

Strength in numbers: Group size enhances individual survival and colony longevity in Damaraland mole-rats *Fukomys damarensis*

Paul Juan Jacobs^{a,*}, Daniel William Hart^a, Jennifer U.M. Jarvis^b, Nigel Charles Bennett^c

^a Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa

^b Department of Biological Sciences, University of Cape Town, Rondebosch, 7700, Cape Town, South Africa

^c Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa

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ABSTRACT

Cooperative behaviour presents an evolutionary paradox because although dispersal may increase direct fitness, many individuals forego reproduction to assist others. In arid-dwelling subterranean mammals, the high energetic costs of underground foraging, together with scarce and patchily distributed food resources are thought to have favoured the evolution of group living and cooperative breeding. These social systems are believed to enhance foraging efficiency and improve the survival prospects of individuals and groups. Using a longitudinal dataset from a wild population of Damaraland mole-rats (*Fukomys damarensis*) in arid central Namibia, we examine how group size predicts survival and persistence at both the individual and group levels. Our findings show that larger groups confer significant apparent survival benefits, that is the probability that an individual survives and remains available for recapture or resighting, reflecting both true survival and site fidelity, and also enhance colony persistence relative to solitary animals or pairs. We further demonstrate that these very small social-unit states are inherently unstable as without increases in group size, they are unlikely to persist within the population for extended periods. Larger groups clearly enhance survival, making remaining in the natal colony more beneficial than dispersing in an arid environment where dispersal is highly risky.

1. Introduction

In arid environments, animals have evolved behavioural, morphological, physiological as well as molecular adaptations that often involve trade-offs (Degen, 2012; Huey et al., 2012; Schwimmer and Haim, 2009). Unpredictable rainfall, patchy resource distribution and extreme temperatures may force many species of animal to adopt strategies that prioritise persistence over immediate reproduction (Céré et al., 2015; Mares et al., 2017). Among these species are the subterranean cooperatively breeding Damaraland mole-rat (*Fukomys damarensis*) which inhabits an arid environment characterised by high temperatures, low and sporadic rainfall patterns and coarse sandy soils, in the thorn-scrub woodland savannas and grasslands of southern Africa (Bennett and Faulkes, 2000; Hart et al., 2026; Mynhardt et al., 2021). Burrow creation and tunnel expansion for foraging in arid environments is extremely energy-demanding (Lovegrove, 1989), and the underground roots and geophytic tubers that serve as food are patchily distributed, further reducing foraging efficiency (Jarvis et al., 1998; Spinks and Plaganyi, 1999). The reduced efficiency associated with subterranean and arid

habitats is thought to favour cooperation among closely related individuals (Griesser et al., 2025). Such cooperation promotes group living and cooperative behaviours and mitigates energetic shortfalls through collective foraging efforts (Burland et al., 2002; Hazell et al., 2000; Mynhardt et al., 2021).

Several alternative hypotheses have further been proposed to explain the persistence of cooperative breeding groups and why some individuals remain in groups rather than pursuing their own independent reproduction. These include kin selection theory (Michod, 1982), the benefits of philopatry hypothesis (Emlen, 1994; Koenig et al., 1992), the habitat saturation hypothesis (Selander, 1964), the group augmentation hypothesis (Kingma et al., 2014), the life-history hypothesis of cooperative breeding (Hatchwell and Komdeur, 2000), the pay-to-stay hypothesis (Hårdling and Kokko, 2003), and the local resource enhancement hypothesis (Perrin and Lehmann, 2001). These hypotheses have been examined across a range of cooperatively breeding taxa through long-term, multi-generational studies. In mammals, extensive research has been done on species such as meerkats (*Suricata suricatta*) (Clutton-Brock, 2002; Scantlebury et al., 2002; Stephens et al., 2005),

* Corresponding author.

E-mail address: pj.jacobs@up.ac.za (P.J. Jacobs).

