

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

2 Running title: No specialisation in naked mole-rats

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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.

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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  $7.0 \pm 1.5$  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  $38.3 \pm 12.3$  g (range 16-74  
165 g), with  $36.1 \pm 11.6$  g for females and  $39.8 \pm 12.5$  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  $216 \pm 61$  d, with a mean time of  $54 \pm 41$  d between sessions. In Pretoria, each  
182 group was observed on three consecutive days. Over all 43 sessions, a mean of  $161 \pm 69$   
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
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Total	169	31.0	4.5	1.8	3.0	22.7	37.0
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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	-	<b>0.59(0.09)</b>	<b>0.63(0.09)</b>	<b>0.58(0.09)</b>	<b>0.70(0.07)</b>
	Eat	<b>0.56(0.13)</b>	-	<b>0.66(0.11)</b>	<b>0.61(0.11)</b>	<b>0.35(0.12)</b>
	Food carry	<b>0.58(0.13)</b>	<b>0.58(0.14)</b>	-	<b>0.34(0.13)</b>	<b>0.61(0.10)</b>
	Nest build	0.22(0.14)	<b>0.45(0.15)</b>	0.13(0.17)	-	<b>0.43(0.11)</b>
	Burrow	<b>0.51(0.11)</b>	0.24(0.14)	<b>0.51(0.13)</b>	0.14(0.14)	-
Male	Active non-help	-	<b>0.60(0.08)</b>	<b>0.65(0.07)</b>	<b>0.78(0.05)</b>	<b>0.77(0.04)</b>
	Eat	<b>0.64(0.08)</b>	-	<b>0.84(0.06)</b>	<b>0.57(0.09)</b>	<b>0.61(0.08)</b>
	Food carry	<b>0.78(0.06)</b>	<b>0.83(0.06)</b>	-	<b>0.61(0.08)</b>	<b>0.64(0.07)</b>
	Nest build	<b>0.66(0.07)</b>	<b>0.58(0.09)</b>	<b>0.70(0.08)</b>	-	<b>0.69(0.06)</b>
	Burrow	<b>0.72(0.06)</b>	<b>0.60(0.08)</b>	<b>0.71(0.07)</b>	<b>0.58(0.09)</b>	-

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.

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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

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715 **Figure Legends**

716

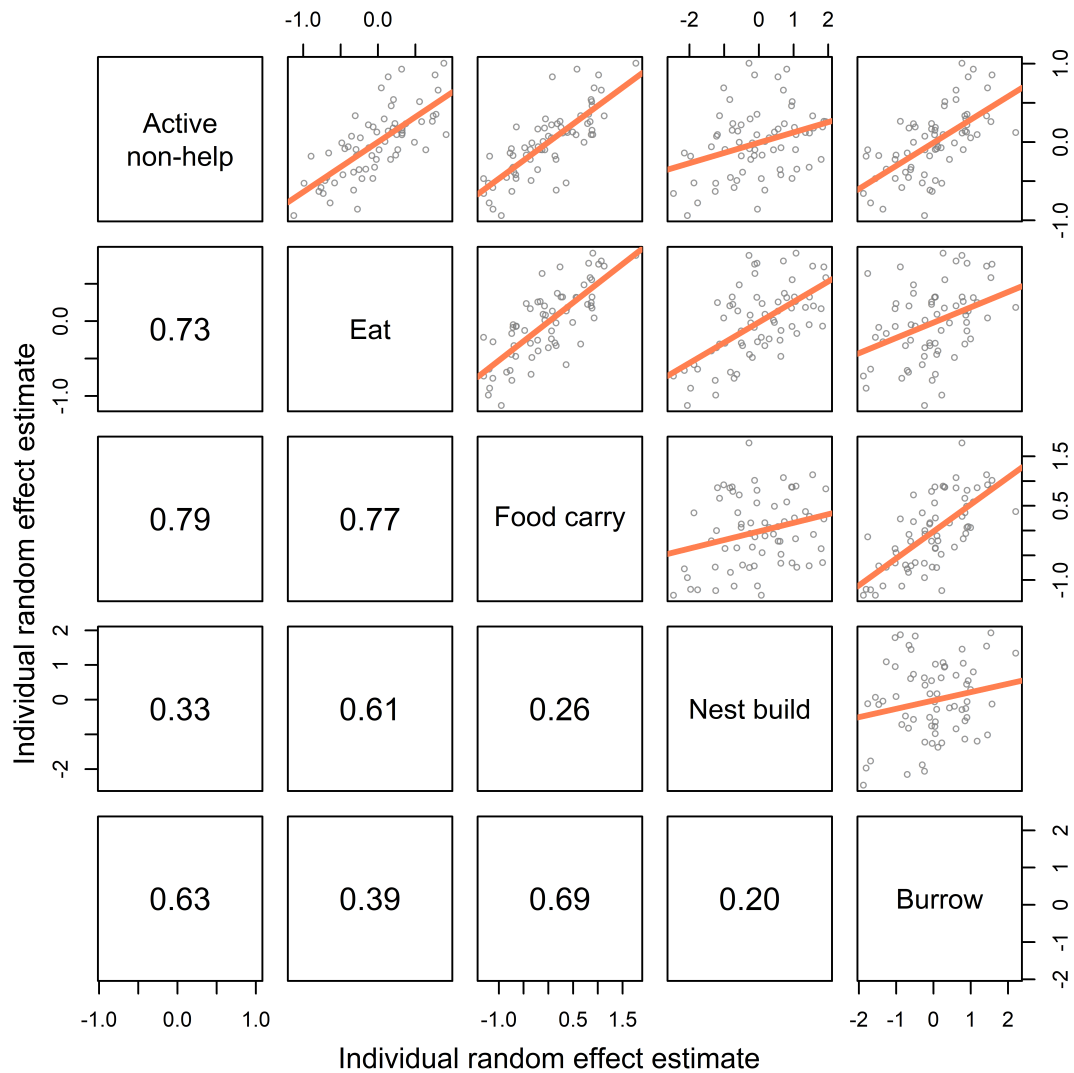
717 **Figure 1:** Within-individual random effects correlations from Model 2 for a) females and b) males. Values in the lower  
718 half of the matrix represent the correlations between the median individual level intercept in the posterior samples for  
719 each behaviour. They are therefore larger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