter the 'trapping interval'). ε_i is the normally distributed error with mean 0 and variance σ^2.

Separate models were fitted to males and females for each size metric, using all information from individuals that were recaptured at least once, and where the recapture interval fell between 90 and 365 days. The female body mass dataset comprised 381 "repeat capture" events (*n* = 193 females, mean/female = 1.96, 1SD = 1.21) and excluded any weight

data from females once they were known to be a breeder, thus removing any artefact of status or pregnancy. The male body mass dataset consisted of n = 456 repeat capture events (n = 214 males, mean/male = 2.13, 1SD = 1.54). The female and male incisor width datasets consisted of 328 and 381 repeat capture events respectively (n = 193 females, mean/female = 1.82, 1SD = 1.16; n = 198 males, mean/male = 1.92, 1SD = 1.33). In each model a random effect of individual identity was specified at the level of the asymptote and the growth rate constant, and to aid convergence, random effects were modelled as uncorrelated. Likelihood ratio tests indicated that the inclusion of a random effect of group identity was not needed.

The initial growth model was extended by incorporating a standardised group size term:

$$S2_i = (A + A_{GS}.GS) - ((A + A_{GS}.GS) - S1_i)e^{-(k + k_{GS}.GS).D_i} + \varepsilon_i$$

Here, A_{GS} and k_{GS} estimate the change in asymptotic mass and growth rate constant with changing group size, GS. Group size was taken as the group size on initial capture, which was highly correlated with recapture group size (r = 0.78, df = 835, p < 0.001). As the results were qualitatively unaffected by excluding incomplete captures, results are presented for all captures. Group size was z-score transformed prior to model fitting, such that A and k are estimated at the mean group size experienced by each sex.

RESULTS

a) Population structure and distribution of group sizes

The mean group size across all captures was 5.91 individuals (1SD = 5.61, max = 26, Figure 1). Of the 84 unique groups that were captured, 49 were of a single individual on the first capture, 94% of which were females (n = 46). Excluding this large number of single individuals, the mean group size was 8.67 individuals (1SD = 5.30), which can be taken to represent the average size of a breeding unit in the population.

Across the duration of the study only one reproductively active 'breeding' female was present at a group at any given time.

b) Status-related survivorship among females

Single females generally exhibited high annual survival rates and disappeared from the population at intermediate rates between those of breeders and those of non-breeders (Figure 2, Table S3); their survival was higher (79.3%) than that of in-group non-breeders (64.2%) and tended to be lower than that of breeders (86.7%). Thus, in-group non-breeders were 1.91 times more likely to disappear than single females (95% CI [1.07,3.43]), and 3.28 times more likely to disappear than breeding females (95% CI [1.84,5.82]). The rate of disappearance of single females was higher than that of breeding females, with the former being 1.71 times more likely to disappear than the latter, though this effect was not significant (95% CI [0.78,3.77], Figure 2c). Group size did not appear to affect the likelihood that non-breeding females (hazard ratio = 1.003, 95% CI [0.973,1.033]) or breeding females (hazard ratio = 1.058, 95% CI [0.970,1.156]) died/disappeared.

Single females maintained good body condition over extended periods, frequently over several years. The body condition of single females was equivalent to that of size-matched non-

breeders (Figure 3), suggesting that solitary living does not affect the ability of individuals to acquire food and maintain mass (condition analyses outlined in Supplementary Material).

c) Within-group recruitment

The rate of recruitment was largely independent of group size. Experimentally created pairs recruited a comparable number of offspring into their group as established groups that were captured and recaptured over the same time period (Figure 4a; Welch's t-test, $t = 0.253$, $df = 14.02$, $p = 0.80$; Figure S7 details capture history after pairing). The recruitment rate in experimental and control groups over the experimental period was comparable to the total recruitment rate over the whole study period (Figure 4a), and environmental conditions across the experimental period were typical of those seen in the Kalahari over a longer time span (Figure S8).

Across the duration of the study, group size was associated with a slight increase in within-group recruitment rate (0.216 ± 0.106, $z = 2.04$, $p = 0.042$, Table S4, Figure 4b). Changing the group size term to reflect the mean group size across the capture and recapture event did not qualitatively affect the result. Increased rainfall in the year prior to first trapping trended towards having a positive effect on recruitment (geometric mean monthly rainfall: 0.159 ± 0.086, $z = 1.85$, $p = 0.065$), but the body mass of the breeding female did not (-0.090 ± 0.089, $z = -1.02$, $p = 0.31$). The inclusion of an interaction between rainfall and group size suggested that the effect of group size on recruitment rate did not depend upon recently experienced weather conditions (0.108 ± 0.080, $z = 1.36$, $p = 0.17$).

d) Early-life growth and adult body mass

In both sexes, increases in group size were associated with a faster growth rate in early life (Figure 5, Table S5). However, growth rates declined more strongly during ontogeny in

larger groups and their members ultimately went on to attain a lower asymptotic body mass (NLMM: male A_{GS} = -8.10 ± 2.02, p < 0.001; female A_{GS} = -9.42 ± 1.47, p < 0.001) (see Figures S9-10, Supplementary Material for further treatment). Increases in group size were also associated with reductions in asymptotic skeletal size in both sexes, though the effect was only supported in females (NLMM: male A_{GS} = -0.047 ± 0.036, p = 0.19; female A_{GS} = -0.113 ± 0.027, p < 0.001, Table S7). In contrast to the body mass models, there was no support for a relationship between group size and the growth rate constant in either sex (Table S7).

DISCUSSION

The idea that there are strong benefits of group-living to breeders is implicit in many discussions surrounding the evolution of sociality in the African mole-rats (Jarvis *et al.*, 1994; Faulkes & Bennett, 2021). However, up until now only a single study of social mole-rats has explored the fitness consequences of group size in a wild population. In this previous study of Damaraland mole-rats, Young et al. (2015) found that reproductive success was higher in large groups, that survival was independent of group size, and that growth rates of juveniles were reduced in larger groups. In captivity, Houslay et al. (2020) also demonstrated that breeding females in larger groups worked less and showed higher fecundity, though juveniles in this and other captive populations grew more slowly in large groups despite being fed *ad libitum* (Bennett & Navarro, 1997; Zöttl *et al.*, 2016a).

Contrary to the long held belief that group size has strong positive effects on breeder fitness in social mole-rats, our detailed demographic analysis of Damaraland mole-rats demonstrates that for our study population, group size effects are often weak and can be offset by costs of breeding in large groups. In other social species, competition within groups can reduce growth (Buston 2003; Heg et al. 2004) and it is possible that similar effects of competition also reduce fitness in mole-rats. Despite the many possible benefits of large group

size, the weakness or absence of positive associations between group size and fitness correlates overall indicates that the inclusive fitness benefits generated by non-breeders are probably low. We suggest that ecological constraints on dispersal should be considered the principal driver of group-living in the African mole-rats and our data provides several lines of evidence that support this suggestion.

A significant proportion of individuals in our study population are females that have dispersed and settled alone in a burrow system. We find that these solitary individuals display high survivorship and good body condition, despite being forced to forage alone and lacking access to other putative benefits of group living, such as the benefits of group defence, or social thermoregulation. Once joined by a male, these nascent pairs often begin breeding immediately and produce pups at a rate which is comparable to that of established groups. This supports the more general picture to emerge from our data that increases in group size are associated with minimal increases in the reproductive output of breeders. We also show that pups born in small groups initially grow more slowly than pups born in large groups but that their subsequent asymptotic mass is higher than that of individuals in larger groups. These are uncommon patterns among cooperatively breeding vertebrates - to which mole-rats are often compared - where the effects of group size on fitness are often strongly positive (Solomon & French, 1997; Russell, 2004; Ebensperger *et al.*, 2012). This is particularly true of singular cooperative breeders like African wild dogs (*Lycaon pictus*), meerkats (*Suricata suricatta*) and dwarf mongooses (*Helogale parvula*), where a breeding pair is responsible for the majority of group-level reproduction and where pairs of individuals usually fail to reproduce successfully without the direct actions of helpers in rearing pups (Rood, 1990; Creel & Creel, 2002; Groenewoud & Clutton-Brock, 2021). We of course recognise that large group sizes can also have negative impacts in these species (e.g. Creel & Creel, 2015), but to find only weak or absent effects

across several parameters as we do in our study is unusual, and challenges the idea that Damaraland mole-rat breeders are reliant on assistance from non-breeders.

Instead of being maintained by selection for reproductive cooperation, group-living in mole-rats may be largely due to ecological constraints on dispersal. Such constraints appear to have been important in the evolution of group-living in rodents generally (Solomon, 2003; Firman *et al.*, 2020), and while often also depending on phylogeny and other aspects of life history (Ebensperger & Blumstein, 2006; Smorkatcheva & Lukhtanov, 2014; Sobrero *et al.*, 2014), the low recapture rate of non-breeding individuals in our study testifies to the high risks of dispersal (which is often overground) for Damaraland mole-rats (see also Hazell *et al.*, 2000). This likely explains why dispersal in this species is concentrated around intermittent periods of rainfall - when the soil is soft enough to facilitate burrow digging (Lovegrove, 1989; Jarvis *et al.*, 1994; Torrents Ticó *et al.*, 2018a)- and why dispersal success is strongly associated with individual quality, such that fast-growing individuals that reach a high pre-departure body mass are most likely to establish independent breeding territories (Torrents-Ticó *et al.*, 2018b). As a result, there is likely to be strong selection on non-breeders to delay dispersal and remain in their natal group until their chances of dispersing successfully are greatest (Jarvis *et al.*, 1998; Bennett & Faulkes, 2000). Breeders, in turn, may tolerate non-breeders as a form of extended parental care even if their retained offspring provide little to no fitness benefits or advantage their future reproduction. This argument implies that maternal tolerance towards offspring beyond their independence may have been a key factor facilitating group-living in the social mole-rats. Observations of parental behaviour in captive mole-rats support this idea. In solitary species, researchers have noted frequent aggression from mothers towards offspring and have therefore stated that natal dispersal is often driven by eviction in these species (Bennett & Faulkes, 2000; Šumbera, Burda & Chitaukali, 2003). By contrast, our observations of captive Damaraland mole-rats indicate that interactions between mothers and offspring are

rarely aggressive, and that evictions of retained offspring from intact family groups are uncommon. It therefore seems likely that most dispersal events from wild mole-rat groups are voluntary.

