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HAL Authorization

Bachelor groups form due to individual choices or environmental disrupters in African striped mice

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ABSTRACT

16

In several mammal species, bachelor groups occur as a regular life history stage between dispersal and
17 becoming the breeding male of a multi-female group. However, it is rarely investigated how such
18 groups come into existence and how males that choose this strategy differ in life history traits from
19 other males. Males of the socially flexible African striped mouse *Rhabdomys pumilio* have been
20 historically reported to adopt one of three alternative tactics, i.e., small group-living philopatric males,
21 intermediate solitary living roaming males, or large group-living territorial males. Here, we describe
22 for the first time, bachelors as a fourth male tactic. Using long-term data from 13 generations of striped
23 mice we show that there are in fact two types of bachelor groups: first, kin bachelor groups formed
24 when all females disappeared, probably due to predation; and second non-kin bachelor groups formed
25 by unrelated males that originate from different groups. Whereas kin bachelor groups occurred more
26 frequently during the non-breeding season, non-kin bachelor groups were most common in the
27 breeding season and had a shorter tenure, since most of these males soon switched to the solitary
28 roaming tactic or the territorial breeder tactic. Importantly, we found that non-kin bachelors were
29 heavier and older than kin bachelors and that they did not differ from solitary roaming males in body
30 mass and age. In summary, we identified two different forms of bachelor groups, kin bachelors whose
31 female group members disappeared and larger non-kin bachelor groups showing traits of an
32 alternative reproductive tactic. Both types of bachelor groups differed in multiple traits, demonstrating
33 that it is important to follow the life histories of individuals to understand the mechanisms leading to
34 alternative tactics.

35

Keywords: alternative reproductive tactics; male-male groups; reproductive success; social flexibility;
36 strategy; thermoregulation

37

38 INTRODUCTION

39 The social organisation of a species describes its composition of social units and is an important part
40 of its social system (Kappeler 2019; Kappeler & Schaik 2002). Species vary in their social organisation
41 from solitary to pair- and- group-living (Shultz, Opie & Atkinson 2011). Variation also occurs within
42 species, especially when both males and females follow alternative social tactics (Lott 1991; Schradin
43 2013). Social organisation can be sex-specific; for example, herd living females and mainly solitary
44 males in African elephants (*Loxodonta africana*), (O'Connell-Rodwell et al. 2011) as well as some
45 artiodactyls (Jaeggi et al. 2020). Groups of bachelor males are another example of a sex specific form
46 of social organisation and have been described mainly in medium sized to large mammals.

47 While there is no generally agreed upon definition of bachelor males, we regard all groups that consist
48 of males only as bachelor groups, independent of the (often unknown) reproductive consequences of
49 being a bachelor male (Roberts 2017), but excluding male groups that meet primarily for mating and
50 breeding, such as leks (Westcott 1994) and colonies (Robisson, Aubin & Bremond 1993). In many
51 species, larger males monopolise access to groups of breeding females. Since the sex ratio in mammals
52 at birth is close to 1:1, the remaining males must live either solitarily or form bachelor groups that
53 consist of males with low competitive abilities as exemplified in species such as Hanuman langurs
54 (*Semnopithecus entellus*; Koenig & Borries 2001), geladas (*Theropithecus gelada*; le Roux & Bergman
55 2012), white rhinoceros (*Ceratotherium simum*; Gartlan 1974), and many antelopes (Jarman 1974;
56 Wirtz 1982). In these species, there is often only one big competitive breeding male per female group,
57 and the remaining males are evicted by the dominant male from the groups at adolescence, being
58 forced into bachelor groups for predator avoidance (Waterman 1997). Bachelor groups seem to occur
59 mainly in mammals, although some have been reported in other taxa. In eider ducks (*Somatetria*
60 *mollissima*) males leave the females after mating and form bachelor groups, while females incubate
61 alone and raise chicks in creches (Burton & Burton 1969). Reports for small mammals below 1kg, which
62 represent the majority of all mammal species, are also rare. The smallest mammal known to have
63 bachelor groups are Cape ground squirrels with a body mass of about 1 kg (Waterman 1997; Wirtz
64 1982).

