

1 **Naked mole-rats (*Heterocephalus glaber*) do not specialise on cooperative tasks**

2 Running title: No specialisation in naked mole-rats

3

4 Susanne Siegmann¹, Romana Feitsch¹, Daniel W. Hart², Nigel C. Bennett², Dustin J. Penn¹ &
5 Markus Zöttl³

6

7

8 ¹ Konrad Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria

9 ² Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria,
10 Pretoria, Gauteng, South Africa

11 ³ Ecology and Evolution in Microbial Model Systems, EEMiS, Department of Biology and
12 Environmental Science, Linnaeus University, SE-391 82 Kalmar, Sweden

13

14

15

16

17 Correspondence: markus.zottl@lnu.se

18

19 **Acknowledgments**

20 We thank the Vienna Zoo for providing access to their mole-rat groups. We are particularly
21 grateful to Anton Weissenbacher, Doris Preininger, Inez Walter and all caretakers for their help
22 and support in this study. We thank Jack Thorley for helpful discussions about the analyses and
23 interpretation of the data.

24

25 **Abstract**

26 It has been proposed that naked mole-rat (*Heterocephalus glaber*) societies resemble those of
27 eusocial insects by showing a division of labour among non-breeding individuals. Earlier studies
28 suggested that non-breeders belong to distinct castes that specialise permanently or temporarily
29 on specific cooperative tasks. In contrast, recent research on naked mole-rats has shown that
30 behavioural phenotypes are continuously distributed across non-breeders and that mole-rats
31 exhibit considerable behavioural plasticity suggesting that individuals may not specialise
32 permanently on work tasks. However, it is currently unclear whether individuals specialise
33 temporarily and whether there is a sex bias in cooperative behaviour among non-breeders. Here
34 we show that non-breeding individuals vary in overall cooperative investment, but do not
35 specialise on specific work tasks. Within individuals, investment into specific cooperative tasks
36 such as nest building, food carrying and burrowing are positively correlated, and there is no
37 evidence that individuals show trade-offs between these cooperative behaviours. Non-breeding
38 males and females do not differ in their investment in cooperative behaviours and show broadly
39 similar age and body mass related differences in cooperative behaviours. Our results suggest
40 that non-breeding naked mole-rats vary in their overall contribution to cooperative behaviours
41 and that some of this variation may be explained by differences in age and body mass. Our data
42 provide no evidence for temporary specialisation, as found among some eusocial insects, and
43 suggests that the behavioural organisation of naked mole-rats resembles that of other
44 cooperatively breeding vertebrates more than that of eusocial insect species.

45

46 Key words:

47 Behavioural specialisation, division of labour, eusociality, cooperative breeding, helping, social
48 evolution

49

50 Introduction

51 Task specialisation among members of social groups is considered a hallmark of social
52 evolution and can lead to improvements in group efficiency (Chittka and Muller 2009, Bourke
53 2011). The most extreme cases of task specialisation are found among social insects, where
54 individuals show divergent developmental trajectories that lead to functionally different and
55 morphologically specialised castes of workers (Wilson 1971, Bourke 2011). Other social insects
56 show temporary specialisation in the absence of morphological specialisation, and workers pass
57 through successive developmental stages that are characterised by temporary specialisation in
58 specific tasks (Seeley 1982, Biedermann and Taborsky 2011, Mersch et al. 2013). In contrast to
59 insects, group living vertebrates rarely show evidence of specialisation, and usually, individuals
60 vary in their overall investment in cooperative tasks depending on the individual's characteristics
61 and environmental conditions (Cockburn 1998, Clutton-Brock et al. 2003). However, the social
62 mole-rats of the family *Bathyergidae* may represent an exception among group-living
63 vertebrates, and it has been controversially debated to what extent their social organisation
64 resembles that of social insects groups (Jarvis 1981, Bennett 1990, Burda 1990, Crespi and
65 Yanega 1995, Bennett and Faulkes 2000, Burda et al. 2000, Scantlebury et al. 2006, Boomsma
66 2013, Boomsma and Gawne 2018).

67 Early research on naked mole-rats (*Heterocephalus glaber*) has suggested that some non-
68 reproductive individuals specialise permanently on specific work-related tasks and that variation
69 in their cooperative behaviour is a consequence of the development of distinct castes – similar to
70 those found in eusocial insects (Jarvis 1981, Jarvis et al. 1991). Variation in growth, body mass
71 and behaviour were thought to be consequences of divergent developmental trajectories, where
72 small-bodied workers specialise in acquiring indirect fitness benefits generated by helping
73 related individuals, and large individuals were thought to maximise chances of direct
74 reproduction by dispersing or replacing the breeder (Jarvis et al. 1991, O'Riain et al. 1996).
75 Other studies suggested that variation in cooperative behaviour of naked mole-rats may instead
76 represent temporary specialisation, similar to age-related polyethisms found in some social
77 insects and that contrasts in behaviour may be explained by age-related changes of behaviour,
78 where individuals pass through stages of development and conduct different tasks depending on
79 their age (Lacey and Sherman 1991, Lacey and Sherman 1997, Faulkes and Bennett 2016).
80 More recent studies have suggested that naked mole-rats show behavioural flexibility and that
81 cooperative behaviour may be adjusted to the group composition and other social and
82 environmental factors (Mooney et al. 2015, Gilbert et al. 2020). However, it remains unclear
83 whether non-breeding naked mole-rats specialise temporarily on specific work-related

84 behaviours, or whether individuals vary mostly in their overall commitment to cooperative
85 behaviours (Thorley et al. 2018, Braude et al. 2021).

86 Evidence from other social mole-rat species challenges the hypothesis that specialisation is
87 common in mole-rats. Several species of the genus *Fukomys* and *Cryptomys* show a similar
88 social organisation to that of naked mole-rats and exhibit high reproductive skew and
89 cooperative foraging, though their groups are usually smaller than naked mole-rat groups
90 (Bennett and Jarvis 1988, Bennett 1990, Jarvis and Bennett 1993, Jarvis et al. 1994). Whereas
91 subordinate Damaraland mole-rats (*Fukomys damarensis*) exhibit differences in their overall
92 investment in cooperation and show age and size-related changes, the individuals do not
93 specialise in specific tasks, and behavioural variation appears to be a consequence of
94 differences in age, growth and body condition among non-breeders (Bennett and Jarvis 1988,
95 Bennett 1990, Zöttl et al. 2016a, Thorley et al. 2018, Torrents-Ticó et al. 2018a). Similarly,
96 research on the cooperatively breeding Micklem's mole-rat (*Fukomys micklemi*) showed that
97 non-breeding individuals lacked task specialisation (Van Daele et al. 2019) and radio-tracking
98 studies of free-living Ansell's mole-rats (*Fukomys ansellii*) did not find evidence for behavioural
99 specialisation (Šklíba et al. 2016). However, sociality has evolved independently in naked mole-
100 rats and their relatives of the genera *Fukomys* and *Cryptomys*, and it is possible that patterns of
101 behavioural organisation differ as a result of larger mean group sizes in naked mole-rats
102 (Bennett and Faulkes 2000, Faulkes and Bennett 2007, Visser et al. 2019).

103 To demonstrate behavioural specialisation, it is necessary to show that individuals trade-off
104 investment in different forms of cooperative behaviours. This would be expected to generate
105 negative correlations between some cooperative behaviours across individuals over a
106 considerable amount of time (English et al. 2015, Thorley et al. 2018). Previous studies of naked
107 mole-rats have sometimes suggested that specialisation occurs on the grounds that individuals
108 of different body mass or age show contrasts in their investment in specific tasks (Jarvis 1981,
109 Jarvis et al. 1991, Lacey and Sherman 1991, Lacey and Sherman 1997), or by showing that
110 different forms of cooperative behaviours load on different axes in principal component analyses
111 (Mooney et al. 2015). However, these patterns do not necessarily imply specialisation on an
112 individual level, and it remains unclear to what extent naked mole-rats specialise in cooperative
113 tasks.

