1   Classification: **Biological Sciences - Evolution**

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3   # Differences in cooperative behaviour among Damaraland

4   # mole-rats are consequences of an age-related polyethism

5

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19

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, *Heterocephlus 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.

34 **Significance**

35

36 Non-reproductive group members of naked and Damaraland mole-rats are thought to be organised

37 in permanent, distinct castes that differ in behaviour and physiology, suggesting that their social

38 organisation resembles that of obligatorily eusocial insects. This study tests predictions about the

39 distribution of cooperative behaviour based on the suggestion that individual differences represent

40 a caste system. Our data provide no evidence that helpers show fixed, divergent developmental

41 pathways, or specialise in particular tasks. Instead, variation in their behaviour appears to represent

42 an age-related polyethism. The results suggest that the behavioural organisation of social mole-rat

43 groups is similar to that of other singular cooperatively breeding vertebrates and that similarities to

44 obligatorily eusocial insects have been overestimated.

45

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

71   development (20-22) (Michener 1974, "narrow sense caste" *sensu* Wilson 1975, Crespi and Yanega

72   1995).

73   This study investigates whether the distribution of labour in Damaraland mole-rats is the result of an

74   age-related polyethism or whether there is evidence of the formation of castes and of permanent

75   differences in behaviour between frequent and infrequent workers, as has been suggested in

76   previous studies of naked mole-rats (13, 17) and Damaraland mole-rats (14). Distinguishing a system

77   of specialised workers that are organised in castes (*sensu* Michener 1974, (21)) from an age-related

78   polyethism requires longitudinal records of behaviour and growth of known-aged individuals. A

79   caste system, as suggested for social mole-rats, would predict that (i) behavioural phenotypes of

80   individuals with different growth trajectories diverge during ontogeny; (ii) the behavioural profiles of

81   individuals are related to their asymptotic body mass rather than their age; (iii) the distribution of

82   cooperative behaviour shows a bi- or multimodal distribution; (iv) individuals specialise permanently

83   in certain tasks, so that some forms of cooperative behaviour show negative correlations among

84   individuals; and that (v) repeatability of cooperative behaviour through ontogeny is high.

85   Alternatively, an age-related polyethism based on state-dependent costs and strategic resource

86   allocation contingent on opportunities to breed would predict that (i) cooperative investment

87   changes with age; (ii) asymptotic body mass is not necessarily related to cooperative behaviour; (iii)

88   cooperative behaviour is continuously distributed; (iv) individuals do not specialise in certain

89   activities so that there are positive correlations in their investment in different cooperative tasks;

90   and (v) cooperative investment should be contingent on an individual's state and life-history, which

91   frequently results in a bias towards to the more philopatric sex and towards fast-growing individuals.

92   Our study tests these predictions about the distribution of cooperative behaviour based on the

93   suggestion that individual differences represent a caste system or represent and age-related

94   polyethism using behavioural data, collected under controlled laboratory conditions on 187 non-

95   reproductive Damaraland mole-rats from 37 colonies between the ages of 60 and 600 days and 75

96   non-reproductive individuals from 13 colonies which were older than 600 days but whose exact age

97   was unknown. Damaraland mole-rats resemble naked mole-rats in social organisation and both

98   species are sometimes referred to as eusocial (13, 14, 23). Groups of Damaraland mole-rats can have

99   up to 41 members and as in naked mole-rats reproduction is limited to the dominant breeding pair

100   (23, 24). Damaraland mole-rats show variation in growth (25, 26) and cooperate in energetically

101   expensive burrow excavation to locate food underground, communal nest-building, carrying food

102   into a communal food store and by providing allo-parental care to the pups born in the group.

103   Investment in these activities varies between and within individuals (16, 23, 27) but it is unknown

104   how investment in cooperative behaviour of non-reproductive individuals is related to growth, age

105   and sex.

