

Classification: **Biological Sciences - Evolution**

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

Authors

Markus Zöttl¹, Philippe Vullioud¹, Rute Mendonça², Miquel Torrents Ticó^{1,3}, David Gaynor², Adam Mitchell³ and Tim Clutton-Brock^{1,2}

¹ *Department of Zoology, University of Cambridge, Cambridge, UK*

² *Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa*

³ *Kalahari Mole-rat Project, Kuruman River Reserve, Van Zylsrus, South Africa*

Corresponding author:

Markus Zöttl: mz338@cam.ac.uk

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

20 **Abstract**

21 In many cooperative breeders, the contributions of helpers to cooperative activities change with age
22 resulting in age-related polyethisms. In contrast, some studies of social mole-rats (including naked
23 mole-rats, *Heterocephalus glaber*, and Damaraland mole-rats, *Fukomys damarensis*) suggest that
24 individual differences in cooperative behaviour are the result of divergent developmental pathways
25 leading to discrete and permanent functional categories of helpers that resemble the caste systems
26 found in eusocial insects. Here we show that, in Damaraland mole-rats, individual contributions to
27 cooperative behaviour increase with age and are higher in fast growing individuals. Individual
28 contributions to different cooperative tasks are inter-correlated and repeatability of cooperative
29 behaviour is similar to that found in other cooperatively breeding vertebrates. Our data provide no
30 evidence that non-reproductive individuals show divergent developmental pathways, or specialise in
31 particular tasks. Instead of representing a caste system, variation in the behaviour of non-
32 reproductive individuals in Damaraland mole-rats closely resembles that found in other
33 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.

46 /body

47 Introduction

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

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

107 Results

108 Age-related and size-related changes in cooperative behaviour

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

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

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

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 4 a-c; 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 5, GLMM; Growth, $p=0.9$; Age², $p=0.11$; 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

181 repeatability found in other cooperatively breeding vertebrates such as meerkats (cf. Baby-sitting:
182 $R=0.17-0.29$, Provisioning $R=0.51$; Raised guarding: $R=0.16$; (29, 30)) and sociable weavers ($R=0.11-$
183 0.30 ; (31)).

184 Sex differences in investment in cooperative behaviour were small, and when present, were biased
185 towards females which, as in other social mole-rats, are the more philopatric sex (Figures 1, 3 and 4,
186 (23, 32, 33)). Early in ontogeny, fast growing females contributed most to cooperative behaviour but
187 this pattern changed later in life with slow growing females showing more cooperative behaviour
188 (Figure 1a). Since males disperse before breeding, they are less likely to benefit from mutual,
189 delayed benefits of cooperation (i.e. group augmentation effects, (34)), which may explain the
190 differences in cooperative behaviour found during the first 600 days of life. Both a sex bias of
191 cooperative behaviour towards the philopatric sex and strategic adjustment of investment in
192 cooperation depending on likely life-history trajectories, is wide-spread among subordinates in
193 cooperative breeders and primitively eusocial insects which typically pass through the same stages
194 of development while maintaining behavioural plasticity to adjust to changes in opportunities to
195 breed (5, 8, 30, 35). Hence, in this aspect too Damaraland mole-rats resemble other cooperatively
196 breeding vertebrate species rather than obligatory eusocial insects.

197 Our results are not consistent with key predictions for the distribution of cooperative behaviour
198 based on a caste system among non-reproductive individuals in Damaraland mole-rats, when
199 applying Michener's original definition of castes as permanent, functionally different groups of
200 individuals that differ in behaviour, physiology, or morphology where the differences are not mere
201 consequences of age (20-22)(Michener 1974, "narrow sense caste" sensu Wilson 1975, Crespi and
202 Yanega 1995). Some definitions of castes include both age-related polyethisms and true castes *sensu*
203 Michener (e.g. "broad sense caste", Wilson 1975 (22)), but when asking questions related to social
204 complexity, behavioural specialisation and the evolution of cooperative breeding it is useful to treat

205 them as mutually exclusive forms of social organisation and apply the original definition of Michener
206 (1974) (21) as we do here.

