

# Differences in cooperative behaviour among Damaraland mole-rats are consequences of an age-related polyethism

Markus Zöttl<sup>1</sup>, Philippe Vullioud<sup>1</sup>, Rute Mendonça<sup>2</sup>, Miquel Torrents Tico<sup>1,3</sup>, David Gaynor<sup>2</sup>, Adam Mitchell<sup>3</sup> and Tim Clutton-Brock<sup>1,2</sup>

<sup>1</sup> *Department of Zoology, University of Cambridge, Cambridge, UK*

<sup>2</sup> *Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa*

<sup>3</sup> *Kalahari Mole-rat Project, Kuruman River Reserve, Van Zylsrus, South Africa*

Corresponding author:

Markus Zöttl: [mz338@cam.ac.uk](mailto:mz338@cam.ac.uk)

Key words: Caste, Division of labour, Cooperative breeding, Eusociality

## Abstract

In many cooperative breeders, the contributions of helpers to cooperative activities change with age resulting in age-related polyethisms. In contrast, some studies of social mole-rats (including naked mole-rats, *Heterocephalus glaber*, and Damaraland mole-rats, *Fukomys damarensis*) suggest that individual differences in cooperative behaviour are the result of divergent developmental pathways leading to discrete and permanent functional categories of helpers that resemble the caste systems found in eusocial insects. Here we show that, in Damaraland mole-rats, individual contributions to cooperative behaviour increase with age and are higher in fast growing individuals. Individual contributions to different cooperative tasks are inter-correlated and repeatability of cooperative behaviour is similar to that found in other cooperatively breeding vertebrates. Our data provide no evidence that non-reproductive individuals show divergent developmental pathways, or specialise in

particular tasks. Instead of representing a caste system, variation in the behaviour of non-reproductive individuals in Damaraland mole-rats closely resembles that found in other cooperatively breeding mammals and appears to be a consequence of age-related polyethism.

### **Significance**

Non-reproductive group members of naked and Damaraland mole-rats are thought to be organised in permanent, distinct castes that differ in behaviour and physiology, suggesting that their social organisation resembles that of obligatorily eusocial insects. This study tests predictions about the distribution of cooperative behaviour based on the suggestion that individual differences represent a caste system. Our data provide no evidence that helpers show fixed, divergent developmental pathways, or specialise in particular tasks. Instead, variation in their behaviour appears to represent an age-related polyethism. The results suggest that the behavioural organisation of social mole-rat groups is similar to that of other singular cooperatively breeding vertebrates and that similarities to obligatorily eusocial insects have been overestimated.

### **Introduction**

In cooperatively breeding vertebrates and primitively eusocial insects, subordinate group members frequently vary widely in their investment in cooperative tasks. These differences are often consequences of state-dependent changes in fitness costs and benefits, which vary with age, growth and sex (1-6), and result in age- and sex-related polyethisms where behaviour varies in relation with opportunities to breed. In cooperatively breeding meerkats (*Suricata suricatta*) for example, fast growing helpers contribute more to overall cooperative behaviour; supplementary feeding increases help; and subordinates do not specialise on certain tasks (3, 4, 7). Similar patterns are widespread among other cooperative breeders from diverse taxa (birds: (8); mammals: (9); fish: (10, 11); primitively eusocial insects: (5, 6)).

It has been suggested that naked mole-rats (*Heterocephalus glaber*) and Damaraland mole-rats (*Fukomys damarensis*) are an exception to this pattern (12-14). In these species, the main cooperative task performed by non-breeding helpers (building a large network of foraging tunnels) is primarily carried out by small individuals of both sexes (12, 14-17) and it has been argued previously that this may be the result of a caste system, similar to those found in some eusocial insect species, where specialised, smaller workers conduct most of the energetically demanding burrowing and remain in this state for their entire life, while larger workers contribute little to cooperative burrowing but specialise in other cooperative tasks including nest building, allo-parental care or colony defence (12, 14). Others have argued that it is premature to assume that naked mole-rats show a caste system since the observed differences in behaviour could be the result of age-related polyethisms as it is not clear whether variation in cooperative behaviour is age-related (18, 19). An important difference is that castes are permanent, functionally different and discrete groups of individuals that differ in behaviour, physiology, or morphology and represent highly specialised strategies whereas variation caused by age-related polyethisms remains plastic throughout development (20-22) (Michener 1974, "narrow sense caste" *sensu* Wilson 1975, Crespi and Yanega 1995).

This study investigates whether the distribution of labour in Damaraland mole-rats is the result of an age-related polyethism or whether there is evidence of the formation of castes and of permanent differences in behaviour between frequent and infrequent workers, as has been suggested in previous studies of naked mole-rats (13, 17) and Damaraland mole-rats (14). Distinguishing a system of specialised workers that are organised in castes (*sensu* Michener 1974, (21)) from an age-related polyethism requires longitudinal records of behaviour and growth of known-aged individuals. A caste system, as suggested for social mole-rats, would predict that (i) behavioural phenotypes of individuals with different growth trajectories diverge during ontogeny; (ii) the behavioural profiles of individuals are related to their asymptotic body mass rather than their age; (iii) the distribution of cooperative behaviour shows a bi- or multimodal distribution; (iv) individuals specialise permanently

in certain tasks, so that some forms of cooperative behaviour show negative correlations among individuals; and that (v) repeatability of cooperative behaviour through ontogeny is high. Alternatively, an age-related polyethism based on state-dependent costs and strategic resource allocation contingent on opportunities to breed would predict that (i) cooperative investment changes with age; (ii) asymptotic body mass is not necessarily related to cooperative behaviour; (iii) cooperative behaviour is continuously distributed; (iv) individuals do not specialise in certain activities so that there are positive correlations in their investment in different cooperative tasks; and (v) cooperative investment should be contingent on an individual's state and life-history, which frequently results in a bias towards the more philopatric sex and towards fast-growing individuals.