106

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

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

133   R^2 =0.10)

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

135   Three main aspects of cooperative behaviour (digging, nest building and carrying food to a

136   communal storage) showed similar development during ontogeny (Figure 3 a-c, Table 1 b-d). Fast

137   growing individuals exhibited higher investment in all three behaviours early in life. Males and fast

138   growing females reduced digging after reaching an age of 300 days (Figure 3 a, Table 1 b) and nest

139   building activity declined in fast growing males and females sooner than in slow growing individuals

140   (Figure 3b, Table 1c). Sex differences were small but females tended to invest more in nest building

141   and showed higher investment in digging and total cooperation until reaching one year of age

142   (Figure 3a, b). Investment in nest building and food carrying decreased in males and females older

143   than one year and females tended to invest more time in nest building (Figure 3b, c, Table 1c,-d).

144   Pairwise across individual comparisons of digging, nest building and food carrying suggested that

145   investment in different aspects of cooperation correlated positively with each aspect (Figure 4 a-c;

146   Digging-Food carrying, estimate=0.39, r^2=0.22, p<0.001, N=177; Digging- Nest building, estimate=0.2,

147   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).

148   Allo-parental care is rare in Damaraland mole-rats and is mainly displayed when offspring in the

149   group are below one month of age. The mean frequency of allo-parental care shown by non-

150   reproductive individuals was not associated with residual body mass or age but females carried pups

151   more frequently than males (Figure 5, GLMM; Growth, p=0.9; Age^2, p=0.11; Age, p=0.34; Sex,

152   Estimate= -0.76, p=0.045, N=226 observations on N=91 individuals). The frequency of allo-parental

153   care was unrelated to any other forms of cooperative behaviour (Allo-parental care − digging,

154   p=0.26, N=86; allo-parental care − food carrying, p=0.61, N=86; allo-parental care − nest building

155   p=0.49, N=86).

156   Discussion

157   Our results provide no indication that behavioural differences in cooperation in Damaraland mole-

158   rats are a consequence of divergent developmental strategies as would be expected in the caste

159   system suggested for social mole-rats (12-14). Investment in cooperation increased with age and

160   was initially higher in fast growing individuals, indicated by high body mass for a given age. This

161   effect was especially pronounced for digging behaviour, the most common and energetically

162   expensive domain of cooperative activities in social mole-rat societies (Figure 3a), and may be

163   caused by higher tolerance for the energetic demands of cooperation in fast growing individuals.

164   Nest building and food carrying also showed differences in development depending on growth

165   trajectories consistent with the prediction of state-dependent life histories (Figure 3b and c). As in

166   many cooperatively breeding species, age was the most important predictor of an individual's

167   contribution to cooperative tasks (Table 1a-c, (3, 8, 11)). Contributions to different cooperative

168   activities are positively correlated across individuals, suggesting that specialisation in cooperative

169   activities does not occur (Figure 4). These patterns resemble distribution of cooperation in other

170   social vertebrate groups where factors that alter the energetic costs of cooperative behaviour often

171   result in changes of investment in cooperation (3, 10, 28)

172   After the age of 600 days, when practically all individuals had reached asymptotic body mass, small

173   and large non-reproductive individuals did not differ in their contributions to cooperative behaviour

174   (Figure 1b). In addition, across individuals known to be younger than 600 days, asymptotic body

175   mass did also not predict investment in cooperation, suggesting that there are no distinct

176   differences in the behavioural phenotype emerging during ontogeny. Behavioural differences during

177   early ontogeny did not translate into the emergence of distinct behavioural castes in any age class of

178   non-reproductive individuals and most of them reduced investment in cooperation when reaching

179   asymptotic body mass (Figure 1 & 2). Individuals maintained plasticity in cooperative behaviour

180   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 thought 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

253   or 24 hours, applying a 4 min sampling interval. Typically 1-2 observers observed 10-20 individuals

254   simultaneously. We obtained a mean observation frequency of 12.2 scan observation sessions per

255   individual over the study period (range 1-35). To maintain the possibility of expressing foraging

256   behaviour during scan observations (i.e. clearing sand from the tunnel system to maintain access to

257   common food sources), we added sand through the vertical pipes every 2 hours. Several observers

258   were involved in carrying out scan observations and usually a single observer would cover a period

259   of 2-3 hours. We excluded individuals that died before reaching the age of 90 days.