With respect to philopatry of non-breeders and cooperative behaviour within groups, our results suggest that Damaraland mole-rat societies resemble those of some group-living birds and other social rodents that live in families but where helper effects are minimal or absent (Ekman, 2006; Drobniak *et al.*, 2015). Siberian jays (*Perisoreus infaustus*) for example, live in groups where recruits remain in their parents' territory, do not breed themselves and play little role in raising their parents subsequent offspring (Ekman & Griesser, 2016). Like in mole-rats, non-breeders in these bird groups delay dispersal due to ecological constraints and because early departure from the group greatly diminishes the chances of successfully establishing a breeding territory (Ekman, Bylin & Tegelström, 1999; Torrents-Ticó *et al.*, 2018b). In their natal group, philopatric offspring participate in group-level collective actions such as coordinated territory defence and - in the case of mole-rats - in communal foraging, though do not directly provision subsequent offspring, and there are likely fitness benefits for all group members that are generated by this form of mutually beneficial cooperation. Similarly, in other social rodents, such as marmots (*Marmota sp.*), and beavers (*Castor sp.*), group members delay their dispersal and engage in shared, mutually beneficial activities such as nest building, burrow/den construction, and huddling for thermoregulation (Blumstein & Armitage, 1999; Busher, 2007; Mayer, Zedrosser & Rosell, 2017). However, the presence of older offspring may also impose costs on breeders and subsequent offspring through enhanced resource competition and intrasexual competition and in Damaraland mole-rats breeders probably tolerate these costs because the benefits either outweigh the costs, so that the prolonged presence of non-breeders comes to a net zero outcome, or because they are prepared to tolerate some costs to their future reproduction as a form of extended parental care.

While our study found little support for clear group size effects on fitness, it remains possible that some benefits of group size only become apparent under extreme environmental conditions, such as during extended droughts (Jarvis *et al.*, 1998; Bourne *et al.*, 2020; Capilla-Lasheras *et al.*, 2021; Groenewoud & Clutton-Brock, 2021), or are masked by counteracting pressures, such as increased competition for food, or elevated parasite burdens (Schmid-Hempel, 2017). There are also other ways in which group-living might benefit individuals which we have not been able to fully investigate in our population thus far. Chief among these is the possibility that larger groups persist for longer than smaller groups (Keynan & Ridley, 2016; Duncan, Manser & Clutton-Brock, 2021). Our finding that group size has little effect on breeder survival, and that single females enjoy high survivorship, downplays the importance of group size on group persistence generally, but the long potential lifespan of Damaraland mole-rats (more than 10 years: Schmidt, Jarvis & Bennett, 2013) might mean that particularly long time series on the order of several decades are needed to critically examine group persistence.

Overall, our data suggest that the idea that some non-breeders have adopted an alternative life-history strategy of lifetime philopatry similar to workers found in eusocial insects is probably incorrect, because non-breeders appear to gain little inclusive fitness from philopatry. Instead, individuals that fail to acquire a breeding position are probably low-quality individuals that show reduced growth rates and lower investments in cooperative behaviour prior to dispersal (Zöttl *et al.*, 2016b; Thorley *et al.*, 2018b; Torrents-Ticó *et al.*, 2018b). While we acknowledge the similarity of Damaraland mole-rat societies to eusocial and cooperative breeders in terms of reproductive skew and reproductive suppression within groups (Faulkes & Bennett, 2016, 2021; Braude *et al.*, 2021), our paper highlights that further similarities relating to the positive effects of helpers on breeder reproduction have been overemphasized.

In this latter aspect, Damaraland mole-rats may be more similar to some group-living birds and social rodents where breeders do not rely on the assistance of helpers.

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ETHICS

The research carried out in this study was approved by the University of Pretoria Animal Ethics Committee (ECO32-13, EC050-16)

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AUTHOR CONTRIBUTIONS

J.T, H.B, and M.Z planned and designed the study. J.T. carried out statistical analyses with input from H.B and M.Z. J.T., H.B, M.Z., and K.F conducted fieldwork and maintained the database. T.C-B. provided access to facilities and infrastructure at the Kuruman River Reserve. J.T. and M.Z wrote the manuscript, with input from all co-authors throughout.

FIGURES

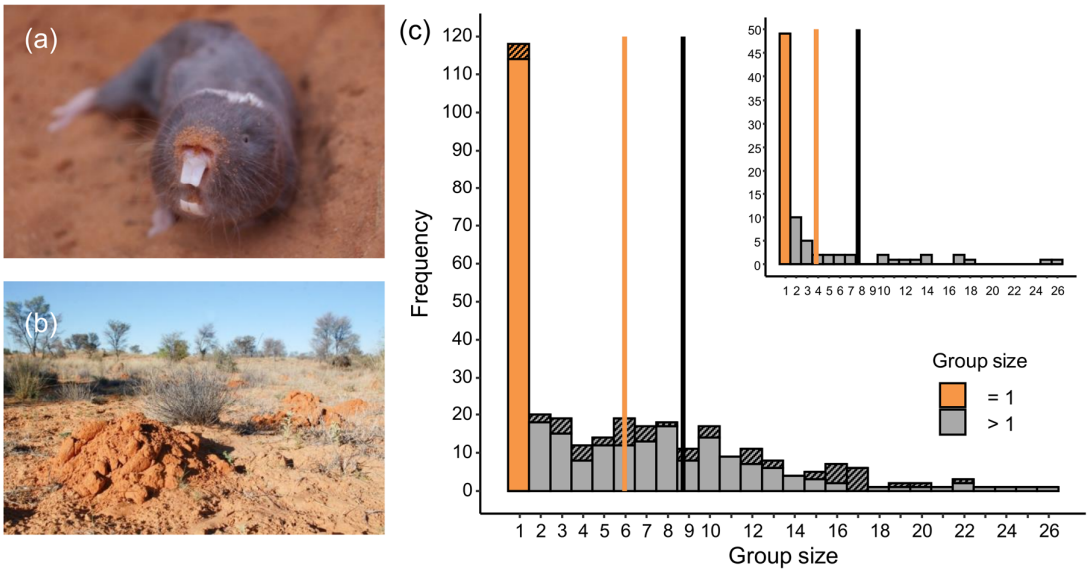


Figure 1. Group sizes for Damaraland mole-rats in the southern Kalahari. (a) An adult Damaraland mole-rat. (b) A line of sand mounds that is created by a group of mole-rats when they dig foraging tunnels underground. (c) The distribution of group sizes in the study population at the Kuruman River Reserve. The main histogram displays group size frequencies across all captures, while the inset histogram displays the group size at first capture for each unique group (n = 82; including single individuals). In each case, a large proportion of the population were captured as single individuals (orange), who were almost exclusively females. The vertical lines display the mean group size either including (orange) or excluding (black) these single individuals, and for all captures, we distinguish between complete and incomplete group captures by hatching the latter (mean for all complete group captures = 5.45, 1SD = 5.51; mean for complete captures of groups > 1 = 8.54, 1SD = 5.32). Removing the 15.2% of incomplete captures had limited influence on the mean group size (not displayed).

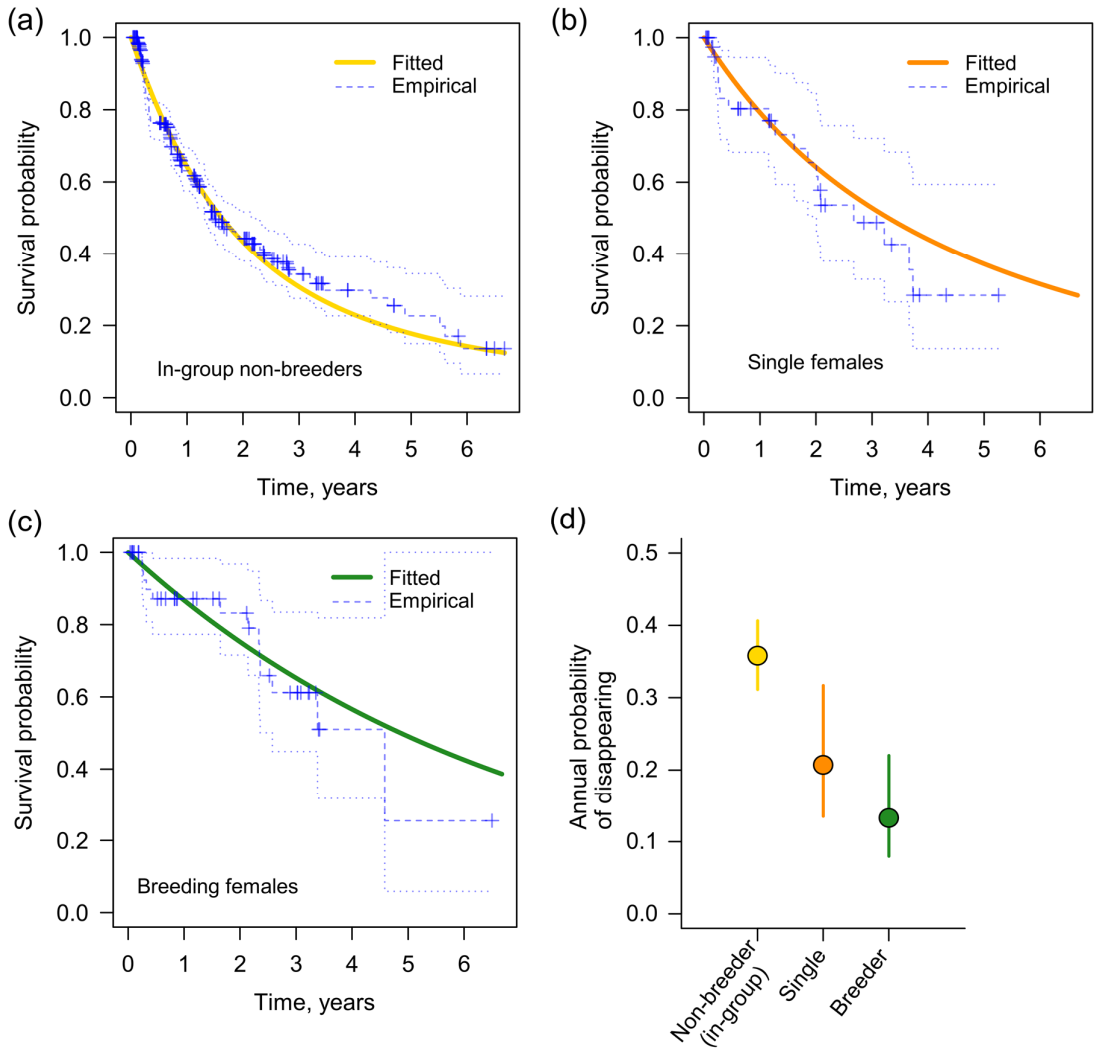


Figure 2. Status-related survivorship in female Damaraland mole-rats: in-group non-breeders (a), single females (b), and breeding females (c). Solid lines display the expected probability of survival from each state and dotted lines display the 'empirical' Kaplan-Meier estimate of survival probability, with crosses denoting cases of censorship. Here, survival strictly refers to disappearance from the study population, and the predicted annual probability of disappearance (mean ± 95% CI) is given in (d). 'Survival' therefore combines cases of in-state mortality with cases of dispersal, where individuals have left their current group and state and are not re-captured thereafter. Dispersal is most likely to account for a large proportion of disappearances from the in-group non-breeder state, and the low incidence of recaptures of individuals thereafter implies that dispersal carries a high cost of mortality. Note that one female had been recaptured as a singleton for 5.26 years by the end-point of the study, and was right-censored at that point.