65 Bachelor males are often overlooked in behavioural studies, even where their existence has been
66 observed. For example, in patas monkeys (*Erythrocebus patas*), bachelor groups have been known for
67 decades (Gartlan 1974) but have received rather little attention thereafter (Ohsawa 2003).
68 Subsequently, the mechanisms leading to the formation of bachelor groups are rarely studied, since in
69 most species it is simply assumed to be an automatically occurring life history stage of waiting males.
70 However, becoming a bachelor is not obligate in all species where bachelor groups occur, and studying
71 how bachelors differ from other males might help us to understand why males choose the bachelor
72 tactic over an alternative tactic. Two possibilities may theoretically give rise to bachelor groups. 1)
73 Environmental disrupters (Schradin 2013) can lead to the formation of bachelor groups when all
74 females of a group die and leave only males behind. While the existence of such bachelor groups would
75 require no further evolutionary explanation as males become bachelors due to stochastic extrinsic
76 factors and not due to individual choice; the observed behaviour of males remaining in a group after
77 all females disappear would still be considered a tactic, albeit, arising from a different mechanism. 2)
78 Alternatively, males could leave mixed sex groups to form bachelor groups. In such instances,
79 evolutionary explanations would be required to give insights into why males choose to leave their
80 groups, why they would prefer to form a bachelor group instead of being solitary and how this
81 ultimately influences their fitness. It has previously been shown that distinguishing whether females
82 chose a solitary breeding tactic or became solitary due to the death of all other group females
83 (environmental disrupter) has important consequences for understanding differences in body mass
84 and stress hormone levels (Hill, Pillay & Schradin 2015a, b).

85 Here we report, to our knowledge for the first time, the occurrence of bachelor males in a mammal
86 with a body mass below 100 g, namely the socially flexible striped mouse *Rhabdomys pumilio* from the
87 arid Succulent Karoo (Schradin et al. 2012). In this species, males can follow alternative social and

88 reproductive tactics (Schradin et al. 2009a). Males are born in the spring breeding season and remain
89 philopatric within their natal group throughout the dry non-breeding season in summer. In the
90 following winter and the spring breeding season, some males remain philopatric, but most males leave
91 their natal group, either becoming solitary living roamers or the breeders of groups of communally
92 breeding females (Schradin et al 2009). Philopatric males are the smallest males with very low
93 reproductive success, breeders the largest males with highest reproductive success, and roamers lie
94 in-between (Schradin & Lindholm 2011). Switching to a tactic of higher reproductive success is
95 associated with having reached a larger body mass and thus higher competitive ability (Schradin &
96 Lindholm 2011). Group-living is associated with thermoregulatory benefits of sharing a nest
97 (Scantlebury et al. 2006), but striped mice are solitary foragers (Schradin & Pillay 2004).

98 The aim of our study was to determine the origin of bachelor groups in African striped mice, and
99 whether bachelor males have traits indicating they represent a waiting tactic (without reproduction)
100 or whether they could represent an alternative reproductive tactic (ART). We expected to identify two
101 types of bachelor males: 1. kin bachelor groups due to environmental disrupters (Schradin 2013), i.e.,
102 cases where all female group members had disappeared, leaving the small philopatric males and the
103 breeding male. 2. non-kin bachelor groups consisting of unrelated males originating from different
104 groups. If non-kin bachelor males represent an ART, we hypothesised that they would be scrotal
105 (sexually mature) and occur mainly during the breeding season. We predicted that males of non-kin
106 bachelor groups (but not of bachelor groups arising from environmental disrupters) would be heavier
107 (more competitive) than philopatric males but lighter than breeding males and would be similar in
108 mass to roaming males. We further predicted non-kin bachelors to be more common when population
109 density is high and the adult sex ratio is male biased, since both would increase competition between
110 males, potentially causing males to leave their natal group and form bachelor groups. Finally, we
111 expected bachelor males to switch to the roaming or breeding tactic when their body mass increased,
112 an indicator of increased competitiveness. We predicted that switching from the bachelor tactic should
113 happen first in former breeding males of kin groups (which are already heavy when the bachelor group
114 forms), then non-kin bachelors (predicted to be of intermediate body mass when becoming a
115 bachelor), and finally in philopatric kin males.