Our study tests these predictions about the distribution of cooperative behaviour based on the suggestion that individual differences represent a caste system or represent an age-related polyethism using behavioural data, collected under controlled laboratory conditions on 187 non-reproductive Damaraland mole-rats from 37 colonies between the ages of 60 and 600 days and 75 non-reproductive individuals from 13 colonies which were older than 600 days but whose exact age was unknown. Damaraland mole-rats resemble naked mole-rats in social organisation and both species are sometimes referred to as eusocial (13, 14, 23). Groups of Damaraland mole-rats can have up to 41 members and as in naked mole-rats reproduction is limited to the dominant breeding pair (23, 24). Damaraland mole-rats show variation in growth (25, 26) and cooperate in energetically expensive burrow excavation to locate food underground, communal nest-building, carrying food into a communal food store and by providing allo-parental care to the pups born in the group. Investment in these activities varies between and within individuals (16, 23, 27) but it is unknown how investment in cooperative behaviour of non-reproductive individuals is related to growth, age and sex.

## Results

### *Age-related and size-related changes in cooperative behaviour*

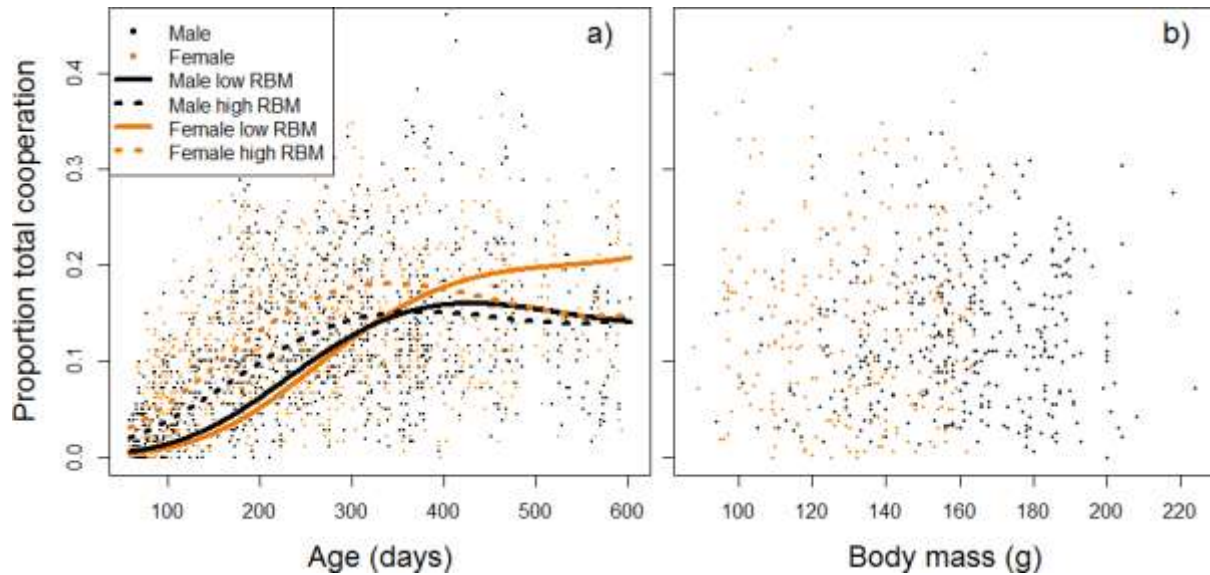
Cooperative behaviour increased with age in both sexes and differed among non-reproductive individuals depending on their residual body mass (Interaction: Sex x Residual body mass x Age; Figure 1a, Table 1a). Males and females with high residual body mass (i.e. fast growing individuals) invested more in cooperative behaviour than individuals with low residual body mass during the first year of their life, but this relationship reversed in the second year when females with low residual body mass showed higher investment in cooperative behaviour than males or females with high residual body mass (Interaction: Sex x Residual body mass x Age; Figure 1a, Table 1a). Across non-reproductive individuals older than 600 days but with unknown exact age, body mass did not predict investment in cooperative behaviour (Figure 1b, GLMM: Body mass: estimate= -0.07,  $p=0.18$ ; Sex: estimate=0.11,  $p=0.34$ ,  $N=644$  observations on  $N=75$  individuals in 13 groups). Asymptotic body mass of known-aged individuals (derived from a Gompertz growth function) was also unrelated to investment in summed cooperative behaviour after the age of 300 days (GLMM, Asymptotic body mass, estimate = 0.02,  $p=0.63$ ,  $N=122$ ) and in all age categories, frequency distribution of total cooperation across individuals showed no evidence for bi- or multimodal distribution (Figure 2 a-d; Hartigans' Dip test for unimodality / multimodality.  $p = 0.53$ ;  $p = 0.98$ ;  $p = 0.81$ ;  $p = 0.95$  for age classes 60-238 days old; 239-418; 419-600; individuals over 600 days of age, respectively).

Repeatability of cooperative behaviour was low when calculated for all individuals of known age, when restricting the analysis to individuals older than 300 days, or when restricting to individuals older than 600 days (Original scale repeatability:  $R=0.018$ ,  $R=0.009$ ,  $R=0.017$ , respectively). After accounting for the effects of age and residual body mass, the repeatability of cooperative behaviour was estimated as  $R=0.154$  including individuals of all ages, and  $R=0.166$  for individuals older than 300 days. The random factor individual identity explained 2% of the variation in the data and including it improved the fit of the model (Log-likelihood ratio test,  $p<0.001$ ). The main model for total

Table 1: Predictors of (a) total workload, (b) digging, (c) nest building and (d) food carrying in Damaraland mole-rats. Reported are coefficients (estimate), standard Errors (SE) and P-values (P) from generalised linear mixed models (GLMM) with logit link function. Bold terms were included in the final, minimal adequate model. Terms in italics were dropped from the final model during model simplification and are displayed with the estimates and probabilities when last included in the model. Sample size of all four models is 2309 observations on 187 subordinate individuals from 37 mole-rat colonies. P values of terms that were included in a higher order interaction are not displayed in the table.