260   We derived four measures of cooperation (total cooperation, digging, food carrying, nest building)

261   from scan observation sessions and extracted proportional investment (how often the behaviour

262   was displayed out of the total number of scans in this session) for each individual. Total cooperation

263   was calculated as the sum of all behaviours that were related broadly to any form of burrow

264   maintenance, foraging, nest building or allo-parental care such as digging in sand, gnawing on tunnel

265   walls, pushing sand into tunnel gaps or dead ends, sweeping sand with the hind legs, moving back to

266   the digging place after having transported sand and transporting food, nest material or pups ((15)

267   for a detailed ethogram). In order to evaluate whether non-reproductive individuals specialise on

268   certain tasks we also derived separate measures of digging (sum of digging in sand, pushing sand

269   into tunnel gaps or dead ends and sweeping sand with the hind legs), nest building and food

270   carrying.

271   Allo-parental care (i.e. when an individual retrieved a pup to the nest) is a rare form of cooperative

272   behaviour in mole-rats and can only be displayed when pups are young. Thus, we recorded all-

273   occurrences of allo-parental care simultaneously to scan observations and used observation sessions

274   for analysis when allo-parental care was observed in this session, which resulted in a data set of 226

275   observations on 91 individuals originating from 58 observation sessions. Of these observations, 198

276   were 12 hour observations and 28 were 24 hour observations but the frequency of allo-parental care

277   recorded per observation did not differ depending on the duration of the observation (GLM,

278 Duration: P=0.13). Including the observation duration in the final model or reducing the data-set to

279 observations of 12 hours did not change the results qualitatively and hence we analysed a pooled

280 sample of 12 and 24 h scan sessions.

281 Statistical analysis

282 To analyse how total cooperative behaviour, digging, nest building and food carrying relates to age,

283 residual body mass and sex we fitted generalised linear mixed models assuming binomial error

284 structure (GLMMs, logit link function) with the proportion of intervals scored with the respective

285 behaviour during a scan session as the response variable. We started with fitting the full model

286 including age, age^2 and age^3 and residual body mass (as index of growth, see SI for details) as

287 covariates and sex and the duration of the observation as a fixed factors. Additionally, we included

288 four 2-way interactions (Age*Residual body mass, Age*Sex, Sex*Residual body mass, Age^2*Residual

289 body mass) and the 3-way interaction (Age* Residual body mass *Sex) to allow the predicted

290 response to differ between sexes and individuals of different residual body mass at different stages

291 of development. All covariates were centred by subtracting the mean from each value and

292 thereafter scaled by dividing the values by the standard deviation. Furthermore, we included the

293 identity of the individual, the scan observation session reference (per mole-rat group) and an

294 observation level count to prevent overdispersion as random factors in all mixed modes models

295 presented in this paper (43). We then employed a stepwise, backwards model simplification

296 procedure (44) until only significant terms remained in the final model. Terms that were dropped in

297 the course of model selection are presented in this paper with the estimates, standard errors and

298 the p-values with which they were last included in the model selection process. Repeatability was

299 calculated following procedures outlined in Nakagawa & Schielzeth (45) using the R package rptR

300 (46). To control for the effect of age, residual body mass and sex we additionally calculated a

301 repeatability estimate using the residuals of a model including these factors. Significance of the

302 random effect individual identity was tested using a log likelihood ratio test and pseudo r^2 was

303   calculated following Nakagawa and Schielzeth (47) using the package MuMIn (48). All models

304   presented were estimated using the software R version 3.2.4 (49) and the packages lme4 (50).

305   Allo-parental brood care was analysed by fitting a GLMM assuming Poisson error structure and log

306   link function with the frequency of allo-parental brood care as the response variable and adding age,

307   age^2, growth and sex as explanatory variables. Because the data set was much smaller we did not

308   attempt to fit an age^3 and we did not include any of the two-way interactions. Again we employed a

309   stepwise, backwards model simplification procedure until only significant terms remained in the final

310   model.