114 In this study, we investigated whether non-breeding individuals in captive naked mole-rat groups
115 specialise across three different cooperative tasks, which are burrowing related activities, nest
116 building and food carrying. To do this, we collected longitudinal behavioural records of 169

117 marked individuals in 11 groups using an instantaneous sampling protocol and analysed the
118 behavioural frequencies with multilevel, multinomial logistic regressions. These generalised
119 linear mixed models are logistic regressions that allow the estimation of within-individual
120 correlation, while also estimating the effects of individual characteristics and environmental
121 effects on behavioural variation (Koster and McElreath 2017, Thorley et al. 2018). Trade-offs
122 between different cooperative behaviours at the individual level would result in negative
123 individual random effects correlations. In contrast, positive correlations would indicate that
124 individuals that perform one cooperative task are also much more likely to perform another kind
125 of cooperative task more frequently.

126 We also investigated whether the expression of cooperative behaviour of naked mole-rats is
127 predicted by individual characteristics (body mass, age) and group size, and whether there is a
128 sex bias in the expression of cooperative behaviour. Variation at these levels and behavioural
129 specialisation are non-mutually exclusive phenomena and do not preclude each other. As such,
130 when addressing questions about behavioural specialisation it is important to include the effects
131 of individual characteristics and group level traits because divergent behavioural trajectories in
132 different tasks may reflect the relative costs and benefits of specific cooperative behaviours at
133 different developmental or life-history stages (McNamara and Houston 1996, Taborsky and
134 Grantner 1998, Heinsohn and Legge 1999, Clutton-Brock et al. 2003).

135

136 **METHODS**

137 **Animals and housing**

138 The study includes data from five groups of naked mole-rats housed at the Vienna Zoo
139 (Tiergarten Schönbrunn) in Austria, and six groups housed at the University of Pretoria in South
140 Africa, with group sizes ranging from 12 to 45 individuals. All animals were born and raised in
141 captivity and housed in tunnel systems made of either transparent PVC or glass. Each group
142 occupied a self-contained tunnel system (3.20–7 m) including at least one nest box and one
143 toilet area. Temperatures in the housing facilities were maintained close to natural burrow
144 conditions at 28°–30°C. The animals were fed *ad libitum* daily on a diet of sweet potatoes,
145 carrots, beetroot, apples and cucumber, and provided with wood wool (Vienna) or paper towel
146 shreds (Pretoria) as nesting material. The boxes (toilet chamber) were cleaned once a day and
147 the food container once a week. During observations, a standardised amount of digging
148 substrate (1 x 200 ml wood shavings) was inserted into the tunnel system every 2 h to provide
149 substrate for burrowing activity.

150 All individuals were identified via passive integrated transponder tags, and prior to
151 observations, the individuals received unique colour marks applied with permanent markers. Sex
152 was determined from the external genitalia (Pretoria) or via molecular sexing using buccal
153 mucosa samples (Vienna). The breeding females were identified by their characteristic genital
154 morphology. In Vienna, we were unable to identify the breeding males in the groups
155 morphologically, and no sexual behaviour was observed during the study. Therefore, we
156 included all individuals except for queens in the behavioural analysis as non-breeders.

157 **Data collection**

158 Data from 169 non-breeding individuals (67 females, 102 males) were included in this study. In
159 Vienna, data were collected from 72 animals between July 2018 and July 2019. Body mass was
160 recorded a mean of 7.0 ± 1.5 times from every animal whenever the group was removed from
161 the tunnel system (e.g. before observation sessions or when taking mucosa samples) by placing
162 them on an electronic scale (accurate to the nearest gram). In Pretoria, data were collected from
163 97 animals in August 2020. Body mass measurements were taken once for each animal before
164 their first observation. The mean body mass for all non-breeders was 38.3 ± 12.3 g (range 16-74
165 g), with 36.1 ± 11.6 g for females and 39.8 ± 12.5 g for males. Ages were known for 91 non-
166 breeders in Pretoria and 8 non-breeders in Vienna. The mean age at the time of observation
167 was 415.4 d, ranging from 140-1254 d.

168 Behavioural data were collected using instantaneous scan sampling. The behaviour of
169 every animal in a group was recorded in 6-10-min intervals, depending on group size. In larger
170 groups, 20 animals were arbitrarily chosen for observation, whereas in groups smaller than 20
171 individuals, all animals were included in the observation. The ethogram included 16 behaviours
172 (Supplementary Table S1), and the observations were recorded on a handheld device using
173 software Animal Behaviour Pro version 1.2 (University of Kent, UK). In Vienna, groups remained
174 in their usual tunnel systems, whereas in Pretoria, they were transferred one day before
175 observation to a tunnel system better suited for observations (Supplementary Figure S1). The
176 animals were allowed 24 h to habituate to the observational tunnels.

177 Observation sessions lasted 6 h and were carried out between 08:00 and 16:00 by the
178 same one or two observers that alternated every 30 min. The observational period was chosen
179 because naked mole-rats show unpredictable activity patterns with considerable inter-individual
180 variation (Riccio and Goldman 2000). In Vienna, each group was observed five times over a
181 mean period of 216 ± 61 d, with a mean time of 54 ± 41 d between sessions. In Pretoria, each
182 group was observed on three consecutive days. Over all 43 sessions, a mean of 161 ± 69
183 sampling events was recorded per individual (range 78-300, see Table 1).

184 **Statistical analysis**

185 Individual correlations between types of cooperative behaviour and the effect of body mass and
186 group size on cooperative behaviour were analysed with the use of three multilevel, multinomial
187 behaviour models that increased in complexity due to the successive inclusion of fixed effect
188 covariates and higher-level random effects (Koster and McElreath 2017). All three models were
189 calculated separately for males and females. Subsequently, we also specified a model for a
190 subset of animals of known age to investigate the effect of age on behaviour and a model for all
191 non-breeders with sex as a predictor variable to quantify behavioural sex differences.

192 The 16 recorded behaviours were grouped into six categories: three types of cooperative
193 behaviour, carrying food, nest building and burrowing (which aggregates all activities related to
194 burrow maintenance such as gnawing at the tunnel walls, digging in or kicking and sweeping
195 substrate), and three non-cooperative behaviour types, resting, eating and active non-help,
196 which summarises all other active behaviours not related to cooperation so that distinction can
197 be made between investment in cooperation and other activities. For most observations, no
198 offspring were present, and the few recorded instances of pup carrying were excluded from the
199 analyses.

200 The Widely Applicable Information Criterion (WAIC) was calculated to evaluate relative
201 model fit, but due to their varying predictors and random effects structure, each of the three
202 Models 1-3 and the comparison of their output provided information relevant to different aspects
203 of our analysis of cooperative behaviour (Watanabe and Opper 2010, Watanabe 2013). The
204 WAIC score was therefore not used for model selection, but rather as an indicator of model
205 quality.

206 Model 1 included only intercepts and random effects for individuals and showed the
207 extent of individual-level variance for each behavioural category as well as the within-individual
208 correlations between the five non-resting behaviours. Since we were interested in individual
209 trade-offs between active behaviours, resting was set as the reference category. This meant that
210 coefficients of the intercepts indicated how much time individuals allocated to the respective
211 behaviours relative to resting. Consequently, the variance of the reference category or
212 correlations between the other behaviours and resting were not calculated.

213 In addition to the individual-level random effects, Model 2 included predictor variables
214 that may be related to the expression of behavioural phenotypes in naked mole-rats. Body mass
215 was added as a fixed effect to test the assumption that maximum body mass influences the
216 cooperative investment of non-breeders. As another well-established predictor of behavioural
217 contributions in cooperative societies the group size was also incorporated as a fixed covariate
218 (Balshine et al. 2001, Fischer et al. 2014, Houslay et al. 2020). Both continuous predictors were
219 z-score transformed before model fitting and specified as first- and second-order polynomials.
220 To control for the origin of the population we also added this variable as a fixed factor with two
221 levels (Vienna/Pretoria). The comparison of individual-level variances between Models 1 and 2
222 gave some indication of the proportion of variance in the behavioural categories that could be
223 explained by the fixed effects. However, the inclusion of predictor variables can increase the
224 higher-level variance estimates in multilevel models, which is why the variances in Model 2
225 should be interpreted with caution (Koster and McElreath 2017). The within-individual
226 correlations between the behavioural responses are not sensitive to this issue, and the changes
227 in correlation estimates relative to Model 1 reflected the impact of the predictor variables on the
228 random effects.