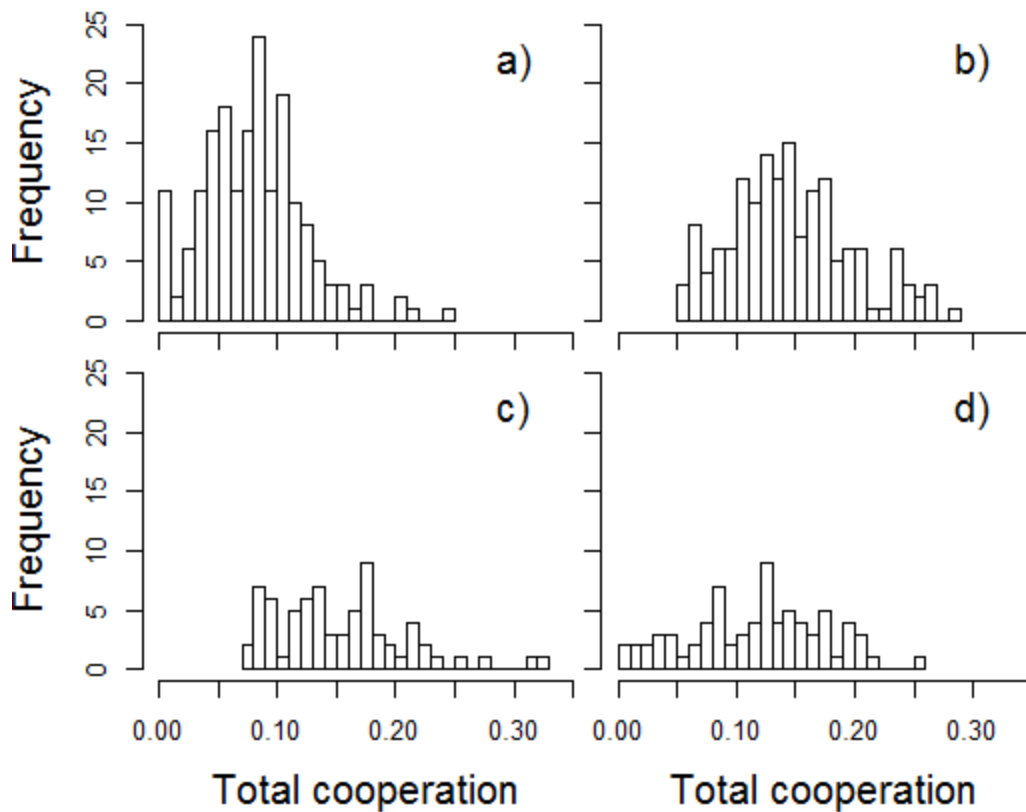
	Estimate	SE	P
a) Total cooperation			
<b>Intercept</b>	<b>-1.84</b>	<b>0.04</b>	
<b>Duration</b>	<b>-0.31</b>	<b>0.06</b>	<b>&lt;0.001</b>
<b>Age</b>	<b>0.35</b>	<b>0.03</b>	
<b>Age<sup>2</sup></b>	<b>-0.46</b>	<b>0.02</b>	
<b>Age<sup>3</sup></b>	<b>0.15</b>	<b>0.01</b>	<b>&lt;0.001</b>
<b>Sex</b>	<b>-0.09</b>	<b>0.05</b>	
<b>Residual body mass</b>	<b>0.19</b>	<b>0.03</b>	
<b>Age*Residual body mass</b>	<b>-0.20</b>	<b>0.02</b>	
<b>Age*Sex</b>	<b>-0.06</b>	<b>0.03</b>	
<b>Sex*Residual body mass</b>	<b>-0.12</b>	<b>0.04</b>	
<b>Age<sup>2</sup>*Residual body mass</b>	<b>0.06</b>	<b>0.01</b>	<b>&lt;0.001</b>
<b>Age*Sex* Residual body mass</b>	<b>0.1</b>	<b>0.03</b>	<b>&lt;0.001</b>
b) Digging			
<b>Intercept</b>	<b>-2.46</b>	<b>0.04</b>	
<b>Duration</b>	<b>-0.33</b>	<b>0.06</b>	<b>&lt;0.001</b>
<b>Age</b>	<b>0.30</b>	<b>0.03</b>	
<b>Age<sup>2</sup></b>	<b>-0.46</b>	<b>0.02</b>	
<b>Age<sup>3</sup></b>	<b>0.15</b>	<b>0.01</b>	<b>&lt;0.001</b>
<b>Sex</b>	<b>-0.07</b>	<b>0.05</b>	
<b>Residual body mass</b>	<b>0.21</b>	<b>0.04</b>	<b>&lt;0.001</b>
<b>Age*Residual body mass</b>	<b>-0.20</b>	<b>0.02</b>	
<b>Age*Sex</b>	<b>-0.05</b>	<b>0.03</b>	
<b>Sex* Residual body mass</b>	<b>-0.12</b>	<b>0.04</b>	
<b>Age<sup>2</sup>*Residual body mass</b>	<b>0.06</b>	<b>0.01</b>	<b>&lt;0.001</b>
<b>Age*Sex* Residual body mass</b>	<b>0.10</b>	<b>0.03</b>	<b>&lt;0.001</b>
c) Nest building			
<b>Intercept</b>	<b>-5.82</b>	<b>0.08</b>	
<b>Age</b>	<b>-0.17</b>	<b>0.08</b>	
<b>Age<sup>2</sup></b>	<b>-0.41</b>	<b>0.05</b>	
<b>Age<sup>3</sup></b>	<b>0.17</b>	<b>0.03</b>	<b>&lt;0.001</b>
<b>Residual body mass</b>	<b>0.04</b>	<b>0.05</b>	
<b>Age*Residual body mass</b>	<b>-0.21</b>	<b>0.05</b>	<b>&lt;0.001</b>
<b>Age<sup>2</sup>*Residual body mass</b>	<b>0.12</b>	<b>0.04</b>	<b>0.002</b>
<i>Sex</i>	<i>-0.15</i>	<i>0.08</i>	<i>0.08</i>
<i>Duration</i>	<i>0.001</i>	<i>0.15</i>	<i>0.99</i>
<i>Sex* Residual body mass</i>	<i>-0.13</i>	<i>0.9</i>	<i>0.11</i>
<i>Age*Sex</i>	<i>-0.06</i>	<i>0.8</i>	<i>0.39</i>
<i>Age*Sex* Residual body mass</i>	<i>0.16</i>	<i>0.08</i>	<i>0.06</i>
d) Food carry			
<b>Intercept</b>	<b>-4.90</b>	<b>0.06</b>	<b>&lt;0.001</b>
<b>Age</b>	<b>0.03</b>	<b>0.05</b>	<b>0.54</b>
<b>Age<sup>2</sup></b>	<b>-0.43</b>	<b>0.04</b>	<b>&lt;0.001</b>
<b>Age<sup>3</sup></b>	<b>0.18</b>	<b>0.02</b>	<b>&lt;0.001</b>
<b>Residual body mass</b>	<b>0.25</b>	<b>0.04</b>	<b>&lt;0.001</b>
<b>Duration</b>	<b>-0.30</b>	<b>0.11</b>	<b>0.006</b>