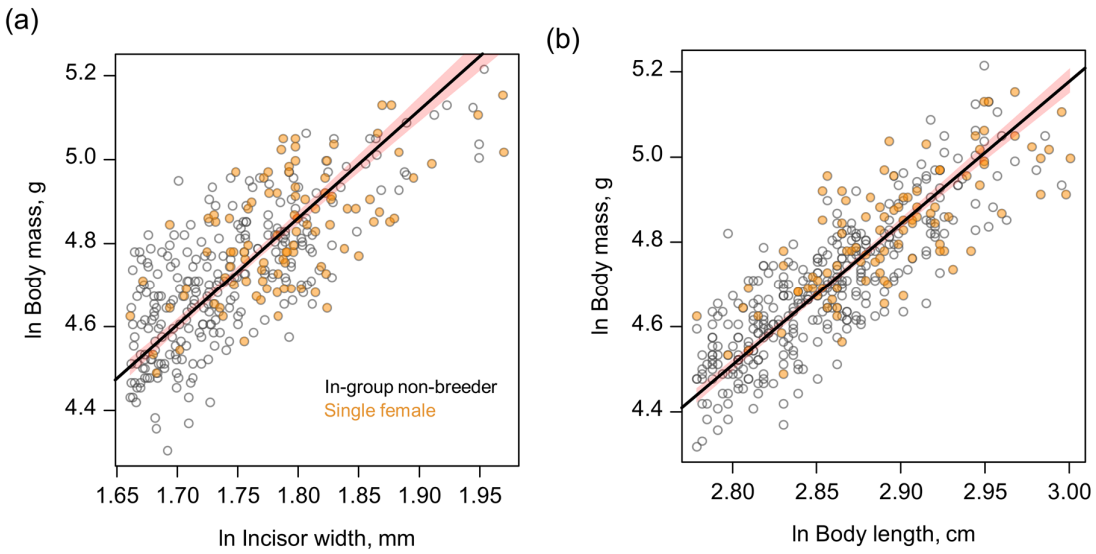


Figure 3. The body condition of dispersed single females compared to size-matched in-group non-breeding females. The principal plots display the scaled major axis regression (SMA) between body mass and incisor width (a), and between body mass and body length (b). Points display the raw data and lines display the predicted regression through all the data, with 95% bootstrapped confidence intervals given by the shaded area. Allowing the two classes of female to have different intercepts and slopes did not improve model fit: the two classes of female did not differ in mean body condition, or in the change in body condition with increasing skeletal size.

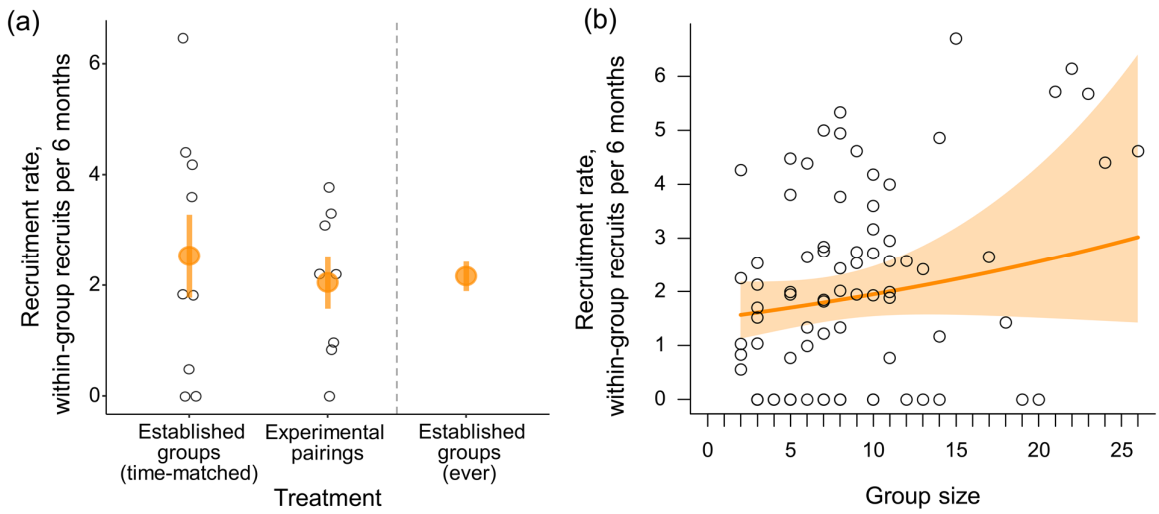


Figure 4. The effect of group size on within-group recruitment. a) The recruitment rate of established groups did not differ from that of newly created pairs when measured over the same time period. The mean rate of recruitment in this experimental period (middle panel in 5a) was similar to the overall mean recruitment rate in the population (right panel in 5a; average of all values in 5b). The larger orange points denote the treatment mean ± 1 SEM. b) In contrast, longitudinal analyses of group size across the duration of study detected a modest effect of increasing group size on the rate of within-group recruitment (0.216 ± 0.106, p = 0.042, GLMM, link-scale); solid line shows the predicted mean and shading shows the 95% confidence intervals. In both panels the black points give raw data, corrected for the trapping interval duration, and in all cases, recruitment has been standardised to a 6-monthly rate according to the time difference between the first capture and the second capture.

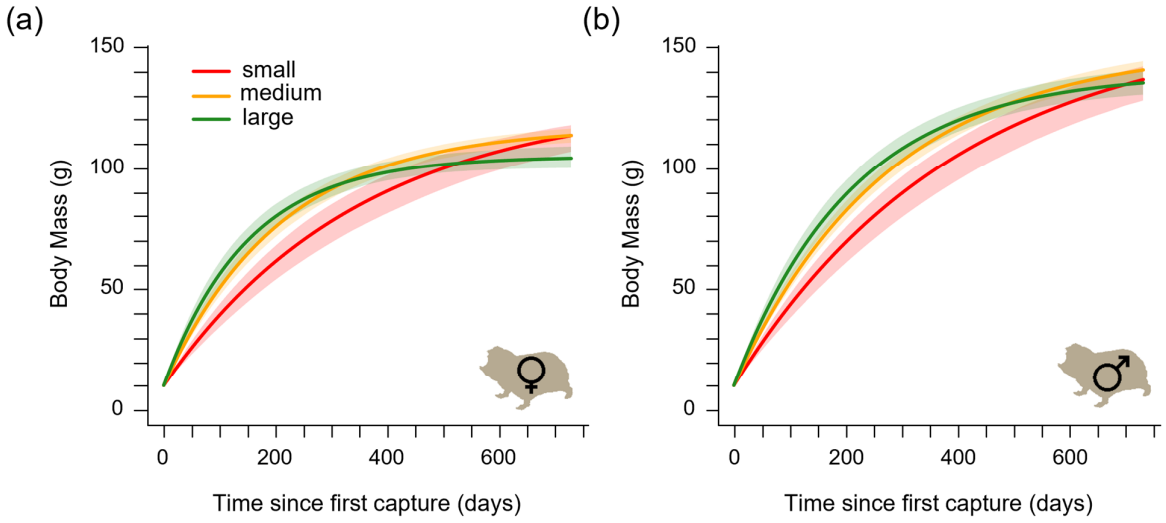


Figure 5. The effect on group size on growth of wild Damaraland mole-rats. Body mass growth depends upon whether the individual was growing in a small (4 individuals, red), medium (12 individuals, orange), or large (20 individuals, green) group. (a) and (b) display the predicted body mass growth of a male or female mole-rat first captured at 10g, the average size of a pup at parturition. Curves are derived from von Bertanlanffy interval equations and show the predicted mean mass, with the shaded areas indicating 95% confidence intervals.