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banded mongooses (*Mungos mungo*) (Cant et al., 2001, 2013), dwarf mongooses (*Helogale parvula*) (Arbon et al., 2024; Creel and Waser, 1994), as well as other group-living African mole-rats (Bathyergidae) (Bennett and Faulkes, 2000; Spinks et al., 2000; Torrents-Ticó et al., 2018b). The ecological pressures associated with environmental constraints will most likely favour philopatry as a survival strategy in Damaraland mole-rat (Perrin and Lehmann, 2001; Spinks et al., 2000; Torrents-Ticó et al., 2018a), however, despite the risks associated with dispersal in arid environments, dispersal occurs frequently enough in wild populations (Finn et al., 2022; Hazell et al., 2000; Mynhardt et al., 2021; Torrents-Ticó et al., 2018a; Young et al., 2010). Dispersal in Damaraland mole-rats is influenced by ecological constraints, temporal windows associated with rainfall and individual condition. Dispersal events typically follow a good rainfall event, when soil conditions are optimal for burrow excavation (Bennett and Faulkes, 2000; Hazell et al., 2000), and the associated energetic costs of digging are optimal (Lovegrove, 1989). Damaraland mole-rats may disperse between colonies, either temporarily or permanently, either above or below ground (Mynhardt et al., 2021). Individuals in better body condition are more likely to disperse, suggesting that size and strength may facilitate the ability to leave the natal colony successfully (Torrents-Ticó et al., 2018a). The success of dispersal in these harsh habitats, is dependent on predation risk (Jarvis and Bennett, 1993) and successful foraging to restore energy reserves during and after dispersal. Once fully dispersed, individuals may form pairs away from the natal colony, allowing new colonies to be established, or enabling individuals to join existing colonies (Hazell et al., 2000; Mynhardt et al., 2021).

This presents a fundamental paradox: while dispersal may offer individuals the opportunity to increase their direct fitness through independent reproduction with non-relatives, survival in Damaraland mole-rats appears to depend on remaining within a cooperative group. Group membership, however, is not without costs. Non-breeders in larger groups may experience reduced growth (Young and Bennett, 2010) and reproductive suppression (Bennett et al., 1993, 1996; Young et al., 2010), whereby female reproduction is inhibited in the presence of the dominant female (Bennett et al., 2022), which further constrains the opportunities for direct fitness gains. Here, we draw on the longest continuous longitudinal dataset from a wild population of Damaraland mole-rats from Dordabis, Namibia, an arid region, to test whether group living does in fact confer a direct evolutionary benefit to individuals and to groups as a whole by enhancing survival.

This longitudinal dataset enables detailed monitoring of repeated individual capture–recapture events, the formation of new groups, and the persistence of established groups over extended periods, a key strength given the species exceptional longevity (Jacobs et al., 2021). The selection pressures associated with increasing group size are multifaceted and often interact in ways that obscure their net fitness consequences. Larger groups may benefit from enhanced cooperative digging (Mendonça et al., 2020), improved foraging efficiency (Spinks and Plaganyi, 1999), more effective thermoregulation (Sumbera, 2019), and increased alloparental care, alongside the broader advantages and disadvantages of helping (Hatchwell and Komdeur, 2000; Houslay et al., 2020; Lehmann and Rousset, 2010; Young and Bennett, 2010). Collectively, these benefits are expected to promote group persistence and, ultimately, individual survival. However, increases in group size may also impose costs, including reduced growth due to intensified competition (Zöttl et al., 2016) and greater opportunities for cheating or diminishing returns to cooperative investment in very large groups (Rotics and Clutton-Brock, 2021; Sachs and Rubenstein, 2007). Our aim was therefore to quantify the net survival benefit or cost of group living in Damaraland mole-rats from Dordabis, Namibia. We therefore test the prediction that larger groups persist longer than solitary individuals or pairs. Finally, if larger groups confer superior survival relative to smaller social units, we expect the most frequently observed group size in the population to approximate the optimal balance between the benefits and costs of group living, providing insight into the prevalence of philopatry

and the constraints on dispersal in this arid-dwelling species.

