Helpers at the nest? The activity patterns of Damaraland mole-rats across reproductive periods

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Data availability

Analyses reported in this article can be reproduced using the data provided by Thorley et al. (2026)

Author Contributions

JT: data curation, conceptualisation, methodology, formal analysis, investigation, writing- original draft. **PV:** data curation, investigation, writing- review and editing. **DS:** data curation, investigation, writing- review and editing. **MZ:** investigation, writing- review and editing. **TCB:** writing- review and editing, project administration, funding acquisition.

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Ethics

The behavioural data used in this study were collected under permits granted by the ethics committee of the University of Pretoria, South Africa (EC089-12, SOP-004-12 and FAUNA 0137/2020), and adhered to the standards outlined in the ASAB/ABS guidelines for the Treatment of Animals in Behavioural Research and Training (ASAB, 2012).

Conflicts of Interest

No conflicts of interest.

Abstract

Individuals help to rear the offspring of other group members in many animal societies. In social mole-rats, conspicuous forms of alloparental care such as allolactation and offspring provisioning are absent, and group members cooperate primarily by digging tunnels to access the tubers on which breeders, and subsequently their offspring, feed. Despite interest in the organisation of mole-rat societies, it remains uncertain how group members adjust their cooperative behaviour across reproductive periods, and the potential for nest attendance to represent a form of direct offspring care has been overlooked. Using observations (~24,000 h) of captive Damaraland mole-rats (*Fukomys damarensis*), we quantified group members' time budgets across reproductive periods and tested whether non-breeders increased their nest attendance following the birth of pups, as expected if nest attendance contributes to alloparental care. Contrary to this prediction, non-breeding individuals of both sexes, as well as breeding males, reduced their nest attendance while increasing their work effort shortly after birth. A similar pattern occurred during late gestation. Breeding females spent more time in the nest, reduced work-related behaviours, and increased feeding activity during these same periods. Thus, we found no evidence that non-breeders care for offspring by increasing nest attendance. The increased work effort by non-breeders during

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reproductive periods may help to support breeders when they are energetically constrained and facilitate access to food resources for dependent pups when they first leave the nest. Our results highlight the importance of distinguishing direct alloparental care from other behavioural changes when interpreting the functional basis of cooperation.

Key words: alloparental care; cooperation, division of labour; helper effects; load-lightening; sociality

Introduction

One of the hallmarks of cooperative breeding is alloparental care, where individuals contribute to the rearing of offspring other than their own (Solomon & French, 1997; Cant, 2012; Koenig and Dickinson, 2016). In many species, these contributions are direct and readily identifiable, including behaviours such as allolactation, offspring provisioning, or the guarding or carrying of young (Clutton-Brock, 2016). However, not all forms of assistance involve direct interactions with offspring. Group members may also contribute through behaviours that support reproduction more indirectly, for example by maintaining territories, defending resources, or investing in shared infrastructure (Packer et al., 1990; Komdeur, 1994; Clutton-Brock, 2009; Koenig et al., 2019). These behaviours can benefit both the individual performing them and other group members but are not directed specifically towards offspring. Distinguishing offspring-directed care from other forms of cooperative activity is important for understanding how helping behaviour is expressed and how reproduction is supported within social groups (West et al., 2021).

This distinction is particularly relevant in systems where direct forms of alloparental care are uncommon or difficult to observe. In such cases, it may be unclear whether specific behaviours primarily support reproduction, provide more general benefits to the group, or are largely self-serving (Dugatkin, 1997; West et al., 2007; Clutton-Brock, 2009; West et al., 2021). Behavioural

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changes associated with reproduction can provide important clues about the functions of putatively cooperative activities. If certain behaviours change when breeders face elevated energetic demands - which in mammals are substantial for pregnancy and lactation (Gittleman and Thompson, 1988; Speakman et al., 2008) - or when offspring are present and dependent, this suggests that they may contribute to reproduction, even when their effects are indirect or difficult to quantify. For example, the fact that meerkats (*Suricata suricatta*) increase their sentinel behaviour when pups are foraging with the group suggests that sentinel behaviour in this context has been selected, at least in part, for its helping benefits (Santema and Clutton-Brock, 2013). Examining how individuals adjust their behaviour across reproductive periods can therefore help to identify which forms of cooperation are most closely associated with supporting breeders and offspring.