116

117 **MATERIAL AND METHODS**

118 *Study site and period*

119 The study was conducted at the Succulent Karoo Research Station (SKRS) at the Goegap Nature
120 Reserve in the Northern Cape Province, South Africa (S29 41.712 E18 01.5, altitude 912 m). This study
121 site receives an average annual rainfall of approximately 160 mm, predominantly in the winter months,
122 where night temperatures often fall below 0°C, whereas summers are typically hot and dry with
123 temperatures reaching approximately 40°C (Schradin and Pillay 2005a). The field site is characterized
124 by sandy areas and patchy bush/shrub distribution (Schradin and Pillay 2004). Data were collected
125 monthly from January 2006 until December 2019, with the exception of April-June 2006.

126 *Trapping, marking, radio-tracking and observation of striped mice*

127 Individuals were live-trapped using Sherman-like metal traps (26x9x9 cm; Schradin and Pillay 2004).
128 Traps were baited using a mixture of bran flakes, raisins, sea salt and sunflower oil. The traps were
129 placed next to bushes containing the nesting sites of groups or roaming individuals. Trapping was done
130 in the early mornings and in the late afternoons but not during the hottest times of the day, when
131 striped mice are mostly inactive (Schradin *et al.* 2007). Body mass measurements were taken during
132 both the morning and afternoon trapping sessions, but for this study, only the morning measurements
133 were used for analysis (mice are heavier in the afternoon due to foraging). Traps were checked every
134 30-45 minutes and trapped mice were weighed (to within 1g until August 2010, and to 0.1g thereafter)
135 using an electronic scale. Males were categorized as either scrotal (testes descended) or non-scrotal
136 (testes inside abdomen; Schradin and Pillay 2005b). Each mouse was marked with two ear tags

137 (National Band and Tag, Newport, KY, USA) and with a unique colour combination of hair dye (Inecto
138 Rapid, Pinetown, South Africa) for identification during behavioural observations. This dye is not
139 known to have any negative effects on the behaviour of striped mice or increase risk of predation
140 (Schradin 2006). Over the years, we monitored between 11 and 16 groups (mean \pm standard deviation;
141 13 ± 1.68). By marking most mice as juveniles, it was possible to record the groups from which most
142 bachelor males originated. Old and unmarked males were assumed to have originated from outside
143 our study site (immigrants); they were ear tagged and marked when they joined the study population.

144 In each group, at least one breeding female was fitted with a radio-collar throughout the year. In
145 addition, during the breeding season, all breeding males, solitary roaming males, and males whose
146 group association was unknown carried radio-collars (Schradin and Pillay 2005b). Individuals were
147 tracked twice a day (alternating morning/afternoon and at night), five times a week, using an AOR
148 8000 wide range receiver and a Telonics RA-14K antenna. By tracking individuals to their nesting sites
149 at night, it was possible to record group composition, to identify the males in each group, and to locate
150 nesting sites for behavioural observations of mice not carrying radio-transmitters.

151 Striped mice typically bask in the sun when they emerge from their nests at sunrise and when they
152 return from foraging at sunset. During this time, it is possible to identify group members due to their
153 individual markings with hair dye, and thus to record group composition. Groups and individuals were
154 directly observed in the mornings (sunrise) and afternoons (sunset) in front of their nests. Each group
155 or individual was observed for two to three consecutive days (both mornings and afternoons), and at
156 least once every two weeks. Observations lasted for 30 to 45 minutes.