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

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

227

228 Methods

229 Study animals and husbandry

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

246 Data collection and data management

247 Data were collected between October 2013 and November 2015. All individuals were weighed
248 weekly until they reached the age of 90 days and thereafter every two weeks using a Sartorius
249 TE4100 electronic scale. Behavioural observations were conducted following a scan and all-
250 occurrence sampling protocol (42) on a handheld Android device operating the software Pocket
251 Observer (Noldus, Wageningen). During the scan sampling we recorded the behaviour of each
252 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, age² and age³ 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, Age²*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, age², growth and sex as explanatory variables. Because the data set was much smaller we did not attempt to fit an age³ 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

326 The laboratory facility at the Kuruman River Reserve is approved by the NSPCA South Africa and all
327 studies are subject to approval by the ethics committee of the University of Pretoria (Permits EC-
328 089-12, EC-009-13 and SOP-004-13).

329

330 Acknowledgements

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

342

- 344 1. McNamara JM & Houston AI (1996) State-dependent life histories. *Nature* 380(6571):215-
345 221.
- 346 2. Heinsohn R & Legge S (1999) The costs of helping. *Trends Ecol Evo* 14:53-57.
- 347 3. Clutton-Brock TH, Russell AF, & Sharpe LL (2003) Meerkat helpers do not specialize in
348 particular activities. *Anim Behav* 66:531-540.
- 349 4. Clutton-Brock TH, *et al.* (2000) Individual contributions to babysitting in a cooperative
350 mongoose, *Suricata suricatta*. *Proc R Soc Lond B* 267(1440):301-305.
- 351 5. Field J, Cronin A, & Bridge C (2006) Future fitness and helping in social queues. *Nature*
352 441(7090):214-217.
- 353 6. Cant MA & Field J (2001) Helping effort and future fitness in cooperative animal societies.
354 *Proc R Soc Lond B* 268(1479):1959-1964.
- 355 7. Russell AF, Sharpe LL, Brotherton PNM, & Clutton-Brock TH (2003) Cost minimization by
356 helpers in cooperative vertebrates. *Proc Natl Acad Sci USA* 100(6):3333-3338.
- 357 8. Cockburn A (1998) Evolution of helping behavior in cooperatively breeding birds. *Ann Rev*
358 *Ecol Systemat* 29:141-177.
- 359 9. Solomon NG & French JA (1997) *Cooperative breeding in mammals* (Cambridge Univ. Press,
360 Cambridge).
- 361 10. Buintjes R, Hekman R, & Taborsky M (2010) Experimental global food reduction raises
362 resource acquisition costs of brood care helpers and reduces their helping effort. *Funct Ecol*
363 24(5):1054-1063.
- 364 11. Buintjes R & Taborsky M (2011) Size-dependent task specialization in a cooperative cichlid
365 in response to experimental variation of demand. *Anim Behav* 81(2):387-394.
- 366 12. Jarvis JU (1981) Eusociality in a mammal: Cooperative breeding in naked mole-rat colonies.
367 *Science* 212(4494):571-573.
- 368 13. Jarvis JUM, Oriain MJ, Bennett NC, & Sherman PW (1994) Mammalian Eusociality - A Family
369 Affair. *Trends Ecol Evol* 9(2):47-51.
- 370 14. Scantlebury M, Speakman J, Oosthuizen M, Roper T, & Bennett N (2006) Energetics reveals
371 physiologically distinct castes in a eusocial mammal. *Nature* 440(7085):795-797.
- 372 15. Bennett NC & Jarvis JU (1988) The social structure and reproductive biology of colonies of
373 the mole-rat, *Cryptomys damarensis* (Rodentia, Bathyergidae). *J Mammal*:293-302.
- 374 16. Bennett N (1990) Behaviour and social organization in a colony of the Damaraland mole-rat
375 *Cryptomys damarensis*. *J Zool Lond* 220(2):225-247.
- 376 17. Jarvis JUM (1991) Reproduction of Naked Mole-Rats. *The biology of the naked mole-rat*, eds
377 Sherman PW, Jarvis JUM, & Alexander RD (Princ. Univ. Press, Princeton, N.J.), pp 358-425.
- 378 18. Lacey EA & Sherman PW (1991) Social organization of Naked Mole-Rat colonies: evidence for
379 divisions of labor. *The Biology of the Naked Mole-Rat*, eds Sherman PW, Jarvis JUM, &
380 Alexander RD (Princeton Univ. Press, Princeton N. J.), pp 275-336.
- 381 19. Lacey EA & Sherman PW (1997) Cooperative breeding in naked mole-rats. *Cooperative*
382 *Breeding in Mammals*, eds Solomon NG & French JA (Cambridge University Press,
383 Cambridge), pp 267-301.
- 384 20. Crespi BJ & Yanega D (1995) The definition of eusociality. *Behav Ecol* 6(1):109-115.
- 385 21. Michener CD (1974) The social behavior of the bees: a comparative study. *The social*
386 *behavior of the bees: a comparative study*, (Harvard University Press, Cambridge,
387 Massachusetts), p 371.
- 388 22. Wilson EO (1975) *Sociobiology* (Belknap Press, Cambridge, Mass.).
- 389 23. Bennett NC & Faulkes CG (2000) *African mole-rats: ecology and eusociality* (Cambridge
390 University Press).
- 391 24. Young AJ & Bennett NC (2013) Intra-sexual selection in cooperative mammals and birds: why
392 are females not bigger and better armed? *Phil Trans R Soc* 368(1631):20130075.