Sex	-0.02	0.09	0.75
Age*Residual body mass	-0.01	0.03	0.53
Age <sup>2</sup> *Residual body mass	-0.03	0.02	0.30
Sex* Residual body mass	-0.01	0.07	0.83
Age*Sex	0.08	0.06	0.12
Age*Sex* Residual body mass	0.08	0.06	0.14



**Figure 1:** Ontogeny of investment in total cooperative behaviour. a) Known-aged males and females exhibiting differential growth rates up to an age of 600 days. Points represent the raw data of 2309 observations of 12 (N=2078) or 24 hours (N=231) per individual. Lines indicate the prediction from the GLMM in Table 1a for fast growing individuals (Residual body mass = 0.3) or slow growing individuals (Residual body mass = -0.3). b) Individuals that were at the start of the study older than 600 days but where the exact age was unknown. N=644 observations on N=75 individuals in 13 groups. See main text for statistical results. Some data points of the raw data are hidden behind the legend or exceed the scaling of the y axes.

cooperation (Table 1a) explained 14.5% of the variation in the data (Conditional  $R^2 = 0.145$ , Marginal  $R^2 = 0.10$ )

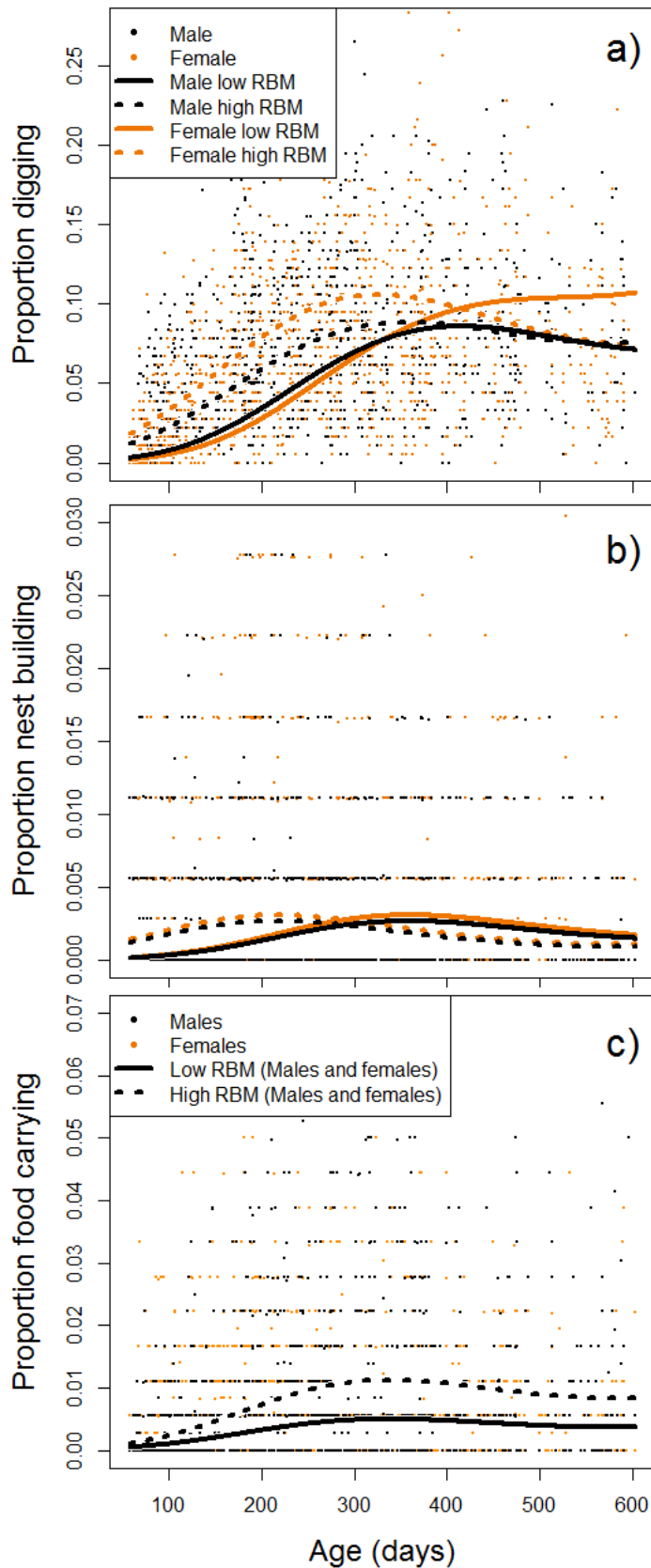


**Figure 2:** Frequency distribution of cooperative investment (mean per individual) in mole-rats of the age a) 60-239 days, b) 240-418 days, c) 419-600 days and d) older than 600 days. Sample sizes are N=182, N=154, N=71, N=75 individuals respectively.