157 *Determination of male tactics*

158 A combination of trapping, radio-tracking and direct observations was used to determine the tactics
159 followed by individual males. If males had previously been trapped at a group as juveniles (body mass
160 $< 25\text{g}$) and still trapped as adults in the same group, they were considered philopatric to this group
161 (Schradin and Yuen 2011; Schoepf and Schradin 2012a). Breeding males were identified as the heaviest
162 scrotal male in its non-natal group; there was never more than one non-natal male per group. Males
163 not sharing a nest with any other mice were considered as solitary roamers (Schradin *et al.* 2012). Two
164 or more males sharing a nest with each other, without any female group member, were identified as
165 bachelor males. Bachelor males were assigned to one of three categories according to relatedness and
166 how the bachelor groups were formed: 1) Kin bachelors: all female members of a group disappeared,
167 leaving behind males, which were related to each other (originate from the same group); 2) Related
168 males of one group which had left their natal group to form a bachelor group. Since this was only
169 observed in one instance where two related males left their natal group to form a bachelor group,
170 these two males were included into the first category for further analysis; 3) Unrelated bachelors:
171 groups consisting of unrelated males that originated from different groups. Thus, we recognised a total
172 of five different male tactics: philopatrics, roamers, breeders, and the two categories of bachelors (kin
173 and non-kin bachelors). Tenure was determined for each bachelor male by counting the number of
174 months that each male continuously shared the same nest with other bachelor males. To determine
175 the body mass at tactic switches, we used the mean body mass of five morning measures before
176 switching to the bachelor tactic or after switching from being a bachelor to next tactic, but within a
177 maximum of 14 days of the tactic switch. The total change in body mass while males were bachelors
178 was measured as the total difference in body mass (g) from the period when males switched to the
179 bachelor tactic and to the period when males changed from bachelor to a different tactic: g/period).

180 *Determination of population density, breeding intensity, sex ratio and ratio of bachelor males*

181 Population densities were calculated as number of adult striped mice per hectare. We determined
182 population density monthly by dividing the entire number of adult individuals ($> 30\text{g}$) by the size of the
183 study area. The size of the study area varied because we always incorporated 10-12 focal groups (this
184 included both breeding groups and bachelor groups) for study, and depending on population density,
185 these groups had larger or smaller territories influencing the size of the study area. For each year, we

186 determined the breeding season as the period when striped mice initiated breeding (6 weeks before
187 pups emerged) to when breeding terminated (6 weeks before last observed pups; Brooks 1982;
188 Schradin and Pillay 2005a). To determine breeding intensity (breeding ratio) in the study population,
189 we divided the number of pups born each month by the number of adult females present on the field
190 site, giving us a continuous measure. Date of birth was calculated for juveniles (body mass below 30g)
191 using their body mass at first capture and a population specific growth curve (Schradin, Schneider &
192 Yuen 2009b). Adult sex ratio was determined from the same data as number of adult males divided by
193 number of adult females. These estimates included individuals from non-focal groups at the periphery
194 of the study area, which did not carry transmitters, and which were not directly observed, but only
195 trapped for information about competing neighbouring groups. In contrast, for the frequency of
196 bachelor males, i.e. the percentage of males following this tactic, only data from males living in focal
197 groups were used, since information about the individual social tactics was less reliable from males in
198 neighbouring groups which were not included in nest observations and radio-tracking.

199 *Ethical note*

200 We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research (Bee et al., 2020). Mice
201 were captured and handled using protocols approved by the Animal Ethics Screening Committee of
202 the University of the Witwatersrand (AESC clearance number: 2007/40/01).

203 *Statistical Analysis*

204 Data were analysed using R Studio V3.6.2 (R Development Core Team, 2006), with tests being accepted
205 as statistically significant when $P \leq 0.05$. We assessed the likelihood of scrotality in the five male tactics
206 and evaluated the season (breeding versus non-breeding) that kin and non-kin bachelors were most
207 likely to occur using Pearson's Chi Squared Tests.

208 Next, we evaluated competitive ability by comparing body mass and age in the five tactics by fitting
209 generalised linear models (GLM) with the "glm" function from the MASS package (Veneables and
210 Ripley, 2002) to the data. For comparison between the different tactics, we standardized data for each
211 year, by using data from the onset of the breeding season in September, as done in previous studies
212 on roaming males (Schradin et al. 2009a). Thus, we calculated the mean body mass of all morning
213 measurements for the month of September for each male. Age was calculated for each male (where
214 data were available) from birth dates, which were calculated using a population specific growth curve
215 based on body mass that is reliable for individuals with a body mass of less than 30g (Schradin,
216 Schneider & Yuen 2009b). Mean body mass was the response variable, age and tactic were fixed effects
217 and male ID and year were introduced as random factors. Following significant effects of age and tactic
218 on male body mass, pairwise comparisons using Wilcoxon rank sum tests, adjusted for multiple
219 comparisons with the Benjamini-Hochberg method (Dunn, 1964) were used to determine where
220 differences were.

