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HAL Authorization

1 **Females of solitary- and group-living sister species of African striped mice show a similar**
2 **social structure following experimentally imposed group-living**

3

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17 species of African striped mice show a similar social structure following experimentally imposed group-living.
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20

21

22 **Abstract**

23 Social systems vary within and between species, ranging along a continuum between solitary-
24 living to complex societies. Social systems are emergent properties of interactions between
25 individuals, and these interactions are often modulated by hormones. We investigated the
26 behavioral and hormonal consequences of experimentally imposed social grouping in two sister
27 species of the African striped mouse *Rhabdomys*, one of which (*R. pumilio*) is group-living in its
28 natural xeric environment, while the other (*R. dilectus*) is solitary-living in its mesic environment.
29 We compared social behavior of triads of age-matched, unfamiliar females of each species, and
30 measured their serum corticosterone and testosterone concentrations in comparison to solitary
31 housed controls. On Day 1, triads of both species displayed mainly amicable behavior. Aggression
32 was rare, but *R. pumilio* females showed more aggression than *R. dilectus* females. Triads of both
33 species shared nests from Day 2 onwards, and amicable behavior increased over time. Neither
34 species differed in hormonal concentration compared to their solitary controls, but *R. dilectus* had
35 1.3x higher serum corticosterone than *R. pumilio*. Serum testosterone did not differ between
36 species or treatments. Neither corticosterone nor testosterone concentration measured at the end
37 of the experiment was related to the duration of amicable behavior shown between triad members
38 at the end of the study. In sum, both species established a similar social structure when housed in
39 non-kin triads in captivity. Both displayed high amicability and little aggression, indicating that
40 environmental factors, such as resource distribution and duration of the breeding season, may be
41 more important determinants of social organization in striped mice than social tolerance.

42

43 **Keywords**

44 communal breeding, group formation, social behavior, solitary-living, group-living, social
45 flexibility

46

47 **Significance statement**

48 Variation in social systems occurs both between and within species, and to date, it is still poorly
49 understood how differences in social tolerance relate to inter-specific variation in social systems.

50 We experimentally imposed social grouping in females of two sister species of the African striped
51 mouse, one naturally group-living and one solitary-living species. We studied interactions between
52 individuals in these experimental groups over 21 days and measured testosterone and
53 corticosterone concentration at the end of the experiment. Both species mainly showed socio-
54 positive behavior and little aggression occurred. Individuals from experimental groups of both
55 species had similar testosterone and corticosterone concentrations compared to solitary-housed
56 control females of the same species. Our results show that both species are tolerant of conspecifics,
57 at least in captivity, indicating that environmental factors might be more important determinants
58 of social organization than social tolerance.

59

60 **Introduction**

61 Variation in social systems occurs both between and within species (Lott 1991; Kappeler et al.
62 2013). This variation is underpinned by the environmental conditions and is physiologically
63 mediated. The mechanisms leading to the formation of the observed variety of social systems are
64 still not well understood (Kappeler et al. 2013). The social system of a species is created by the
65 behavior of individuals, with whom they group (social organization), with whom and how they
66 interact (social structure), with whom they mate (mating system) and who they care for (care
67 system; Kappeler, 2019). One important component of all forms of sociality is the nature of the
68 interactions between individuals (Hinde 1976).

69 Group-living is typically associated with frequent interactions between group members and
70 these interactions can be both amicable (e.g. grooming, body contact) and agonistic (e.g. chasing,
71 fighting) (Silk 2007; Kappeler et al. 2013). Aggression can occur over access to resources or
72 mating partners, and to establish a social hierarchy (Creel 2001; Silk 2007). Group size can
73 influence rates of agonistic interactions, for example, occurrence of agonistic interactions between
74 female primates increases with group size (Wheeler et al. 2013). Typically, individuals are less
75 tolerant of unrelated individuals (especially of the same sex) than of relatives (Clutton-Brock
76 2016). Interactions between individuals of solitary species are generally less well-studied
77 (Kappeler and van Schaik 2002), but studies have revealed that great diversity exists also in solitary
78 mammals (Woodroffe and Macdonald 1993). For example, males of some solitary species form
79 alliances (Lührs and Kappeler 2013), some solitary foraging species form ‘spatial groups’ or
80 sleeping associations that are characterized by home-range overlap and friendly interactions
81 among members (Wiens and Zitzmann 2003; Dammhahn and Kappeler 2009; Lührs and Kappeler
82 2013; Graw et al. 2019), and others show social tolerance at food or water sources (Elbroch et al.

83 2017; Tichon et al. 2020). There is a dynamic feedback between how constituent individuals
84 behave towards each other, which leads to a particular social organization of a population, and in
85 turn affects the behavior of individuals in that population (Kappeler and van Schaik 2002; Schradin
86 et al. 2018). To date, it is still poorly understood how differences in social tolerance relate to inter-
87 specific variation in social systems.

88 While external drivers underpin social interactions, various internal factors, such as
89 hormones and neuropeptides, modulate interactions between individuals (McCall and Singer 2012;
90 Hofmann et al. 2014). Testosterone is an important modulator of social interactions, influencing
91 aggression, territory defense, sexual behavior, and is itself influenced by social status (Staub and
92 De Beer 1997; Soto-Gamboa et al. 2005). Some species show increased testosterone secretion in
93 response to social interactions, and high concentration of testosterone can be linked to social
94 aggression (Wingfield et al. 1990; Goymann et al. 2007; Tibbetts and Crocker 2014). Testosterone
95 also potentially increases risk-taking behavior because of its association with inhibition of the
96 hypothalamus-pituitary-adrenal (HPA) axis that reduces anxiety (Aikey et al. 2002; McCall and
97 Singer 2012; Raynaud and Schradin 2014). Glucocorticoid hormones, corticosterone or cortisol,
98 are released via stimulation of the HPA axis in response to stressors, for example aggression from
99 a conspecific (Sapolsky et al. 2000). Glucocorticoid hormones mobilize glucose to provide energy
100 in response to stressors, and increased circulating levels are considered as a stress response
101 (Rubenstein 2007). It has been proposed that a generalized endocrine profile of chronic stress does
102 not exist, but social stress is associated with a glucocorticoid increase in many species (Zayan
103 1991; Dickens and Romero 2013). Solitary and social species experience social stress differently
104 (Blanchard et al. 2001). For example, several social primate species mount a stress response when
105 separated from conspecifics (Zayan 1991), and female yearling tuco-tuco, *Ctenomys sociabilis*,