311   To evaluate whether asymptotic body mass is associated with investment in total cooperation (i.e.

312   sum of all cooperative behaviours) we used a generic Gompertz growth function of the package

313   nlme (51). We fitted a growth curve for each individual and extracted the predicted asymptotic body

314   mass. In 15 out of 151 cases the prediction was higher than the maximum weight of mole-rats in our

315   laboratory population (i.e. ~240 gramm) and these cases were excluded for this analysis. We

316   subsequently fitted a GLMM with binomial error structure with total cooperative investment as the

317   response and the asymptotic body mass as a covariate. Here, we included only scan observation

318   sessions on individuals older than 300 days (N=122) as this is the age were the first individuals of our

319   population reach asymptotic body mass. We included the same random error structure as in

320   previous analysis in this model.

321   To address the question whether mole-rats specialise in certain tasks we calculated the mean

322   frequency of the respective cooperative task (digging, nest building and food carrying) per individual

323   (N=177) and for a subset of individuals (N=86) for allo-parental care. The values were log-

324   transformed and pairwise correlations were analysed using linear models.

325   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).

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343   References

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.   Bruintjes 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.   Bruintjes 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. *Behavl 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, Taborsky 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, & Taborsky 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.).

444 50.   Bates D, Maechler M, & Bollinge B (2011) lme4: Linear mixed-effects models using S4
445   classes.), R package version 0.999375-42.
446 51.   Pinheiro J, D. B, DebRoy S, D S, & Team RDC (2012) nlme: Linear and Nonlinear Mixed Effects
447   Models. R package version 3.1-104.).
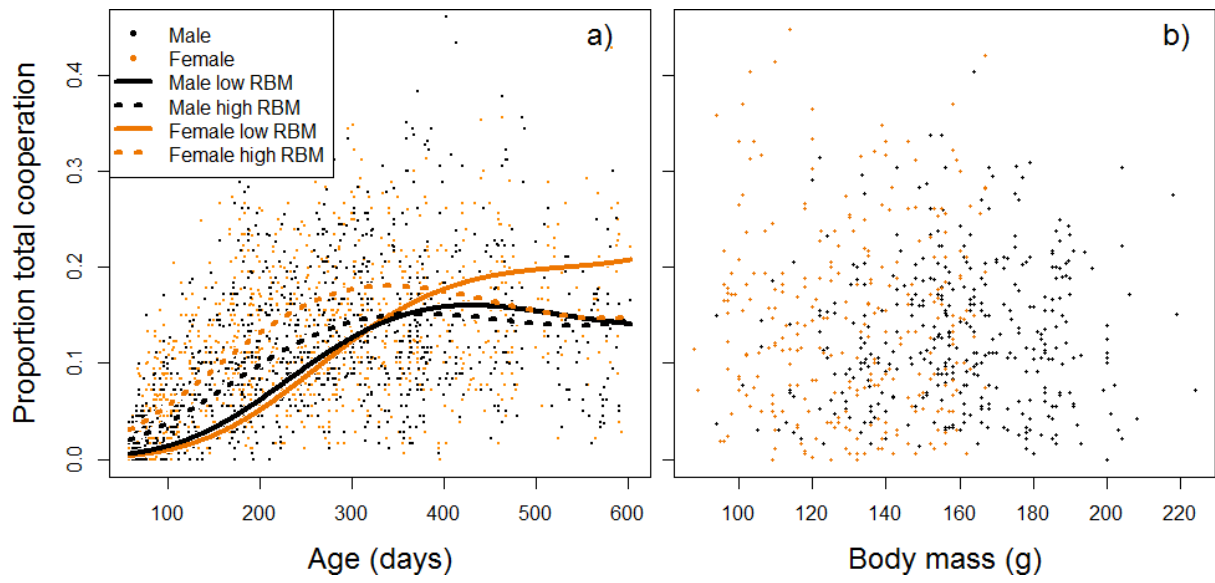
448