229 The structure of Model 3 was further expanded to include random effects at the level of
230 observation session and group, while maintaining the set of fixed effects from the previous
231 model. Random effects for sessions were incorporated to account for temporal pseudo-
232 replication created by recording the same individuals repeatedly throughout one session. Group-

233 level random effects were introduced to adjust for clustering of the data by group. The complex
234 random effects structure of this model affects the interpretation of the individual random effects
235 and their correlations: individual-level variance estimates did not reflect variation across all the
236 individuals of the population, but within-group variations and as a result, individual-level
237 correlations in this model did not represent individual trade-offs between behavioural responses.
238 However, including higher-level random effects improved the overall model fit and allowed a
239 more precise estimation of the fixed effects. As a result, Model 3 was particularly suited for
240 analysing the effects of the predictor variables on cooperative investment.

241 We expanded the structure of Model 3 to investigate the effect of age on behaviour for
242 the subset of 99 non-breeders of known age by including age as a fixed effect (as a first-,
243 second- and third-order polynomial) and litter as a random effect for Model 3a. Additionally, we
244 applied Model 3b, which also retained the random and fixed effects structure of Model 3 but
245 incorporated sex as a categorical predictor, to the whole dataset.

246 Models were fitted and analysed in a Bayesian framework with the R packages *rstan*
247 (Stan Development Team 2020) and *rethinking* (McElreath 2020). Instead of the conventional
248 Markov chain Monte Carlo algorithms, *rstan* employs Hamiltonian Monte Carlo chains, which are
249 more efficient at achieving sufficiently mixed posterior distributions (Monnahan et al. 2017). We
250 used three chains of 2000-3000 iterations for model fitting, half of which were devoted to the
251 warm-up. To ensure adequate mixing of the chains, a non-centred parameterisation of the
252 varying effects was realised with a Cholesky decomposition of the variance-covariance matrices
253 (Koster and McElreath 2017). Additionally, we assigned weakly informative priors to the fixed
254 effect parameters and variance-covariance matrices that prevent overfitting while influencing the
255 posterior distribution as little as possible (Koster and McElreath 2017). To diagnose potential
256 problems with chain mixing and convergence, we examined the trace plots and rank histograms
257 of the chains as well as the effective number of samples and the Gelman-Rubin convergence
258 diagnostic ($R^2 < 1.1$) (McElreath 2020).

259 The correlations between random effects were considered significant if the 95% credible
260 intervals of their posterior distributions did not include zero. The interpretation of the coefficients
261 of the fixed effects is complicated because they do not represent the direct effect of the predictor
262 on the probability of exhibiting a certain behaviour due to their relationship to the reference
263 category. Following Koster and McElreath (2017), we instead calculated the predicted
264 probabilities and their credible intervals in order to visualise the impact of body mass, group size
265 and age on behaviour. Probabilities were based on fixed effects only while averaging over

266 random effects. Prediction intervals cannot be used to test categorical predictor variables for
267 significance, because they contain uncertainty from all covariates, and so to examine differences
268 in behaviour between females and males, we calculated the contrasts between the predicted
269 probabilities for the two groups (Koster and McElreath 2017). Statistical significance was inferred
270 if the 95% credible intervals of the predicted differences did not span zero. All statistical
271 analyses were performed in R (R Core Team, 2020).

272 **Ethical statement**

273 The protocol used in this study was approved by the animal ethics committee of the University of
274 Pretoria NAS099/2020 and Department of Agriculture land reform and rural development
275 12/11/1/8 (1595JD).

276

277 RESULTS

278 Individual-level trade-offs

279 Comparison with the WAIC showed that model fit improved with increased model complexity
280 (Supplementary Table S2). Effects of the predictor variables are therefore presented for Model 3
281 and its variants 3a and 3b, while within-individual correlations are taken from Model 1 and 2.

282 We found no evidence of task specialisation of non-breeding naked mole-rats between
283 any of the three cooperative tasks. Individual-level random effect correlations between any two
284 of the observed behaviours (excluding the reference category resting) were positively correlated
285 across both sexes and negative correlations were notably absent, indicating that there were no
286 trade-offs between different cooperative behaviours within individuals (Table 2, Supplementary
287 Tables S3 and S4 for random effects correlations on all levels from Models 1, 2 and 3 for
288 females and males, respectively). Individuals that performed more of one cooperative behaviour
289 were also more likely to engage in other cooperative behaviours: mole-rats who were more
290 frequently observed carrying food engaged more often in nest building (females: $\rho_{3,4} = 0.34 \pm$
291 0.13 ; males: $\rho_{3,4} = 0.61 \pm 0.08$), and burrowing (females: $\rho_{3,5} = 0.61 \pm 0.10$; males: $\rho_{3,5} = 0.64 \pm$
292 0.07), while individuals who burrowed relatively more also allocated more of their time to nest
293 building (females: $\rho_{4,5} = 0.43 \pm 0.11$; males: $\rho_{4,5} = 0.69 \pm 0.06$; values from Model 1, Table 2,
294 upper half of each matrix). Most correlations remained robust after controlling for the influence of
295 the fixed effects on behaviour in Model 2, though nest building was no longer significantly
296 correlated to other cooperative tasks in females (Figure 1; Table 2, lower half of each matrix).
297 The positive correlations remained qualitatively unchanged when limiting the dataset to include
298 only individuals that were observed over a long period in the population from Vienna
299 (Supplementary Figure S2, Supplementary Table S5). However, despite remaining positive, a
300 small number of correlations, notably nest building to food carrying within the population in
301 Vienna did not reach significance among females, presumably because the sample size was
302 limited to 19 females.

303 Effects of body mass, group size and age

304 Individual-level variances changed only to a small extent with the inclusion of fixed effects in
305 Model 2 compared to Model 1, indicating that body mass, group size and population account for
306 only a small proportion of individual-level behavioural variation (Supplementary Table S6). The
307 behavioural changes attributed to the fixed effect estimates (body mass, group size, age) were
308 also estimated with a high degree of uncertainty, suggesting that these individual and group

309 characteristics were relatively poor predictors of cooperative behaviour of naked mole-rats in
310 both populations. However, some attenuated general trajectories were notable in the
311 visualisation of the predicted probabilities (Figures 2, 3 and 4).

312 Body mass had similar effects on male and female non-breeders (Figure 2,
313 Supplementary Table S7). Food carrying increased with larger body mass, whereas burrowing
314 activity decreased with larger body mass in both sexes. Individuals with intermediate body
315 masses engaged mostly in nest-building activity. Group size had overall no convincing effect on
316 the cooperative and non-cooperative behaviour of naked mole-rats (Figure 3, Supplementary
317 Table S7). Individuals in larger groups rested more and furthermore showed less non-helping
318 activity. Investment in food carrying peaked at intermediate group sizes in both sexes and
319 burrowing showed a similar quadratic relationship in females. In contrast, burrowing declined
320 and resting increased with larger group sizes in males. Females performed less nest building in
321 larger groups, whereas no such trend was apparent for males.

322 Overall, the animals became less active with age, as seen by the increase of resting
323 behaviour over time (Figure 4, Supplementary Table S7). In accordance with this trend,
324 investment in burrowing behaviour decreased for both sexes during the first 2.5 years of life. The
325 effect of age on some behaviours seems sex-dependent: time allocated to food carrying
326 declined after 1.5 years in females, whereas in males, food carrying increased with age and
327 reached its peak at around 2 years. Nest building behaviour showed the inverse trends, with
328 males expressing nest-building more frequently with age and females displaying a steep decline
329 after 1.5 years.

330 **Sex differences in cooperative behaviour**

331 Whereas some sex differences existed in relation to age, overall, sex differences in cooperative
332 and non-cooperative behaviour were minor and non-significant, with the exception of females
333 spending marginally more time eating (Model 3b). Both sexes were equally likely to carry food,
334 engage in nest building and burrowing after controlling for the effects of body mass, group size
335 and population (Figure 5).

336

337 **Table 1:** Descriptive summary statistics for the observational data used in this study split by group, population, sex
 338 and body mass. Population-level differences are also illustrated in Supplementary Figure S3.