2. Materials and methods

2.1. Study animals

The Damaraland mole-rat is a subterranean rodent inhabiting the arid and semi-arid regions of southern Africa (Bennett and Faulkes, 2000). Colonies of 2–40 individuals are organised around a single dominant breeding female and up to three breeding males, while the remaining colony members are reproductively suppressed and function as non-breeding helpers (Burland et al., 2002; Jarvis and Bennett, 1993). The species is unusually long-lived for a small rodent, with individuals reported to survive for over 15 years in captivity and more than 10 years in the wild (Bennett and Faulkes, 2000; Dammann and Burda, 2007).

2.2. Study population

Between April 1988 and March 2002, a longitudinal field study of Damaraland mole-rats was conducted, near Dordabis, Namibia. Fieldwork was undertaken on the farm Garib, located approximately 120 km southeast of Windhoek (22°58'S 17°41'E). The size of the study site ranged between 124,800 and 235,000 m² over the course of the study. The climate of this region is modified tropical continental type with two seasons each year, a brief rainy (December–March) and long dry period (April–November) (Supplementary Figs. S1–S3).

2.3. Trapping of mole-rats

Mole-rat groups were captured biannually (one period between December to May or between June to November) by excavating short trenches across active molehill lines to access the underlying tunnels, followed by the placement of modified Hickman live traps baited with sweet potato (Hickman, 1979). Traps were checked every 1–3 h between 06:00 and 22:00. Upon capture, body mass was measured using a precision scale (Ohaus CS2000), which was accurate to the 0.1 g and rounded to the nearest gram. Once a group had been fully trapped out, indicated by a lack of burrowing activity at the site for 36 h, any unmarked individuals (identified by sex, body mass, and natural coat patterns) were permanently marked using toe clipping (Burland et al., 2004; Jarvis et al., 1998). Entire groups were then released together back into their original burrow systems the day following the 36 h of no burrowing activity to prevent other mole-rats from occupying the burrows. A group was defined as all individuals captured from a single, contiguous burrow system. In most cases, all members of a group were caught at a single trap site. However, in some instances, individuals caught at distant trap sites were later identified as belonging to the same group. This was confirmed either by prior knowledge of group compositions and capturing instances, absence of a dominant breeding female at one of the sites, or through recapture of released individuals at the other site. The dominant breeding female in each group (of which there was only ever one) was identified by her perforate vagina and/or swollen teats, validated by post-mortem observations in previous studies (Burland et al., 2004). Breeding males were more difficult to discern from the longitudinal data (Torrents-Ticó et al., 2018b). Sex was determined based on external genital morphology (Bennett and Faulkes, 2000). Groups were captured to monitor individual identity, sex, body mass, group composition, and to record capture series. During this period, a total of 1955 unique captures (138 groups) were recorded, comprising 1000 males and 950 females.

2.4. Data handling

The first analysis focused on a subset of individuals ($n = 123$: Female = 66; Male = 55; Unk = 2) that had, at some point during the study, been captured either as part of a breeding pair or in a solitary state. For each

of these individuals, life history data were compiled from the point of first capture until their final recorded disappearance. At each capture event, the number of individuals present in their group was recorded, allowing us to track changes in group affiliation and size over time.

The second analysis used 126 unique groups, which were considered to have been completely captured out, based on capturing protocol to ensure correct representation of actual group size. Our study focused strictly on group size and apparent survival, in addition to sex and body mass. Breeding status was not performed for these analyses for two reasons. Firstly, due to the uncertainty of breeding male's identification. Secondly, not all breeding females had their body mass recorded at the time of capture. By not investigating breeding status, we were able to retain a larger sample size for sequential captures over time, which is important for apparent survival analyses.

2.5. Statistical analysis

All statistical analyses were performed using R version 4.3.3 (Team, 2021). To estimate individual apparent survival/persistence of the 123 individuals that were ever in a solitary or paired state as a function of group size, we employed a multi-state Markov model using the *msm* package (Jackson, 2011). We defined three states for this model (see supplementary material for more details).