221 We then examined the influence of population density, sex ratio and breeding ratio on the occurrence
222 of kin and non-kin bachelor groups by fitting GLMs, specifying a Poisson distribution. Here, the number
223 of bachelors that occurred was the response, population density, sex ratio, breeding ratio and their
224 interactions were introduced as fixed effects, and year was introduced as a random factor. Analysis of
225 variance tests (ANOVAs) were used to assess: 1) whether male body mass changed during their time
226 (tenure) as bachelors and whether this change was influenced by the tactic prior to becoming a
227 bachelor and 2) whether the subsequent tactic employed by bachelors was influenced by the body
228 mass at the time of switching. Finally, the influence of kinship and tactic employed prior to becoming
229 bachelors on tenure (total duration spent as bachelors) was evaluated by fitting a GLM. Tenure (time)
230 was introduced as the response while kinship and prior tactic were fixed effects. For all GLMs, we
231 conducted backward model reduction to select the minimum adequate model.

232

233 RESULTS

234 *Origin of bachelor groups*

235 We observed 108 bachelors in 40 bachelor groups comprising of 2-5 individuals (mean mean \pm SD: 2.65
236 \pm 1.004) from 2006 to 2019. We identified two main types of bachelor males: (a) 60 males in 22 kin
237 bachelor groups (56 %), in which all females had disappeared leaving behind the male group members
238 (offspring and breeding male of the group); and (b) 48 males in 18 non-kin bachelor groups (44 %),
239 which were formed by males originating from different natal groups (Fig 1). Overall, 70 % of all
240 bachelors had previously been philopatric.

241

242 *Scrotality and seasonality of bachelors.*

243 Independent of tactic, adult males at the start of the breeding season were more likely to be scrotal
244 than non-scrotal ($\chi^2 = 74.39_{df=4}$; $P < 0.001$, Pearson's Chi square test). Specifically, 99 % of breeders (N
245 = 164), 99 % of roamers, ($N = 68$), 66 % of philopatrics ($N = 162$), 80 % of kin bachelors ($N = 15$) and 86
246 % ($N = 11$) of non-kin bachelors were scrotal. Kin bachelors were more common during the non-
247 breeding season than the breeding season ($\chi^2 = 16.09_{df=1}$; $P < 0.001$, Pearson's Chi square test; Fig 2).
248 In contrast, non-kin bachelors were more frequent in the breeding season than the non-breeding
249 season ($\chi^2 = 16.09_{df=1}$; $P < 0.001$, Pearson's Chi square test; Fig 2).

250

251 *Influence of population density and sex ratio on the occurrence of bachelors*

252 Sex ratio was a significant predictor of the number of kin bachelors that occurred (GLM, $\chi^2 = 11.81_{df=1}$;
253 $P = 0.016$) whereas breeding opportunities, population density and the interaction between population
254 density and sex ratio were not significant predictors (GLM, $P > 0.05$). Thus, more kin bachelors occurred
255 in a population with a male biased sex ratio (Fig 3a). Conversely, for non-kin bachelors, population
256 density was a significant predictor (GLM, $\chi^2 = 18.32_{df=1}$; $P = 0.009$) while sex ratio, breeding ratio,
257 population density or the interaction effects were not significant (GLM, $P > 0.05$). Thus, more non-kin
258 bachelors occurred in conditions of low to intermediate population density, but none at very high
259 population densities (Fig 3b).

260

261 *Comparison of body mass and age in five tactics at the start of the breeding season*

262 Male body mass at the start of the breeding season (September) was significantly related to both tactic
263 (GLM, $P < 0.001$; $\chi^2 = 93.38_{df=4}$) and age (GLM, $P < 0.001$; $\chi^2 = 59.12_{df=1}$). Pairwise comparisons of body
264 mass in the tactics revealed that philopatrics were the lightest, breeders the heaviest and roamers
265 were of intermediate body mass (Table 1; Fig. 4a). Additionally, we found that non-kin bachelors were
266 significantly heavier than kin bachelors. Kin bachelors were significantly lighter than breeders and
267 roamers but did not differ from philopatric males. Non-kin bachelors were significantly heavier than
268 philopatrics, lighter than breeders but did not differ from roaming males

269 Similar results were observed when age was analysed by tactic (Table 1; Fig 4b). Pairwise comparisons
270 revealed that philopatrics were the youngest, breeders the oldest, while roamers were of intermediate
271 age. Kin bachelors did not differ in age from philopatrics but were younger than males of all other
272 tactics. Non-kin bachelors were older than philopatrics and kin bachelors but did not differ in age from
273 both breeding and roaming males.