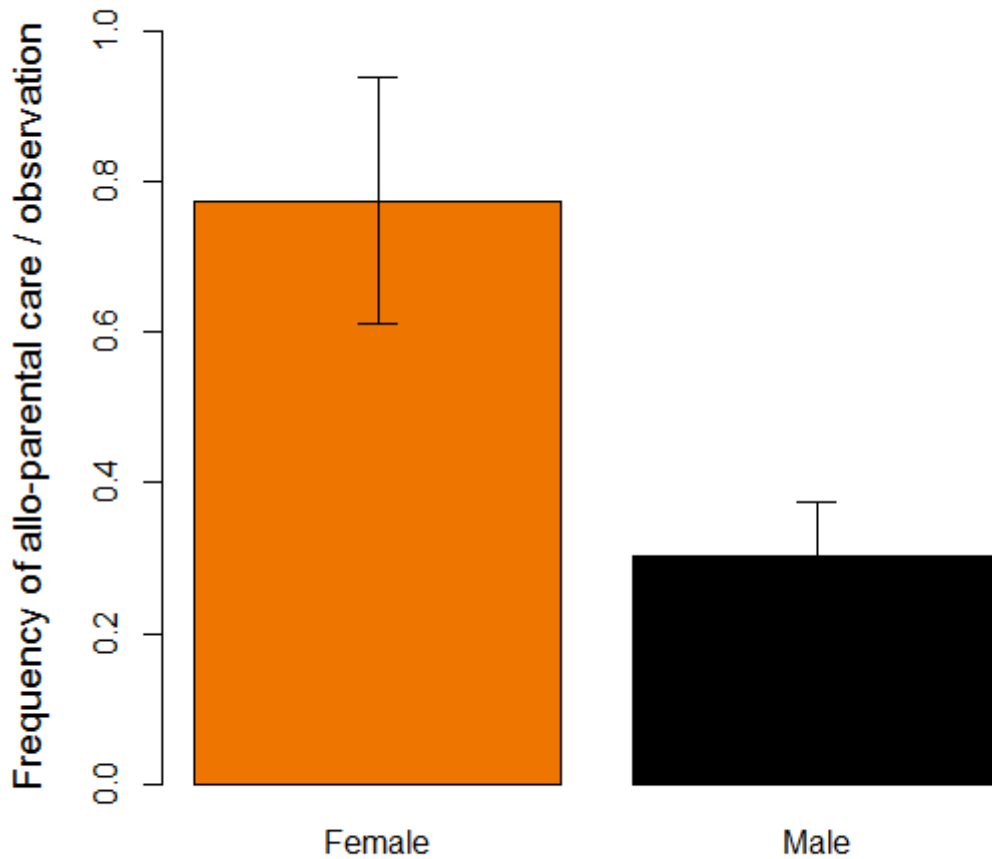
*Ontogeny of investment in digging, nest building, food carrying and allo-parental care*

Three main aspects of cooperative behaviour (digging, nest building and carrying food to a communal storage) showed similar development during ontogeny (Figure 3 a-c, Table 1 b-d). Fast growing individuals exhibited higher investment in all three behaviours early in life. Males and fast growing females reduced digging after reaching an age of 300 days (Figure 3 a, Table 1 b) and nest building activity declined in fast growing males and females sooner than in slow growing individuals (Figure 3b, Table 1c). Sex differences were small but females tended to invest more in nest building and showed higher investment in digging and total cooperation until reaching one year of age (Figure 3a, b). Investment in nest building and food carrying decreased in males and females older than one year and females tended to invest more time in nest building (Figure 3b, c, Table 1c,-d). Pairwise across individual comparisons of digging, nest building and food carrying suggested that investment in different aspects of cooperation correlated positively with each aspect (Figure S2)





**Figure 3:** Ontogeny of investment in (a) digging, (b) nest building and (c) carrying food by males and females exhibiting different growth rates. Points represent raw data of observations of 12 (N=2078) or 24 hours (N=231) per individual. Lines indicate the prediction from the GLMM in Table 1b, 1c and 1d. Some data points of the raw data are hidden behind the legend or exceed the scaling of the y axes.



**Figure 4:** Mean frequency of allo-parental care provided by females and males during 12 (198) and 24 hours (28) observations. Bars represent mean  $\pm$  SE, N=226 observations on 91 individuals. See main text for statistics.

(Digging-Food carrying, estimate=0.39,  $r^2=0.22$ ,  $p<0.001$ , N=177; Digging- Nest building, estimate=0.2,  $r^2=0.14$   $p<0.001$ , N=177; Food carrying- Nest building, estimate=0.21,  $r^2=0.01$ ,  $p=0.069$ , N=177).

Allo-parental care is rare in Damaraland mole-rats and is mainly displayed when offspring in the group are below one month of age. The mean frequency of allo-parental care shown by non-reproductive individuals was not associated with residual body mass or age but females carried pups more frequently than males (Figure 4, GLMM; Growth,  $p=0.9$ ; Age<sup>2</sup>,  $p=0.11$ ; Age,  $p=0.34$ ; Sex,

Estimate= -0.76,  $p=0.045$ ,  $N=226$  observations on  $N=91$  individuals). The frequency of allo-parental care was unrelated to any other forms of cooperative behaviour (Allo-parental care – digging,  $p=0.26$ ,  $N=86$ ; allo-parental care – food carrying,  $p=0.61$ ,  $N=86$ ; allo-parental care – nest building  $p=0.49$ ,  $N=86$ ).