Group	N	Percentage of total observations					
		Active non-help	Eat	Food carry	Nest build	Burrow	Rest
A (Vienna)	12	32.1	4.8	0.9	2.6	21.9	37.7
B (Vienna)	18	29.7	3.9	1.2	6.4	24.3	34.5
C (Vienna)	13	46.3	1.7	0.5	3.6	23.3	24.5
D (Vienna)	18	46.1	5.4	4.7	4.6	26.7	12.5
H (Vienna)	11	49.8	5.6	2.2	5.2	40.6	20.4
1 (Pretoria)	14	24.7	6.7	2.2	3.0	18.9	44.6
4 (Pretoria)	18	19.9	3.2	1.3	0.4	23.6	51.7
5 (Pretoria)	11	16.8	6.2	1.3	0.6	12.8	62.3
6 (Pretoria)	18	26.1	6.2	3.6	0.0	25.5	38.5
7 (Pretoria)	18	22.4	3.5	1.3	1.4	13.4	58.0
10 (Pretoria)	18	24.1	6.9	1.7	4.9	7.4	54.8
Vienna	72	37.4	3.8	1.7	4.0	27.0	26.2
Pretoria	97	22.3	5.4	1.9	1.7	16.9	51.8
Females	67	27.6	5.3	1.9	3.1	18.8	43.2
Males	102	32.8	4.1	1.7	3.0	24.8	33.6

Small (<35g)	72	28.5	4.6	1.8	2.7	20.6	41.8
Medium (35-55g)	75	31.5	4.4	1.5	3.2	22.2	37.2
Large (>55g)	22	34.8	4.5	2.6	3.0	28.6	26.5
<hr/>							
Total	169	31.0	4.5	1.8	3.0	22.7	37.0
<hr/>							

339

340

341 **Table 2:** Correlations of individual-level random effects across responses from Model 1 and 2 for both sexes.

Sex	Behaviour	Behaviour				
		Active non-help	Eat	Food carry	Nest build	Burrow
Female	Active non-help	-	0.59(0.09)	0.63(0.09)	0.58(0.09)	0.70(0.07)
	Eat	0.56(0.13)	-	0.66(0.11)	0.61(0.11)	0.35(0.12)
	Food carry	0.58(0.13)	0.58(0.14)	-	0.34(0.13)	0.61(0.10)
	Nest build	0.22(0.14)	0.45(0.15)	0.13(0.17)	-	0.43(0.11)
	Burrow	0.51(0.11)	0.24(0.14)	0.51(0.13)	0.14(0.14)	-
Male	Active non-help	-	0.60(0.08)	0.65(0.07)	0.78(0.05)	0.77(0.04)
	Eat	0.64(0.08)	-	0.84(0.06)	0.57(0.09)	0.61(0.08)
	Food carry	0.78(0.06)	0.83(0.06)	-	0.61(0.08)	0.64(0.07)
	Nest build	0.66(0.07)	0.58(0.09)	0.70(0.08)	-	0.69(0.06)
	Burrow	0.72(0.06)	0.60(0.08)	0.71(0.07)	0.58(0.09)	-

342 The upper half of the matrix lists correlations from Model 1, the lower half correlations from Model 2. Reported values
 343 are means from the posterior samples (SD in parenthesis); parameters in bold indicate estimates where the 95%
 344 credible intervals do not span zero.

345

346 **Discussion**

347 Our results provide no indication that naked mole-rats in these captive groups specialise
348 temporarily or permanently in specific work-related tasks and instead suggest that within
349 individuals all work-related tasks correlate positively with each other. Overall, individuals show
350 variation in total activity levels that trade-off against resting duration, whereas investment in all
351 recorded behaviours, including burrowing, nest building and food carrying, correlate positively
352 with each other. As such, naked mole-rat non-breeders vary in their general commitment to
353 cooperative behaviour that may be linked to some differences in age, body size, metabolism and
354 group size. Their behavioural types can be characterised along a one-dimensional syndrome
355 varying from individuals that show long periods of activity and that engage frequently in all forms
356 of work-related cooperative behaviour to individuals that show shorter periods of activity and
357 engage less frequently in all forms of cooperative behaviour.

358 Our results do not support previous suggestions that naked mole-rats specialise on specific
359 tasks, either temporarily or permanently (Jarvis 1981, Jarvis et al. 1991, Lacey and Sherman
360 1991, Lacey and Sherman 1997). These studies inferred specialisation from size-related
361 variation in cooperative behaviour by showing that burrowing, nest building and food carrying
362 follow divergent size-dependent trends. However, the individuals were mostly of unknown age
363 and it has been found that size and age-related differences may not necessarily be the result of
364 specialisation, but instead are often consequences of the relative costs and benefits to
365 individuals at different life stages (McNamara and Houston 1996, Faulkes and Bennett 2016,
366 Zöttl et al. 2016a, Gilbert et al. 2020). The results of our study also represent a clear example
367 where size and age-related variation can exist despite a positive correlation of engagement in
368 different tasks within individuals. One of the most important studies advancing the case that
369 naked mole-rats may specialise on specific tasks used a principal component analysis to
370 investigate whether individuals specialise across territory defence, pup care and work-related
371 tasks and show that these three types of behaviours load on different axes (Mooney et al. 2015).
372 However, specialisation at the individual level may be expected to result in the loading of
373 different cooperative tasks with opposite directionality on the same axis and this has yet to be
374 shown. Our study was unable to assess how territory defence and pup carrying relates to other
375 cooperative tasks such as nest building, food carrying and burrowing because pup care
376 behaviour is only shown in times when offspring are very small and territory defence needs to be
377 elicited by introducing foreign conspecifics, predators or predator scent. Future research is now
378 needed to clarify how these behaviours relate to each other in a similar analytical framework as

379 we used in this study and to explicitly test whether the investment in pup care and territory
380 defence are traded-off against investment in other tasks at the individual level.

381 Although the idea of specialization of non-breeders in mole-rat species is interesting and has
382 attracted widespread attention, recent longitudinal studies suggest that individuals rarely
383 specialise. Mole-rats within the genera *Fukomys* and *Cryptomys* show body size related
384 changes in cooperative behaviour and individuals can vary widely in the frequency of burrowing
385 behaviour (Bennett and Jarvis 1988, Bennett 1990, Burda 1990, Bennett 1992, Jarvis et al.
386 1994, Spinks et al. 1999, Scantlebury et al. 2006). However, longitudinal studies of Damaraland
387 mole-rats of known ages have shown that individuals do not trade-off investment in cooperative
388 behaviours and that the general patterns of the distribution of cooperative behaviour across
389 individuals are similar to those of naked mole-rats shown in this study (Zöttl et al. 2016a, Thorley
390 et al. 2018, Zöttl et al. 2018, Gilbert et al. 2020). Evidence from field studies of other *Fukomys*
391 species also supports the notion that the behavioural similarity of mole-rats societies with
392 obligatorily eusocial insects has probably been overemphasized in the past and evidence for
393 specialisation, divergent developmental trajectories or bimodal trait distributions across
394 individuals are rare (Faulkes and Bennett 2016, Šklíba et al. 2016, Zöttl et al. 2016b, Van Daele
395 et al. 2019, Voigt et al. 2019).

396 Our results are consistent with growing evidence suggesting that the distribution of cooperative
397 behaviour across individuals in social mole-rat societies is similar to that of many other
398 cooperatively breeding mammals and birds. In most cooperatively breeding mammals and birds,
399 individuals vary in the overall commitment to cooperative behaviours. In meerkats and banded
400 mongooses, for example, different helping behaviours are positively correlated to each other and
401 divergent developmental trajectories are absent (Carter et al. 2014, Sanderson et al. 2015),
402 though individuals vary by age, sex and opportunities to breed (Clutton-Brock et al. 2001,
403 Clutton-Brock et al. 2003, Cant et al. 2016, Clutton-Brock and Manser 2016). Similarly, in
404 cooperatively breeding birds, individuals show positively co-varying variation across individuals
405 in specific cooperative tasks such as chick feeding and nest defence (van Asten et al. 2016,
406 Teunissen et al. 2020) and although some notable exceptions exist (Arnold et al. 2005), the
407 majority of studies suggest that across avian and mammalian cooperative breeders task
408 specialisation is rare.