The African mole-rats (Bathyergidae) provide an interesting system in which to examine different forms of cooperation. These subterranean rodents live either solitarily or in stable groups ranging from a few individuals in some species (Yeboah and Dakwa, 2002) to several hundred in the case of the naked mole-rat (*Heterocephalus glaber*, Brett 1991; Faulkes and Bennett, 2021). In the social species, groups typically comprise a single breeding female and, in most cases, a single breeding male, alongside offspring from multiple successive litters (Sherman et al., 1991; Bennett and Faulkes, 2000; Patzenhauerová et al., 2013). Group members perform energetically costly excavation and maintenance of extensive burrow systems, which is normally considered as a form of cooperative foraging because it sustains access to the underground storage organs of plants on which all individuals feed (Jarvis and Bennett, 1993; Lovegrove, 1989; Faulkes and Bennett, 2021). In contrast to many other cooperatively breeding mammals, direct forms of offspring provisioning are rare or absent in mole-rat societies. Allolactation does not occur, while reports of pup feeding via allocoprophagy are few, contentious, and largely restricted to naked mole-rats

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(Burda, 1989; Watarai et al., 2018; Braude et al., 2021; Buffenstein et al., 2022). Non-breeders do carry nest material and retrieve pups that wander from the nest prematurely in captivity (Zöttl et al., 2016, 2018; Begall et al., 2021), but the frequency and significance of these behaviours under natural conditions is unclear.

One potentially important but largely overlooked behaviour in social mole-rats is nest attendance by non-breeding group members. This omission is striking because mole-rat pups are highly altricial, being born naked, blind, and possessing limited thermoregulatory capacity for several weeks postpartum (Burda, 1990; Jarvis, 1991; Bennett & Faulkes, 2000; Šumbera, 2019). In other rodents, communal nesting and huddling by group members can substantially improve offspring thermoregulation and survival (Hayes et al., 2000; Gilbert et al., 2010). Interactions with alloparents can also influence offspring development through increased tactile stimulation and social contact (Kenkel et al., 2017), while mothers can also benefit by having more time to forage while group members attend offspring (Auclair et al., 2014). Together, these findings suggest that the extent and timing of nest attendance by group members could influence offspring development in mole-rats if individuals adjust their allocation of time to the nest during early reproduction. Nest attendance may therefore represent a form of direct alloparental care in a system where other forms of offspring provisioning are lacking.

Here, we examine behavioural changes across reproductive episodes in Damaraland mole-rats (*Fukomys damarensis*) to assess whether group members adjust their behaviour in ways consistent with direct offspring care or the broader support of reproduction. Using nearly 24,000 hours of behavioural observations from captive groups housed in semi-natural tunnel systems (Figure 1A), we quantified nest attendance, work, and feeding activity across the reproductive periods of breeding females. We predicted that, following parturition, non-breeders would increase

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their nest attendance, consistent with a role in direct alloparental care when offspring are present and their thermoregulatory and care needs are greatest. We also examined work behaviour to test whether reproductive periods are associated with broader changes in activity that could indirectly support reproduction, with time spent eating providing context for how changes in work might be accommodated. Increased work during reproductive periods could support breeders and pups by maintaining or enhancing access to communal food resources. Previous studies of mole-rats have documented variation in activity budgets and work effort among breeders and non-breeders, as well as across group sizes (e.g., Mooney et al., 2015; Zöttl et al., 2016; Thorley et al., 2018; Francioli et al., 2020; Gilbert et al., 2020; Houslay et al., 2020; Rotics et al., 2025; Siegmann et al., 2025), but whether these behaviours change systematically across reproductive periods has not been studied to date.

Materials And Methods

Study population

Observations were conducted on a captive Damaraland mole-rat population at the Kalahari Research Centre in South Africa (-26.979º, 21.833º) between 2013 and 2024. Established in October 2013 from wild-caught groups in the surrounding duneveld, the population was later expanded by pairing unrelated individuals and typically comprised dozens of groups, including both wild-caught animals of unknown age and lab-born individuals of known age (Zöttl et al., 2016). Wild groups in the surrounding population averaged 8.7 ± 5.30 individuals (excluding solitary individuals, range = 2–26; Thorley et al., 2023), while the captive groups in this study averaged 7.9 ± 5.5 individuals across all observation sessions (range = 2–26).

Animals were housed in tunnel systems constructed from PVC pipes. The pipes were modified to have transparent viewing windows so that animals could be easily observed (Figure

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1A). The tunnel systems featured various compartments that functioned as a nestbox, a toilet, a food store, and a waste box. Vertical pipes were incorporated to allow the introduction of sand collected from nearby dunes, which promoted natural digging behaviour and required animals to remove sand to access food placed in peripheral tunnels. Animals were fed twice daily on a diet primarily consisting of sweet potato and cucumber, and tissue paper was provided as nesting material. Tunnel system design varied with group size so that larger groups occupied tunnels of increased length. The rooms in which groups were housed were maintained at 19–21°C, temperatures that fall within the range recorded in natural Damaraland mole-rat burrows (Roper et al., 2001) and closely matches soil temperatures measured at depths used for nesting, particularly during winter (Streicher, 2011).