106 that live and breed alone have higher glucocorticoid levels than females that live and breed within
107 their natal group (Woodruff et al. 2013). In contrast, solitary species can experience stress in
108 response to social interactions with conspecifics, such as in the golden hamster, *M. auratus*, which
109 experiences immune-system decline in groups, with a shorter life span as group size increases
110 (Wommack et al. 2003). Moreover, group-living animals can experience social buffering,
111 displaying reduced corticosterone response to a stressful situation due to the presence of
112 conspecifics to which they are socially bonded, potentially via inhibition of the HPA axis (Sachser
113 et al. 1998; Hennessy et al. 2009; Young et al. 2014).

114 The African striped mouse, genus *Rhabdomys*, is a small (adult body mass 30 - 90g)
115 diurnal, murid rodent, widely distributed throughout southern Africa, occurring in a variety of
116 biomes from semi-arid deserts (160 mm rainfall per annum) to moist grasslands (700-1000 mm
117 rainfall per annum) (Skinner and Chimimba 2005). Our study considers two closely related species
118 of *Rhabdomys*: *R. pumilio* occurring in xeric environments and *R. dilectus* in mesic areas of South
119 Africa (Rambau et al. 2003). Molecular data places the divergence between the species at
120 approximately 3.1 million years ago (du Toit et al. 2012). Distinct differences in sociality exist
121 between these species in nature. *R. pumilio* in the arid Succulent Karoo is facultatively group-
122 living (Schradin and Pillay 2003, 2004), and is socially flexible, switching to solitary-living under
123 very low population density during the breeding season (but not during the non-breeding season)
124 (Schradin et al. 2010a, 2012). In free-living *R. pumilio*, individuals of both sexes have lower
125 corticosterone concentrations after switching from group-living to solitary-living during the
126 breeding season (Schoepf and Schradin 2013). Female *R. pumilio* which breed solitarily have
127 lower baseline corticosterone concentrations when compared to their group-living counterparts,
128 but do not differ in testosterone concentrations (Hill et al. 2015). Weanling *R. pumilio* show a more

129 pronounced stress response to separation from their natal group compared to weanling *R. dilectus*,
130 indicating that philopatry and group-living may be more important for young *R. pumilio* compared
131 to young *R. dilectus* that typically disperse at weaning (Mackay et al. 2014). The grassland species,
132 *R. dilectus*, is solitary-living, with individual home ranges overlapping mainly with home ranges
133 of the opposite sex (Schradin and Pillay 2005). While variation in hormonal response in *R. pumilio*
134 has been well investigated, a comparison of the hormonal profile with the closely related *R.*
135 *dilectus* is lacking.

136 In this study we investigated 1) whether *R. dilectus*, a naturally solitary-living species,
137 tolerates conspecifics and forms groups under experimental conditions, 2) whether social
138 interactions differ between both species and how interactions change over time when
139 experimentally kept in groups, and 3) how circulating corticosterone and testosterone
140 concentrations correlate with social behaviors and the social contexts (imposed group-living vs
141 solitary-housed). First, we investigated whether or not three unrelated, unfamiliar conspecific
142 female *Rhabdomys* display the social tolerance necessary to facilitate and initiate social group
143 formation, and whether tolerance (nest sharing and amicability) of conspecifics is maintained over
144 time in each species (referred to as stable groups in this study). We predicted that *R. pumilio* triads
145 show less aggression and more amicable behavior compared to *R. dilectus* triads, and that these
146 differences would occur already at the beginning of nest cohabitation. We hypothesized that
147 associating with conspecifics would be more stressful physiologically for *R. dilectus* than *R.*
148 *pumilio*. We predicted that 1) social groups of both species would have greater concentrations of
149 corticosterone and testosterone than solitary-housed controls of both species, due to social stress
150 and competition experienced in groups, 2) testosterone and corticosterone concentrations to

151 correlate positively with aggression and to be higher in the more aggressive triads and species, and
152 3) testosterone and corticosterone concentrations to correlate negatively with amicable behavior.

153

154 **Materials and Methods**

155 *Study Species*

156 In the semi-arid Succulent Karoo, *R. pumilio* is facultatively group-living and usually forms social
157 groups that consist of one breeding male, up to four closely related breeding females and their
158 philopatric offspring (Schradin and Pillay 2003, 2004). Group members share a nest, interact
159 amicably and bask together at dawn and dusk, and defend a common territory, but forage solitarily
160 during the day (Schradin and Pillay 2005). *R. pumilio* is socially flexible, switching to solitary-
161 living under very low population density during the breeding season, but not during the non-
162 breeding season (Schradin et al. 2010a, 2012). Individuals of both sexes have lower corticosterone
163 concentrations when solitary than in a group (Schoepf and Schradin 2013). Female *R. pumilio*
164 which breed solitarily have lower baseline corticosterone concentrations when compared to their
165 group-living counterparts, but the solitary breeders do not differ from the group-living females in
166 testosterone concentrations (Hill et al. 2015).

167 The grassland species, *R. dilectus*, is solitary-living, with individual home ranges
168 overlapping mainly with home ranges of the opposite sex (Schradin and Pillay 2005). *R. dilectus*
169 occurs at lower population density than *R. pumilio*, indicating that lower population density
170 promotes solitary-living (Schradin and Pillay 2005). The breeding season (7 months; October to
171 April) of *R. dilectus* is more than double that of *R. pumilio* (3 months; August to November)
172 (Schradin and Pillay 2005; Skinner and Chimimba 2005).

173

174 *Study Animals*

175 Experiments took place in the Milner Park Animal Unit at the University of the Witwatersrand,
176 Johannesburg, South Africa. The striped mice used in this study were from existing captive
177 colonies. The naturally group-living species, *Rhabdomys pumilio*, originated from the Goegap
178 Nature Reserve in the semi-arid Succulent Karoo of South Africa (average rainfall of 160 mm per
179 annum, winter rainfall). The naturally solitary-living species, *Rhabdomys dilectus*, originated from
180 the moist grassland in central South Africa (average rainfall of 700 mm per annum, summer
181 rainfall). All individuals were F2 or F3 captive born.