- 393 25. Bennett N & Navarro R (1997) Differential growth patterns between successive litters of the
394 eusocial Damaraland mole-rat, *Cryptomys damarensis*, from Namibia. *J Zool Lond*
395 241(3):465-473.
- 396 26. Young AJ, Jarvis JU, Barnaville J, & Bennett NC (2015) Workforce Effects and the Evolution of
397 Complex Sociality in Wild Damaraland Mole Rats. *Am Nat* 186(2):302-311.
- 398 27. Gaylard A, Harrison Y, & Bennett NC (1998) Temporal changes in the social structure of a
399 captive colony of the Damaraland mole-rat, *Cryptomys damarensis*: the relationship of sex
400 and age to dominance and burrow-maintenance activity. *J Zool Lond* 244:313-321.
- 401 28. Clutton-Brock TH, *et al.* (1999) Selfish sentinels in cooperative mammals. *Science*
402 284(5420):1640-1644.
- 403 29. English S, Nakagawa S, & Clutton-Brock T (2010) Consistent individual differences in
404 cooperative behaviour in meerkats (*Suricata suricatta*). *J Evol Biol* 23(8):1597-1604.
- 405 30. Carter AJ, English S, & Clutton-Brock TH (2014) Cooperative personalities and social niche
406 specialization in female meerkats. *J Evol Biol* 27(5):815-825.
- 407 31. Leighton GM & Vander Meiden L (2016) Sociable Weavers Increase Cooperative Nest
408 Construction after Suffering Aggression. *PloS one* 11(3):e0150953.
- 409 32. O'Riain MJ, Jarvis JUM, & Faulkes CG (1996) A dispersive morph in the naked mole-rat.
410 *Nature* 380(6575):619-621.
- 411 33. Hazell R, Bennett N, Jarvis J, & Griffin M (2000) Adult dispersal in the co-operatively breeding
412 Damaraland mole-rat (*Cryptomys damarensis*): a case study from the Waterberg region of
413 Namibia. *J Zool Lond* 252(01):19-25.
- 414 34. Kingma SA, Santema P, Taborisky M, & Komdeur J (2014) Group augmentation and the
415 evolution of cooperation. *Trends Ecol Evol* 29(8):476-484.
- 416 35. Zöttl M, Chapuis L, Freiburghaus M, & Taborisky M (2013) Strategic reduction of help before
417 dispersal in a cooperative breeder. *Biol Lett* 9(1).
- 418 36. Choe JC & Bernard J. Crespi e (1997) *The Evolution of Social Behaviour in Insects and*
419 *Arachnids* (Cambridge University Press).
- 420 37. Bourke A (2011) *Principles of Social Evolution* (Oxford University Press, Oxford).
- 421 38. Faulkes CG & Bennett NC (2016) Damaraland and naked mole-rats: Convergence of social
422 evolution. *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior*.
423 (Cambridge Univ. Press, Cambridge) pp 338.
- 424 39. Faulkes CG, *et al.* (1997) Ecological constraints drive social evolution in the African mole-
425 rats. *Proceedings of the Royal Society of London B: Biological Sciences* 264(1388):1619-1627.
- 426 40. Jarvis J & Bennett N (1993) Eusociality has evolved independently in two genera of
427 bathyergid mole-rats—but occurs in no other subterranean mammal. *Behav Ecol Sociobiol*
428 33(4):253-260.
- 429 41. Mooney SJ, Filice DC, Douglas NR, & Holmes MM (2015) Task specialization and task
430 switching in eusocial mammals. *Anim Behav* 109:227-233.
- 431 42. Altmann J (1974) Observational Study of Behavior: Sampling Methods. *Behav* 49:227-265.
- 432 43. Harrison XA (2014) Using observation-level random effects to model overdispersion in count
433 data in ecology and evolution. *PeerJ* 2:e616.
- 434 44. Crawley M (2007) *The R book* (Wiley Publishing).
- 435 45. Nakagawa S & Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a
436 practical guide for biologists. *Biol Rev* 85(4):935-956.
- 437 46. Schielzeth H & Nakagawa S (2010) rptR: Repeatability estimation for Gaussian and non-
438 Gaussian data), R package version 0.6.405/r52.
- 439 47. Nakagawa S & Schielzeth H (2013) A general and simple method for obtaining R² from
440 generalized linear mixed-effects models. *Methods Ecol Evol* 4(2):133-142.
- 441 48. Barton K (2016) MuMIn: Multi-Model Inference.), R package version 1.15.6.
- 442 49. R Core Development Team (2011) R: A language and environment for statistical computing.
443 R Foundation for Statistical Computing. (Vienna, Austria.).