Individuals from each group were identified using uniquely coloured dye marks applied to their white head patch. Individuals were also implanted with a passive integrated transponder (PIT) tag on capture or in early life. Animals were weighed regularly on an electronic balance (Sartorius TE4100) and sexed based on external genital morphology. Breeding females were identified based on their breeding history and the presence of swollen teats and a perforate vagina (Bennett & Jarvis, 1988). In most cases, breeding males were known with high confidence because groups were either founded by a single breeding pair (male offspring will not mate with their mother) or because genetic paternity analyses confirmed that all offspring within a group were sired by a single male. In a small number of cases where multiple paternity was detected, males known to have sired offspring were excluded from analyses as we could not identify a single breeding male unambiguously (~7% of all observations).

Pregnancy in breeding females was monitored regularly through weight gain and abdominal swelling and confirmed by abdominal palpation to detect foetuses. Towards the end of

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gestation, nest boxes were checked every 2-3 days for pups. The distribution of pairing-to-birth intervals, together with the lower bound of the inter-birth interval distribution, suggests a gestation length of approximately 95-100 days (Figure S1). Pups remained in the nest for several weeks post-birth, gradually spending more time outside of the nest and beginning to consume solid food. Weaning typically occurs at around 28 days (Bennett & Faulkes, 2000).

Behavioural observations

Behavioural data were collected using instantaneous scan sampling (Altmann, 1974). We have previously used this approach to investigate mole-rat behaviour in this system (Zöttl et al., 2016; Thorley et al., 2018), including the effects of group size on work effort during late gestation (Houslay et al., 2020), but we have not yet examined behavioural changes across reproductive episodes. Observation sessions were generally conducted as part of longitudinal behavioural monitoring, for example in relation to the age of group members (Zöttl et al, 2016), rather than being scheduled according to reproductive periods. Nevertheless, the extensive sampling effort over the project's history resulted in substantial coverage of gestation and post-birth periods (Figure 1B). Any observations conducted during experiments that were known to affect activity budgets were excluded from the analysis (e.g., Vullioud et al., 2021), irrespective of the reproductive status of the breeding female at the time. To avoid confounding overlapping reproductive events, we also excluded observation periods in which a new pregnancy occurred during the post-birth phase of a previous litter (0–90 days). The final dataset consisted of 1982 observation sessions conducted on 133 unique groups. On average, each group was observed 14.9 ± 12.8 times (mean ± SD, median = 10, range = 1-62). Groups had a single breeding female at any given time, but because groups were sampled repeatedly, an average of 1.5 ± 0.6 breeding females were represented per group (mean ± SD, median = 1, range = 1-3). A total of 102 breeding females

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were represented across all observations, and groups were observed during the reproductive periods of 98 of these females.

Each observation session lasted approximately 12 hours (11.98 ± 0.17; mean ± SD; range = 10.0 to 12.6 hours), with scans of all group members conducted every four minutes. We recorded behaviour using a 17-category ethogram (Table S1). Here, we were interested in resting behaviour, working behaviour, and eating behaviour. Resting normally involves individuals being in the nest (and not visible). Individuals sometimes huddle outside of the nest in the tunnels, though this is rare (0.93% of observed rest events), so we only consider rest periods in the nest. For working behaviour, we aggregated four behaviours related to the excavation and movement of sand, which in the wild is crucial for maintaining burrow systems and locating new food sources: digging (using extrabuccal teeth and front paws to dig in sand), sweeping (sweeping sand with hind paws through the tunnel system), kicking (pushing sand into tunnel gaps with the hind paws or nose), and locomotion between work (moving between episodes of the other three behaviours). During observations sand was added to the tunnel system at 2-hour intervals to sustain opportunities for work-related behaviours.

Statistical analyses

To investigate changes in resting, working, and eating behaviour across reproductive episodes, we categorised each observation session according to its timing relative to birth. We classified observations as occurring during the gestation period (-90 to -1 days), the post-birth period (0-90 days), or in non-reproductive periods (< -90 days or > 90 days). We further divided gestation and post-birth into discrete phases. Gestation was separated into the first trimester (-90 to -61 days), second trimester (-60 to -31 days), early third trimester (-30 to -15 days), and late third trimester (-14 to -1 days). Post-birth was divided into the early first trimester (0–14 days),

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late first trimester (15–30 days), second trimester (31–60 days), and third trimester (61–90 days). We used finer temporal bins close to birth because we anticipated that behavioural changes could be concentrated around these periods. Although reproductive timing could alternatively be modelled as a continuous variable, categorisation allowed direct statistical comparisons among reproductive phases and with non-reproductive periods.