409 Whereas most research on cooperatively breeding mammals is often limited to observational
410 data and relies on longitudinal studies of life-history variation, cooperatively breeding cichlids
411 have emerged as some of the most promising and innovative study systems to investigate
412 divergent developmental trajectories and individual specialisation among cooperatively breeding

413 vertebrates (Arnold and Taborsky 2010, Brintjes and Taborsky 2011, Taborsky et al. 2013,
414 Fischer et al. 2017). The reproductive ecology of these fish shares many of the characteristics
415 with cooperatively breeding birds and mammals. They live in stable groups with high
416 reproductive skew and up to 25 helpers that engage in different forms of cooperative behaviour
417 (Taborsky and Limberger 1981, Taborsky 1984, 1985). Helpers that vary in relatedness to the
418 breeders can either stay in the territory and help or disperse and breed independently (Taborsky
419 and Limberger 1981, Bergmuller et al. 2005, Dierkes et al. 2005, Heg et al. 2011, Hellmann et al.
420 2016), and cooperative behaviour is used to appease the dominant breeders and prevent
421 punishment and eviction (Bergmuller and Taborsky 2005, Zöttl et al. 2013b, Fischer et al. 2014,
422 Naef and Taborsky 2020). Experimental manipulations of the social environment and predation
423 pressure have long-lasting effects on the behavioural phenotype and the physiology of helpers
424 that may be related to variation life-histories and could adapt some individuals for extended
425 philopatry and others to dispersal (Taborsky et al. 2013, Fischer et al. 2015, Fischer et al. 2017,
426 Antunes et al. 2020), though it remains unclear whether divergent phenotypes are a result of
427 adaptation, or of developmental constraints, and whether long-lasting developmental effects
428 overshadow the capacity to adapt to stochastically arising breeding or dispersal opportunities
429 (Bergmuller et al. 2005, Zöttl et al. 2013a, English et al. 2015). In contrast to predictions about
430 the distribution of investment in specific tasks among specialised helpers, these cichlids show
431 positive correlations between territory defence and maintenance tasks (Le Vin et al. 2011), and it
432 remains unclear if developmental effects lead to some trade-offs between different tasks in
433 cooperatively breeding cichlids.

434 Our study suggests that burrowing frequency in naked mole-rats decreased with age and body
435 mass, which is consistent with recent research on age-related behavioural variation in naked
436 mole-rats (Gilbert et al. 2020). Nest building peaked at intermediate body mass at the age of two
437 years and food carrying increased in heavier individuals. These patterns are broadly similar to
438 those in Damaraland mole-rats, and the general decline of burrowing behaviour coincides with
439 the age and body mass at which individuals in the wild disperse from their natal group
440 (Hochberg et al. 2016, Zöttl et al. 2016a, Torrents-Ticó et al. 2018a). While breeders and non-
441 breeders show long lifespans in captivity (Dammann and Burda 2006, Buffenstein 2008, Schmidt
442 et al. 2013, Ruby et al. 2018), most non-breeders in the wild disappear from their natal groups
443 when they reach approximately 2-3 years of age, and subsequently either become breeders in a
444 new group or die during dispersal (but see Young et al. 2015, Hochberg et al. 2016,
445 Torrents-Ticó et al. 2018b). Those that remain in the group have been found to gain body mass
446 and become less active (Jarvis et al. 1991, O'Riain et al. 1996, Thorley et al. 2018). This

447 relationship is reflected in our groups, as male non-breeders rested more as they aged, and time
448 spent on most cooperative activities peaked at around 1.5-2 years or generally decreased with
449 age.

450 Our data reveal that sex differences in work-related cooperative behaviour of naked mole-rats
451 are minor and body mass and age-related patterns are broadly similar in male and female non-
452 breeding individuals. This is consistent with previous studies (Jarvis et al. 1991, Lacey and
453 Sherman 1997, Gilbert et al. 2020), and it is possible that as in other social mole-rats species,
454 sex-differences are limited to allo-parental care behaviour which we were unable to record in this
455 study (Bennett 1990, Zöttl et al. 2016a, Thorley et al. 2018, Zöttl et al. 2018). The lack of sex-
456 differences contrasts with the distribution of cooperative behaviours in many other cooperatively
457 breeding species where sex differences are common and often linked to sex differences in
458 philopatry (Clutton-Brock et al. 2002). In mole-rats the duration of philopatry differs only
459 marginally between males and females (Braude 2000, Hazell et al. 2000, Torrents-Ticó et al.
460 2018b, Hochberg et al. 2016) and could be the underlying reason for similar investment in
461 cooperative behaviour across both sexes in naked and other social mole-rat species. However,
462 many sex differences in the behaviour of mammals only manifest after sexual maturity, and an
463 alternative explanation for the lack of sex differences in naked mole-rat non-breeders is that non-
464 breeders are hormonally pre-pubescent and therefore show little sex-specific variation (Faulkes
465 et al. 1990, 1991 and 1994).

466 **Conclusion**

467 Naked and Damaraland mole-rats have been proposed to share many of the traits of the
468 obligatory eusocial insects, including task specialisation among workers. Our study suggests
469 that task specialisation among different work-related tasks does not occur, which is consistent
470 with recent studies on the distribution of cooperative behaviour among non-reproductive
471 individuals of other mole-rat species. In contrast, individuals that contribute more to a specific
472 task are also more likely to engage in a different task, suggesting that individuals primarily vary
473 in their overall investment in cooperative behaviour. Our data suggest that naked mole-rats show
474 similar behavioural organisation to other cooperatively breeding vertebrates where involvement
475 in different tasks is commonly positively correlated within individuals and that similarity to the
476 obligatorily eusocial insects has been overemphasized.

477 **Funding**

478 This research has been funded by a grant by the Crafoord Foundation (2018-2259) and by a
479 grant from the Swedish Research Council (2017-05296) to Markus Zöttl.

480 **Author contributions**

481 MZ conceived the study. SS and RF collected the data with assistance from all authors. SS
482 analysed the data. MZ and SS wrote the first draft of the paper. All authors commented and
483 edited the manuscript.

484 **Conflict of Interest**

485 We declare no conflict of interest.

486 **Significance statement**

487 It has been controversially discussed whether non-breeders in naked mole-rats belong to distinct
488 castes that specialise permanently or temporarily in specific cooperative tasks. In this paper we
489 show that non-breeding individuals vary in overall cooperative investment, but do not specialise
490 on specific work tasks. Our data provide no evidence for temporary specialisation and suggests
491 that the behavioural organisation of naked mole-rats resembles that of other cooperatively
492 breeding vertebrates more than that of eusocial insect species.