50. Bates D, Maechler M, & Bollinger B (2011) lme4: Linear mixed-effects models using Eigen and
classes.), R package version 0.999375-42.
51. Pinheiro J, D. B, DebRoy S, D S, & Team RDC (2012) nlme: Linear and Nonlinear Mixed Effects
Models. R package version 3.1-104.).

Figure Legends

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.

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.

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.

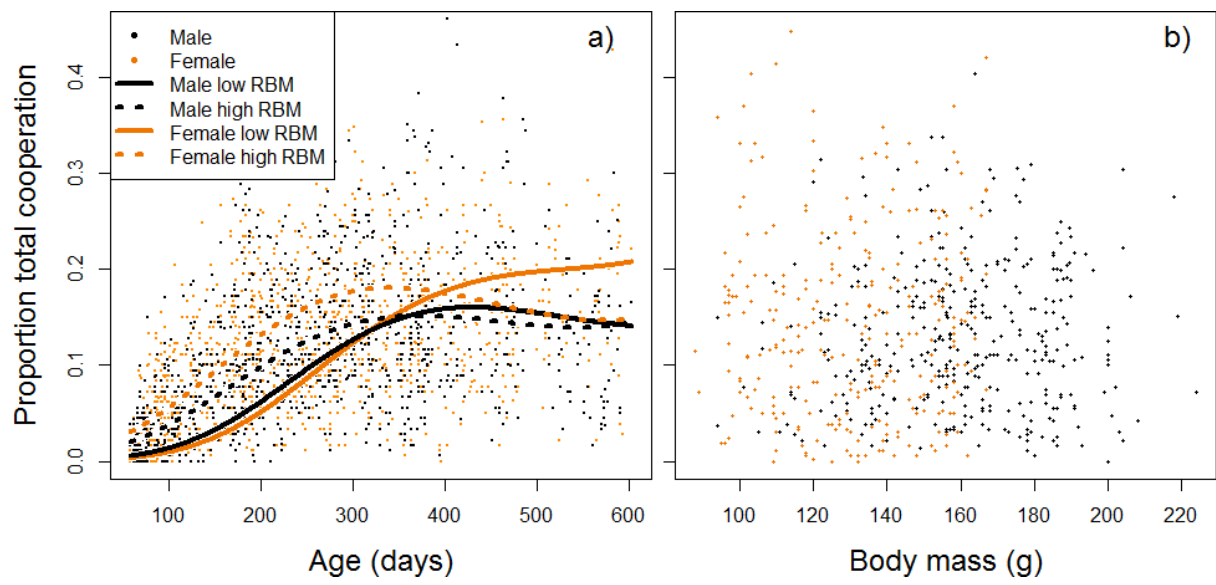
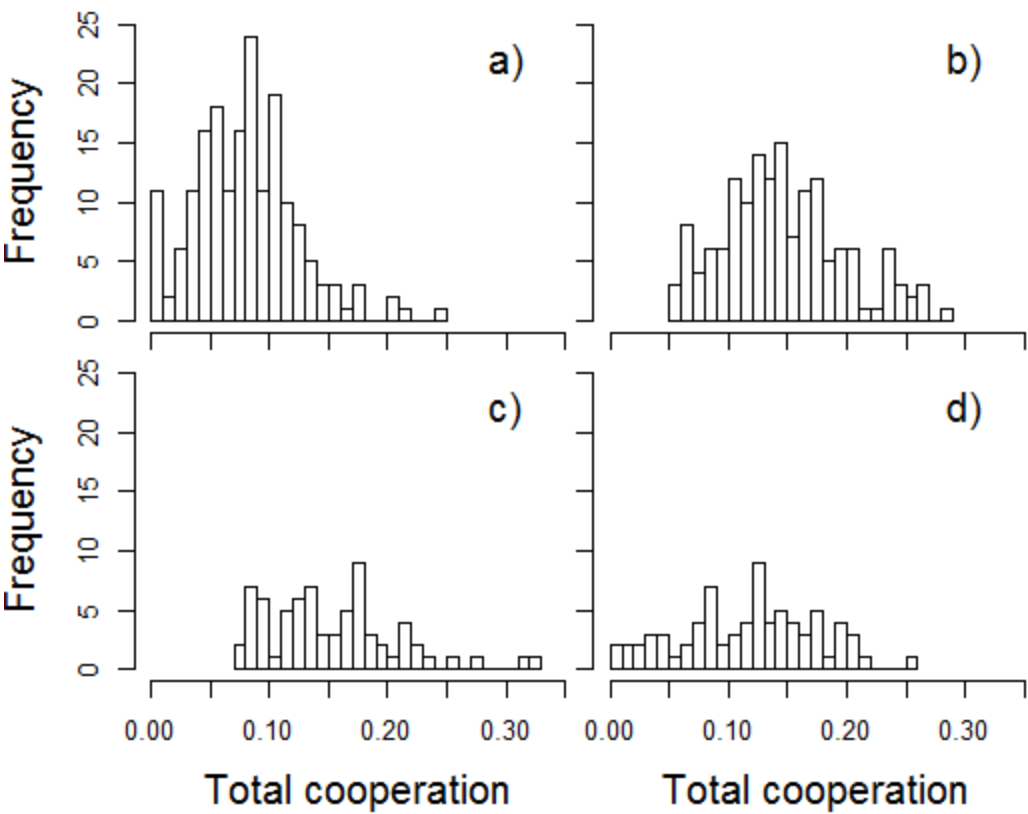


Figure 1



475 [Figure 2](#)