To model the effects of reproductive status and reproductive period on individual behaviours, we fit generalized linear mixed models (GLMM) with a binomial error distribution. The response variable in each case was the proportion of time engaged in each behaviour (observed scans/total scans). As predictor variables, we included the reproductive period, individual status (breeding/non-breeding female/male), and their interaction. Since breeding individuals were always adults, we restricted the analysis to non-breeding individuals that were known to be older than 1.5 years of age at the time of the observation to ensure a representative comparison. We also included group size and body weight, which we modelled with quadratic terms to allow for potential non-linear effects. These continuous predictors were z-score transformed before model fitting. Lastly, we included random intercepts for individual identity (n = 632), group identity (n = 133), and the observation session (n = 1982).

We were principally interested in the contrasts arising from the interaction between reproductive period and status, specifically: (i) within-status differences across reproductive periods relative to the non-reproductive period, and (ii) between-status differences in each reproductive period. To assess these contrasts from each GLMM, we fitted each model in a Bayesian framework using the 'brms' package (Bürkner, 2018) in R version 4.6.1 (R Core Team, 2026). A key advantage of a Bayesian approach here is that it allows us to directly estimate posterior distributions for all contrasts of interest and make probability statements about group

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differences. By comparison, a frequentist approach would require multiple comparison adjustments to control for type I errors, which can substantially reduce statistical power when evaluating large numbers of biologically relevant contrasts. Contrasts were calculated from the estimated marginal means of fitted models using the 'emmeans' package (Lenth & Piaskowski, 2026).

For each model we ran four chains of 2000 iterations, of which 1000 were dedicated to the warm-up, and used weakly informative priors for fixed effects. Convergence and model fit were assessed using standard diagnostics and posterior predictive checks. To interpret the strength and uncertainty of effects, we report posterior means and 95% credible intervals derived from posterior draws, along with the probability of direction ($p_{+/-}$, Makowski et al., 2019), defined as the proportion of the posterior distribution lying above or below zero in the direction of the median. We interpret effects with $p_{+/-} < 0.90$ as unlikely to exist, $0.90 < p_{+/-} < 0.95$ as having a moderately probability of existence, and $p_{+/-} \geq 0.95$ as having a high probability of existence.

Results

The time budgets of the different classes of individuals showed distinct temporal patterns across reproductive episodes (Figure 2). While breeding females increased their nest attendance during late gestation and early post-birth, all other group members decreased their nest attendance over the same period. In general, the more time individuals spent in the nest, the less time they spent contributing to work.

After an initial decline during early gestation, breeding females steadily increased their nest attendance through gestation and into early post-birth (Table S2). The strongest increase

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relative to non-reproductive periods occurred in the final two weeks of pregnancy (β = 0.167 [95% CrI: 0.061, 0.275], p_+ = 0.999) and the first two weeks post-birth (β = 0.363 [0.251, 0.474], p_+ = 1.000), coinciding with lactation and high pup dependency. Predicted resting time in the nest rose from 68.3% [95% CrI: 65.7, 70.9] during non-reproductive periods to 75.7% [73.0, 78.1] immediately post-partum. Working time declined over the same interval before increasing again as pups developed (Table S3).

In contrast, non-breeding females, non-breeding males, and breeding males reduced their time in the nest and increased their time spent working across gestation and into early post-birth. The largest declines in nest attendance occurred either side of birth (Table S2). In both breeding and non-breeding males, reductions in nest time were significant across most reproductive periods, whereas in non-breeding females, only late gestation and early post-birth differed significantly from the non-reproductive baseline (Table S2B).

The concurrent increase in working time during reproductive periods represented relatively large effects (Table S2). In non-breeding females, predicted work time rose from 4.7% [4.0, 5.6] during non-reproductive periods to 7.5% [6.3, 9.1] in the first two weeks post-birth (β = 0.502 [0.365, 0.633], p_+ = 1.000). Non-breeding males showed a similar increase from 5.8% [4.9, 6.8] to 9.7% [8.1, 11.6] (β = 0.549 [0.413, 0.682], p_+ = 1.000), while breeding males increased further from 5.3% [4.4, 6.4] to 14.1% [11.4, 17.4] (β = 1.072 [0.878, 1.268], p_+ = 1.000). Over a 12-hour observation period, these changes corresponded to an additional 20.2, 28.1, and 63.4 minutes of work, respectively.