274

275 *Post bachelor tactics*

276 Males significantly gained weight during their tenure as bachelors (Anova; $F = 3_{df=2}$; $P = 0.0339$, Fig 5).
277 Total change in body mass during the bachelor tactic was significantly influenced by the tactic which
278 males had employed prior to becoming bachelors (Anova; $F = 3_{df=2}$; $P = 0.034$, Fig 5). Specifically, kin
279 bachelors which had been philopatric prior to becoming bachelors increased body mass the most;
280 while kin bachelors that had previously been breeders showed the smallest increase in body mass (Fig
281 5). Kin bachelors were more likely to die or disappear from the population than non-kin bachelors ($P =$
282 0.004 , Fisher's Exact Test). Bachelors that did not disappear (presumably due to death) went on to
283 become roamers and breeders (Fig 6). Of the 24 surviving kin bachelors, 16 became breeders and 8
284 became roamers. Kin bachelors that became breeders were not heavier than roamers (Anova; $F =$
285 $0.749_{df=1}$; $P = 0.391$; Fig 6). Similarly, of the 32 surviving non-kin bachelors, 16 went on to become
286 roamers and 16 went on to become breeders, again with no significant difference in body mass (Anova;
287 $F = 1.21_{df=1}$; $P = 0.283$; Fig 6).

288

289 *Tenure of bachelor groups*

290 Overall, bachelor groups were maintained for a period of 1-5 months (1.88 ± 1.31) after which they
291 disbanded (Fig 7). Tenure in bachelor groups was longest for kin philopatrics (GLM, $P < 0.001$, $2.274 \pm$
292 1.39), shortest in kin breeders (GLM, $P = 0.0316$, 1.59 ± 1.060) and was not significantly influenced by
293 other tactics (GLM, $P > 0.05$), with males in non-kin bachelor groups having a similar tenure
294 independent of their previous tactic (Fig. 6).

295

296 **DISCUSSION**

297 Males in several animal species exhibit variation in social and reproductive behaviour, which is often
298 associated with differences in body condition. For example, young and old, small and large males
299 regularly make use of alternative behavioural tactics in order to optimise their fitness (Gross 1996;
300 Taborsky 2008). The occurrence of bachelor groups has recently been reported in the second largest
301 land mammal (i.e. Asian elephants, *Elephas maximus*), where they represent a unique life history
302 strategy for male elephants that are confronted by landscapes that have been altered by
303 anthropogenic activities (Srinivasaiah et al. 2019). Here, we report for the first time, the existence of
304 bachelor groups in a mammalian species that is much less than 1kg in body mass and provide evidence
305 that it represents an important life history stage for males of intermediate competitive ability.

306 Using data from 13 generations, we first showed that bachelor groups in the socially flexible African
307 striped mouse arise as a consequence of two main mechanisms: 1) through the disappearance of all
308 group females, leaving behind kin males in a bachelor group; and 2) when unrelated males form
309 bachelor groups. We then showed that both kin and non-kin bachelors differ in seasonality of
310 occurrence and in traits which are known indicators of competitive ability in striped mice, i.e. body
311 mass, age, and scrotality (Schradin et al 2009a). Specifically, kin bachelor groups were more common
312 during the non-breeding season and comprised of the large breeding male, which soon disappeared
313 or moved into another group, and small philopatric males, which remained bachelors until the next
314 breeding season. Non-kin bachelors were most common during the breeding season, nearly all of them
315 were reproductively active, and their body mass was similar to that of solitary roamers. Finally, we
316 found that non-kin bachelors had a short tenure and, after increasing their body mass, soon switched
317 to the solitary roaming or the group-living breeder tactic. This indicates that non-kin bachelors might
318 represent an alternative reproductive tactic that is similar to roaming males, but with the advantage
319 of social thermoregulation by huddling in a nest at night, which is known to be an important
320 mechanism for reducing energy expenditure in this species (Scantlebury et al, 2006).