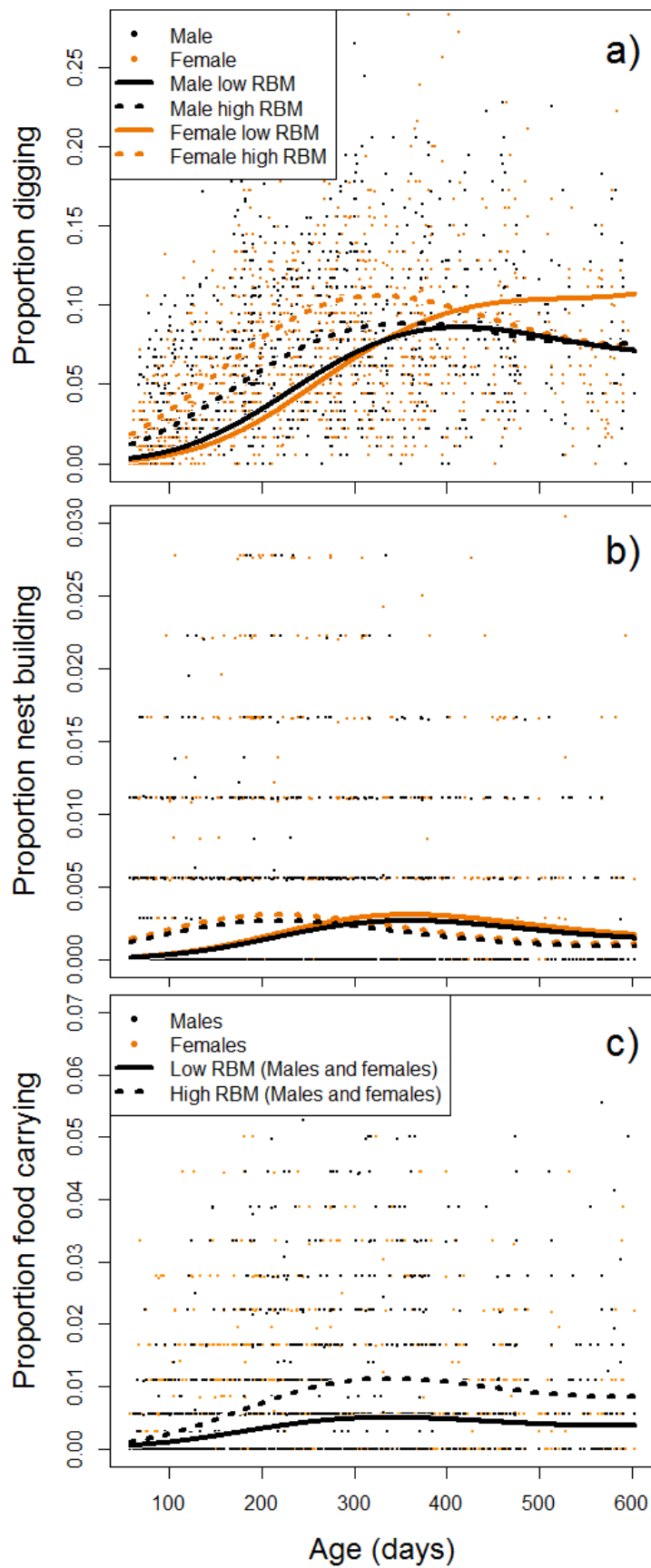