SUPPLEMENTARY MATERIAL

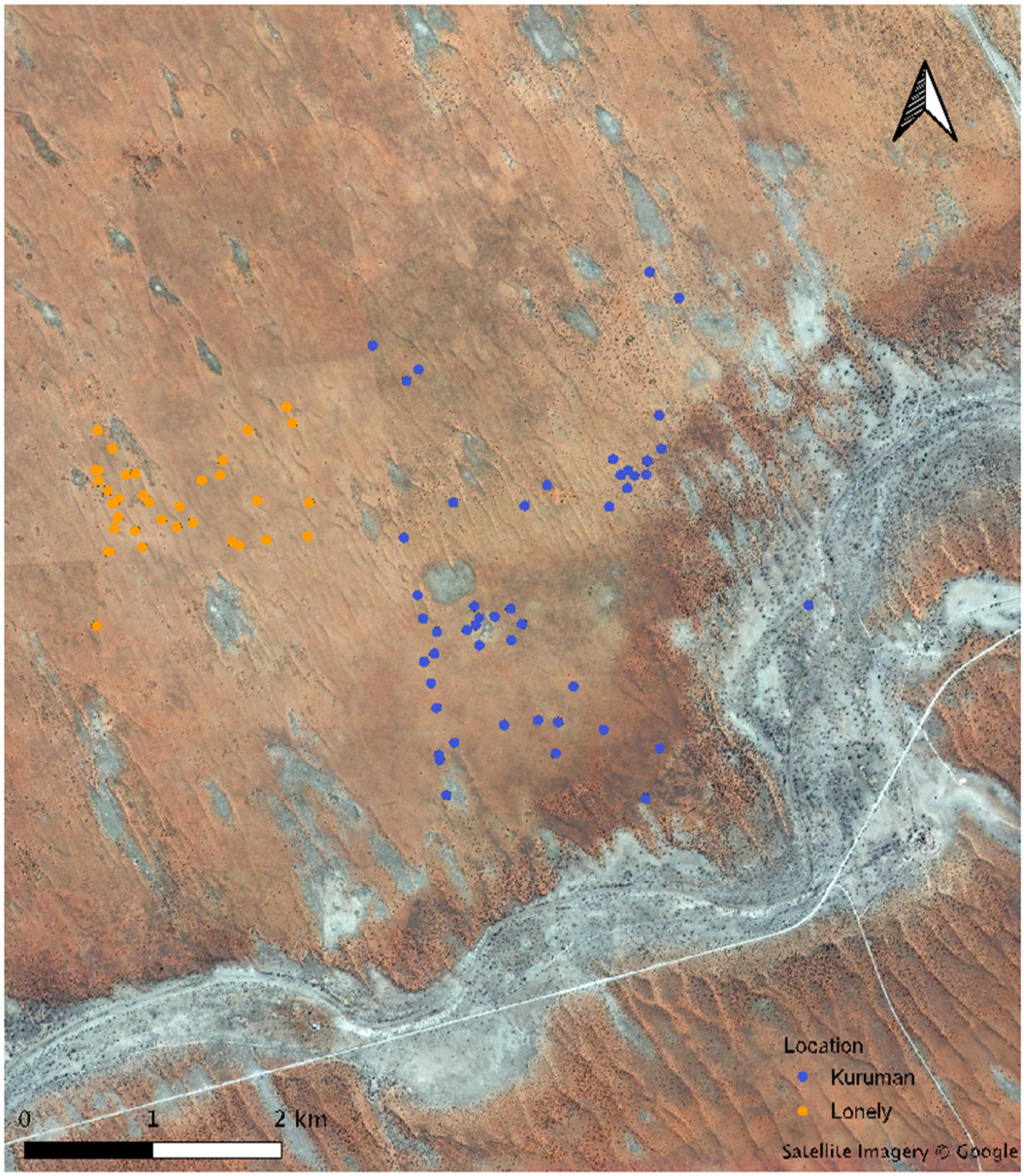


Figure S1. The trapping locations of Damaraland mole-rats groups captured at the Kuruman River Reserve and Lonely farm between 2013 and 2020. Each group is noted by a point which marks the centroid of all group captures, with the point colour corresponding to location, "Kuruman" or "Lonely". Note that with only one exception, mole-rat groups were distributed entirely within the red 'arenosol' soils, where their principal food (Gemsbok cucumber) is found. The one exception to this pattern was a single dispersing female who temporarily burrowed in an area of calcareous soils, which appear light grey from satellite. These calcareous soils highlight the path of the long dried up Kuruman river as it passes through the reserve.

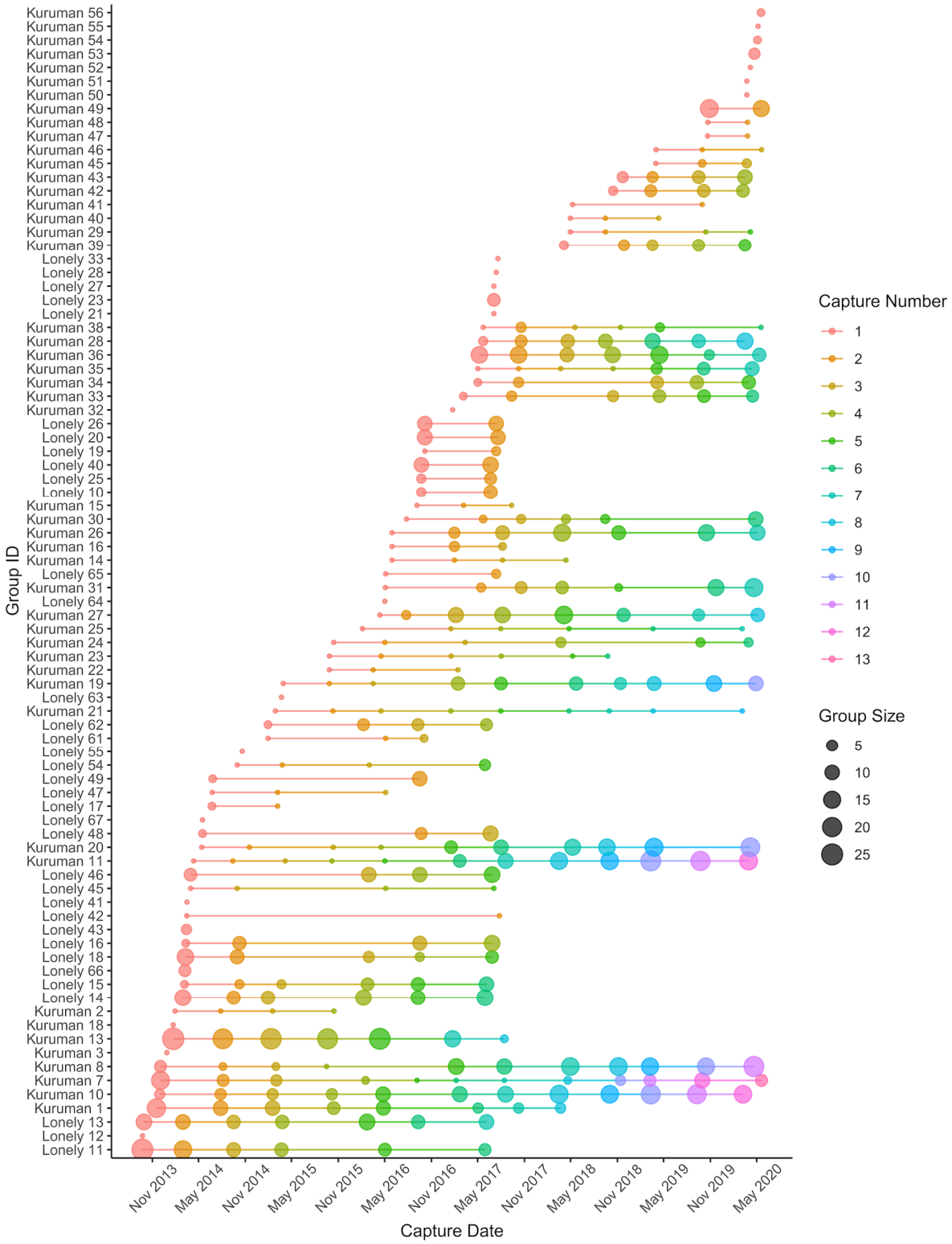


Figure S2. The history of trapping effort of Damaraland mole-rats groups in and around the Kuruman River Reserve. Each unique group has its own row, where successive capture events are denoted by points moving right along the x-axis. The size of the points is proportional to the size of the group at each capture event.

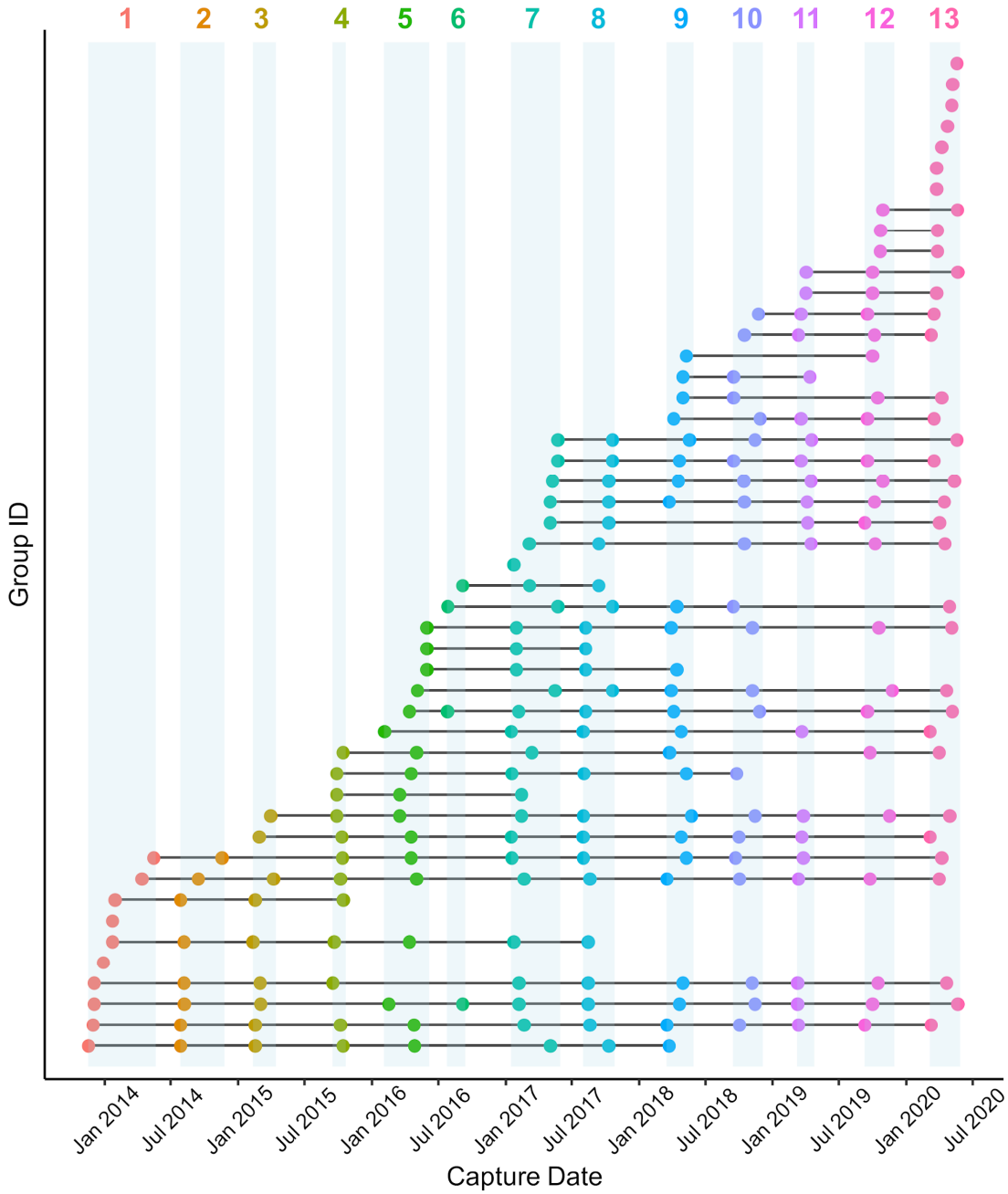


Figure S3. The history of trapping effort for Damaraland mole-rat groups at the Kuruman River Reserve in the Kalahari, separated into discrete trapping windows. Periods are defined by any break in trapping effort of more than 2 months. By doing so, it can be seen that no group is captured twice within a trapping period. Also, most groups are captured in successive trapping periods, with very few groups 'skipping' trapping windows- with the exception of period 6, where only a few groups were recaptured. In the few other cases where groups skips a trapping period, this is because no mounds were visible throughout the period, and when this occurs, it is not known whether a group had collapsed/disappeared or was present underground but not digging.