321 In support of our expectations, two types of bachelor groups occurred, arising as a result of two
322 different mechanisms. Firstly, we observed bachelor groups that formed as a result of environmental
323 disrupters (Schradin 2013); where individuals were forced into the bachelor tactic (kin bachelor

324 groups). Kin bachelor groups formed when all females of a group disappeared (presumably due to
325 predation), leaving behind males. Secondly, we observed bachelor groups that formed due to social
326 flexibility, where individuals can switch reversibly between tactics (Schradin et al., 2012). These were
327 the non-kin bachelor groups, which consisted of unrelated males that originated from different groups.
328 Importantly, we report that there was one instance where two related males left their natal group to
329 form a bachelor group. More than half of bachelor groups (56%) formed due to environmental
330 disrupters (Schradin 2013), indicating that following the bachelor tactic often does not reflect
331 individual male choices to form groups consisting of males only, but may be the result of stochastic
332 extrinsic factors. Similar observations where stochastic extrinsic factors such as the death of important
333 group members impose changes in tactics and social organisation (Schradin, 2018) have been reported
334 in other species. For example, in pair-living Scandinavian wolves (*Canis lupus lupus*), the death of one
335 of the pair members results in the other becoming temporarily solitary (Milleret et al. 2017). Similarly,
336 in striped mice, the death of all but one adult female group member gives rise to female solitary
337 breeders (Hill et al. 2015). Whether an alternative tactic is due to social flexibility or environmental
338 disrupters can have significant influences on physiology (Hill et al. 2015b) and is also expected to
339 influence fitness (Hill et al. 2015a).

340 At the start of the breeding season, both kin and non-kin bachelors were sexually mature and
341 physiologically capable of breeding, as indicated by them being scrotal (Schradin et al. 2012). Since
342 male striped mice cannot obtain a breeding position within their natal groups (Schradin et al. 2010),
343 reproductive opportunities during the breeding season may encourage males to disperse. This may
344 explain the significantly higher incidence of non-kin bachelor males in the breeding season than in the
345 non-breeding season. Conversely, more kin bachelor males were observed during the non-breeding
346 season than in the breeding season. This is likely due to the non-breeding season being much longer
347 (nine months) than the breeding season (three months) which would make the death of all females in
348 a group more likely, subsequently leading to a higher likelihood of the occurrence of kin bachelor
349 groups. Similarly, a male-biased sex ratio was a significant predictor of number of kin bachelor groups
350 that occurred. For non-kin bachelors, population density was a significant predictor, with more
351 bachelors occurring in conditions of low to intermediate population density. This indicates that
352 demographic factors may play an important role in constraining dispersal. A high population density
353 may result in a lack of available territories (Emlen 1982a; Bergmuller et al. 2005), which hinders
354 sexually mature individuals from choosing a dispersal tactic. Thus, reproductive competition during
355 the breeding season, coupled with empty territories into which males can disperse (low population
356 density) seem to favour dispersal leading to the formation of non-kin bachelor groups.

357 Body condition, reflected by an individual's age, body mass or size is an important factor in the
358 determination of reproductive tactics in many species (Brockmann & Taborsky 2008; Gross
359 1996), including striped mice (Schradin et al. 2009a). Interestingly, we found that non-kin bachelors
360 were significantly heavier than kin bachelors and philopatrics, lighter than breeders but did not differ
361 in body mass from roaming males. The finding that males which choose to disperse and become
362 bachelors (non-kin bachelors) were heavier and older than males which were forced to become
363 bachelors (kin bachelors) lies within our expectations since similar findings have been reported in
364 female striped mice. Group-living females which became solitary by leaving a communal group differed
365 in individual traits from those forced to do so by environmental disrupters by being heavier and having
366 lower stress hormone levels (Hill et al. 2015). That individuals of the same observed behavioural tactic
367 can differ in important traits such as body mass, age, and hormone levels in both male and female
368 striped mice highlights the importance of distinguishing between environmental disrupters versus
369 social flexibility as mechanisms leading to these tactics.