## **Discussion**

Our results provide no indication that behavioural differences in cooperation in Damaraland mole-rats are a consequence of divergent developmental strategies as would be expected in the caste system suggested for social mole-rats (12-14). Investment in cooperation increased with age and was initially higher in fast growing individuals, indicated by high body mass for a given age. This effect was especially pronounced for digging behaviour, the most common and energetically expensive domain of cooperative activities in social mole-rat societies (Figure 3a), and may be caused by higher tolerance for the energetic demands of cooperation in fast growing individuals. Nest building and food carrying also showed differences in development depending on growth trajectories consistent with the prediction of state-dependent life histories (Figure 3b and c). As in many cooperatively breeding species, age was the most important predictor of an individual's contribution to cooperative tasks (Table 1a-c, (3, 8, 11)). Contributions to different cooperative activities are positively correlated across individuals, suggesting that specialisation in cooperative activities does not occur (Figure 4). These patterns resemble distribution of cooperation in other social vertebrate groups where factors that alter the energetic costs of cooperative behaviour often result in changes of investment in cooperation (3, 10, 28)

After the age of 600 days, when practically all individuals had reached asymptotic body mass, small and large non-reproductive individuals did not differ in their contributions to cooperative behaviour (Figure 1b). In addition, across individuals known to be younger than 600 days, asymptotic body mass did also not predict investment in cooperation, suggesting that there are no distinct differences in the behavioural phenotype emerging during ontogeny. Behavioural differences during

early ontogeny did not translate into the emergence of distinct behavioural castes in any age class of non-reproductive individuals and most of them reduced investment in cooperation when reaching asymptotic body mass (Figure 1 & 2). Individuals maintained plasticity in cooperative behaviour which resulted in low to moderate estimates of repeatability, that were comparable to the levels of repeatability found in other cooperatively breeding vertebrates such as meerkats (cf. Baby-sitting:  $R=0.17-0.29$ , Provisioning  $R=0.51$ ; Raised guarding:  $R=0.16$ ; (29, 30)) and sociable weavers ( $R=0.11-0.30$ ; (31)).

Sex differences in investment in cooperative behaviour were small, and when present, were biased towards females which, as in other social mole-rats, are the more philopatric sex (Figures 1, 3 and 4, (23, 32, 33)). Early in ontogeny, fast growing females contributed most to cooperative behaviour but this pattern changed later in life with slow growing females showing more cooperative behaviour (Figure 1a). Since males disperse before breeding, they are less likely to benefit from mutual, delayed benefits of cooperation (i.e. group augmentation effects, (34)), which may explain the differences in cooperative behaviour found during the first 600 days of life. Both a sex bias of cooperative behaviour towards the philopatric sex and strategic adjustment of investment in cooperation depending on likely life-history trajectories, is wide-spread among subordinates in cooperative breeders and primitively eusocial insects which typically pass through the same stages of development while maintaining behavioural plasticity to adjust to changes in opportunities to breed (5, 8, 30, 35). Hence, in this aspect too Damaraland mole-rats resemble other cooperatively breeding vertebrate species rather than obligatory eusocial insects.

Our results are not consistent with key predictions for the distribution of cooperative behaviour based on a caste system among non-reproductive individuals in Damaraland mole-rats, when applying Michener's original definition of castes as permanent, functionally different groups of individuals that differ in behaviour, physiology, or morphology where the differences are not mere consequences of age (20-22)(Michener 1974, "narrow sense caste" sensu Wilson 1975, Crespi and

Yanega 1995). Some definitions of castes include both age-related polyethisms and true castes *sensu* Michener (e.g. "broad sense caste", Wilson 1975 (22)), but when asking questions related to social complexity, behavioural specialisation and the evolution of cooperative breeding it is useful to treat them as mutually exclusive forms of social organisation and apply the original definition of Michener (1974) (21) as we do here.

Previous behavioural studies in Damaraland mole-rats found patterns that were regarded as consistent with caste formation among non-reproductive individuals in some groups. However, they were not able to determine whether variation in the behaviour of individuals was the result of a caste system or was a product of age-related changes in cooperative behaviour since the ages of many individuals were unknown (14-16, 27). Our data support the suggestion that the social organisation of Damaraland mole-rats resembles that of other cooperative breeding vertebrates rather than that of obligatorily eusocial insect societies where true castes with fixed developmental trajectories occur in several lineages, including termites, ants, aphids and thrips (36, 37).

Our study raises the question whether naked and Damaraland mole-rats differ in their behavioural organisation or whether the scarcity of longitudinal data of known-aged individuals in studies of naked mole-rats has encouraged observers to attribute contrasts in behaviour to the formation of castes. Sociality has evolved independently in Damaraland and naked mole-rats and the similarity of their breeding systems is regarded as a striking example for convergent evolution (38-40) so it is possible that differences in behavioural organisation of the species might exist between these two species. However, the results of some studies do not support the suggestion that castes exist in naked mole rats. In some colonies, body weight and work load were negatively correlated and smaller individuals performed more maintenance and foraging behaviour (12, 17). Others found the opposite pattern (18, 19) and a recent study showed that, contrary to a caste system, naked mole-rats maintain behavioural plasticity throughout development (41), which is consistent with the patterns found in Damaraland mole-rats in this study.

## Methods

### *Study animals and husbandry*

The animals used in this study were either wild caught Damaraland mole-rats or their offspring, who had been produced and raised under captive conditions. Animals were captured around the Kuruman River Reserve in the Northern Cape South Africa between February and September 2013. The mole-rats were either maintained in their original group (i.e. the group in which they were captured) or new groups were established by pairing one male and one female that originated from different groups. All individuals were dye-marked to allow individual recognition and carried a passive implantable transponder for identification. This paper includes data from a total of 37 groups comprising 13 wild caught groups and 24 laboratory-founded groups ranging in size from 3 to 26 individuals. All groups were housed in PVC tunnel systems that included compartments for nesting and food storage, toilet areas and one large box. The upper halves of the tubes had a transparent PET window enabling close behavioural observation. All tunnel systems included one to three vertical pipes in the periphery of the tunnels that led sand into the tunnel system. Depending on group size, the length of tunnel systems varied between 4 and 16 meters (see SI Figure 1). Twice a day the mole-rats were fed *ad libitum* with sweet potatoes and cucumbers and the vertical pipes were refilled with clean sand. Once a day the pipes were cleaned and confined toilet areas were rinsed with hot water. Occasionally apples, squash and potatoes were offered to enrich the diet.