493

494 References

- 495
- 496 Antunes, D. F., M. Reyes-Contreras, G. Glauser and B. Taborsky (2020). "Early social experience has life-
- 497 long effects on baseline but not stress-induced cortisol levels in a cooperatively breeding fish." *Hormones*
- 498 *and Behaviour* **128**: 104910.
- 499 Arnold, C. and B. Taborsky (2010). "Social experience in early ontogeny has lasting effects on social skills
- 500 in cooperatively breeding cichlids." *Animal Behaviour* **79**: 621-630.
- 501 Arnold, K. E., I. P. Owens and A. W. Goldizen (2005). "Division of labour within cooperatively breeding
- 502 groups." *Behaviour* **142**(11-12): 1577-1590.
- 503 Balshine, S., B. Leach, F. Neat, H. Reid, M. Taborsky and N. Werner (2001). "Correlates of group size in a
- 504 cooperatively breeding cichlid fish (*Neolamprologus pulcher*)." *Behavioral Ecology and Sociobiology*
- 505 **50**(2): 134-140.
- 506 Bennett, N. (1990). "Behaviour and social organization in a colony of the Damaraland mole-rat
- 507 *Cryptomys damarensis*." *Journal of Zoology* **220**(2): 225-247.
- 508 Bennett, N. (1992). "The locomotory activity patterns of a functionally complete colony of *Cryptomys*
- 509 *hottentotus hottentotus* (Rodentia: Bathyergidae)." *Journal of Zoology* **228**(3): 435-443.
- 510 Bennett, N. C. and C. G. Faulkes (2000). African mole-rats: ecology and eusociality, Cambridge University
- 511 Press.
- 512 Bennett, N. C. and J. U. Jarvis (1988). "The social structure and reproductive biology of colonies of the
- 513 mole-rat, *Cryptomys damarensis* (Rodentia, Bathyergidae)." *Journal of Mammalogy* **69**(2): 293-302.
- 514 Bergmuller, R., D. Heg and M. Taborsky (2005). "Helpers in a cooperatively breeding cichlid stay and pay
- 515 or disperse and breed, depending on ecological constraints." *Proceedings of the Royal Society B:*
- 516 *Biological Sciences* **272**(1560): 325-331.
- 517 Bergmuller, R. and M. Taborsky (2005). "Experimental manipulation of helping in a cooperative breeder:
- 518 helpers 'pay to stay' by pre-emptive appeasement." *Animal Behaviour* **69**: 19-28.
- 519 Biedermann, P. H. and M. Taborsky (2011). "Larval helpers and age polyethism in ambrosia beetles."
- 520 *Proceedings of the National Academy of Sciences of the United States of America* **108**(41): 17064-17069.
- 521 Boomsma, J. J. (2013). "Beyond promiscuity: mate-choice commitments in social breeding." *Philosophical*
- 522 *Transactions of the Royal Society of London B: Biological Sciences* **368**(1613): 20120050.
- 523 Boomsma, J. J. and R. Gawne (2018). "Superorganismality and caste differentiation as points of no
- 524 return: how the major evolutionary transitions were lost in translation." *Biological Reviews* **93**(1): 28-54.
- 525 Bourke, A. (2011). Principles of Social Evolution, Oxford University Press.
- 526 Braude, S. (2000). "Dispersal and new colony formation in wild naked mole-rats: evidence against
- 527 inbreeding as the system of mating." *Behavioral Ecology* **11**(1): 7-12.
- 528 Braude, S., S. Holtze, S. Begall, J. Brenmoehl, H. Burda, P. Dammann, D. Del Marmol, E. Gorshkova, Y.
- 529 Henning and A. Hoeflich (2021). "Surprisingly long survival of premature conclusions about naked
- 530 mole-rat biology." *Biological Reviews* **96**: 376-393.
- 531 Brintjes, R. and M. Taborsky (2011). "Size-dependent task specialization in a cooperative cichlid in
- 532 response to experimental variation of demand." *Animal Behaviour* **81**: 387-394.
- 533 Buffenstein, R. (2008). "Negligible senescence in the longest living rodent, the naked mole-rat: insights
- 534 from a successfully aging species." *Journal of Comparative Physiology B* **178**(4): 439-445.
- 535 Burda, H. (1990). "Constraints of pregnancy and evolution of sociality in mole-rats with special reference
- 536 to reproductive and social patterns in *Cryptomys hottentotus* (Bathyergidae, Rodentia) 1." *Journal of*
- 537 *Zoological Systematics and Evolutionary Research* **28**(1): 26-39.
- 538 Burda, H., R. L. Honeycutt, S. Begall, O. Locker-Grütjen and A. Scharff (2000). "Are naked and common
- 539 mole-rats eusocial and if so, why?" *Behavioural Ecology and Sociobiology* **47**: 293-303.
- 540 Cant, M. A., H. J. Nichols, F. J. Thompson and E. I. Vitikainen (2016). "Banded mongooses: demography,
- 541 life history, and social behavior." In: *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution,*
- 542 *and Behavior*. W. D. Koenig and L. D. Janis (Eds.), Cambridge University Press: 318-337.

- 543 Carter, A. J., S. English and T. H. Clutton-Brock (2014). "Cooperative personalities and social niche
544 specialization in female meerkats." *Journal of Evolutionary Biology* **27**(5): 815-825.
- 545 Chittka, L. and H. Muller (2009). "Learning, specialization, efficiency and task allocation in social insects."
546 *Communicative & Integrative Biology* **2**(2): 151-154.
- 547 Clutton-Brock, T. H., P. N. M. Brotherton, M. J. O'Riain, A. S. Griffin, D. Gaynor, R. Kansky, L. Sharpe and
548 G. M. McIlrath (2001). "Contributions to cooperative rearing in meerkats." *Animal Behaviour* **61**: 705-
549 710.
- 550 Clutton-Brock, T. H. and M. Manser (2016). "Meerkats: cooperative breeding in the Kalahari." In:
551 *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior*. W. D. Koenig and J. L.
552 Dickinson (Eds.), Cambridge University Press: 294-317.
- 553 Clutton-Brock, T. H., A. F. Russell and L. L. Sharpe (2003). "Meerkat helpers do not specialize in particular
554 activities." *Animal Behaviour* **66**: 531-540.
- 555 Clutton-Brock, T. H., A. F. Russell, L. L. Sharpe, A. J. Young, Z. Balmforth and G. M. McIlrath (2002).
556 "Evolution and development of sex differences in cooperative behavior in meerkats." *Science* **297**(5579):
557 253-256.
- 558 Cockburn, A. (1998). "Evolution of helping behaviour in cooperatively breeding birds." *Annual Review of*
559 *Ecology, Evolution, and Systematics* **29**: 141-177.
- 560 Crespi, B. J. and D. Yanega (1995). "The definition of eusociality." *Behavioral Ecology* **6**(1): 109-115.
- 561 Dammann, P. and H. Burda (2006). "Sexual activity and reproduction delay ageing in a mammal." *Current*
562 *Biology* **16**(4): R117-R118.
- 563 Dierkes, P., D. Heg, M. Taborsky, E. Skubic and R. Achmann (2005). "Genetic relatedness in groups is sex-
564 specific and declines with age of helpers in a cooperatively breeding cichlid." *Ecology Letters* **8**(9): 968-
565 975.
- 566 English, S., L. E. Browning and N. J. Raihani (2015). "Developmental plasticity and social specialization in
567 cooperative societies." *Animal Behaviour* **106**: 37-42.
- 568 Faulkes, C., Abbott, D., and Jarvis, J. (1990). Social suppression of ovarian cyclicity in captive and wild
569 colonies of naked mole-rats, *Heterocephalus glaber*. *Reproduction* **88**(2): 559-568.
- 570 Faulkes, C., Abbott, D. and Jarvis, J. (1991). Social suppression of reproduction in male naked mole-rats,
571 *Heterocephalus glaber*. *Reproduction* **91**(2): 593-604.
- 572 Faulkes, C., Trowell, S., Jarvis, J., and Bennett, N. (1994). Investigation of numbers and motility of
573 spermatozoa in reproductively active and socially suppressed males of two eusocial African mole-rats,
574 the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Cryptomys damarensis*).
575 *Reproduction* **100**(2): 411-416.
- 576 Faulkes, C. G. and N. C. Bennett (2007). "African mole-rats: social and ecological diversity." In: *Rodent*
577 *Societies: an Ecological and Evolutionary Perspective*. J. O. Wolff and P. W. Sherman (Eds.), University of
578 Chicago Press: 427-437.
- 579 Faulkes, C. G. and N. C. Bennett (2016). "Damaraland and naked mole-rats: Convergence of social
580 evolution." In: *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior*. W. D.
581 Koenig and L. D. Janis (Eds.), Cambridge University Press: 338-352.
- 582 Fischer, S., M. Bessert-Nettelbeck, A. Kotschal and B. Taborsky (2015). "Rearing-group size determines
583 social competence and brain structure in a cooperatively breeding cichlid." *The American Naturalist*
584 **186**(1): 123-140.
- 585 Fischer, S., L. Bohn, E. Oberhammer, C. Nyman and B. Taborsky (2017). "Divergence of developmental
586 trajectories is triggered interactively by early social and ecological experience in a cooperative breeder."
587 *Proceedings of the National Academy of Sciences of the United States* **114**(44): E9300-E9307.
- 588 Fischer, S., M. Zöttl, F. Groenewoud and B. Taborsky (2014). "Group-size-dependent punishment of idle
589 subordinates in a cooperative breeder where helpers pay to stay." *Proceedings of the Royal Society B:*
590 *Biological Sciences* **281**(1789): 20140184.

591 Gilbert, J. D., S. J. Rossiter and C. G. Faulkes (2020). "The relationship between individual phenotype and
592 the division of labour in naked mole-rats: it's complicated." *PeerJ* **8**: e9891.

593 Hazell, R., N. Bennett, J. Jarvis and M. Griffin (2000). "Adult dispersal in the co-operatively breeding
594 Damaraland mole-rat (*Cryptomys damarensis*): a case study from the Waterberg region of Namibia."
595 *Journal of Zoology* **252**(1): 19-25.

596 Heg, D., S. Rothenberger and R. Schurch (2011). "Habitat saturation, benefits of philopatry, relatedness,
597 and the extent of co-operative breeding in a cichlid." *Behavioral Ecology* **22**(1): 82-92.

598 Heinsohn, R. and Legge, S. (1999). "The costs of helping." *Trends in Ecology and Evolution* **14**: 53-57.

599 Hellmann, J. K., M. G. Sovic, H. L. Gibbs, A. R. Reddon, C. M. O'Connor, I. Y. Ligocki, S. Marsh-Rollo, S.
600 Balshine and I. M. Hamilton (2016). "Within-group relatedness is correlated with colony-level social
601 structure and reproductive sharing in a social fish." *Molecular Ecology* **25**(16): 4001-4013.