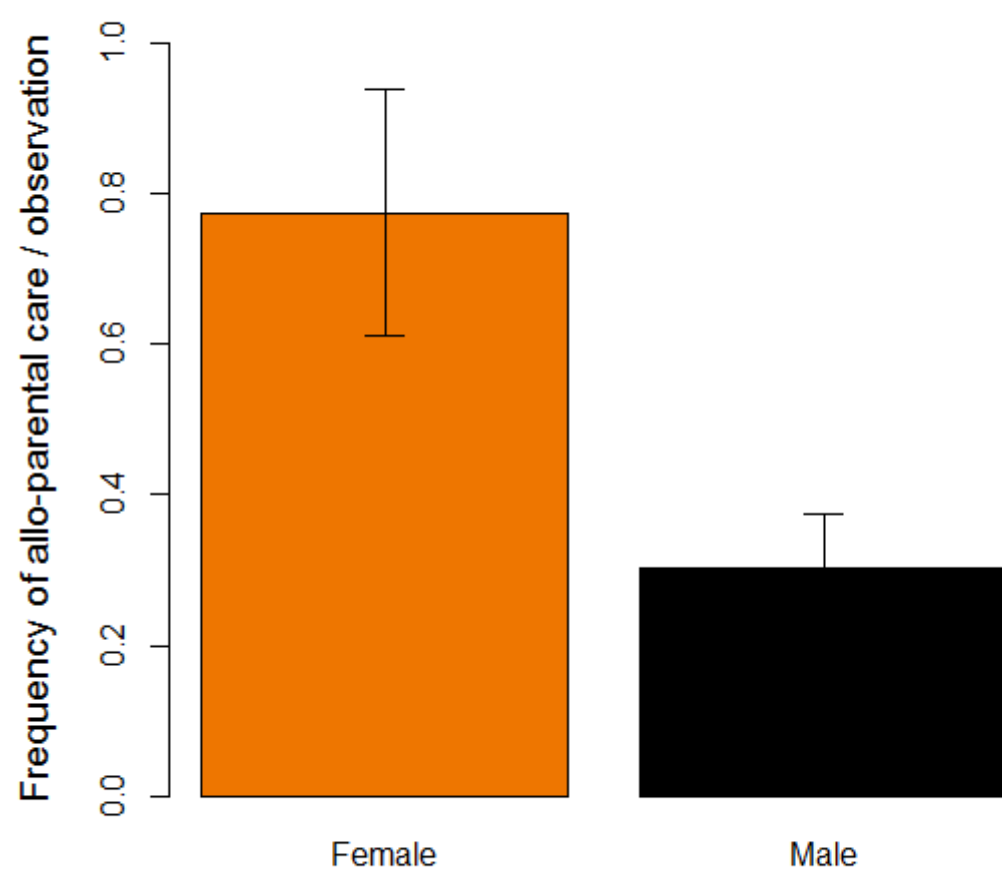