- State 1: Individuals captured either alone or as part of a pair,
- State 2: Individuals captured in groups of three or more,
- State 3: An absorbing state representing disappearance or presumed death or apparent survival from the population, as direct observable deaths and reappearing after disappearing were not observed.

State 1 and state 2 are transient states, which means animals can move between them (transitioning) or simply, go from being alone or as a pair to a group of three or more and vice versa. The absorbing state (State 3) refers to a state that once entered, it is permanent, such that individuals that disappear from the population cannot return to being solitary or as a pair or in a group of three or more (see supplementary material for more details). Due to sparse data, numerical inconsistencies and convergence issues associated with solitary individuals, we combined solitary and paired individuals of both sexes into a single state. For individuals not recaptured, we added an additional observation six months after their last known capture to account for the uncertainty surrounding their disappearance, following the approach of interval coding by Jackson (2011). Similarly, for individuals captured during the final trapping window at each site, an additional censored row was added under the assumption they were alive at the dataset's conclusion. The model estimated transition (the movement between different and same state) probabilities between states, which allowed us to derive state-dependent apparent survival probabilities. We visualised apparent survival trajectories using the built-in plot function from the *msm* package, comparing individuals that are solitary or paired versus those in a group size of three or more. Hazard ratios and relative likelihoods were interpreted based on 95 % confidence intervals (CIs); intervals that did not include 1.0 were considered indicative of biologically meaningful effects, with emphasis also placed on the magnitude of effect sizes. We compared survival between grouping categories (solitary/pair versus grouped) using Kaplan–Meier curves generated from the Markov chain survival object, and assessed differences with a log-rank test using the *survdiff* function from the *survival* package).

To assess whether the effect of group size on survival was non-linear, we first ran a Cox proportional hazards model using the *survival* package (Therneau and Lumley, 2015). The model used centered group size as the response variable. We plotted the subsequent martingale residuals, where the locally smoothed trend (red line) showed no systematic curvature across the observed range of group sizes, supporting the assumption of a linear relationship (Supplementary Fig. S4). Therefore, we modelled the effect of group size on apparent survival as linear.

To analyse the persistence of animals that were ever caught in a solitary or pair state, we used a Cox proportional hazards mixed effects models using the *coxme* package (Therneau, 2015). We modelled the effects of group size, individual body mass, sex and their interaction on apparent survival, with animal identity and group identity included as random effects. These analyses used 121 of the 123 individuals in the Markov model as the sex of two individuals were unknown. We repeated the analysis by categorising groups into two classes—solitary or pair versus groups of three or more, to strictly separate solitary and pairs from group sizes of three or more. Sex was not retained in any of the model outputs.

The group persistence of the 126 unique groups was also analysed as a function of group size, with group identity as a random effect. The Cox model assumes that hazard ratios remain constant over time. To test this assumption, we examined Schoenfeld residuals for group size using the *survival* package (Therneau and Lumley, 2015). The residuals showed no significant time-dependent deviations for all models (see Fig. S4, S5 and S6), confirming that the proportional hazards assumption was satisfied.

It is important that similar to the study by Hazell et al. (2000) that noted that despite up to 60 % of adults leaving their natal colony within 16 months of adulthood, fewer than 10 % are later observed founding new groups. As dispersal and evasion of recapture were possible, this dataset reflects apparent survival, limited to individuals for whom multiple capture records existed. Although this can reflect sampling effort, it is impossible to separate deaths occurring while colony members were extending the natal foraging burrows and losses occurring during dispersal. Thus, survival in this regard refers to apparent survival, which involves all leading causes to disappearance and can underestimate actual survival.