602 Hochberg, M. E., R. J. Noble and S. Braude (2016). "A hypothesis to explain cancers in confined colonies
603 of naked mole rats." *BioRxiv*: 079012.

604 Houslay, T. M., P. Vulllioud, M. Zöttl and T. H. Clutton-Brock (2020). "Benefits of cooperation in captive
605 Damaraland mole-rats." *Behavioral Ecology* **31**(3): 711-718

606 Jarvis, J. U. and N. Bennett (1993). "Eusociality has evolved independently in two genera of bathyergid
607 mole-rats—but occurs in no other subterranean mammal." *Behavioral Ecology and Sociobiology* **33**(4):
608 253-260.

609 Jarvis, J. U., M. O'Riain and E. McDaid (1991). "Growth and factors affecting body size in naked mole-
610 rats." In: *The Biology of the Naked Mole-Rat*. P. W. Sherman, J. U. Jarvis and R. D. Alexander (Eds.),
611 Princeton University Press: 358-383.

612 Jarvis, J. U. (1981). "Eusociality in a mammal: Cooperative breeding in naked mole-rat colonies." *Science*
613 **212**(4494): 571-573.

614 Jarvis, J. U., M. J. O'Riain, N. C. Bennett and P. W. Sherman (1994). "Mammalian eusociality: a family
615 affair." *Trends in Ecology and Evolution* **9**(2): 47-51.

616 Koster, J. and R. McElreath (2017). "Multinomial analysis of behavior: statistical methods." *Behavioral*
617 *Ecology and Sociobiology* **71**(9): 138.

618 Lacey, E. A. and P. W. Sherman (1991). "Social organization of Naked Mole-Rat colonies: evidence for
619 divisions of labor." In: *The Biology of the Naked Mole-Rat*. P. W. Sherman, J. U. Jarvis and R. D. Alexander
620 (Eds.), Princeton University Press: 275-336.

621 Lacey, E. A. and P. W. Sherman (1997). "Cooperative breeding in naked mole-rats." In: *Cooperative*
622 *Breeding in Mammals*. N. G. Solomon and J. A. French (Eds.), Cambridge University Press: 267-301.

623 Le Vin, A. L., B. K. Mable, M. Taborsky, D. Heg and K. E. Arnold (2011). "Individual variation in helping in a
624 cooperative breeder: relatedness versus behavioural type." *Animal Behaviour* **82**: 467-477.

625 McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and Stan* (Second
626 Edition). CRC Press, <https://xcelab.net/rm/statistical-rethinking/>

627 McNamara, J. M. and A. I. Houston (1996). "State-dependent life histories." *Nature* **380**(6571): 215-221.

628 Mersch, D. P., A. Crespi and L. Keller (2013). "Tracking individuals shows spatial fidelity is a key regulator
629 of ant social organization." *Science* **340**(6136): 1090-1093.

630 Monnahan, C. C., J. T. Thorson and T. A. Branch (2017). "Faster estimation of Bayesian models in ecology
631 using Hamiltonian Monte Carlo." *Methods in Ecology and Evolution* **8**(3): 339-348.

632 Mooney, S. J., D. C. Filice, N. R. Douglas and M. M. Holmes (2015). "Task specialization and task switching
633 in eusocial mammals." *Animal Behaviour* **109**: 227-233.

634 Naef, J. and M. Taborsky (2020). "Commodity-specific punishment for experimentally induced defection
635 in cooperatively breeding fish." *Royal Society open science* **7**(2): 191808.

636 O'Riain, M. J., J. U. Jarvis and C. G. Faulkes (1996). "A dispersive morph in the naked mole-rat." *Nature*
637 **380**(6575): 619-621.

638 R Core Team (2020). R: A language and environment for statistical computing. R Foundation for
639 Statistical

640 Computing, Vienna, Austria, <https://www.R-project.org/>
641 Riccio, A. P. and B. D. Goldman (2000). "Circadian rhythms of locomotor activity in naked mole-rats
642 (*Heterocephalus glaber*)." *Physiology & Behavior* **71**(1-2): 1-13.
643 Ruby, J. G., M. Smith and R. Buffenstein (2018). "Naked mole-rat mortality rates defy Gompertzian laws
644 by not increasing with age." *elife* **7**: e31157.
645 Sanderson, J. L., I. Stott, A. J. Young, E. I. K. Vitikainen, S. J. Hodge and M. A. Cant (2015). "The origins of
646 consistent individual differences in cooperation in wild banded mongooses, *Mungos mungo*." *Animal*
647 *Behaviour* **107**: 193-200.
648 Scantlebury, M., J. Speakman, M. Oosthuizen, T. Roper and N. Bennett (2006). "Energetics reveals
649 physiologically distinct castes in a eusocial mammal." *Nature* **440**(7085): 795-797.
650 Schmidt, C. M., J. U. Jarvis and N. C. Bennett (2013). "The long-lived queen: reproduction and longevity in
651 female eusocial Damaraland mole-rats (*Fukomys damarensis*)." *African Zoology* **48**(1): 193-196.
652 Seeley, T. D. (1982). "Adaptive significance of the age polyethism schedule in honeybee colonies." *Behavioural Ecology and Sociobiology* **11**: 287-293.
653 Šklíba, J., M. Lövy, H. Burda and R. Šumbera (2016). "Variability of space-use patterns in a free living
654 eusocial rodent, Ansell's mole-rat indicates age-based rather than caste polyethism." *Scientific Reports* **6**:
655 37497.
656 Spinks, A. C., T. A. Branch, S. Croeser, N. C. Bennett and J. U. Jarvis (1999). "Foraging in wild and captive
657 colonies of the common mole-rat *Cryptomys hottentotus hottentotus* (*Rodentia: Bathyergidae*)." *Journal*
658 *of Zoology* **249**(2): 143-152.
659 Stan Development Team (2020). "RStan: the R interface to Stan." R package version 2.21.2, [http://mc-](http://mc-stan.org/)
660 [stan.org/](http://mc-stan.org/)
661 Taborsky, B., L. Tschirren, C. Meunier and N. Aubin-Horth (2013). "Stable reprogramming of brain
662 transcription profiles by the early social environment in a cooperatively breeding fish." *Proceedings of*
663 *the Royal Society B: Biological Sciences* **280**(1753): 20122605.
664 Taborsky, M. (1984). "Broodcare helpers in the cichlid fish *Lamprologus brichardi* - their costs and
665 benefits." *Animal Behaviour* **32**: 1236-1252.
666 Taborsky, M. (1985). "Breeder-helper conflict in a cichlid fish with broodcare helpers - an experimental
667 analysis." *Behaviour* **95**: 45-75.
668 Taborsky, M. and Limberger, D. (1981). "Helpers in Fish." *Behavioural Ecology and Sociobiology* **8**: 143-
669 145.
670 Taborsky, M. and Grantner, A. (1998). "Behavioural time-energy budgets of cooperatively breeding
671 *Neolamprologus pulcher* (Pisces: Cichlidae)." *Animal Behaviour* **56**: 1375-1382.
672 Teunissen, N., S. A. Kingma and A. Peters (2020). "Nest defence and offspring provisioning in a
673 cooperative bird: individual subordinates vary in total contribution, but no division of tasks among
674 breeders and subordinates." *Behavioral Ecology Sociobiology* **74**(7): 1-9.
675 Thorley, J., R. Mendonça, P. Vulllioud, M. Torrents-Ticó, M. Zöttl, D. Gaynor and T. Clutton-Brock (2018).
676 "No task specialization among helpers in Damaraland mole-rats." *Animal Behaviour* **143**: 9-24.
677 Torrents-Ticó, M., N. C. Bennett, J. U. Jarvis and M. Zöttl (2018a). "Growth affects dispersal success in
678 social mole-rats, but not the duration of philopatry." *Biology Letters* **14**(2): 20180005.
679 Torrents-Ticó, M., N. C. Bennett, J. U. Jarvis and M. Zöttl (2018b). "Sex differences in timing and context
680 of dispersal in Damaraland mole-rats (*Fukomys damarensis*)." *Journal of Zoology* **306**(4): 252-257.
681 van Asten, T., M. L. Hall and R. A. Mulder (2016). "Who cares? Effect of coping style and social context on
682 brood care and defense in superb fairy-wrens." *Behavioral Ecology*: arw096.
683 Van Daele, P. A., N. Desmet, R. Šumbera and D. Adriaens (2019). "Work behaviour and biting
684 performance in the cooperative breeding Micklem's mole-rat *Fukomys micklei* (*Bathyergidae*,
685 *Rodentia*)." *Mammalian Biology* **95**: 69-76.
686 Visser, J. H., N. C. Bennett and B. J. van Vuuren (2019). "Phylogeny and biogeography of the African
687 *Bathyergidae*: a review of patterns and processes." *PeerJ* **7**: e7730.
688

689 Voigt, C., A. Ter Maat and N. C. Bennett (2019). "No evidence for multimodal body mass distributions and
690 body mass-related capture order in wild-caught Damaraland mole-rats." *Mammalian Biology* **95**: 123-
691 126.