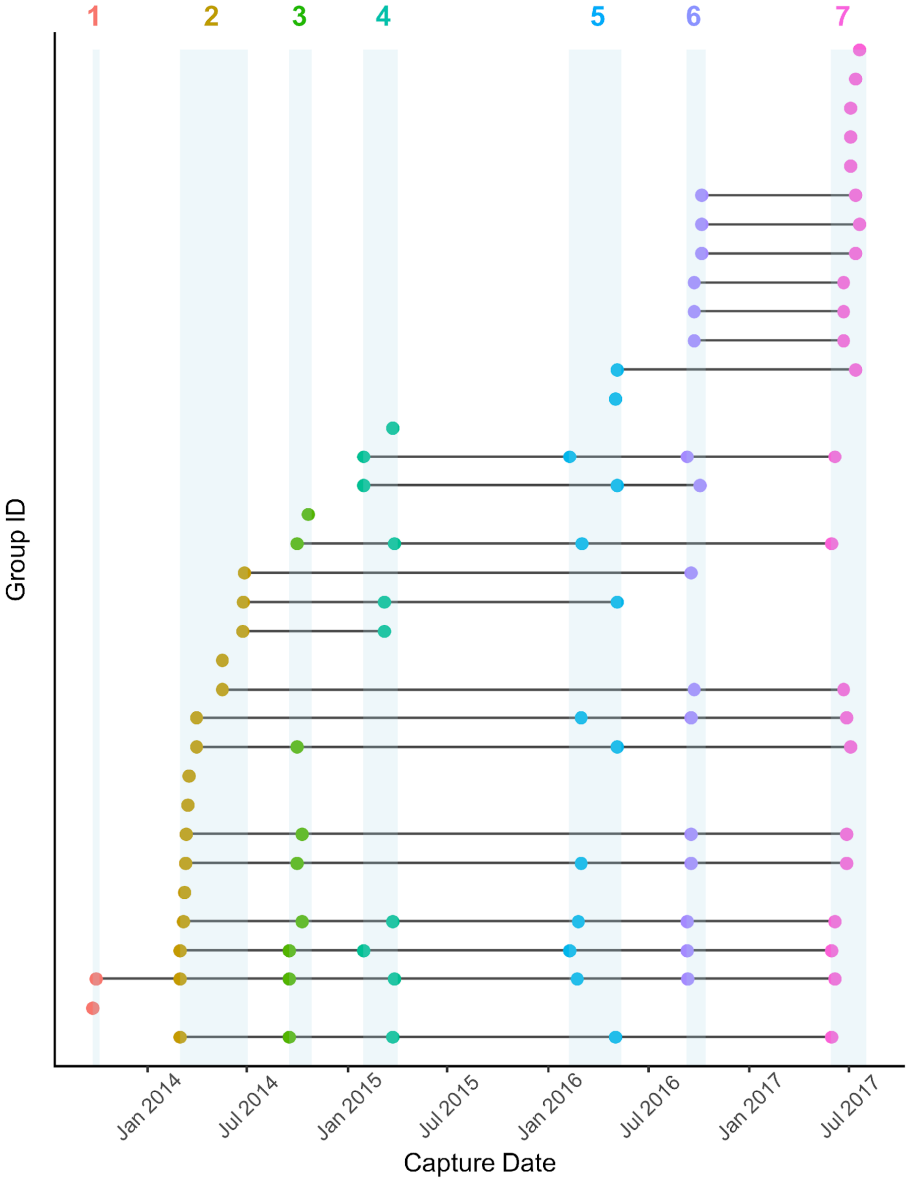


Figure S4. The history of trapping effort for Damaraland mole-rat groups at "Lonely" in the Kalahari, separated into discrete trapping windows. Periods are defined by any break in trapping effort of more than 2 months. By doing so, it can be seen that no group is captured twice within a trapping period. Also, most groups are captured in successive trapping periods, with very few groups 'skipping' trapping windows- with the exception of period 6, where only a few groups were recaptured. In the few other cases where groups skips a trapping period, this is because no mounds were visible throughout the period, and when this occurs, it is not known whether a group had collapsed/disappeared or was present underground but not digging.

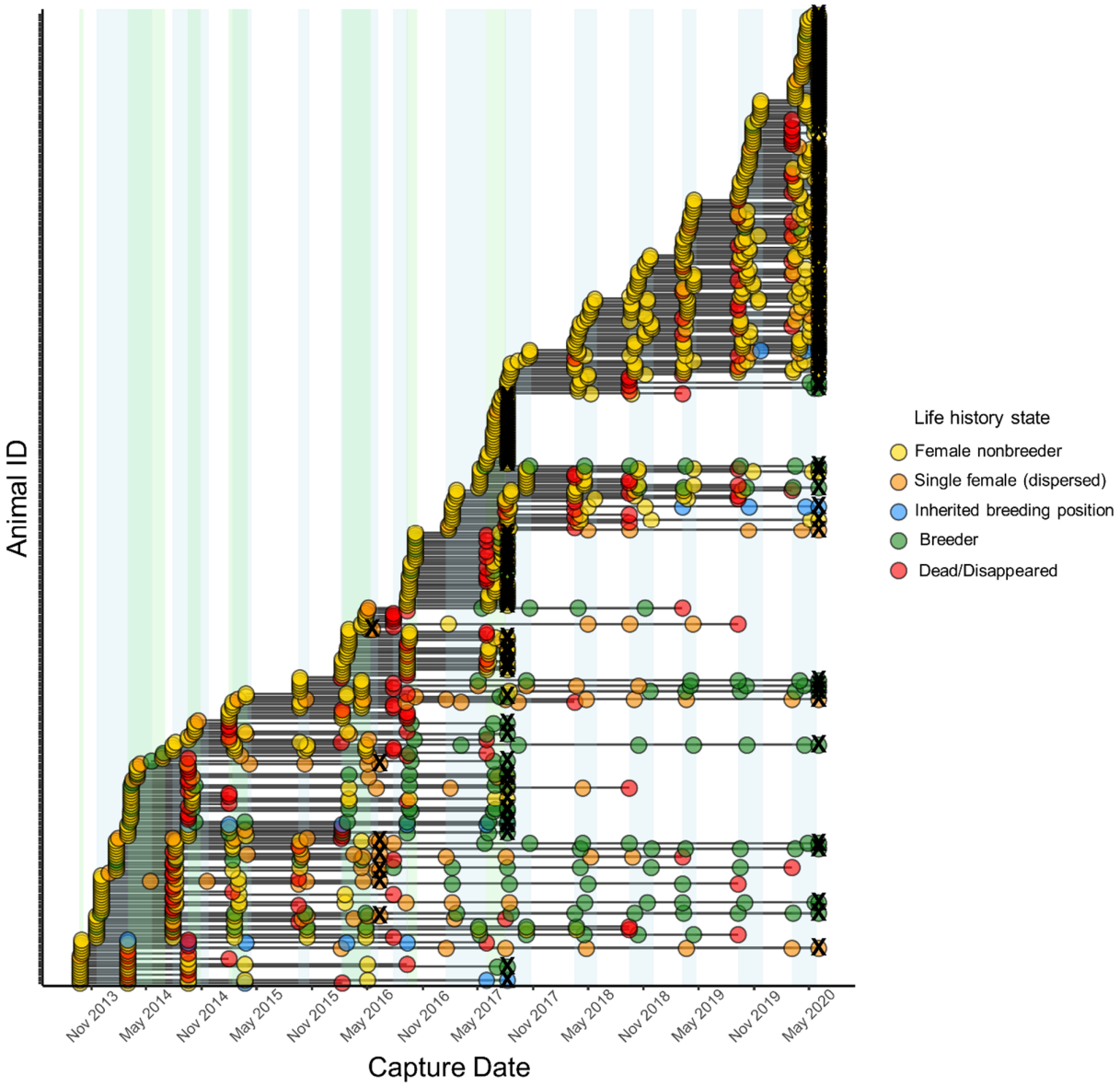
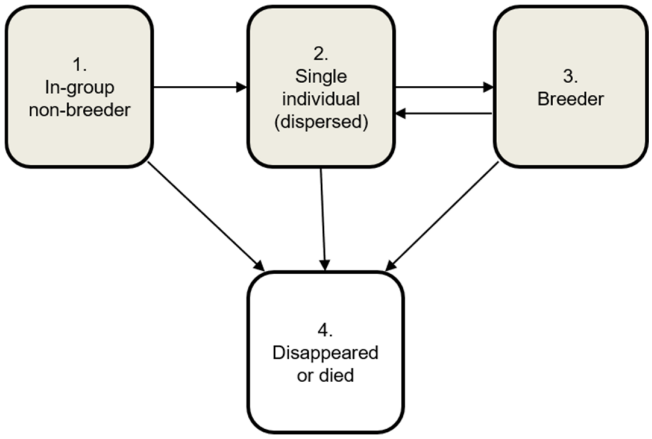


Figure S5. The fates of female Damaraland mole-rats capture from 2013-2020. Though analysed together, the fate/current state of female non-breeders at the Kuruman River Reserve and Lonely were assessed separately since they took advantage of different trapping windows (KRR- blue shaded areas; Lonely; green shaded areas). Individual states at any given time are female non-breeder, single female (who has dispersed from her natal group), an out-of-natal group breeder (again dispersed), and disappeared/died. In a small number of cases females also acquired dominance in their natal group (when an immigrant male had moved in previously). For individuals that were not recaptured at some point before the final trapping period in either location, it was assumed that the individual had died or disappeared at some point between their last capture and start of the next trapping window; as handled by the models. Additionally, individuals captured in the last trapping period at each location were assumed to have persisted in their current state to the end of the period, where they were right-censored (**X**).



$$Q = \begin{pmatrix} q_{11} & q_{12} & 0 & q_{14} \\ 0 & q_{22} & q_{23} & q_{24} \\ 0 & 0 & q_{33} & q_{34} \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Figure S6. Multi-state model for the life history transitions of female Damaraland mole-rats, with associated Q matrix. In a small number of cases where individuals were experimentally paired (i.e. given a male when formerly present as a single female and analysed in other papers; e.g. Thorley et al. 2018 Proc. R. Soc. B, 285: 20180897), they were also right-censored at the point of pairing so that any transitions from single female to breeder did not include this experimental component. In all cases, the multi-state model was parameterised so that the timing between transitions was not known exactly, but was estimated under Markov assumptions- this includes the timing of death/disappearance.

The condition of single females

To compare the body condition of single females and in-group non-breeding females we performed standardised major axis regressions of body mass on two skeletal size traits: incisor width and body length. We included body length as this is a more conventional linear measurement of skeletal size in mammals. Incisor width was measured as noted in the main text. Body length was measured dorsally from the front of the snout to the tip of the tail using a tape measure (to an accuracy of 1mm). As for incisor width, each measurement was taken in duplicate by two observers, and we here use the average of these two measures. For each skeletal measurement we filtered out any in-group non-breeding females whose skeletal size was less than the minimum size trait found in single females. This meant that the two classes of female were size-matched skeletally, such that any difference in condition would reflect increased bodily reserves for a given skeletal size.