These behavioural shifts resulted in a marked divergence in activity budgets between breeding females and other group members during key reproductive stages (Tables S2C and S3C, Figure S3). In late gestation, breeding females spent more time in the nest (71.8% [68.9, 74.7])

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and less time working (4.9% [4.1, 6.0]) than non-breeding females (65.0% [61.6, 68.2]; 7.1% [6.0, 8.8]), non-breeding males (63.4% [59.9, 66.7]; 9.1% [7.7, 11.0]), or breeding males (63.6% [59.7, 67.3]; 10.9% [8.7, 13.4]). These differences were amplified in early post-birth, with breeding females spending 75.7% [73.0, 78.1] of time in the nest and only 4.6% [3.8, 5.2] working, compared with lower nest attendance and higher work rates in non-breeding females (65.8% [62.5, 69.0]; 7.5% [6.3, 9.1]), non-breeding males (64.3% [60.9, 67.6]; 9.7% [8.1, 11.6]), and breeding males (60.6% [56.4, 64.5]; 14.1% [11.4, 17.4]); all contrasts, $p_+/p_- = 1.000$. Outside reproductive periods, activity budgets were broadly similar across classes, with individuals spending approximately 68-70% of time in the nest and 4-6% working on average.

Unlike resting and working behaviour, time spent eating remained relatively stable across reproductive stages (Table S4), accounting for approximately 5% of daily activity (Figure 2). The main exception was a modest upward trend in eating time among breeding females as gestation progressed (late gestation $\beta = 0.090$ [0.009, 0.173], $p_+ = 0.987$). This was followed by a more pronounced increase during late lactation ($\beta = 0.318$ [0.218, 0.421], $p_+ = 1.000$) and in the period 30-60 days after birth ($\beta = 0.237$ [0.152, 0.323], $p_+ = 1.000$).

Time budgets were also influenced by body mass and group size (Figure S2). Heavier individuals, who were often older, spent more time resting and less time working, while individuals in larger groups worked significantly less and rested more.

Discussion

Outside of a handful of laboratory-based assays (Mooney et al, 2015; Zöttl et al., 2018; Watarai et al., 2018), the extent to which non-breeding individuals in mole-rat societies engage in offspring-directed care has received little attention, despite social mole-rats frequently being described as cooperative breeders and, more controversially, as eusocial, both of which are defined

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in part by the presence of alloparental care (Crespi and Yanega, 1995; Lukas and Clutton-Brock, 2012). By quantifying individual behaviour across the reproductive periods of large numbers of groups, we found no evidence that non-breeders increase their nest attendance following the birth of pups. Contrary to this primary prediction, nest attendance declined in non-breeding males and females, suggesting that direct alloparental care through nest-based behaviours may be limited in this species, despite the potential thermoregulatory benefits of huddling in mole-rats (Kotze et al., 2008; Šumbera, 2019; but see Vavrušková et al., 2022) and the prevalence of communal nesting, huddling, and allonursing in other rodents (Hayes, 2000; Gilbert et al., 2010; Tang-Martínez and Congdon, 2016).

Nest attendance does not in itself constitute direct offspring care, and non-breeders may provide care through interactions with pups inside the nest that were not detectable using our scan-based observations. Nevertheless, nest attendance provides the opportunity for such interactions to occur, and the absence of any increase in nest attendance by either sex offers little support for the idea that direct care intensifies during reproductive periods. The fact that breeding males also spent more time outside of the nest following parturition also raises questions about paternal involvement in pup rearing. Male assistance to breeding females was first proposed as an important component in the evolution of mole-rat sociality more than three decades ago (Burda, 1990). However, almost no studies have reported on paternal contributions to offspring care since, perhaps reflecting the generally limited involvement of breeding males. To our knowledge, one of the only studies to examine paternal care was carried out in Damaraland mole-rats and found that breeding males carried pups less frequently than any other class of group member when given the opportunity (Zöttl et al., 2018).

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Instead of increasing nest attendance, reproductive periods were associated with pronounced and consistent shifts in work-related behaviours across non-breeding females, non-breeding males, and breeding males, with individuals spending more time engaged in work-related activities during late gestation and early lactation. In contrast, breeding females increased their nest attendance during these periods, especially after parturition when offspring were present and maternal demands are expected to be greatest. Breeding females also increased their feeding activity during late gestation and early lactation, while changes in their work effort were more equivocal. Although breeding females reduced their work levels over the course of gestation, this reflected a decrease from an elevated peak earlier in pregnancy, and work effort during late gestation or lactation was not significantly lower than during non-reproductive periods.

The increased work effort of most group members is expected to lead to a net increase in total group-level work output during the period of highest reproductive demand. Over a 12-hour observation period, the magnitude of the individual responses was considerable: non-breeding females and males increased their work effort by approximately 20 (+60%) and 28 (+67%) minutes respectively, on average, while breeding males exhibited an even stronger response. In a wild setting, where time budgets are very similar to our captive set-up (Rotics et al., 2025), this increase in work effort scaled across group members could benefit breeders and offspring by improving access to food (Jarvis and Bennett, 1993; Jarvis et al., 1994; Jarvis et al., 1998; Spinks et al., 2000), principally through the excavation of new tunnels to locate previously inaccessible food resources.