3. Results

The majority of captured groups consisted of individuals found in pairs, with an overall mean group size of 9 for the population (Fig. 1). Only 22 solitary mole-rats (14 females and 8 males) were captured across the 14-year study period. For females, the median duration of persistence in the population following their first recorded occurrence as solitary or paired was 0.54 years, ranging from 0 years (individuals never seen again after initial capture) to 5.97 years. Of these, 23 females were observed to persist for more than 1 year after their first solitary or paired capture, while 43 did not. For males, the median duration of persistence was 0.38 years, ranging from 0 to 3.41 years. Only 15 males were observed to persist beyond 1 year, compared with 40 that did not.

Group size had a strong positive effect on individual survival, as demonstrated by both the MSM (Fig. 2A–C; Table S1), the Cox proportional mixed effect hazards models (Table 1) and the Kaplan Meier log-rank test. Individuals captured alone or in pairs exhibited lower persistence compared to grouped animals Kaplan Meier log-rank test ($\chi^2 = 44.9$, $df = 1$, $p < 0.0001$). The probability of remaining in the solitary/pair state for an entire year was only 14.8 % (Fig. 2B; Table S1). In contrast, 31.0 % of individuals in the solitary/pair state are predicted to become groups of three or more within one year (Fig. 2B; Table S1). However, a substantial 54.2 % of individuals in the solitary/pair state disappeared from the population within a year, indicating a high mortality or emigration risk associated with small (<3) group size (Fig. 2C; Table S1). For individuals already in groups (≥ 3 members), persistence within that state was much higher, with a 50.3 % probability of remaining in a group from one year to the next (Fig. 2B; Table S1). The risk of disappearance for these group-dwelling individuals was markedly lower, at 29.9 % (Fig. 2C; Table S1), supporting the concept that group living compared to paired and solitary states provides a survival advantage. Overall, the apparent risk of disappearance was reduced in individuals that increased in group size, or maintained a larger group size compared to remaining in a solitary or paired state for an extended period (Fig. 2C; Table S1).