### *Data collection and data management*

Data were collected between October 2013 and November 2015. All individuals were weighed weekly until they reached the age of 90 days and thereafter every two weeks using a Sartorius TE4100 electronic scale. Behavioural observations were conducted following a scan and all-occurrence sampling protocol (42) on a handheld Android device operating the software Pocket Observer (Noldus, Wageningen). During the scan sampling we recorded the behaviour of each individual based on an ethogram of 17 behaviours for observation sessions with the duration of 12

or 24 hours, applying a 4 min sampling interval. Typically 1-2 observers observed 10-20 individuals simultaneously. We obtained a mean observation frequency of 12.2 scan observation sessions per individual over the study period (range 1-35). To maintain the possibility of expressing foraging behaviour during scan observations (i.e. clearing sand from the tunnel system to maintain access to common food sources), we added sand through the vertical pipes every 2 hours. Several observers were involved in carrying out scan observations and usually a single observer would cover a period of 2-3 hours. We excluded individuals that died before reaching the age of 90 days.

We derived four measures of cooperation (total cooperation, digging, food carrying, nest building) from scan observation sessions and extracted proportional investment (how often the behaviour was displayed out of the total number of scans in this session) for each individual. Total cooperation was calculated as the sum of all behaviours that were related broadly to any form of burrow maintenance, foraging, nest building or allo-parental care such as digging in sand, gnawing on tunnel walls, pushing sand into tunnel gaps or dead ends, sweeping sand with the hind legs, moving back to the digging place after having transported sand and transporting food, nest material or pups ((15) for a detailed ethogram). In order to evaluate whether non-reproductive individuals specialise on certain tasks we also derived separate measures of digging (sum of digging in sand, pushing sand into tunnel gaps or dead ends and sweeping sand with the hind legs), nest building and food carrying.

Allo-parental care (i.e. when an individual retrieved a pup to the nest) is a rare form of cooperative behaviour in mole-rats and can only be displayed when pups are young. Thus, we recorded all-occurrences of allo-parental care simultaneously to scan observations and used observation sessions for analysis when allo-parental care was observed in this session, which resulted in a data set of 226 observations on 91 individuals originating from 58 observation sessions. Of these observations, 198 were 12 hour observations and 28 were 24 hour observations but the frequency of allo-parental care recorded per observation did not differ depending on the duration of the observation (GLM,

Duration:  $P=0.13$ ). Including the observation duration in the final model or reducing the data-set to observations of 12 hours did not change the results qualitatively and hence we analysed a pooled sample of 12 and 24 h scan sessions.

### *Statistical analysis*

To analyse how total cooperative behaviour, digging, nest building and food carrying relates to age, residual body mass and sex we fitted generalised linear mixed models assuming binomial error structure (GLMMs, logit link function) with the proportion of intervals scored with the respective behaviour during a scan session as the response variable. We started with fitting the full model including age,  $\text{age}^2$  and  $\text{age}^3$  and residual body mass (as index of growth, see SI for details) as covariates and sex and the duration of the observation as a fixed factors. Additionally, we included four 2-way interactions (Age\*Residual body mass, Age\*Sex, Sex\*Residual body mass,  $\text{Age}^2$ \*Residual body mass) and the 3-way interaction (Age\* Residual body mass \*Sex) to allow the predicted response to differ between sexes and individuals of different residual body mass at different stages of development. All covariates were centred by subtracting the mean from each value and thereafter scaled by dividing the values by the standard deviation. Furthermore, we included the identity of the individual, the scan observation session reference (per mole-rat group) and an observation level count to prevent overdispersion as random factors in all mixed modes models presented in this paper (43). We then employed a stepwise, backwards model simplification procedure (44) until only significant terms remained in the final model. Terms that were dropped in the course of model selection are presented in this paper with the estimates, standard errors and the p-values with which they were last included in the model selection process. Repeatability was calculated following procedures outlined in Nakagawa & Schielzeth (45) using the R package rptR (46). To control for the effect of age, residual body mass and sex we additionally calculated a repeatability estimate using the residuals of a model including these factors. Significance of the random effect individual identity was tested using a log likelihood ratio test and pseudo  $r^2$  was



calculated following Nakagawa and Schielzeth (47) using the package MuMIn (48). All models presented were estimated using the software R version 3.2.4 (49) and the packages lme4 (50).

Allo-parental brood care was analysed by fitting a GLMM assuming Poisson error structure and log link function with the frequency of allo-parental brood care as the response variable and adding age, age<sup>2</sup>, growth and sex as explanatory variables. Because the data set was much smaller we did not attempt to fit an age<sup>3</sup> and we did not include any of the two-way interactions. Again we employed a stepwise, backwards model simplification procedure until only significant terms remained in the final model.

To evaluate whether asymptotic body mass is associated with investment in total cooperation (i.e. sum of all cooperative behaviours) we used a generic Gompertz growth function of the package nlme (51). We fitted a growth curve for each individual and extracted the predicted asymptotic body mass. In 15 out of 151 cases the prediction was higher than the maximum weight of mole-rats in our laboratory population (i.e. ~240 gramm) and these cases were excluded for this analysis. We subsequently fitted a GLMM with binomial error structure with total cooperative investment as the response and the asymptotic body mass as a covariate. Here, we included only scan observation sessions on individuals older than 300 days (N=122) as this is the age where the first individuals of our population reach asymptotic body mass. We included the same random error structure as in previous analysis in this model.