182

183 *Husbandry*

184 We conducted experiments under partially controlled environmental conditions: 14:10 light: dark
185 cycle (lights on at 05h00); 30-60% rH; and a room temperature of 24-28°C. We randomly formed
186 approximately 40 breeding pairs per species simultaneously before experiments began. Breeding
187 pairs were housed in clear Labotec™ cages (L x H x W: 425mm x 150mm x 240mm), containing
188 a PVC nest-box (L x H x W: 98mm × 64mm × 77mm), ±3cm wood shavings, a handful of
189 *Eragrostis* grass (± 20g) and ± 5g of paper tissue provided for nesting material. We provided a
190 cardboard tube (L x D: 99mm x 38mm) and a small wooden block for chewing for enrichment.
191 The daily diet included 5g Epol® mouse cubes, approximately 5g fresh fruit or vegetables and
192 approximately 2g millet per mouse (millet was gradually increased to 4g for pregnant and lactating
193 females); water was provided *ad libitum*.

194 At 20 days of age, pups produced from the breeding pairs were weaned and housed alone
195 for a further 30 days in Labotec™ cages, furnished and enriched as described. *R. dilectus* young
196 typically disperse at weaning (around day 16), whereas *R. pumilio* young typically delay dispersal,

197 although they disperse earlier when population density is low (Willan and Meester 1989; Schradin
198 and Pillay 2004; Schradin 2005; Schoepf and Schradin 2012a). Thus, solitary living at young age
199 occurs naturally in both species. From these juveniles, we used a total of 40 *R. pumilio* and 40 *R.*
200 *dilectus* females in this study. We focused our study on females because groups in *R. pumilio* are
201 usually made up of multiple breeding females with one breeding male (Schradin et al. 2012).

202

203 *Experimental design*

204 At approximately 43 days of age (one week prior to forming triads), we marked all striped mice
205 using commercial hair dye (Innecto™, Pinetown, South Africa) to allow for individual
206 identification. We assigned three unrelated, age-matched conspecific females randomly to a triad,
207 and we formed a total of 10 triads per species. Each triad was housed together from approximately
208 50 days old to approximately 85 days old in an aluminum tank with a clear Perspex front (L x H x
209 W: 460mm x 350mm x 300mm) and a wire-mesh lid. These tanks contained wood shavings for
210 bedding, and grass and nesting material, as described under husbandry (above). Tanks contained
211 three separate nest boxes of equal size (L x H x W: 100mm x 77mm x 63.5mm) to prevent forced
212 cohabitation of the triad. The feeding regime followed the diet described above. Before we initiated
213 behavioral data collection, we directly observed interactions for 20 min immediately after
214 introducing the three mice into experimental tanks on Day 1, so that triads could be terminated if
215 excessive fights occurred. We observed no fights in any of the triads during this period. Following
216 this 20-minute direct observation period, we filmed the triads from 09h00-12h00 using Sony
217 Handycam® video cameras; striped mice are most active during this period (Pillay 2000). We
218 filmed triads on Days 1, 3, 6, 10, 15, and 21 of triad formation and we manually scored the behavior
219 of females (Table S1) from video footage using a stopwatch. It was not possible to score behavior

220 blindly for several reasons: due to the timing of birth within a species that allowed triad formation
221 to start earlier for *R. pumilio* than for *R. dilectus*, because the same researchers were responsible
222 for husbandry, individual markings, triad formation and filming and scoring of behavior; and
223 because the marking of mice was visible in the video recordings. As age-matched controls for
224 hormonal comparison to triads (below), we maintained ten females per species in solitary housing
225 from 50 to 85 days of age. We marked these individuals and placed them in new cages on the same
226 days as experimental triads. Control animals were housed in Labotec™ cages prepared as
227 described above.

228 To investigate the initiation of group formation in the two species, we scored the three
229 hours (09h00-12h00) of footage from Day 1 of triad formation, recording the frequency of all
230 interactions between all members of the triad. We recorded dyadic interactions between members
231 of each triad, including which animal initiated an interaction, which mouse they initiated the
232 interaction toward, the manner of the approach (amicable or aggressive), and the response
233 (aggressive or avoidance) of the approached mouse (Table S1). We calculated the frequency of
234 aggressive approaches, amicable approaches, avoidance, and aggressive responses to an approach
235 from these data from Day 1 (behaviors defined in Table S1).

236 We scored the duration of amicable and aggressive interactions between dyads within each
237 triad from the video footage recorded on Days 1, 3, 6, 10, 15 and 21 of experimental triad
238 formation, and we recorded the presence of nest cohabitation from direct observation. We recorded
239 the duration of behaviors continuously for 15-minutes during the period of most activity of the
240 three hours of video footage recorded for all triads on the 6 non-consecutive days over the 21-days
241 of sampling. We used the same 15 min slots for each triad. We recorded nest cohabitation (yes/no)
242 using direct observation at times when the mice were resting or asleep, usually between 14h00-

243 15h00. This was done every day following the formation of triads and we used this information to
244 confirm whether group formation had occurred in a triad (Schradin et al. 2010b; Schoepf and
245 Schradin 2012b).