Figure 3



480

481 [Figure 4](#)

482

483

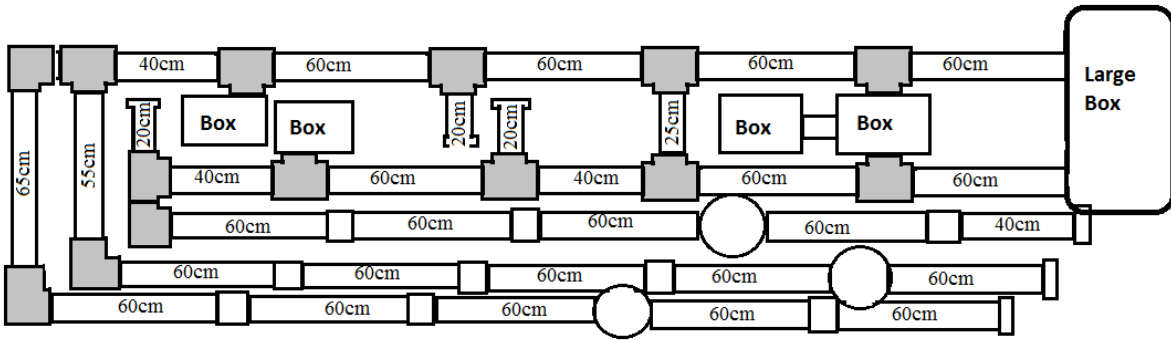
484 Table 1: Predictors of (a) total workload, (b) digging, (c) nest building and (d) food carrying in Damaraland mole-rats.
 485 Reported are coefficients (estimate), standard Errors (SE) and P-values (P) from generalised linear mixed models
 486 (GLMM) with logit link function. Bold terms were included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