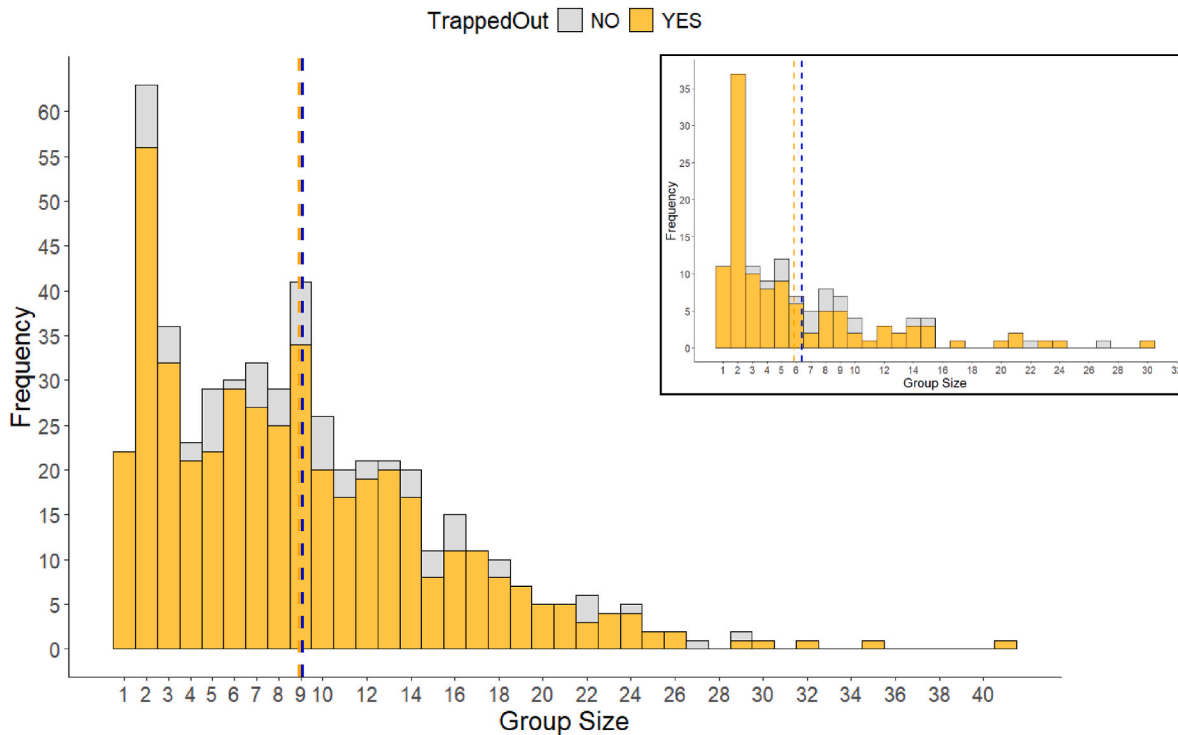


Fig. 1. The distribution of group sizes in the study population of Damaraland mole-rats (*Fukomys dmamarensis*) from Dordabis, Namibia, from 1988 to 2002. The main histogram displays group size frequencies across all captures, where yellow represents colonies fully trapped out and grey for colonies not completely trapped out. The inset histogram displays the group sizes at first capture. The dashed lines indicate the mean group size across all captures that only include completely trapped out (yellow) or not completely trapped out (grey) groups.

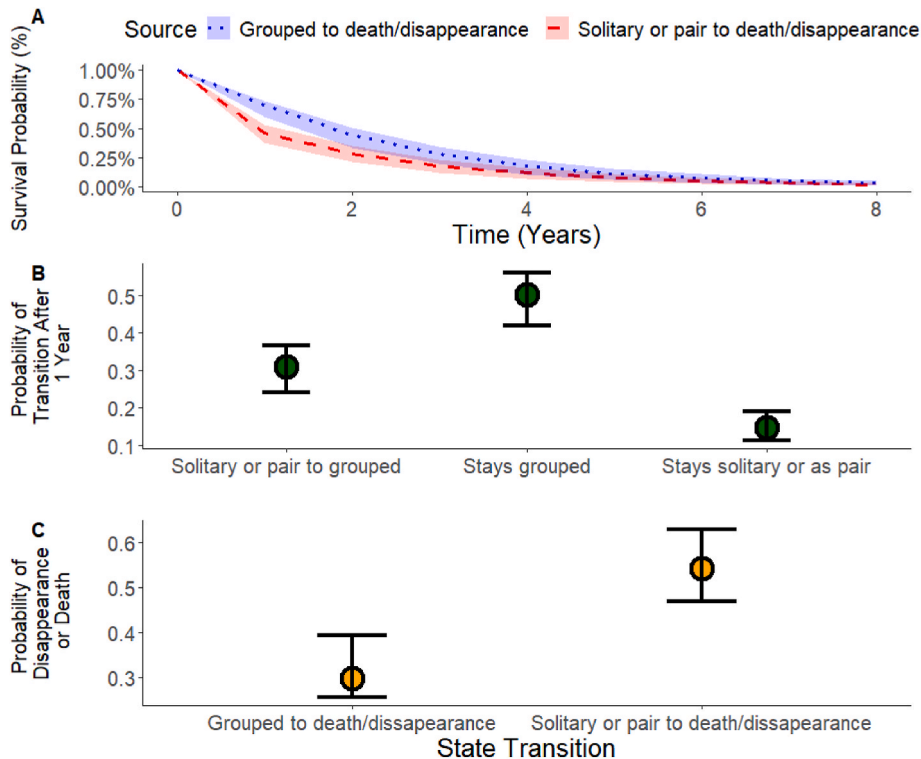


Fig. 2. The multiple Markov chain A) state-related survivability curve, B) the state transition probabilities between solitary/pair and group size of 3 or more states after 1 year and C) state transition probabilities to death/disappearance after 1 year of Damaraland mole-rats (*Fukomys dmamarensis*). “Disappearance/Death” combines cases where individuals died within their group (*in-situ* mortality) and cases where mortality occurred during dispersal (when individuals left their current group and state and were not recaptured thereafter). The multi-state model combined information on individuals that have all been in a solitary or pair state during their life history (n = 123).