Standardised major axis regression was proposed by Peig & Green (2008) as a superior regression method for the scaling of mass on linear body measurements than ordinary least squares methods, and has been widely adopted in studies on mammals since. Briefly, we performed a standardised major axis regression of ln body mass against the natural log of each skeletal measurement using the *smatr* package (Warton et al. 2012). In both cases, we initially fitted a model which allowed the slope and intercept to vary according the class of female, but for both skeletal measurement neither the intercept (teeth width LRT: $\chi^2_1 = 1.04$, $p = 0.31$; body length LRT: $\chi^2_1 = 0.09$, $p = 0.76$) nor the slope (teeth width LRT: $\chi^2_1 = 1.31$, $p = 0.25$; body length width LRT: $\chi^2_1 = 2.53$, $p = 0.11$) significantly different between single females and in-group non-breeders. **This indicates that single females and in-group non-breeders did not differ in their condition**.

We therefore present the results of the scaling relationship where all females were assumed to following the same scaling relationship; modelled by a single slope and intercept (Figure 3 in main manuscript, incisor width intercept = 2.41, 95% CI = -0.08 – 0.56, incisor width slope = 2.57, 95% CI = 2.39 – 2.75; body length intercept = -4.83, 95% CI = -5.33 – -4.33, body length slope = 3.34, 95% CI = 3.17 – 3.52).

The scaled mass index of each measurement can be calculated using the following formula:

$$SMI = M_i \left(\frac{L_0}{L_i}\right)^{b_{SMA}}$$

Where M_i and L_i are the body mass and skeletal measurement of individual *i*, b_{SMA} is the scaling exponent estimated by the SMA regression of *M* on *L*, and L_0 is the arithmetic mean value of the population sample. The scaled mass index of single females and in-group non-breeding females are contrasted below in the inset boxplots.

References:

Peig, J. & Green, A.J. (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118, 1883-1891.

Warton, D.I., Duursma, R.A., Falster, D.S., & Taskinen, S. (2012) smatr 3- an R package for estimation of allometric lines. *Methods in Ecology and Evolution* 3(2), 257-259.

Experimental Pairings

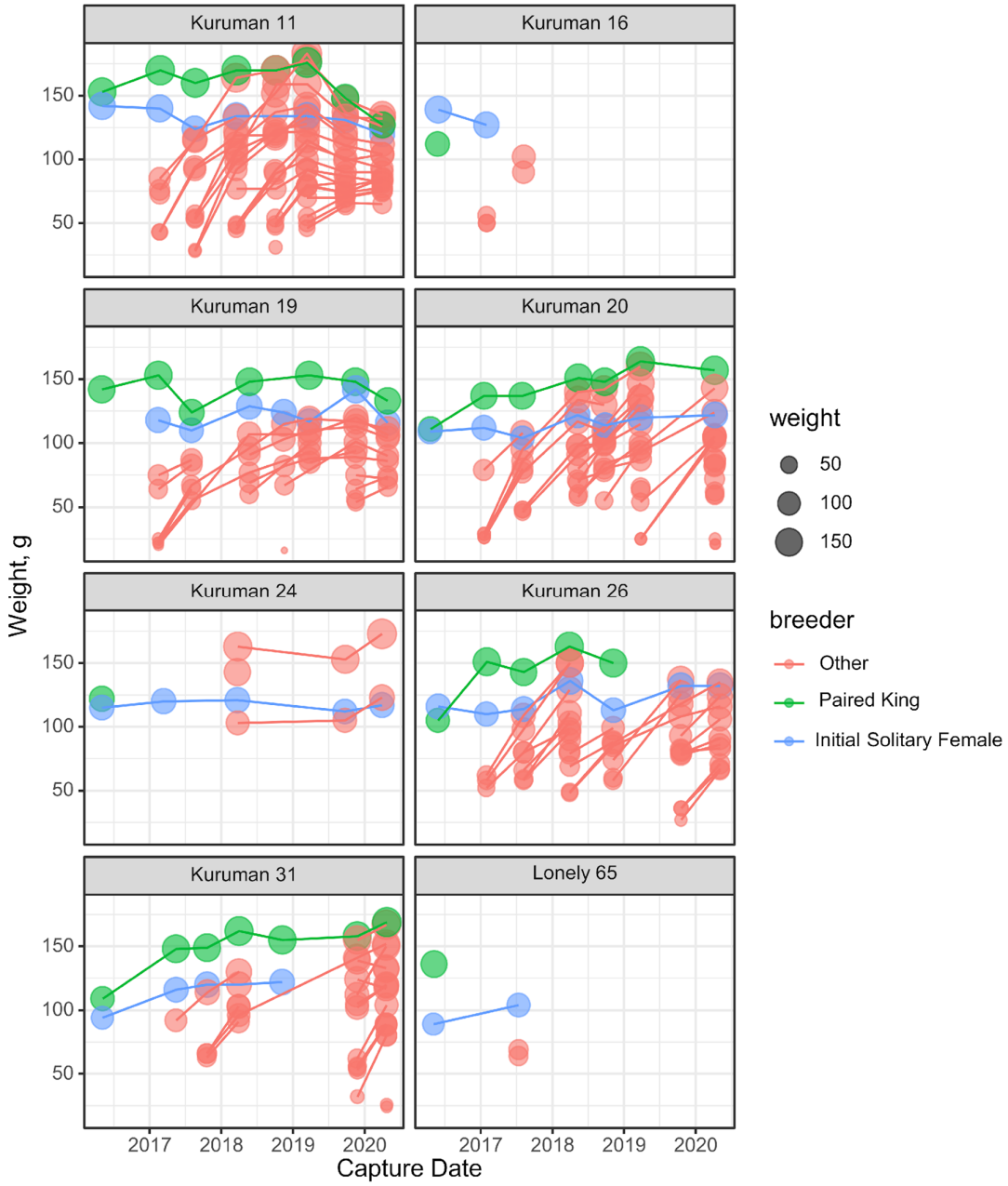


Figure S7. Group structure and trapping history of groups that were created experimentally with the addition of an unfamiliar male to the burrow systems of single females. In most cases newly created pairings commenced breeding shortly after pairing, as indicated by the recruitment of 'other' individuals into the group following the initial pairing.

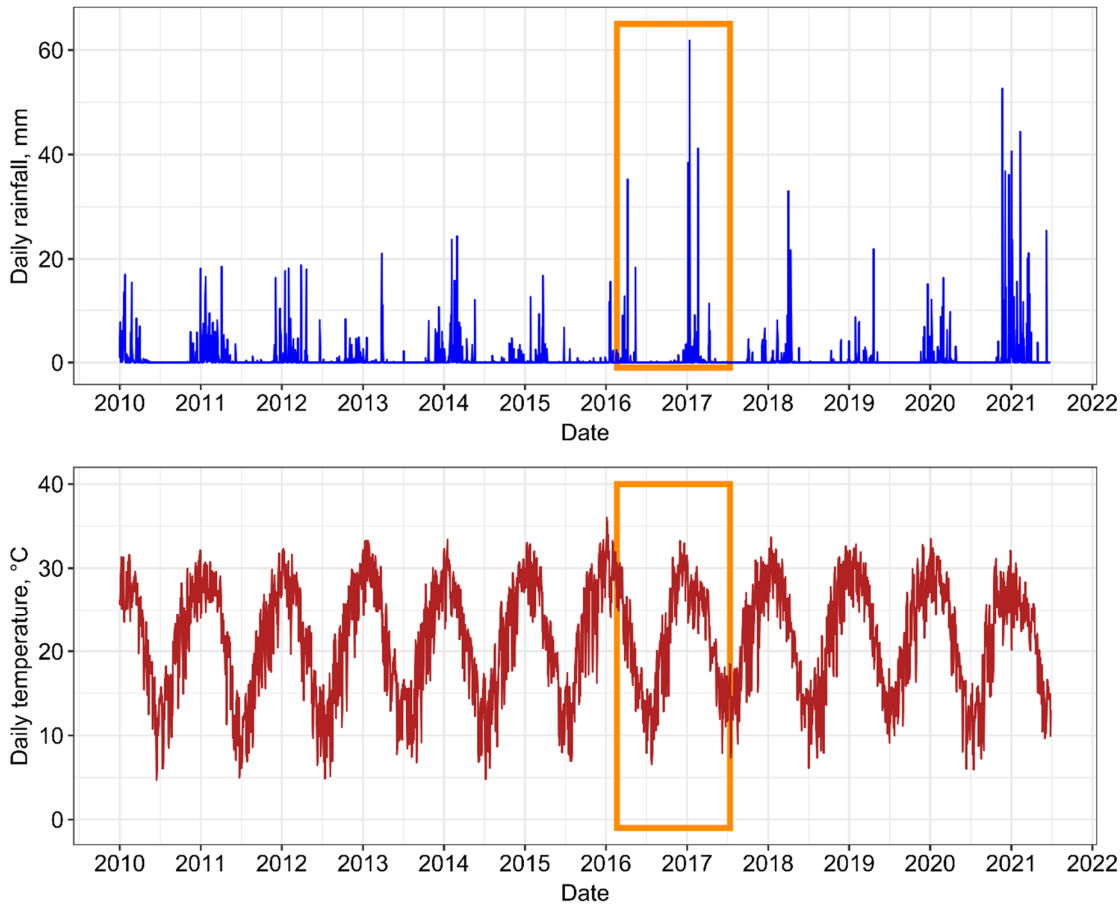


Figure S8. The timing of the experimental pairings in relation to climatic variation at the Kuruman River Reserve. Upper and lower panels document the long-term daily rainfall (mm) and daily average temperature at the field site. The orange rectangle demarcates the period within which experimentally created pairs and established groups (which served as controls) were captured and recaptured. Climate data taken from NASA's GMAO MERRA-2 assimilation model and GEOS 5.12.4 FP-IT.