Increased work effort might also improve access to food by contributing to the maintenance and filling of food stores. As in various mole-rat species, Damaraland mole-rats maintain centralised caches of food close to the nest (Bennett and Faulkes, 2000; Faulkes and Bennett, 2016), moving tubers or parts of tubers from peripheral tunnels to more central locations. It has

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been hypothesised that these food stores serve to buffer energetic constraints on breeders during reproduction (Young and Bennett, 2010) and could also provide pups with readily accessible food during early development. In our captive population, individuals readily cached food in boxes that were provided (Figure 1), but the design of our observations did not allow us to quantify patterns of food storage and consumption. Clarifying how increased work contributes to food storage, and how stored food is subsequently exploited by breeders and pups, would help to determine whether food storage primarily functions to provision breeders and pups, or instead serves as a more general strategy that reduces travel costs for all group members. Several testable predictions can be made in this regard: (1) non-breeders increase food deposition during late gestation and lactation; (2) breeding females preferentially exploit food from stores close to the nest during peak energetic demand; and (3) pups preferentially exploit food from stores close to the nest during early development. Evidence from wild populations partially supports the second prediction, with accelerometry-based assessments of feeding postures suggesting that breeders preferentially feed on stored rather than in situ (i.e. peripheral) food resources (Rotics et al., 2025).

The proximate drivers of the increased activity of non-breeders during key reproductive stages remain unclear. Potential cues could include behavioural, hormonal, or chemical signals from the breeding female, as well as cues from dependent pups. One possible behavioural explanation is that breeders become less tolerant of group members during critical reproductive periods, as is commonly observed in a wide range of cooperatively and communally breeding species, including various rodents (Ebensperger, 1998; Clutton-Brock et al., 2010; Ferrari et al., 2021). Reduced tolerance at the nest could cause non-breeders to spend more time outside the nest, where they engage in foraging and burrow maintenance. This behavioural mechanism seems a parsimonious explanation for our results, though the nature of such interactions in Damaraland

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mole-rats warrants further study. In naked mole-rats, early work suggested that breeders could stimulate non-breeders to work via aggressive 'shoving' behaviour (Reeve, 1992), but this has since been challenged (Jacobs and Jarvis, 1996; Clarke and Faulkes, 2001). Such a mechanism also seems unlikely to operate in Damaraland mole-rats, where overt aggression in stable groups is generally rare (though it does occur and is usually associated with known cases of reproductive conflict). Thus, if reduced tolerance by breeders contributes to increased non-breeder activity, we suggest that it is more likely to manifest through subtler, less aggressive forms of dominance that alter non-breeders' access to or time spent in the nest.

Hormonal or chemical signals from the breeding female may also play a role. In naked mole-rats, Edwards et al. (2021) found that the estradiol levels of non-breeders rose during the breeder's pregnancy and were correlated with her hormone levels, suggesting that her reproductive state can in principle influence the physiology of all group members, and thus affect their behaviour (see also Watarai et al., 2018). Recent work has also identified a breeder-derived chemical signal produced during reproduction that influences the social behaviour and reproductive physiology of non-breeding individuals in naked mole-rat societies, with the compound also detected at low levels in breeding females of several *Fukomys* species (Khallaf et al., 2026). While such results demonstrate that breeder-mediated hormonal or chemical cues can directly impact the behaviour of group members in a mammal, evidence for such effects in Damaraland mole-rats is currently lacking, and effects on cooperative behaviour remain speculative. Ultimately, behavioural and physiological processes are likely to be interrelated, and future work integrating behavioural observations with physiological measurements can provide valuable insights into the proximate drivers of context-dependent contributions by non-breeders in mole-rat societies.

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There are relatively few studies of cooperative and communal breeding mammals with which to compare our results directly. Although nest or natal-den attendance has been described in various species in qualitative terms, quantitative research on the contributions of non-breeding group members in this aspect of care has focused largely on carnivores. In some social mongooses, including meerkats and banded mongooses (*Mungos mungo*), non-breeding helpers babysit pups at the natal burrow while other group members forage, sometimes remaining with pups for the entire day. In meerkats, dominant breeders rarely babysit (Clutton-Brock et al., 2000), whereas both breeders and non-breeders babysit frequently in banded mongooses and the number of babysitters is positively associated with pup survival (Cant 2003). In grey wolves (*Canis lupus*) and African wild dogs (*Lycaon pictus*), by contrast, breeding females spend most of their time at the natal den during early pup development while other pack members forage (Malcolm and Marten 1982; Ruprecht et al. 2012), a pattern which more closely resembles what we observed in Damaraland mole-rats. Studies of communal-breeding rodents have also examined nest attendance from the perspective of offspring: in colonial tuco-tucos (*Ctenomys sociabilis*), for example, the proportion of time that nests were unattended decreases as the number of adults sharing a burrow system increases (Izquierdo and Lacey, 2008). Although these studies provide useful comparative context, differences in life history complicate direct comparisons with mole-rats. Further studies investigating nest attendance in other group-living rodents would therefore be particularly valuable for establishing the extent to which the patterns we observed in mole-rats are shared across species.