449 Figure Legends

450 Figure 1: Ontogeny of investment in total cooperative behaviour. a) Known-aged males and females
451 exhibiting differential growth rates up to an age of 600 days. Points represent the raw data of 2309
452 observations of 12 (N=2078) or 24 hours (N=231) per individual. Lines indicate the prediction from
453 the GLMM in Table 1a for fast growing individuals (Residual body mass = 0.3) or slow growing
454 individuals (Residual body mass = -0.3). b) Individuals that were at the start of the study older than
455 600 days but where the exact age was unknown. N=644 observations on N=75 individuals in 13
456 groups. See main text for statistical results. Some data points of the raw data are hidden behind the
457 legend or exceed the scaling of the y axes.

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

461 Figure 3: Ontogeny of investment in (a) digging, (b) nest building and (c) carrying food by males and
462 females exhibiting different growth rates. Points represent raw data of observations of 12 (N=2078)
463 or 24 hours (N=231) per individual. Lines indicate the prediction from the GLMM in Table 1b, 1c and
464 1d. Some data points of the raw data are hidden behind the legend or exceed the scaling of the y
465 axes.

466 Figure 4: Mean frequency of allo-parental care provided by females and males during 12 (198) and
467 24 hours (28) observations. Bars represent mean ± SE, N=226 observations on 91 individuals. See
468 main text for statistics.
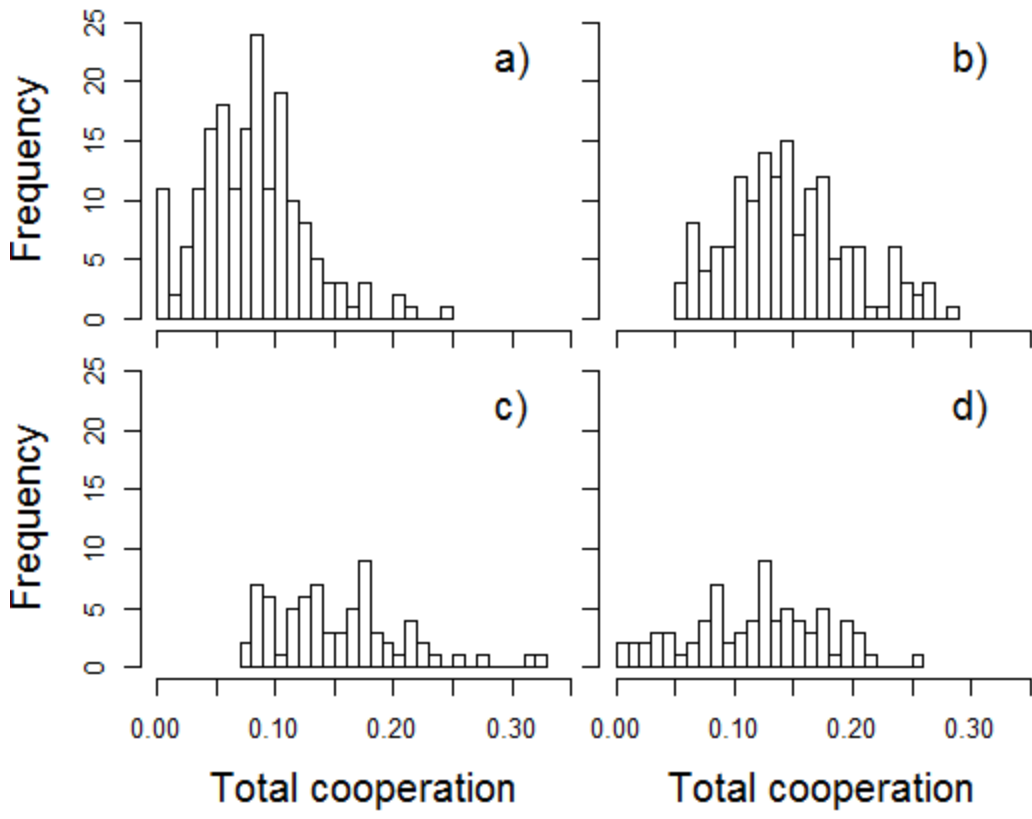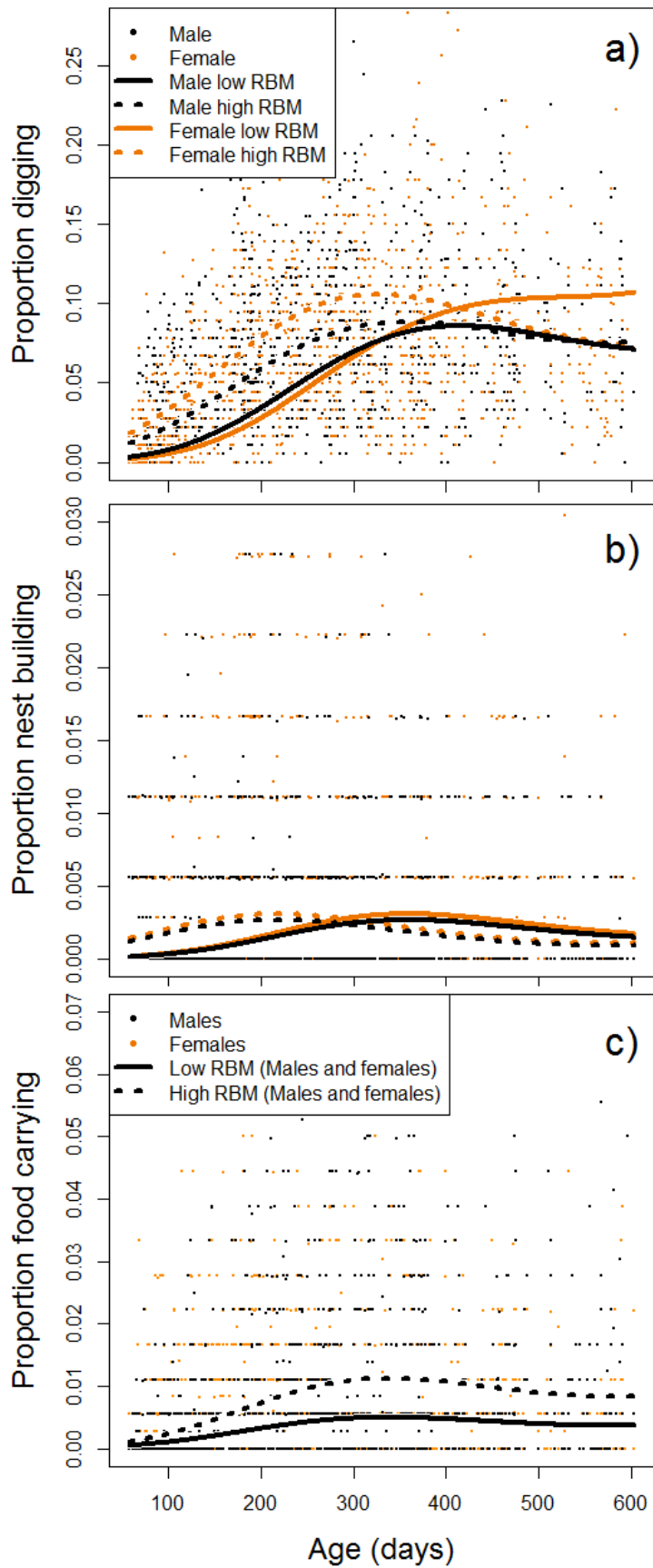
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471 Figure 1