246 At approximately Day 35 (85 days of age), we euthanized all subjects (triads and controls)
247 through isoflurane inhalation and collected blood to measure serum corticosterone and
248 testosterone. Mice were euthanized and blood collected within 2-3 minutes of first handling to
249 minimize the effect of the stress of handling on the circulating corticosterone concentrations. Mice
250 were confirmed dead by testing for a pulse, then immediately decapitated and we collected
251 approximately 500 μ L of blood in an Eppendorf™ tube from the trunk of the animal. Following
252 the methods described by Schradin (2008), we kept blood samples at room temperature for 1.5
253 hours to allow for coagulation before being centrifuged at 8000 rpm for 10 minutes. Subsequently,
254 we pipetted the serum into another Eppendorf™ tube and centrifuged for a further 10 minutes at
255 8000 rpm. We then pipetted the serum into two different aliquots (20 μ L of serum for
256 corticosterone, and 50 μ L for testosterone) which were stored at -20°C. We measured hormone
257 concentrations using enzyme-immunoassays, performed at the University of Strasbourg, France,
258 using commercial kits from IBL Hamburg, specific to each hormone, following the procedures
259 validated for striped mice by (Schradin 2008). For both hormones, serial dilution of striped mouse
260 sample pools (2 for each hormone) paralleled the standard curve and the slopes were not different
261 (Schradin 2008). Intra- and inter-assay variability was determined with pools from wild striped
262 mice. For testosterone, inter-assay variability for one pool with 6 samples was 15.6%. For
263 corticosterone, inter-assay variability (5 samples) for two pools were 11.5% and 15.6%. Intra-
264 assay variability was only determined for corticosterone for both pools and was 10.2% (5 samples)
265 and 4.6% (8 samples). Hormone concentrations are expressed as ng/ml of serum.

266

267 *Data analysis*

268 We analyzed all data in R v.3.6.2 (R Core Team 2019). We calculated the percentage of triads that
269 shared a nest for each species and used a Fisher's Exact Test to assess whether the species differed
270 in nest cohabitation. We terminated one *R. dilectus* triad on Day 4 due to excessive fighting, and
271 the video footage of one *R. pumilio* triad was corrupted and not available for analysis of behavioral
272 interactions. We did not consider the *R. pumilio* triad in the data analysis of the Day 1 interactions
273 and excluded both triads from the analysis of the behavior over the 21-day sampling period,
274 resulting in data set of n = 9 triads for both species for these analyses. However, we included both
275 triads in the nest cohabitation percentage calculation. For the hormonal analysis, we excluded the
276 *R. dilectus* triad that was terminated early, and thus we analyzed data from 9 *R. dilectus* triads (n
277 = 27 individuals), 10 *R. pumilio* triads (n = 30 individuals), and 10 individually-housed controls
278 per species.

279

280 Interactions on Day 1 of triad formation

281 We analyzed the frequency of the type of approaches (amicable or aggressive) and responses to an
282 approach (aggressive or avoidance) on Day 1 using a multivariate analysis of variance
283 (MANOVA). We used the square-root of the approach and response behaviors to reduce
284 heteroscedasticity. We included species as a categorical predictor and we used the frequency of
285 aggressive approaches, amicable approaches, avoidance of approaches, and aggressive responses
286 to approaches as multiple response variables. We assessed species differences in the proportion of
287 aggressive approaches to amicable approaches and the proportion of avoidance behavior to
288 aggressive responses using Fisher's Exact Tests for Count Data.

289

290 Behavior during 6 non-consecutive days of sampling over 21 days

291 We used linear mixed models (LMMs), using ‘lme4’ package (Bates and Maechler 2010), to
292 analyze species differences and temporal changes in the duration of amicable and aggressive
293 behavior displayed during the 6 days of observation during 3 weeks of the study. We fitted two
294 LMMs, one for each behavior, with either aggression or amicable behavior as the response
295 variable, and species and Day, and the interaction between species and Day as fixed factors in the
296 model. We included Triad ID as a random effect. We used Wald Chi-square tests (type III) to
297 calculate χ^2 statistics and *p* values using the ‘car’ package (Fox and Weisberg 2011). We assessed
298 model assumptions by inspecting Q–Q plots and by plotting model residuals against fitted values.
299 Prior to running each model, we checked for multi-collinearity by calculating variance inflation
300 factors (Zuur et al. 2010) for the predictor variables using the ‘vif’ function in the ‘car’ package
301 (Fox and Weisberg 2011). Vifs did not indicate collinearity (all vifs<2).

302

303 Hormone concentrations

304 We analyzed the influence of species and treatment on corticosterone and testosterone
305 concentrations using a LMM per hormone with Gaussian error structure. We used the square root
306 of testosterone to reduce heteroscedasticity when fitting the model. In both models, we included
307 species, treatment and their interaction as fixed factors. We included treatment group ID (i.e. triad
308 and control group) and litter ID as random effects. We included litter ID to account for the litter
309 from which females were derived having possible influences on group dynamics, as litter mates
310 were assigned to different triads or as controls. We then performed post-hoc analyses using the
311 ‘emmeans’ function from the ‘emmeans’ package (Lenth 2021) to determine pairwise differences

312 in hormone levels between species and treatment groups. We adjusted p values using the Tukey
313 method. Since corticosterone suppresses testosterone secretion in some species (Soto-Gamboa et
314 al. 2005; Deviche et al. 2014), we used a Pearson's product-moment correlation to assess whether
315 the two hormones were correlated ($n = 77$).

316 To establish the relationship between the hormonal profiles and social behavior, we
317 calculated the total duration of amicable and aggressive behavior shown by each of the 18 triads
318 during the 15-minute observation slot on Day 21, which were the behavioral data collected closest
319 in time to when the endocrine measurements were taken. Both species showed no aggressive
320 behavior on Day 21, and thus we did not examine the relationship between aggressive behavior
321 and endocrine levels. We fitted two LMMs with Gaussian error structure. We used hormone
322 concentration (corticosterone or square root of testosterone) as the response variable and included
323 the duration of amicable behavior on Day 21, its quadratic term, species, and the interaction
324 between behavior and species as fixed factors.. We included triad ID as random effect in both
325 LMMs. We checked model assumptions by inspecting Q–Q plots and by plotting model residuals
326 against fitted values and by using the ‘performance’ package (Lüdecke et al. 2021).