692 Watanabe, S. and M. Opper (2010). Asymptotic equivalence of Bayes cross validation and widely
693 applicable information criterion in singular learning theory. *Journal of Machine Learning Research* **11**:
694 3571-3594.

695 Watanabe, S. (2013). A widely applicable Bayesian information criterion. *Journal of Machine Learning*
696 *Research* **14**: 867-897.

697 Wilson, E. O. (1971). *The insect societies*, Bellknap Press.

698 Young, A. J., J. U. Jarvis, J. Barnaville and N. C. Bennett (2015). "Workforce Effects and the Evolution of
699 Complex Sociality in Wild Damaraland Mole Rats." *The American Naturalist* **186**(2): 302-311.

700 Zöttl, M., L. Chapuis, M. Freiburghaus and M. Taborsky (2013b). "Strategic reduction of help before
701 dispersal in a cooperative breeder." *Biology Letters* **9**(1): 20120878.

702 Zöttl, M., D. Heg, N. Chervet and M. Taborsky (2013a). "Kinship lowers alloparental care where helpers
703 pay-to-stay." *Nature Communications* **4**: 1341.

704 Zöttl, M., P. Vulllioud, K. Goddard, M. Torrents-Ticó, D. Gaynor, N. C. Bennett and T. Clutton-Brock (2018).
705 "Allo-parental care in Damaraland mole-rats is female biased and age dependent, though independent of
706 testosterone levels." *Physiology & Behavior* **193**: 149-153.

707 Zöttl, M., P. Vulllioud, R. Mendonça, M. T. Ticó, D. Gaynor, A. Mitchell and T. Clutton-Brock (2016a).
708 "Differences in cooperative behavior among Damaraland mole rats are consequences of an age-related
709 polyethism." *Proceedings of the National Academy of Sciences* **113**(37): 10382-10387.

710 Zöttl, M., Thorley, J., Gaynor, D., Bennett, N. C., & Clutton-Brock, T. (2016b). Variation in growth of
711 Damaraland mole-rats is explained by competition rather than by functional specialization for different
712 tasks. *Biology Letters*, 12(12).

713

714

715 **Figure Legends**

716

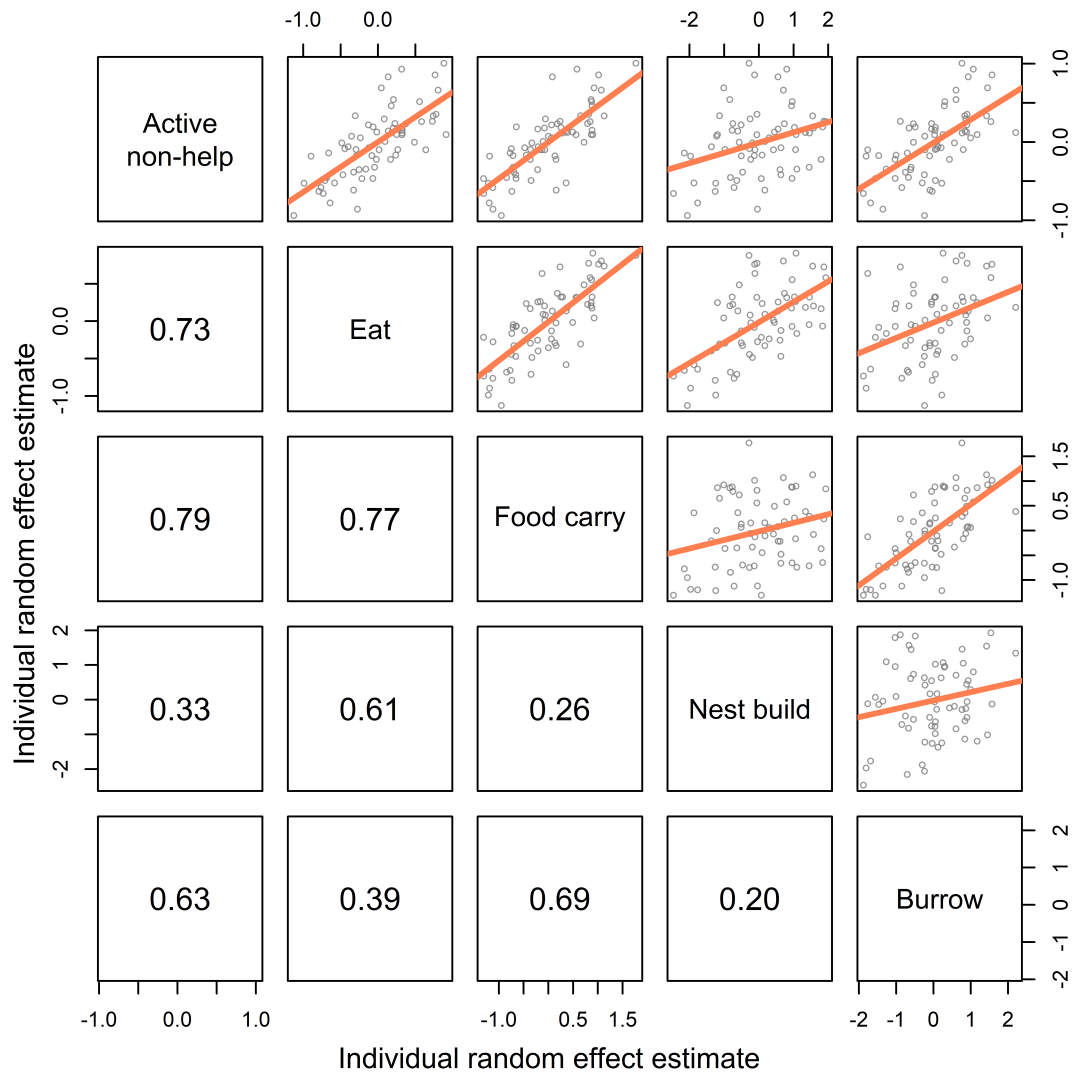
717 **Figure 1:** Within-individual random effects correlations from Model 2 for a) females and b) males. Values in the lower
718 half of the matrix represent the correlations between the median individual level intercept in the posterior samples for
719 each behaviour. They are therefore larger than the correlations presented in Table 2 that are taken directly from the
720 variance-covariance matrices of the posterior samples.

721 **Figure 2:** Model predictions of response behaviours as a function of body mass for **a)** females and **b)** males. All other
722 fixed covariates are held at the sample mean and predictions are made at the population level for individuals from
723 Vienna. Shaded regions show the 89% percentile intervals calculated from the posterior samples of Model 3 for each
724 sex.

725 **Figure 3:** Model predictions of response behaviours as a function of group size for **a)** females and **b)** males. All other
726 fixed covariates are held at the sample mean and predictions are made at the population level for individuals from
727 Vienna. Shaded regions show the 89% percentile intervals calculated from the posterior samples of Model 3 for each
728 sex.

729 **Figure 4:** Model predictions of response behaviours as a function of age for **a)** females and **b)** males. All other fixed
730 covariates are held at the sample mean. Shaded regions show the 89% percentile intervals calculated from the
731 posterior samples of Model 3a for each sex.

732 **Figure 5:** Model predictions of response behaviours as a function of sex (67 female non-breeders and 102 male non-
733 breeders). All other fixed covariates are held constant at the sample mean. The confidence intervals are the 89%
734 percentile intervals as calculated from the posterior samples of Model 3b.

(a)**(b)**