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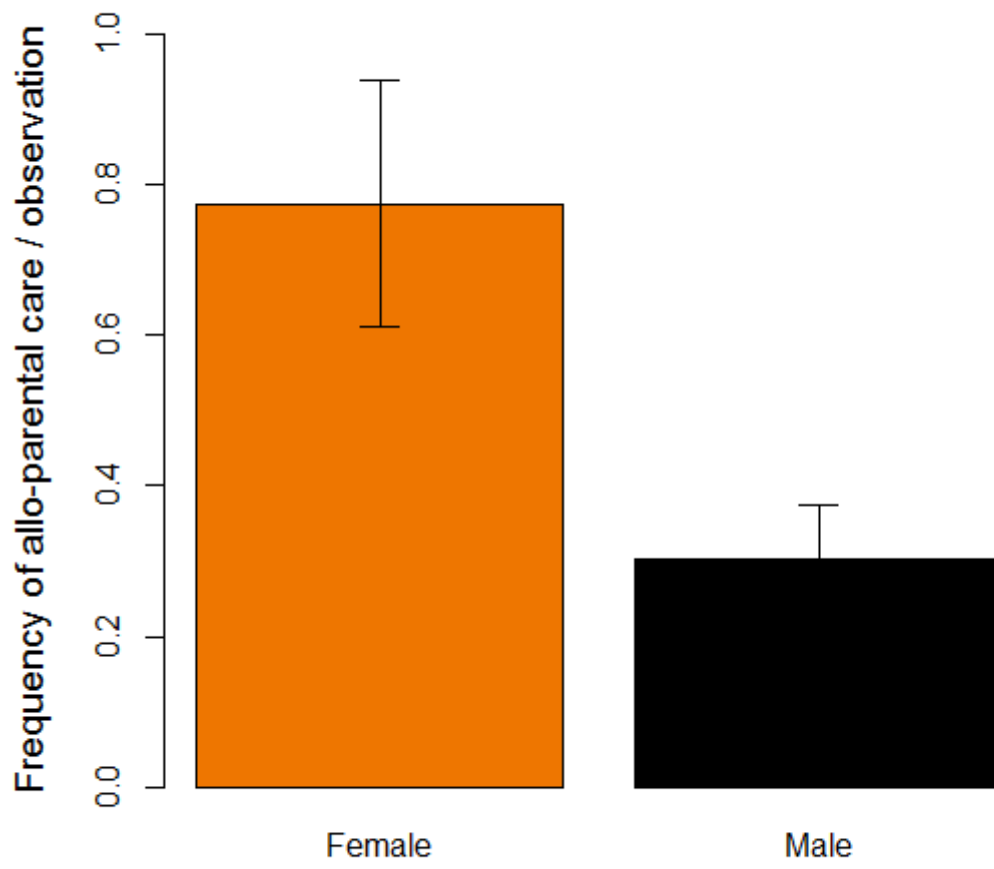
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Figure 2

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Figure 3

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Figure 4

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a) Total cooperation	Estimate	SE	P
Intercept	**-1.84**	**0.04**	
Duration	**-0.31**	**0.06**	**<0.001**
Age	**0.35**	**0.03**	
Age^2	**-0.46**	**0.02**	
Age^3	**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**	
Age^2*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**	
Age^2	**-0.46**	**0.02**	
Age^3	**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**	
Age^2*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**	
Age^2	**-0.41**	**0.05**	
Age^3	**0.17**	**0.03**	**<0.001**
Residual body mass	**0.04**	**0.05**	
Age*Residual body mass	**-0.21**	**0.05**	**<0.001**
Age^2*Residual body mass	**0.12**	**0.04**	**0.002**
Sex	-0.15	0.08	0.08
Duration	*0.001*	*0.15*	*0.99*
Sex Residual body mass*	*-0.13*	*0.9*	*0.11*
*Age*Sex*	*-0.06*	*0.8*	*0.39*
*Age*Sex* Residual body mass*	*0.16*	*0.08*	*0.06*
d) Food carry			
Intercept	**-4.90**	**0.06**	**<0.001**
Age	**0.03**	**0.05**	**0.54**
Age^2	**-0.43**	**0.04**	**<0.001**
Age^3	**0.18**	**0.02**	**<0.001**

Residual body mass	**0.25**	**0.04**	**<0.001**
Duration	**-0.30**	**0.11**	**0.006**
Sex	*-0.02*	*0.09*	*0.75*
*Age*Residual body mass*	*-0.01*	*0.03*	*0.53*
*Age^2*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*