327

328 **Results**

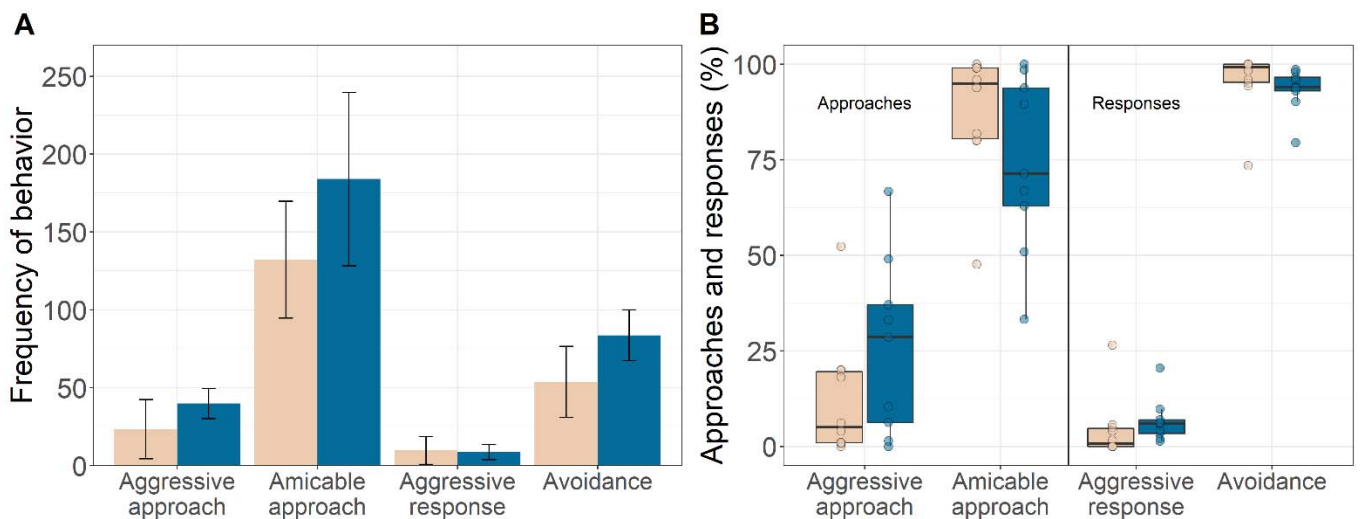
329 Females of both species cohabited nests, with all three females sharing one nest from Day 2 for
330 100% of *R. pumilio* triads (10 of 10 triads) and 90% of *R. dilectus* triads (9 of 10 triads; Fisher's
331 Exact Test: $p > 0.99$). One *R. dilectus* triad did not cohabit a nest and was terminated on Day 4 due
332 to excessive fighting.

333

334 Interactions on Day 1 of triad formation

335 Species was not a significant predictor ($F_{1,14} = 1.03$, $p = 0.43$) of the type of approaches and
 336 responses to an approach on Day 1 of triad formation (Fig. 1A). Triads of *R. pumilio* showed a
 337 total of 2015 approaches (359 aggressive and 1656 amicable approaches) and triads of *R. dilectus*
 338 showed a total of 1556 approaches (234 aggressive and 1322 amicable approaches). Triads of *R.*
 339 *pumilio* showed a total of 832 responses (753 avoidance and 79 aggressive responses) and triads
 340 of *R. dilectus* showed a total of 635 responses (538 avoidance and 97 aggressive responses). There
 341 was a species difference in the proportion of aggressive approaches to amicable approaches
 342 (Fisher's Exact Test for Count Data: $P = 0.03$, odds ratio = 1.22, 95% CI = 1.02 – 1.47; Fig. 1B)
 343 and in the proportion of avoidance behavior to aggressive responses ($P = 0.0009$, odds ratio = 1.72,
 344 95% CI = 1.24 – 2.39; Fig. 1B). Both species showed more amicable approaches than aggressive
 345 approaches, but in *R. pumilio* proportions were more skewed towards aggressive approaches
 346 compared to *R. dilectus* (Fig. 1B). Both species showed more often avoidance behavior compared
 347 to aggressive responses, and again, in *R. pumilio* proportions were more skewed towards
 348 aggressive responses compared *R. dilectus* (Fig. 1B).

349
 350



351

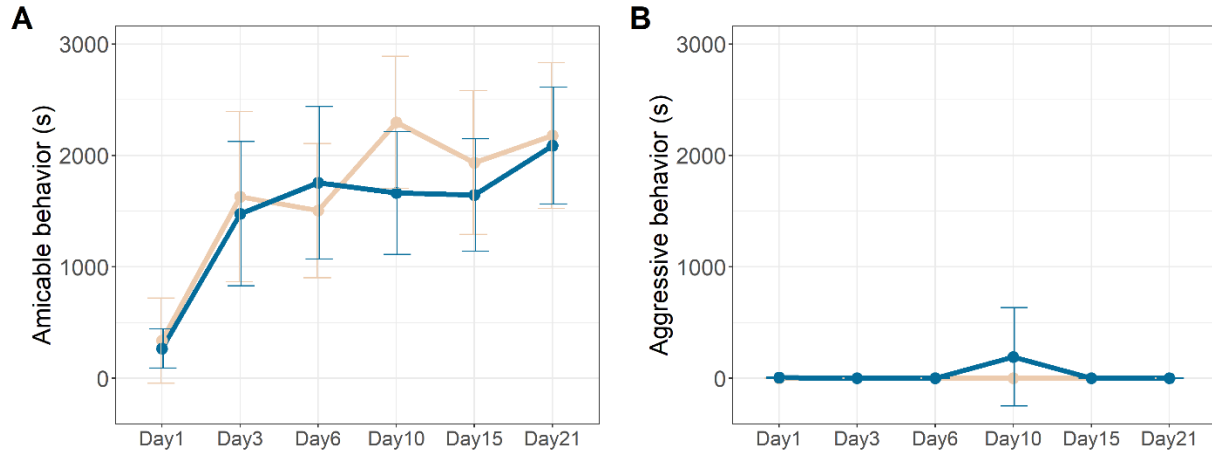
352 **Fig 1** Aggressive and amicable approaches, aggressive responses and avoidance behavior between
353 triad members on Day 1 (observation of 3 hrs) of triad formation in two species of *Rhabdomys*
354 (beige = solitary *R. dilectus*, blue = group-living *R. pumilio*). (A) Frequencies of approaches and
355 responses are shown. Columns indicate mean frequency and error bars show the standard error.
356 (B) Percentages of approaches (aggressive vs. amicable) and responses (aggressive vs. avoidance)
357 are shown. Boxplot center line represents the median, lower and upper box limits represent the 1st
358 and 3rd quartile (IQR), whiskers minimum and maximum values of nonoutlier data ($\pm 1.5 \times \text{IQR}$)
359 and outliers are indicated by small filled circles (n = 10 for *R. dilectus* triads, n = 9 for *R. pumilio*
360 triads)