Lastly, it remains unknown whether the behavioural patterns we observe in captivity generalise to wild populations of mole-rats, where variation in food availability and differing travel and work costs may alter the balance between nest-based and foraging behaviours. Understanding whether behavioural changes around reproduction translate into measurable fitness benefits is also

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of fundamental importance, especially given recent work suggesting that helper effects on reproductive success in Damaraland mole-rats can be small (Thorley et al., 2023; though see Young and Bennett, 2015). Emerging technologies such as accelerometry and automated behavioural tracking offer promising avenues for resolving these questions in natural settings, although logistical constraints may still limit their application in subterranean systems. Carefully controlled experimental studies in captivity may therefore provide the best means of investigating behavioural mechanisms, including breeder influence, eviction, or infanticide, which are common in other cooperative and communal breeders (Clutton-Brock et al. 2010; Lukas & Huchard, 2019) but remain poorly understood in mole-rats.

In conclusion, our study demonstrates that non-breeding Damaraland mole-rats adjust their behaviour in a finely tuned, reproduction-dependent manner, primarily through changes in work effort rather than increased nest attendance. Our results support the idea that flexibility in workload allocation plays a key role in maintaining group function and supporting reproduction, although the fitness consequences of this flexibility remain uncertain and may not necessarily reflect adaptive processes. By revealing how reproductive state structures cooperative effort, our work provides a foundation for future research on the ecological and evolutionary drivers of helping behaviour in mole-rats and other mammals.

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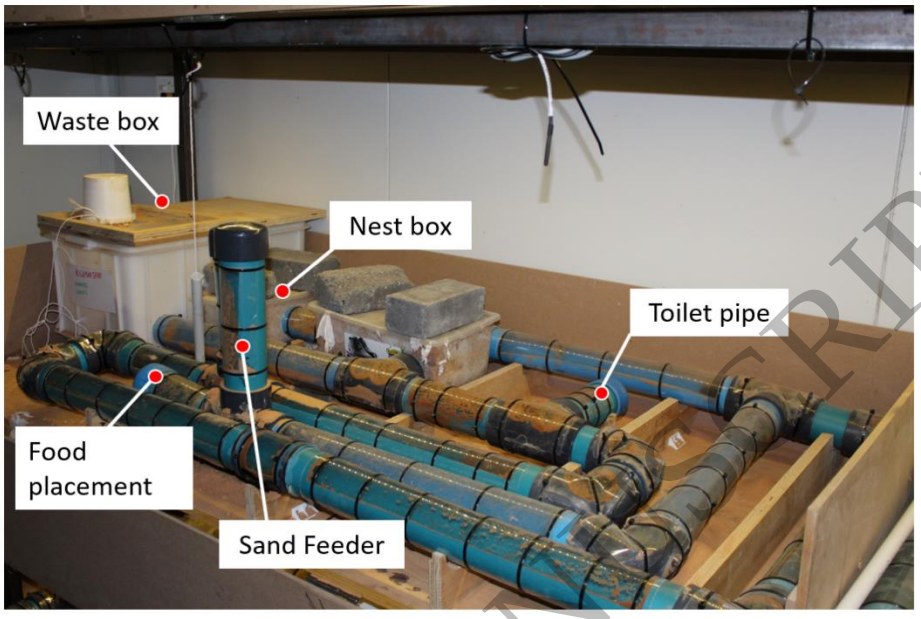
Figure Legends

Figure 1. Tunnel system design and observational sampling effort. (A) A typical tunnel system, with key features highlighted. This represents a medium-sized tunnel system, used for groups of Damaraland mole-rats containing 4-10 individuals. (B) The distribution of observational sampling effort across the reproductive episodes of breeding females. The plot includes 1240 observation sessions across 402 distinct reproductive periods, where each session consisted of ~ 12 hours of instantaneous scan sampling of all group members on a given day. Analyses also included 742 observation sessions conducted outside of the 180-day reproductive window.