To address the question whether mole-rats specialise in certain tasks we calculated the mean frequency of the respective cooperative task (digging, nest building and food carrying) per individual (N=177) and for a subset of individuals (N=86) for allo-parental care. The values were log-transformed and pairwise correlations were analysed using linear models.

## **Ethical note**

The laboratory facility at the Kuruman River Reserve is approved by the NSPCA South Africa and all studies are subject to approval by the ethics committee of the University of Pretoria (Permits EC-089-12, EC-009-13 and SOP-004-13).

## **Acknowledgements**

We thank Nigel Bennett for helpful discussions, advice and insightful comments on an earlier draft of this manuscript. We thank Jack Thorley, Katy Goddard, Kyle Finn, Sally Bornbusch, Sean McGregor, Laura Higgs, Rita Leal, Rachel Kwok, Romain Fuerst, Francesco Santi, Natasha Waite, Holly English, Nathan Katlein and Candice Baan for help with the data collection and Nikki Raihani for helpful discussions and advice. The comments of Dominic Cram, Alecia Carter and Petter Tibblin have improved the manuscript substantially. Tim Vink and Ian Stevenson provided invaluable assistance with data management and logistic support, and Christina Kooper, Ijon Kooper, JP Netshanger, Steven Koper, Dawid Van Wyk were a great help in taking care of our study animals. We thank the Kalahari Research Trust for access to the research facilities and Marta Manser and the University of Zurich for their contribution to maintaining the Kalahari Research Centre. This study was funded by an European Research Council grant to THCB (294494).

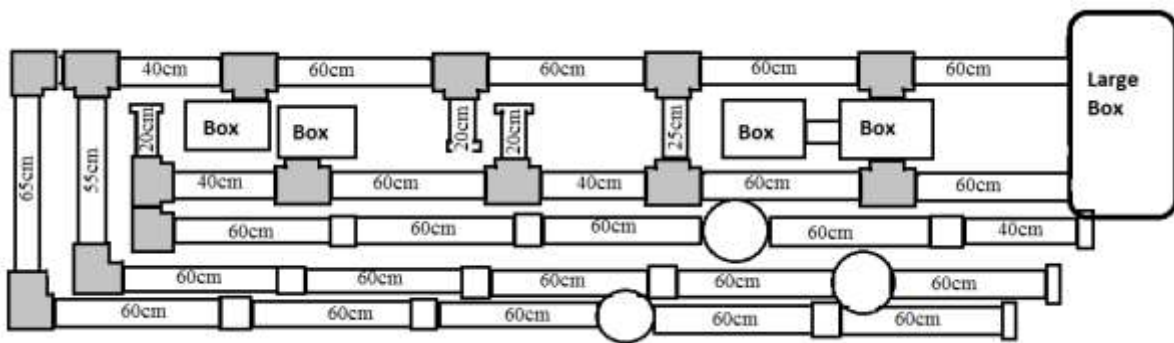
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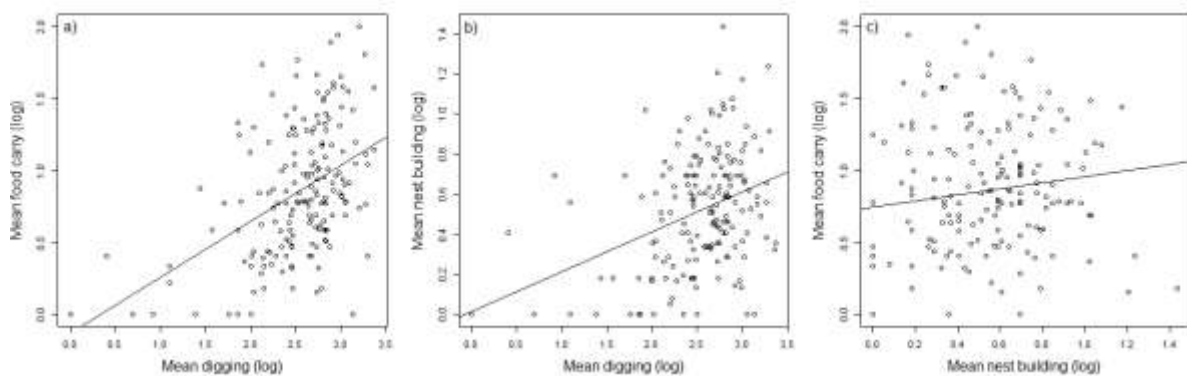
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## Supplementary information



Supplementary Information Figure 1: One example of the tunnel system cages used during the study.



Supplementary Information Figure 2: Pairwise comparisons between investment in a) digging and food carrying, b) digging and nest building and c) nest building and food carrying. Plotted are the natural logarithms of the mean frequency of different cooperative tasks over the duration of this study per individual (N=177). See main text for statistics.

### *Residual body mass*

As an index of growth we used residual body mass from linear models including age and age<sup>2</sup> as explanatory variables. Mean residual body mass during the fast growth period in early ontogeny (between 90 days and 300) explains 72% of the variation found in mean residual body mass after the age of 450 days when most individuals reached asymptotic body mass and ceased weight gain (linear model, N=80 individuals, Estimate=1.1±0.07, r<sup>2</sup>=0.72, P<0.001). This suggests that high residual body mass at any point in life is tightly linked to fast growth trajectories and high asymptotic body mass late in life. Additionally, individuals which show high residual body mass at a given point in life have shown faster mean weight gain over their life previous to this measurement compared to individuals with low residual body mass, which links residuals body mass tightly to growth trajectories. Because

males grow faster than females and we were primarily interested in relative variation of growth within males and within females we used separate models for each sex to derive a relative measure of growth. For statistical analysis we used the closest measurement of residual body mass to the behavioural observation and averaged measures with equal distance to the observation.