361

362 Behavior over 21 days

363 Species was not a significant predictor of amicable behavior duration ($\chi^2_1 = 0.04$, $p = 0.83$), nor
364 was there a significant interaction between species and Day ($\chi^2_5 = 4.49$, $p = 0.48$). Day was a
365 significant predictor of duration of amicable behavior ($\chi^2_5 = 53.56$, $p < 0.001$; Fig. 2A). Post hoc
366 tests revealed that amicable behavior duration was significantly lower on Day 1 than the
367 subsequent days ($p < 0.0001$), and the duration of amicable behavior on Day 21 was significantly
368 greater than on Day 3 ($p = 0.01$) and Day 6 ($p = 0.02$; Fig. 2). In both species, amicable behavior
369 occurred more frequently than aggressive behavior during the study (Fig. 2B). Species ($\chi^2_1 = 0.009$,
370 $p = 0.92$), Day ($\chi^2_5 = 0.00$, $p = 1.00$) and their interaction ($\chi^2_5 = 5.55$, $p = 0.35$; Fig. 2B) did not
371 affect aggressive behavior.

372



373

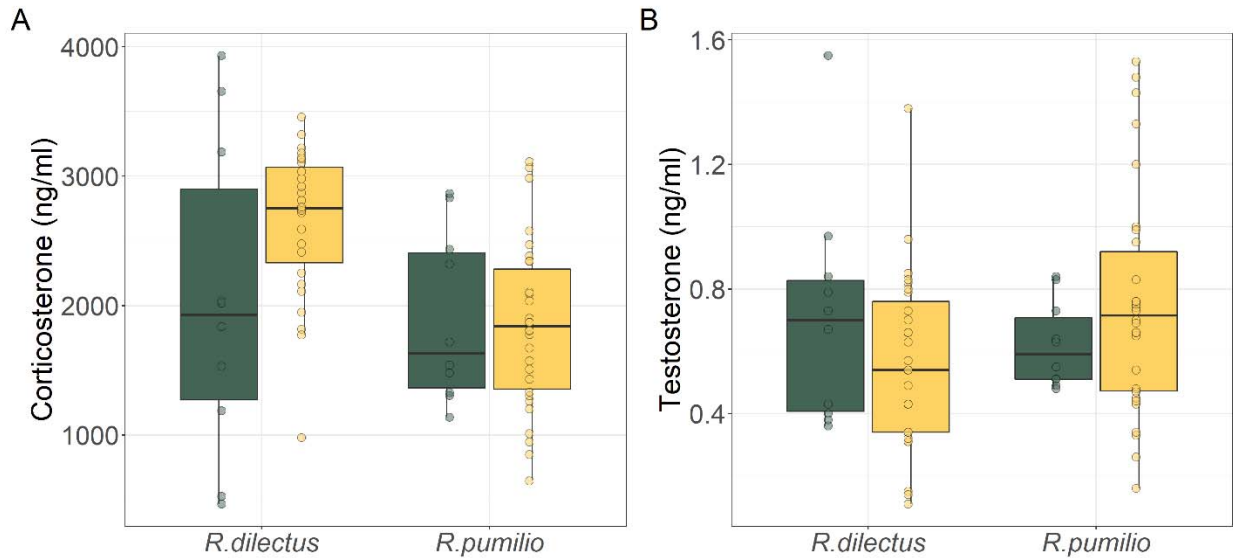
374 **Fig. 2** Duration of (A) amicable and (B) aggressive behavior of two species of *Rhabdomys* (*R.*
 375 *pumilio* in blue and *R. dilectus* in beige) housed in triads over 21 days. Data (15 min observations
 376 per day) are displayed as mean and 95% confidence interval

377

378 Hormone concentrations

379 Testosterone and corticosterone were not correlated (Pearson's product-moment correlation: $t = -$
 380 1.42, $df = 75$, $p = 0.15$, $r = -0.16$). Species ($\chi^2_1 = 3.86$; $p = 0.049$) was a significant predictor of
 381 circulating corticosterone concentrations. *R. dilectus* had higher corticosterone concentrations
 382 (mean \pm SD: control: 2038.2 ± 1215.7 ng/ml, triad: 2644.7 ± 566.7 ng/ml) than *R. pumilio* (control:
 383 1896.4 ± 655.9 ng/ml, triad: 1838.2 ± 641.0 ng/ml). Treatment ($\chi^2_1 = 1.06$; $p = 0.30$) was not a
 384 predictor of corticosterone concentrations, nor was there an interaction between species and
 385 treatment ($\chi^2_1 = 2.09$; $p = 0.14$). Pairwise comparisons of corticosterone concentrations between
 386 species and treatment groups showed no significant differences (all $P > 0.09$; Fig. 3A). Both species
 387 had similar testosterone concentrations (*R. dilectus*: control: 0.71 ± 0.36 ng/ml, triad: 0.56 ± 0.28
 388 ng/ml; *R. pumilio*: control: 0.62 ± 0.13 ng/ml, triad 0.75 ± 0.36 ng/m). Testosterone concentration

389 was not significantly predicted by species ($\chi^2_1 = 1.70$; $p = 0.19$), treatment ($\chi^2_1 = 0.11$; $p = 0.76$),
390 or an interaction between species and treatment ($\chi^2_1 = 2.08$; $p = 0.14$; Fig. 3B).
391



392
393 **Fig 3** Serum (A) corticosterone and (B) testosterone concentrations of two species of *Rhabdomys*.
394 Comparisons are shown between two treatments: triads (in yellow) and solitary-housed females
395 (controls, in green). Boxplots show median values as well as 1st and 3rd quartiles and points
396 represent individual values ($n = 27$ for *R. dilectus* triads, $n = 30$ for *R. pumilio* triads, $n = 10$ for
397 controls of each species)
398

399 Neither corticosterone nor testosterone concentration showed a relationship with the
400 duration of amicable behavior shown between triad members on Day 21 (Table 1; Fig. 4).