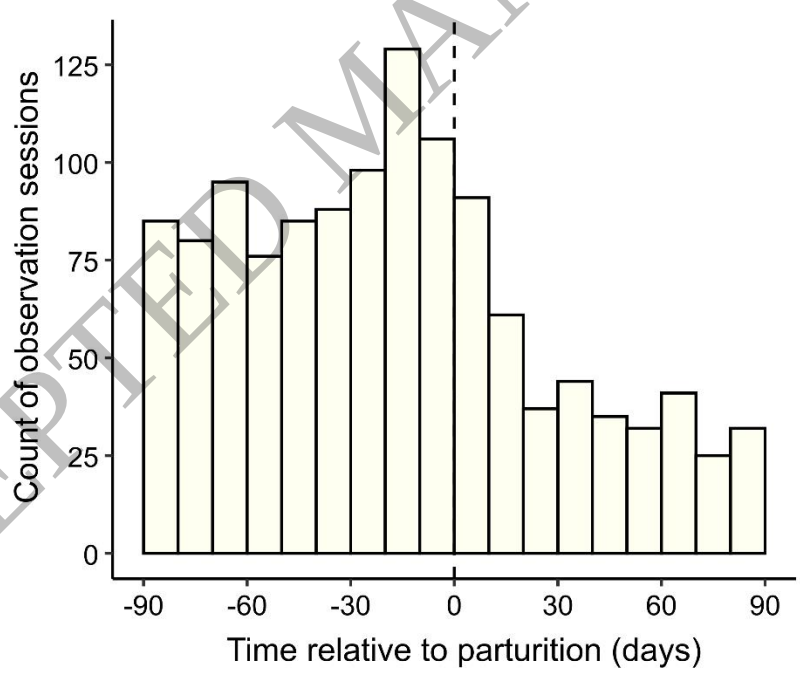
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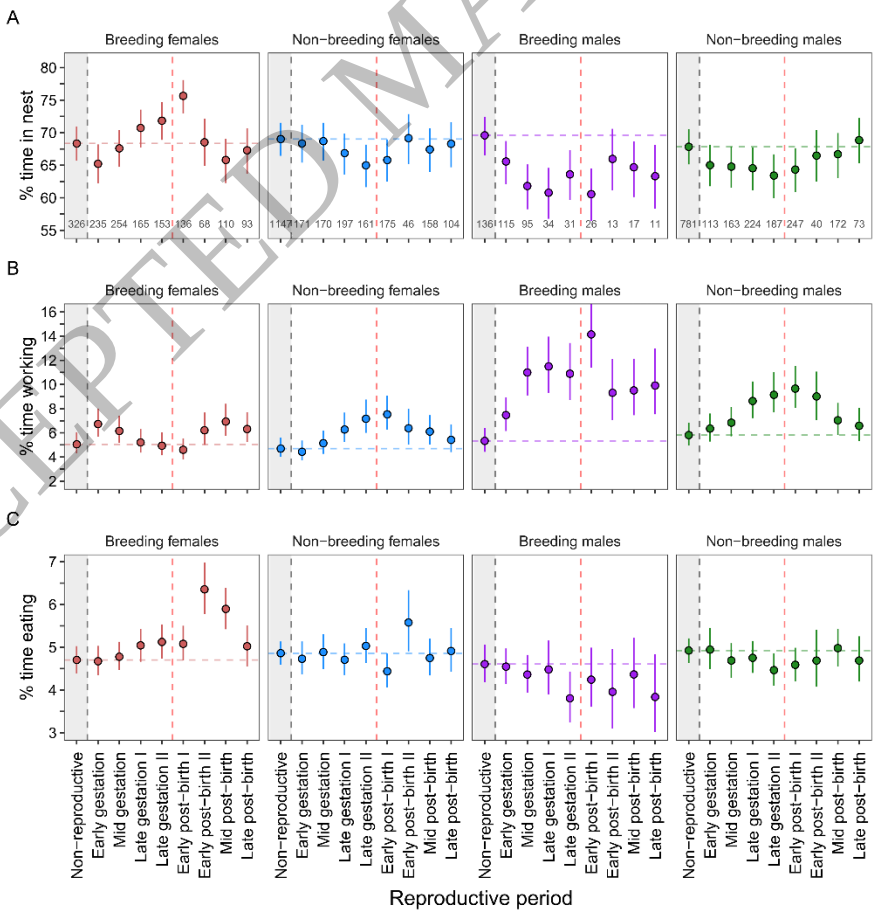
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Figure 2. Damaraland mole-rat time budgets across reproductive episodes. The percentage of time that mole-rats spent in the nest (A), working (B), and eating (C) across reproductive stages. Points show model-predicted means and 95% credible intervals for breeding and non-breeding males and females. The horizontal dashed line in each panel indicates the predicted value during non-reproductive periods. Vertical dashed lines delineate reproductive stages, separating non-reproductive periods from gestation and post-birth periods; the red dashed line indicates birth. Reproductive stages comprise early and mid-gestation, two late-gestation intervals immediately preceding birth, two early post-birth intervals immediately following birth, and subsequent mid and late post-birth periods. Predictions were generated as conditional effects for individuals of mean body mass (151 g) in groups of 11 individuals.



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