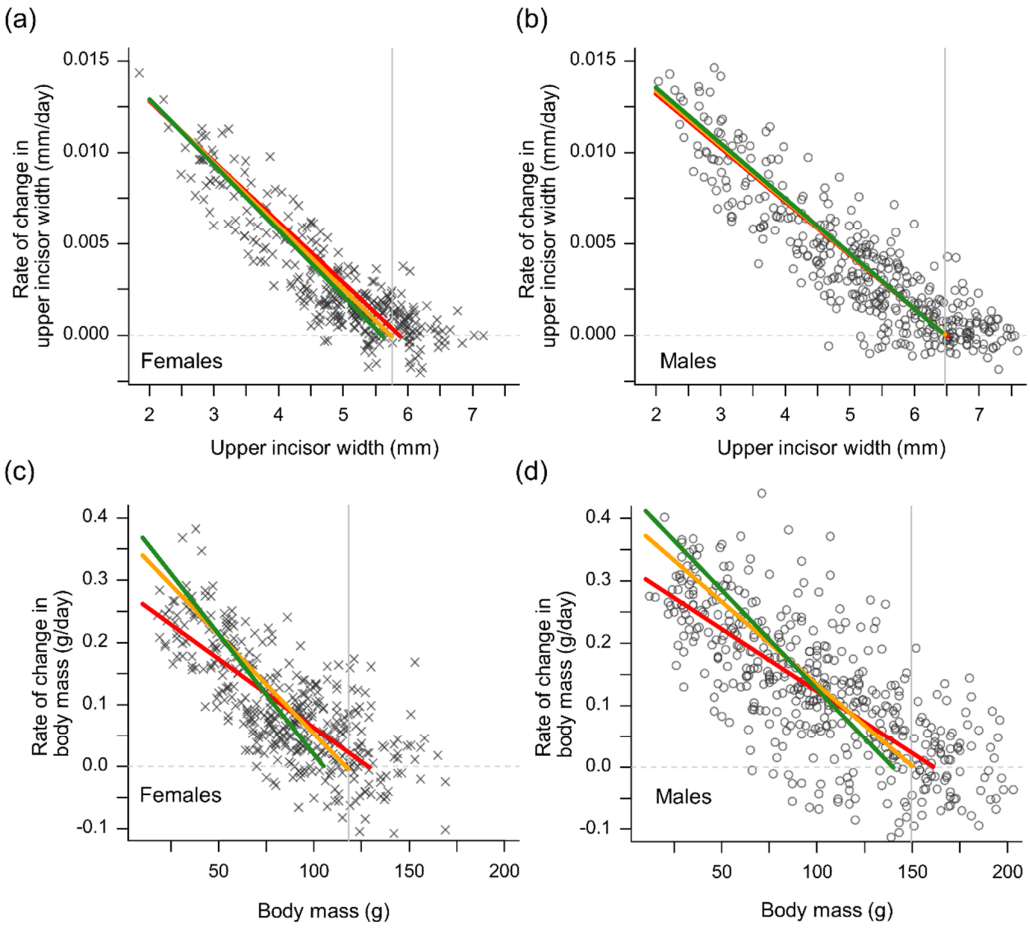


Figure S9.The rate of change in incisor width and body mass for females (a, c) and males (b, d) with variation in initial size and group size. Each point represents the change in incisor width or body mass across two captures - a capture and a recapture. Note that with increasing initial size, the slope of the change in size metric converges on the estimated population-level asymptotes (vertical lines).

Group size and adult body mass

Because the parameters of the von-Bertalanffy growth curve covary with one another (as parameterised), it is not possible to dissociate the effect of group size on the growth rate constant, *k*, from the effect of group size on asymptotic mass, *A*; *k* itself contributes to the estimation of *A*. We therefore carried out additional analyses to clarify the effect of group size on adult body mass.

For all the males and females whose growth was modelled by the interval equations (Figure S7), we extracted weight information for all the times that they were captured at least one year after first being captured at less than 1 year of age (< 100g for males, < 80g for females). The weights information therefore represented the body mass of all non-breeding individuals captured beyond 1 year of age, with most data coming from individuals far older than this. This generated a data set of 152 weights from 73 males, and 111 weights from 65 females. At the same time, we calculated the average group size that each of these individuals had experienced in their first year life; for some individuals we had only one value across this period, for others we had up to 3 measures.

The mass of individuals in adulthood of either sex was then modelled according to their current group size and the group size that they experienced in early life (< 1 year of age). The two terms were not strongly correlated (r = 0.26 in males, r = 0.04 in females), and in both the male and the female data sets the variance inflation factor of the two terms was < 1.07. Both early life group size and adult group size could therefore be fitted together in the same model. Adult body mass was fitted in a linear mixed effects model (Gaussian error), with average group size in the first year specified as a continuous variable, and group size in adulthood specified as a categorical variable with three levels: small, medium, and large, separated into the tertiles in each data set. For males at 1-9 (small), 10-16 (medium), >16 (large); for females at 1-7 (small), 8-15 (medium), >15 (large). An additional variable noting the quarterly period of the year was also included (Jan-Mar; Apr-Jun; Jul-Sep; Oct-De). Group size in early life was standardised prior to model fitting, and a random effect of individual identity, nested within group identity, was specified in each case. Models were fitted in the *lme4* package in R. Model outputs are presented in tables S9, and visualised in Figure S8.

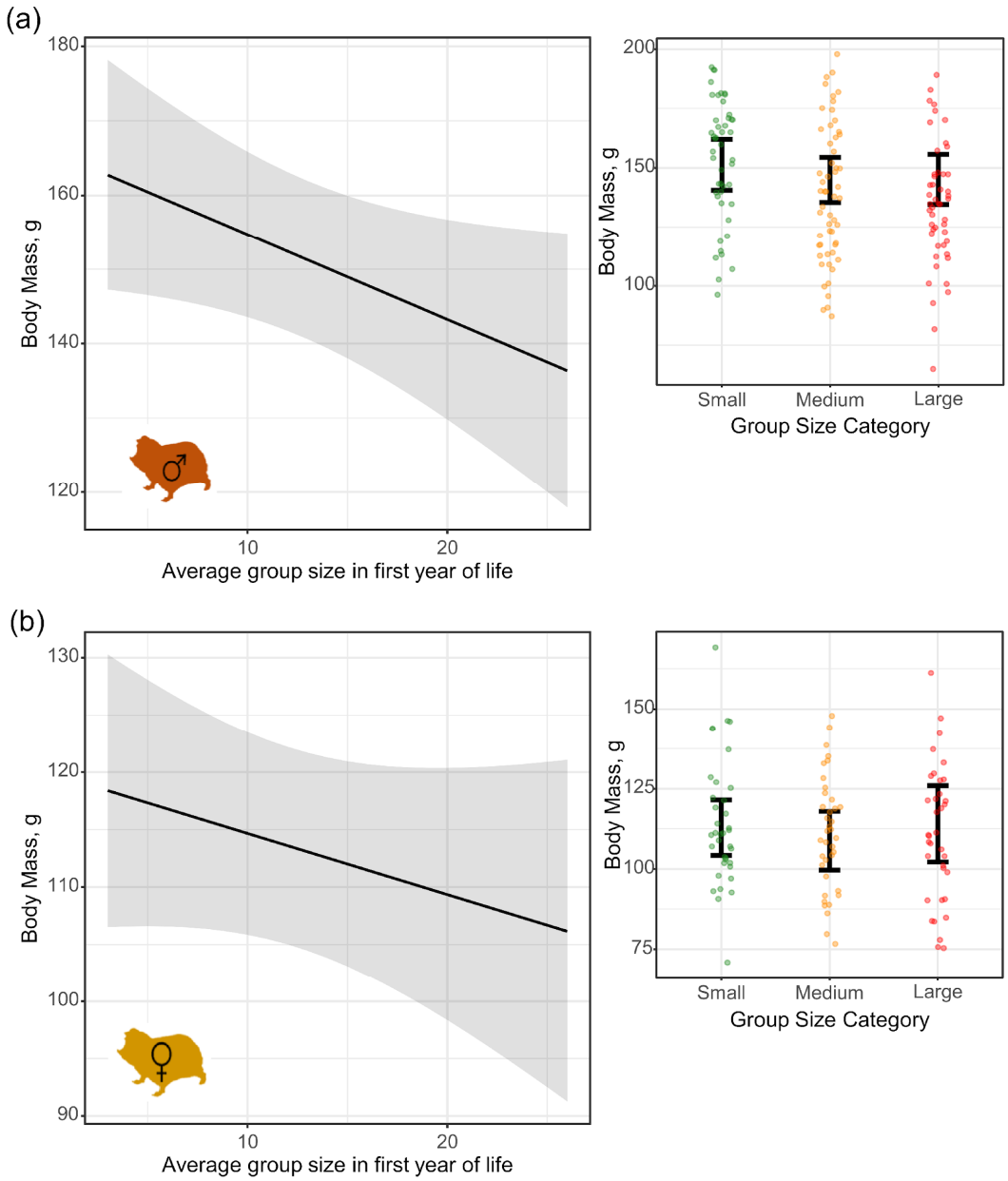


Figure S10. Adult body mass of non-breeding male (a) and female (b) Damaraland mole-rats. Left panels display the predicted effect of average group size in the first year of life on adult mass (< 100g for males, < 80g for females), as estimated from linear mixed effects models (table S11). In both cases, increases in group size during early life reduces body mass in adulthood. By contrast, current group size in adulthood has no effect on adult body mass, as displayed in the right panels. Points denote the raw data across all individuals, with error bars denoting the predicted marginal effects across three group size categories. Group size categories were separated at the tertiles within each data set; for males at 1-9 (small), 10-16 (medium), >16 (large); for females at 1-7 (small), 8-15 (medium), >15 (large). Post-hoc tests performed on the linear mixed effects models found that in neither sex did group size in adulthood have a significant effect on adult body mass ($p > 0.46$ in all contrasts). Note that group size in adulthood was categorised largely for the purpose of visualisation; treating the term as a continuous variable did not qualitatively affect the results.

Table S1. Sum of captures at the Kuruman River Reserve for each trapping period. Recapture rate was calculated as the number of recaptured individuals divided by the total number of individuals captured in the same trapping period. By the end of the first trapping period, two individuals had already been recaptured within new groups (hence 2.6 % recapture rate). Mean recapture rate (N recaptures / N captures within a trapping period, excluding the first trapping period) at Kuruman was 73.1 %, and 54.8% at Lonely.

Location	Trapping Period	Period Start	Period End	N Groups	N Males	N Females	N Ind	N New Ind	N Recap Ind	Recap %
Kuruman	1	2013-11-17	2014-05-21	10	35	41	76	74	2	2.6%
Kuruman	2	2014-07-27	2014-11-24	8	19	28	47	9	38	80.9%
Kuruman	3	2015-02-10	2015-04-14	9	21	28	49	7	42	85.7%
Kuruman	4	2015-09-16	2015-10-22	12	13	30	43	8	35	81.4%
Kuruman	5	2016-02-04	2016-06-06	17	20	38	58	15	43	74.1%
Kuruman	6	2016-07-25	2016-09-12	4	2	4	6	1	5	83.3%
Kuruman	7	2017-01-16	2017-05-30	27	68	51	119	68	51	42.9%
Kuruman	8	2017-07-31	2017-10-26	24	67	61	128	40	88	68.8%
Kuruman	9	2018-03-17	2018-05-30	24	79	70	149	46	103	69.1%
Kuruman	10	2018-09-14	2018-12-04	22	71	68	139	34	105	75.5%
Kuruman	11	2019-03-09	2019-04-24	20	83	75	158	41	117	74.1%
Kuruman	12	2019-09-09	2019-11-30	24	93	97	190	65	125	65.8%
Kuruman	13	2020-03-05	2020-05-27	35	114	128	242	60	182	75.2%
Lonely	1	2013-09-23	2013-10-06	3	20	18	38	38	0	0.0%
Lonely	2	2014-03-01	2014-07-03	17	40	45	85	58	27	31.8%
Lonely	3	2014-09-16	2014-10-27	9	19	29	48	13	35	72.9%
Lonely	4	2015-01-29	2015-04-02	10	14	20	34	9	25	73.5%
Lonely	5	2016-02-08	2016-05-12	13	24	41	65	30	35	53.8%
Lonely	6	2016-09-09	2016-10-13	16	55	54	109	66	43	39.4%
Lonely	7	2017-05-30	2017-08-02	24	85	72	157	67	90	57.3%

Table S2. Summary of the analyses carried out in the paper, with information on the data used.