Table 1

Cox mixed-effects model outputs for apparent mole-rat survival. Hazard ratios (HR) with exact 95 % confidence intervals (CI) and p-values are shown. Models are separated into individuals (n = 119) that were ever selfish or in a pair state using 1) continuous scaled group size, (2) solitary and paired versus grouped categories. The (3) model includes all groups as single entities (n = 126). HR < 1 indicates reduced hazard (higher survival) and HR > 1 indicates increased hazard (reduced survival). Models with the best AIC are presented for each model type.

Model	Variable	HR (95 % CI)	p-value
Individuals: Scaled Group Size × Mass	GroupSize_c	0.24 (0.12–0.47)	0.0001
	Mass	1.01 (0.98–1.03)	0.616
	GroupSize_c × Mass	1.01 (1.00–1.01)	0.004
Individuals: GroupCategory × Mass	Group Category	<0.001 (<0.001–0.012)	0.0005
	Mass	0.97 (0.95–0.99)	0.004
	Group Category × Mass	1.04 (1.01–1.07)	0.009
All groups: Scaled Group Size	GroupSize_c	0.80 (0.67–0.95)	0.003

4. Discussion

Our 14-year longitudinal study of a wild Damaraland mole-rat population in Dordabis, Namibia, provides strong empirical support for the statement that long-standing group living provides a clear evolutionary advantage with larger groups showing enhanced individual survival, making it more beneficial to remain in the natal colony than to disperse in search of reproductive opportunities. Solitary individuals were rare in our study population, and most likely represent solitary individuals that during dispersal pair up to form a new reproductive cohort. However, both field data and model predictions show that solitary and paired states were generally short-lived and typically became larger groups within a year, greatly enhancing survival prospects. Consistent with this, individuals initially captured solitary, or in pairs, were rarely recaptured in the same state. Notably, sex did not remain in the final models, suggesting that the survival benefits of group living apply similarly to both sexes. The cost–benefit framework of increased group size of our long-term data reveals a distinct group size threshold of 9, suggesting this group size may represent an optimal size at which the costs and benefits of group living are optimal. The tail end of larger groups beyond this point may reflect diminishing returns, where additional members no longer accrue “increased” survival benefits and may even introduce increased competition or social conflict such that the costs begin to outweigh the benefits. Together, these findings highlight the critical role of sociality in enhancing survival and ensuring persistence in this arid-dwelling rodent species.

While group living gives a clear evolutionary benefit, dispersal in Damaraland mole-rats remains a key evolutionary strategy, with individuals attempting it to maximise direct fitness despite substantial risks (Finn et al., 2022; Hazell et al., 2000; Mynhardt et al., 2021; Torrents-Ticó et al., 2018b). In our study, fewer males were found in a solitary or paired state compared to females, suggesting that males may preferentially join pre-existing groups, whereas females are more likely to establish new colonies independently (Mynhardt et al., 2021). Because our survival analyses focused on solitary and paired states, they did not capture male dispersal into established groups, where males can still benefit from the survival advantages of larger group sizes. Males may also disperse further in search of lone females (Mynhardt et al., 2021), and such extended dispersal is known to be physiologically costly (Spinks et al., 2000). This could result in reduced recapture rates if males move beyond the study area, thereby underestimating their apparent

survival. Nonetheless, even if our estimates represent apparent rather than true survival, the highly significant results from our hazard models highlight the stark disparity between solitary/pair states and grouped states. Moreover, our findings suggest that the transition from solitary or paired individuals into larger groups typically occurs within a single rainy season, as these smaller states rarely persisted for more than a year.