401
402 **Table 1** Results of the linear mixed models to test for an association between the total duration of
403 amicable behavior shown in a triad on Day 21 and corticosterone and testosterone concentration

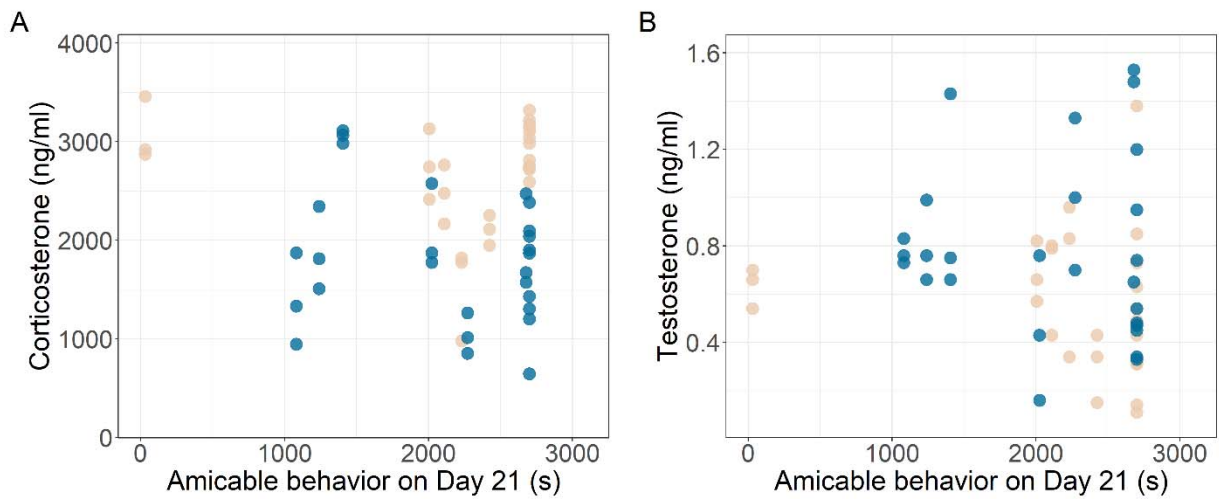
404 of two species of *Rhabdomys*. Factors in bold type indicate significant predictors of hormone
 405 concentration

<i>Predictors</i>	Corticosterone			Testosterone		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	2545	2060 – 3031	<0.0001	0.74	0.62 – 0.87	<0.0001
Duration amicable behavior on Day21	16	-426 – 457	0.945	-0.05	-0.16 – 0.06	0.386
Duration amicable behavior on Day21 ²	82	-59 – 324	0.505	-0.01	-0.07 – 0.05	0.703
Species[<i>R. pumilio</i>]	-797	-1345 – -248	0.004	0.12	-0.02 – 0.26	0.081
Random Effects						
σ^2 / ICC	144398 / 0.66			0.03 / 0.23		
Marginal R ² / Conditional R ²	0.317 / 0.767			0.119 / 0.323		

406 σ^2 = variance of the random effect ‘triad’; ICC = Intraclass coefficient of variation.
 407 The marginal R² considers only the variance of the fixed effects, while the conditional R² takes
 408 both the fixed and random effects into account.

409

410



411

412 **Fig 4** Serum corticosterone and testosterone concentrations in relationship to the duration of
413 amicable behavior on Day 21 in triads of two species of *Rhabdomys* (*R. pumilio* in blue and *R.*
414 *dilectus* in beige).

415

416 **Discussion**

417 Surprisingly, females of both the group-living and the solitary-living species of the African striped
418 mice formed stable non-kin groups characterized by amicable interactions with corticosterone and
419 testosterone levels comparable to their solitary controls. Overall, aggression was rare and both
420 species showed more amicable approaches than aggressive approaches and more avoidance
421 behavior than aggressive responses. But in *R. pumilio* proportions were more skewed towards
422 aggressive approaches and aggressive responses compared *R. dilectus*.

423 Nest cohabitation occurred in all *R. pumilio* triads and 90% of *R. dilectus* triads, and in all
424 those triads already by the second day of triad formation. Nest cohabitation was then maintained
425 for the remaining duration of the study. We had not expected the naturally solitary-living *R.*
426 *dilectus* to form groups as readily as the natural group-living *R. pumilio*. Sharing a nest with
427 conspecifics requires social tolerance and is often used as an indication of group-living (Andrews
428 and Belknap 1993; Rusu and Krackow 2004; Schradin et al. 2010a; Schoepf and Schradin 2012b).
429 Our study thus indicates that differences in the social organization between both *Rhabdomys*
430 species under natural conditions may not be due to species differences in social tolerance. The
431 similarity in social interactions between both species implies that environmental factors, such as
432 resource distribution and the duration of the breeding season, could be more important
433 determinants of social organization in free-living *Rhabdomys* than social tolerance (Schradin 2005;
434 Schradin and Pillay 2005). However, we studied both species in a single context (non-kin triads)

435 and results may vary if, for example, the number of animals per cage was decreased or increased,
436 in the presence of a male or when studied under semi-natural conditions.

437 We expected *R. pumilio* to be more tolerant of conspecifics than *R. dilectus*, but initially
438 on Day 1 *R. pumilio* showed a higher proportion of aggressive approaches and aggressive
439 responses toward conspecifics than *R. dilectus*. Naturally occurring groups of *R. pumilio* typically
440 consist of extended family members (Schradin and Pillay 2004), which are territorially aggressive
441 towards striped mice of other groups (Schradin 2004), so using unrelated females here may have
442 promoted aggression on Day 1. Importantly, amicable behavior was also common on Day 1 and
443 consistently increased in the first week after the mice started cohabiting, remaining high
444 throughout the second and third week of the study. Behaviors such as allogrooming facilitates
445 social recognition of group members (Kerth 2007) and the increasing duration of amicable
446 behavior between group members over time may be the result of increased familiarity between
447 group members. Importantly, amicable behavior was the predominant behavior displayed in triads
448 of both *Rhabdomys* species, indicating not only social tolerance but social attraction facilitating
449 group formation in both species. Female free-tailed bats, *Tadarida teniotis*, are more amicable
450 toward familiar than unfamiliar conspecifics (Ancillotto and Russo 2014). Similarly, meadow
451 voles, *M. pennsylvanicus*, that form unrelated communal nesting groups in winter, reduce agonistic
452 and increase amicable interactions toward group-members, but display heightened aggression
453 toward unfamiliar non-group members (Kawata 1990). In captivity, but not in the wild, meadow
454 voles readily form partner preferences for both same-sex and opposite-sex conspecifics (Beery et
455 al. 2009; Madrid et al. 2020). These differences in behavior between captive and wild individuals
456 of the same species show that animals in captivity may exhibit behaviors that they do not normally
457 exhibit under free-living conditions, highlighting the need to study species both in captivity and in

458 the wild. It is important to note that the use of non-kin may have resulted in fewer differences
459 between the species because neither species lived in their typical social organization (solitary or
460 with extended family members), and it would be important to repeat this study using related
461 females.