Analysis	Data	Total rows of data	Total unique inds	Total unique groups	Included incomplete captures	Method	Comments
Status-related survivorship in females	All capture events from females, irrespective of age (weight) at first capture. Additional rows generated for when individuals disappeared or were right-censored. "*Fates_Allfemales.csv*"	F: 1315	F: 362	F: 80	Yes	Multi-state Markov model. .	- Right-censored individuals that were still present for the last trapping window at either study location. - Four states: i- in-group non-breeder, ii- single female, iii- breeder, iv - disappeared/dead - Figure 2, Table S3
Growth: body mass	Body mass across successive capture events (a capture and recapture) "*FieldMR_Growth_BodyMass.csv*"	F: 381 M: 456	F: 193 M: 214	F: 48 Male: 39	NA	Non-linear mixed effects model with von Bertalanffy interval equation. Males and females analysed separately.	- Removed breeding females so that pregnancy weights not included. - Only chose recaptures falling 100-365 days after the first capture. - Figure 5, Figure S9, Table S5 - Follow-up analysis to check effect of group size on asymptotic mass (above; Figure S10)
Growth: incisor width	Incisor width across successive capture events (a capture and recapture) "*FieldMR_Growth_TeethWidth.csv*"	F: 328 M: 381	F: 180 M: 198	F: 47 Male: 38	NA	Non-linear mixed effects model with von Bertalanffy interval equation. Males and females analysed separately.	- Only chose recaptures falling 100-365 days after the first capture. - Figure S9, Table S7
Body condition of females	All body mass measurements with an associated skeletal trait measurement (either teeth width of body length) "*FieldMR_SingleFemaleCondition_BodyLength.csv*" "*FieldMR_SingleFemaleCondition_TeethWidth.csv*"	F incisor width: 353 F body length: 419	F incisor width: 177 F body length: 213	F incisor width: 64 F body length: 67	NA	Scaled major axis regression of ln(body mass) ~ ln(skeletal trait). In both cases, a separate slope of intercept for	-Included information from females that were either an in-group non-breeder or a single female. As the main question was whether single females had a similar body condition to in-group non-breeding females, we only considered in-group non-breeders when their skeletal trait was greater than the smallest recorded value in single females

						single females was not supported.	(i.e. removing young females still in their natal group to ensure this didn't bias allometric scaling). - Figure 3
Within-group recruitment rate (longitudinal)	All complete group captures and recaptures separated by 100-365 days. "*FieldMR_Recruitment_Longitudinal.csv*"	78 capture-recapture events	NA	33 groups	No	Generalised linear mixed effects model with Poisson error distribution. Included offset term for time interval.	-Within-group recruits classed as all new individuals in the group on recapture that were less than year of age (body mass < 80g for females, body mass < 100g for males")" - Only included groups if capture history indicated the presence of a breeding female. - Figure 4; Table S4
Within-group recruitment rate (experimental)	The number of new recruits on the first recapture of experimentally created pairs, which were compared to the number of recruits in established groups captured across the same time period. "*FieldMR_Recruitment_Experimental.csv*"	Pairings: 8 Time-matched groups: 9	NA	NA	No	t-test on recruitment rate	- Figure 4

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Table S3. Status-related survivorship. Probability of transitioning between states over a one-year and a two-year period. Transition probabilities estimated from a multi-state model fitted to all females that were captured across the duration of the study. n = 362 females. Estimates related to survival probability are filled in grey. Confidence intervals estimated using the delta method.

Transition	1 year probability (95% CI)	2 year probability (95% CI)
in-group non-breeder → in-group non-breeder	0.525 (0.466, 0.568)	0.276 (0.221, 0.323)
in-group non-breeder → single female	0.069 (0.047, 0.097)	0.078 (0.051, 0.110)
in-group non-breeder → breeder	0.048 (0.031, 0.077)	0.079 (0.055, 0.115)
in-group non-breeder → dead/disappeared	0.358 (0.314, 0.411)	0.567 (0.513, 0.624)
single female → single female	0.612 (0.469, 0.716)	0.375 (0.217, 0.506)
single female → breeder	0.181 (0.104, 0.312)	0.267 (0.155, 0.404)
single female → dead/disappeared	0.207 (0.131, 0.318)	0.358 (0.249, 0.512)
breeder → single female	-	-
breeder → breeder	0.867 (0.777, 0.921)	0.752 (0.600, 0.849)
breeder → dead/disappeared	0.133 (0.079, 0.223)	0.248 (0.151, 0.400)

Table S4. The recruitment rate of offspring into groups in Damaraland mole-rats in the wild. Recruitment was modelled with a generalised linear model with negative binomial error distribution. Models were fitted to n = 77 group-level recapture events in 33 distinct breeding groups. All estimates are provided on the link scale (log-link), and continuous variables are z-score transformed. Models also included an offset for the log(time between capture and recapture).

	Mean Estimate	Std. Error.	z-value	p-value
Fixed effects				
Intercept	-4.538	0.108		
Group Size	0.216	0.106	2.04	**0.042**
Breeder mass	-0.090	0.089	-1.02	0.309
Rainfall	0.159	0.086	1.85	0.065
Random effect	**Variance**	**Std Dev**		
Group ID (n = 33)	0.129	0.359		

Table S5. Body mass growth of Damaraland mole-rats in the wild. Model summaries provide estimates from the non-linear mixed effects that incorporated group size into von Bertalanffy interval equations. Models were fitted to n = 381 recapture events in females, and n = 456 recapture events in males. Estimates provide the population mean for the fixed effects, the standard deviation for the random effects.

Females	**Mean Estimate**	**Std. Error.**	**t-value, df**	**p-value**
Fixed effects				
A	118.26	2.01	58.72, 185	**< 0.001**
A_{GS}	-9.42	1.47	6.41, 185	**< 0.001**
K	0.00447	0.00003	16.02, 185	**< 0.001**
k_{GS}	0.00155	0.00032	4.90, 185	**< 0.001**
Random effect	**Variance**	**Residual**		
A ~ 1|AnimalID	15.79	9.18		
k ~ 1|AnimalID	Negligible			
Males	**Mean Estimate**	**Std. Error.**	**t-value, df**	**p-value**
Fixed effects				
A	149.70	2.84	52.74, 239	**< 0.001**
A_{GS}	-8.10	2.02	4.00, 239	**< 0.001**
k	0.00368	0.00002	17.90, 239	**< 0.001**
k_{GS}	0.00084	0.00020	4.36, 239	**0.001**
Random effect	**Variance**	**Residual**		
A ~ 1|AnimalID	21.47	12.51		
k ~ 1|AnimalID	Negligible			

Table S6. The adult body mass of mole-rat non-breeders. Female and male mass was modelled using a linear mixed effects model with Gaussian error distribution. In either case, models were fitted to non-breeding individuals that were captured at least one year after they were first captured at less than 1 year of age (< 100g for males, < 80g for females). They therefore represent the average body mass of all non-breeding individuals captured beyond 1 year of age, with most data coming from individuals far older than this. Group size categories were separated at the tertiles within each data set; for males at 1-9 (small), 10-16 (medium), >16 (large); for females at 1-7 (small), 8-15 (medium), >15 (large). n = 65 unique females from 25 groups. n = 73 unique males from 23 groups. See **Figure S10**.

Females (n = 111)	**Mean Estimate**	**Std. Error.**	**t-value, df**	**Chisq, df**	**p-value**
Fixed effects					
Intercept	112.95	4.41			
Adult group size: medium	-4.12	4.62	-0.892	1.23, 2	0.54
Adult group size: large	1.15	6.27	0.183		
Yearly quarter: second	-4.55	3.87	-1.178	1.90, 3	0.59
Yearly quarter: third	-4.15	4.11	-1.009		
Yearly quarter: fourth	-2.06	3.97	-0.511		
Early life group size	3.08	2.62	-1.176	1.23, 1	0.27
Random effect	**Variance**	**Std Dev**			
Animal ID:Group ID	162.2	12.73			
Animal ID	114.6	10.71			
Residual	128.5	11.34			
Males (n = 152)	**Mean Estimate**	**Std. Error.**	**t-value, df**		
Fixed effects					
Intercept	151.30	5.44			
Adult group size: medium	-6.39	4.49	-1.423	2.13, 2	0.34
Adult group size: large	-6.15	5.36	-1.148		
Yearly quarter: second	-14.22	3.36	-4.238	27.15, 3	<0.001
Yearly quarter: third	-15.53	3.24	4.789		
Yearly quarter: fourth	-12.03	3.57	-3.373		
Early life group size	-6.56	3.33	-1.967	2.99, 1	0.084
Random effect	**Variance**	**Std Dev**			
Animal ID:Group ID	493.2	22.21			
Animal ID	159.4	12.62			
Residual	141.0	11.88			

Table S7. Incisor width growth of Damaraland mole-rats in the wild. Model summaries provide estimates from the non-linear mixed effects that incorporated group size into von Bertalanffy interval equations. Models were fitted to n = 328 recapture events in females, and n = 381 recapture events in males. Estimates provide the population mean for the fixed effects, the standard deviation for the random effects.

Females	**Mean Estimate**	**Std. Error.**	**t-value, df**	**p-value**
Fixed effects				
A	5.75	0.04	147.60, 145	**< 0.001**
A_{GS}	-0.11	0.04	4.17, 145	**< 0.001**
K	0.0053	0.0002	26.23, 145	**< 0.001**
k_{GS}	0.0031	0.0002	1.37, 145	0.17
Random effect	**Variance**	**Residual**		
A ~ 1|AnimalID	0.39	0.16		
k ~ 1|AnimalID	Negligible			
Males	**Mean Estimate**	**Std. Error.**	**t-value, df**	**p-value**
Fixed effects				
A	6.48	0.05	132.11, 180	**< 0.001**
A_{GS}	-0.05	0.04	1.32, 180	0.19
k	0.00429	0.0001	31.19, 180	**< 0.001**
k_{GS}	0.00007	0.0001	0.48, 180	0.64
Random effect	**Variance**	**Residual**		
A ~ 1|AnimalID	0.47	0.20		
k ~ 1|AnimalID	Negligible			