The costs and benefits of dispersal appear to lie along a continuum shaped by environmental context, individual condition, and social structure (Bonte et al., 2012). This continuum is influenced by key ecological constraints of group living, such as rainfall, which affects both the energy required for burrowing (Lovegrove, 1989) and primary productivity (Zhu and Southworth, 2013). Rainfall may greatly influence post-dispersal survival probabilities, as favourable conditions can improve an individual's chances of surviving (Bennett and Faulkes, 2000; Faulkes et al., 1997). Some individuals occupy the portion of the spectrum where dispersal is viable and may maximise fitness gains, for example through larger body mass or increased energy reserves (Hazell et al., 2000; Torrents-Ticó et al., 2018a, 2018b). This is especially important regarding the energetic costs associated with digging (Lovegrove, 1989; Vleck, 1979). However, not all individuals meet the prerequisites for safe dispersal, and in a long-lived species such as the Damaraland mole-rat, selection may favour behaviours that optimise lifespan (survival) rather than immediate reproduction (Crone, 2001). Under this framework, the survival benefits of group living likely select for a fitness trade-off favouring survival over reproduction, buffering individuals against extrinsic mortality risks and promoting cooperative behaviour within natal groups as an indirect fitness benefit (Faulkes and Bennett, 2021).

There are some shortcomings to our study, where detection bias, dispersal variability and the potential for recapture avoidance suggest that our findings be interpreted with caution. Since individuals are only observed when trapped, disappearance may reflect true mortality or undetected emigration, meaning that apparent survival can underestimate actual survival. This issue is especially relevant after dispersal, when individuals may move beyond the trapping area entirely and therefore evade further detection. In addition, the exact timing of death could rarely be confirmed, and many mortality events had to be estimated from the last known capture, introducing additional uncertainty into survival models. Despite these limitations, our results clearly infer the noticeable survival differences between solitary or paired individuals and those in larger groups are consistent across both field data and model outputs, reflecting a genuine biological pattern rather than merely a sampling artefact.

Our study demonstrates that the cumulative advantages of group living allow Damaraland mole-rats to withstand ecological stressors better, resulting in improved long-term survival. The benefits of cooperative group living, including enhanced survival and persistence, clearly outweigh the costs, supporting the notion that group living, which gave rise to sociality and cooperative behaviour, is central to the life-history strategy of this species. A study by Thorley et al. (2023) of a southern Kalahari population of Damaraland mole-rats found that, although group living remained common, some individuals could maintain a solitary state with high survivorship for extended periods. While rainfall and soil properties were similar across populations, spatial variation in food resource distribution was stated as a potential factor that may influence the costs and benefits of group living (Thorley et al., 2023). Our findings provide evidence to this claim, where food availability differs between the populations, where in Dordabis, food resources are primarily small clumps of bulbs and geophytes, whereas in the Kalahari, large tubers are more common. The population differences in food resources may have contributed to the individual survival contrasts of the current study. Overall, our findings highlight how ecological pressures, individual condition, social structure and food resource distribution interact to shape survival strategies, emphasising the role of sociality in buffering individuals against environmental challenges. Our

findings contribute to how ecological constraints, dispersal costs, social buffering, and, in particular, food resource availability have shaped the evolution of group living.

CRedit authorship contribution statement

Paul Juan Jacobs: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Daniel William Hart:** Writing – review & editing, Conceptualization. **Jennifer U.M. Jarvis:** Writing – review & editing, Resources, Investigation, Funding acquisition. **Nigel Charles Bennett:** Writing – review & editing, Project administration, Investigation, Conceptualization.

Ethics

The project and protocols were approved by the ethics committee at the University of Cape Town and the animals were captured under permit from the Namibian Department of Nature Conservation. The current manuscript analysed the longitudinal data and did not require new ethics for experimentation or analyses.

Data availability statement

The data supporting the findings of this study, including the individual- and group-level survival data as well as the data pertaining to the survival of individuals since their solitary or paired state have been deposited in the Open Science Framework (OSF) and can be accessed through the following link https://osf.io/cq64p/?view_only=9a7aee741f674a12b7c53ed0de6a534c.

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Declaration of competing interest

We have nothing to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2025.105540>.

Data availability

Data will be made available on request.

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