a) Total cooperation	Estimate	SE	P
Intercept	-1.84	0.04	
Duration	-0.31	0.06	<0.001
Age	0.35	0.03	
Age²	-0.46	0.02	
Age³	0.15	0.01	<0.001
Sex	-0.09	0.05	
Residual body mass	0.19	0.03	
Age*Residual body mass	-0.20	0.02	
Age*Sex	-0.06	0.03	
Sex*Residual body mass	-0.12	0.04	
Age²*Residual body mass	0.06	0.01	<0.001
Age*Sex* Residual body mass	0.1	0.03	<0.001
b) Digging			
Intercept	-2.46	0.04	
Duration	-0.33	0.06	<0.001
Age	0.30	0.03	
Age²	-0.46	0.02	
Age³	0.15	0.01	<0.001
Sex	-0.07	0.05	
Residual body mass	0.21	0.04	<0.001
Age*Residual body mass	-0.20	0.02	
Age*Sex	-0.05	0.03	
Sex* Residual body mass	-0.12	0.04	
Age²*Residual body mass	0.06	0.01	<0.001
Age*Sex* Residual body mass	0.10	0.03	<0.001
c) Nest building			
Intercept	-5.82	0.08	
Age	-0.17	0.08	
Age²	-0.41	0.05	
Age³	0.17	0.03	<0.001
Residual body mass	0.04	0.05	
Age*Residual body mass	-0.21	0.05	<0.001
Age²*Residual body mass	0.12	0.04	0.002
<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			
Intercept	-4.90	0.06	<0.001
Age	0.03	0.05	0.54
Age²	-0.43	0.04	<0.001
Age³	0.18	0.02	<0.001

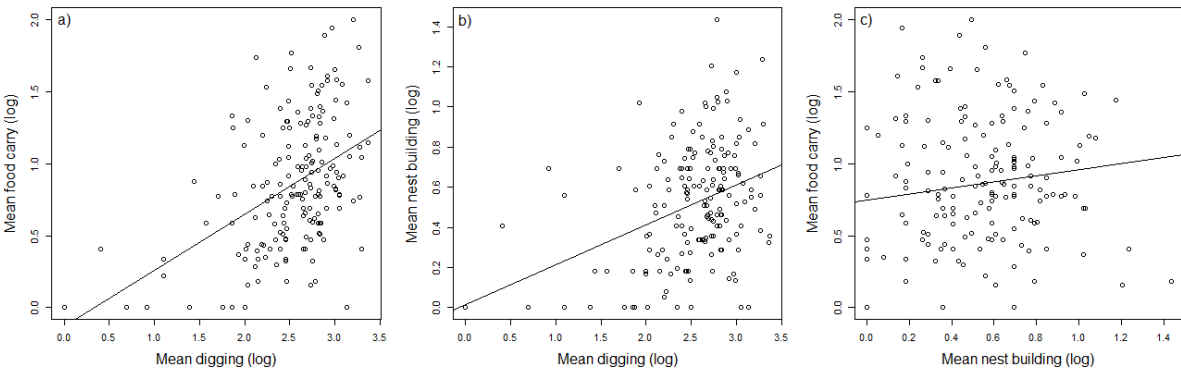
Residual body mass	0.25	0.04	<0.001
Duration	-0.30	0.11	0.006
<i>Sex</i>	<i>-0.02</i>	<i>0.09</i>	<i>0.75</i>
<i>Age*Residual body mass</i>	<i>-0.01</i>	<i>0.03</i>	<i>0.53</i>
<i>Age²*Residual body mass</i>	<i>-0.03</i>	<i>0.02</i>	<i>0.30</i>
<i>Sex* Residual body mass</i>	<i>-0.01</i>	<i>0.07</i>	<i>0.83</i>
<i>Age*Sex</i>	<i>0.08</i>	<i>0.06</i>	<i>0.12</i>
<i>Age*Sex* Residual body mass</i>	<i>0.08</i>	<i>0.06</i>	<i>0.14</i>

490

491



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 age² 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, r²=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

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

515

516

517