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492   Supplementary information
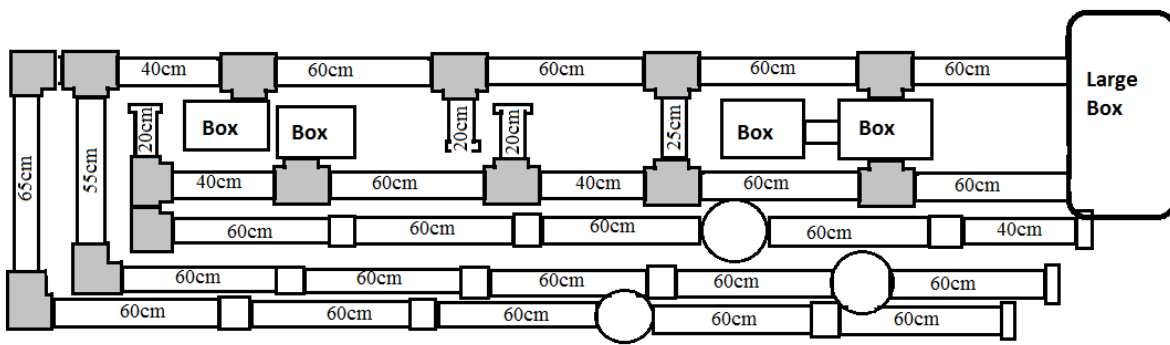
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494   **Supplementary Information Figure 1: One example of the tunnel system cages used during the study.**
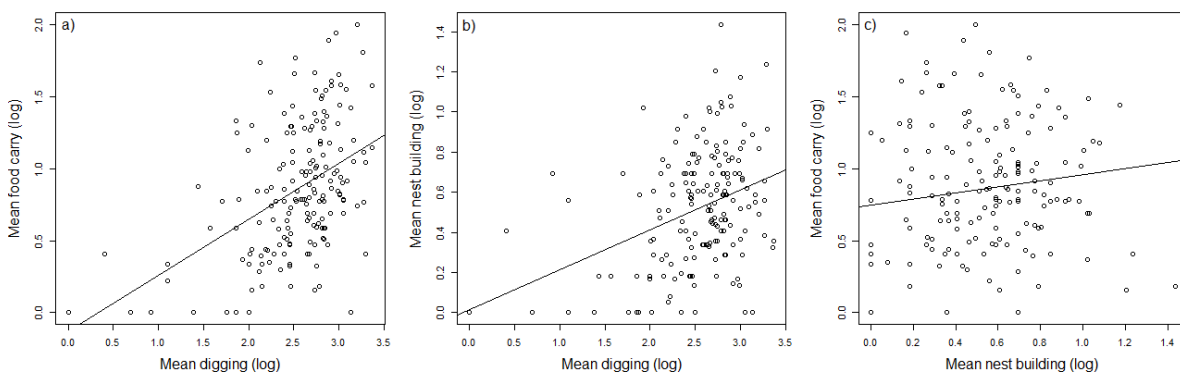
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496   **Supplementary Information Figure 2: Pairwise comparisons between investment in a) digging and food carrying, b)**
497   **digging and nest building and c) nest building and food carrying. Plotted are the natural logarithms of the mean**
498   **frequency of different cooperative tasks over the duration of this study per individual (N=177). See main text for**
499   **statistics.**

500

501   Residual body mass

502   As an index of growth we used residual body mass from linear models including age and age^2 as

503   explanatory variables. Mean residual body mass during the fast growth period in early ontogeny

504   (between 90 days and 300) explains 72% of the variation found in mean residual body mass after the

505   age of 450 days when most individuals reached asymptotic body mass and ceased weight gain (linear

506   model, N=80 individuals, Estimate=1.1±0.07, r^2=0.72, P<0.001). This suggests that high residual body

507   mass at any point in life is tightly linked to fast growth trajectories and high asymptotic body mass

508   late in life. Additionally, individuals which show high residual body mass at a given point in life have

509   shown faster mean weight gain over their life previous to this measurement compared to individuals

510   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.

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