462 We expected *R. dilectus* to be more physiologically stressed during associations with
463 conspecifics than *R. pumilio*, expressed as higher corticosterone concentrations in triads compared
464 to solitary housed females. We found no support for this prediction, and triads of both species had
465 similar corticosterone levels as solitary-housed controls of their own species.

466 With the exception of one *R. pumilio* triad, little aggression occurred after Day 1, which
467 prevented analysis of the relationship between aggressive behavior and hormonal profiles.
468 Testosterone was not related to amicable behavior. We expected triads to have greater
469 concentrations of testosterone than solitary-housed controls of both species, due to competition
470 within groups. However, there was no difference in circulating testosterone concentrations
471 between the two species, regardless of social setting (triad vs. solitary control). Similarly, previous
472 studies found no differences in testosterone concentration between solitary and group-living
473 female *R. pumilio* (Schoepf and Schradin 2013; Hill et al. 2015). Together these studies do not
474 support the hypothesis that testosterone has an important role in the regulation of social behavior
475 of female *Rhabdomys*. However, it may be important to repeatedly measure testosterone
476 throughout the process of triad formation when most aggression occurred to better assess species
477 differences. It has been proposed that, in females, selection may have favored independence of
478 aggression from testosterone concentration because elevated concentrations of testosterone could
479 interfere with normal ovulation or produce detrimental maternal effects, such as a decrease in the
480 expression of maternal behavior (Gandelman 1973; Svare 1980; O'Neal et al. 2008). Similar to

481 findings in many other mammalian and avian species, our results indicate that female aggression
482 might be independent of testosterone in contrast to male aggression (Payne and Swanson 1972;
483 Elekonich and Wingfield 2000; Davis and Marler 2003; Sannen et al. 2004; Jawor et al. 2006;
484 Littlefield 2010).

485 Inter-specific variation does not only occur in social systems, but also in hormone levels
486 (Guindre-Parker 2018). Inter-specific variation in testosterone levels is best explained by
487 differences in breeding season length and mating system (Husak et al. 2021). While mean
488 testosterone levels can vary between 0 and 5 ng/ml in mammals (Husak et al. 2021), variation in
489 glucocorticoid levels is more extreme (Chrousos et al. 1982; Guindre-Parker 2018). For example
490 catarrhine primates have cortisol levels of around 300 ng/ml and some platyrrhine primates have
491 1000-2000 ng/ml (Chrousos et al. 1982; Coe and Levine 1995). Similarly, house mice (*Mus*
492 *musculus*) have basal corticosterone levels of between 100 and 150 ng/ml (Veenema et al. 2003),
493 prairie voles (*Microtus ochrogaster*) of between 630 and 850 ng/ml (DeVries et al. 1995), while
494 female striped mice (*R. pumilio*) have up to 2000 ng/ml during the breeding season (Schradin 2008;
495 Hill et al. 2020). While several studies investigated inter-specific differences in stress response
496 (Crespi et al. 2013), understanding variation in basal glucocorticoid levels received less attention
497 (Guindre-Parker 2018; Schoenemann and Bonier 2018). One important first question would be
498 whether very high basal levels observed in one species also occur in closely related species from
499 another environment, allowing for an assessment of phylogeny versus environment on basal levels
500 of glucocorticoids. We show that both *Rhabdomys* species have corticosterone concentrations that
501 are higher than those of most mammals, indicating that the high corticosterone concentrations are
502 a phylogenetic remnant of a common ancestor and we predict that other *Rhabdomys* species will
503 share this trait with the two species examined here. Comparative studies of basal glucocorticoid

504 levels in mammals would be needed to address why some species have such high basal
505 glucocorticoid levels.

506

507 *Conclusion*

508 Ours is one of few studies assessing how social structure develops when two sister species, that
509 naturally differ in their social organization, are experimentally forced to live in groups.
510 Surprisingly, we found a very similar social structure in both species, characterized by high
511 amicability and little aggression, making cohabitation possible in 19 out of 20 triads. Whether *R.*
512 *dilectus* shows flexibility in its social organization under natural conditions, similar to *R. pumilio*,
513 is unknown and needs to be studied in the future, but here we showed that this species has the
514 capacity to do so. Ongoing studies in some parts of its range provide anecdotal information of *R.*
515 *dilectus* sometimes forming small social groups, but the reasons for, and the demographic
516 composition of, such group-living are not always apparent (Dufour et al. 2019).

517

518 **Supplementary Information** Supplementary material is available

519

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524

525 **Author's contributions**

526 KJH and NP conceptualized the project and designed experiments; KJH and CC collected data;
527 KJH and CC coded behavioral data; CS measured hormone concentrations; KJH and RR
528 performed statistical analyses; KJH and RR drafted the initial version of the manuscript and all
529 authors gave final approval for publication; NP and CS raised financial support.

530

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534

535 **Data availability** All data analyzed during this study are included as supplementary information
536 files.

537

538 **Code availability** Code will be uploaded as supplementary material during revision or upon
539 acceptance.

540

541 **Declarations**

542 **Conflict of interest**

543 The authors declare that they have no conflict of interest.

544

545 **Ethical approval**

546 All animal protocols adhered to the guidelines set forth by the Animal Behaviour
547 Society/Association for the Study of Animal Behaviour. This study was approved by the animal
548 ethics screening committee at the University of the Witwatersrand (AESC number: 2012/28/2A).

549

550 **Consent to participate** Not applicable.

551

552 **Consent for publication** Not applicable.

553

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