370 In male striped mice, the largest males are dominant breeders that defend territories wherein there
371 are groups of two to four breeding females (Schradin et al 2009a). Thus, body mass is important for
372 territory defence as well as for the maintenance of social and reproductive tactics (Schradin et al
373 2009a). Non-kin bachelors may thus be seen as males which are large enough to disperse, possibly due
374 to the pressures of within-group reproductive competition (Schradin et al 2009b), but not competitive

375 enough to obtain and defend a territory. This is common in many species, where forming bachelor
376 groups is a tactic employed by less competitive males which may be excluded by territorial or resident
377 males (Gartlan 1974; Owen-Smith 1975). These bachelor males form coalitions while they wait to
378 secure a reproductive position in a group (e.g. patas monkey *Erythrocebus patas*; Gartlan 1974) or
379 while they wait to gain a territory (e.g. white rhinoceros *Ceratotherium simum*; Owen-Smith 1975). In
380 our study, tenure of non-kin bachelor males was short compared to kin-bachelors and most males
381 switched soon to another tactic (some disappeared), indicating that this also represents an
382 intermediate life history tactic.

383 A change in body condition is known to elicit a change in social or reproductive tactic in some species
384 (John 1993; Hill et al., 2015). This is also true for male striped mice, which begin their life as philopatric
385 and can later switch to either the roaming or breeding tactic when their body mass increases (Schradin
386 et al 2009b). Our results revealed that males significantly increased their body mass while in bachelor
387 groups. Kin bachelors that had previously been philopatric gained the most body mass while in
388 bachelor groups, and they also had the longest tenure. Kin bachelors that had previously been breeders
389 were able to leave bachelor groups the fastest (had the shortest tenure), possibly because they were
390 already large breeding males before the disappearance of all females, and thus did not need extended
391 periods of time to gain body mass and become more competitive for a tactic change. Non-kin bachelors
392 also gained significant body mass, although in a relatively shorter tenure as kin bachelors. Interestingly,
393 while most kin bachelors disappeared from the population (61%), most non-kin bachelors (66%)
394 managed to switch to the roaming or breeding tactic; tactics which are known to lead to reproductive
395 success (Schradin et al. 2012). These results predict that non-kin bachelors should have significantly
396 higher fitness than kin bachelors, and that the roaming tactic likely confers higher fitness than the
397 bachelor tactic.

398 Alternative reproductive tactics (ARTs) occur where investment in reproduction can be exploited by
399 competitors of the same sex (Taborsky 2008), such that high reproductive competition leads to the
400 evolution of alternative tactics to obtain reproductive opportunities, especially for less competitive
401 males (Alonzo 2008). Whether non-kin bachelor groups in striped mice represent a real ART remains
402 unknown, since we do not know the reproductive consequences. Nevertheless, it is interesting to note
403 that some males chose to form bachelor groups over the alternatives to either stay at home as
404 philopatric males or to become solitary roamers. Remaining a philopatric male is associated with
405 extremely low reproductive success, which is ten times higher in roamers (Schradin & Lindholm 2011),
406 which might explain why older and heavier males leave their natal groups and become roamers, even
407 though this is associated with high energetic costs (Rimbach et al. 2019). One of the main reasons of
408 group-living in striped mice is reduced costs of thermoregulation at night, since sleeping in huddling
409 groups decreases these costs by up to 30% (Scantlebury et al. 2006). Thus, we posit that non-kin
410 bachelor groups are best interpreted as an ART similar to the roaming tactic but with reduced energetic
411 costs of solitary sleeping. Kin bachelors comprise of mostly previously philopatric males, have the
412 longest tenure and gain the most body mass during their tenure as bachelors. Thus, we posit that these
413 are very small males that might otherwise have remained philopatric until at least the next breeding
414 season but were forced to be bachelors by environmental disrupters.

415

416 **Conclusions**

417 Here we report, for the first time, bachelor groups in the striped mouse, by far the smallest mammal
418 for which this male tactic has been reported. Previous findings demonstrated that female striped mice
419 which breed solitarily because they left their communal groups differ from those forced to do so by
420 environmental disrupters (Hill et al. 2015a, b). The current study now shows that distinguishing the
421 conditions under which striped mice males become bachelors also has important implications for
422 individual traits. Our results indicate that individuals following the same behavioural tactic can differ
423 in life history traits depending on the mechanism that gave rise to observed tactic, which should also
424 be considered in other species with alternative tactics.

425

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432

433 DECLARATION OF INTERESTS

434 The authors declare no conflicting interests.

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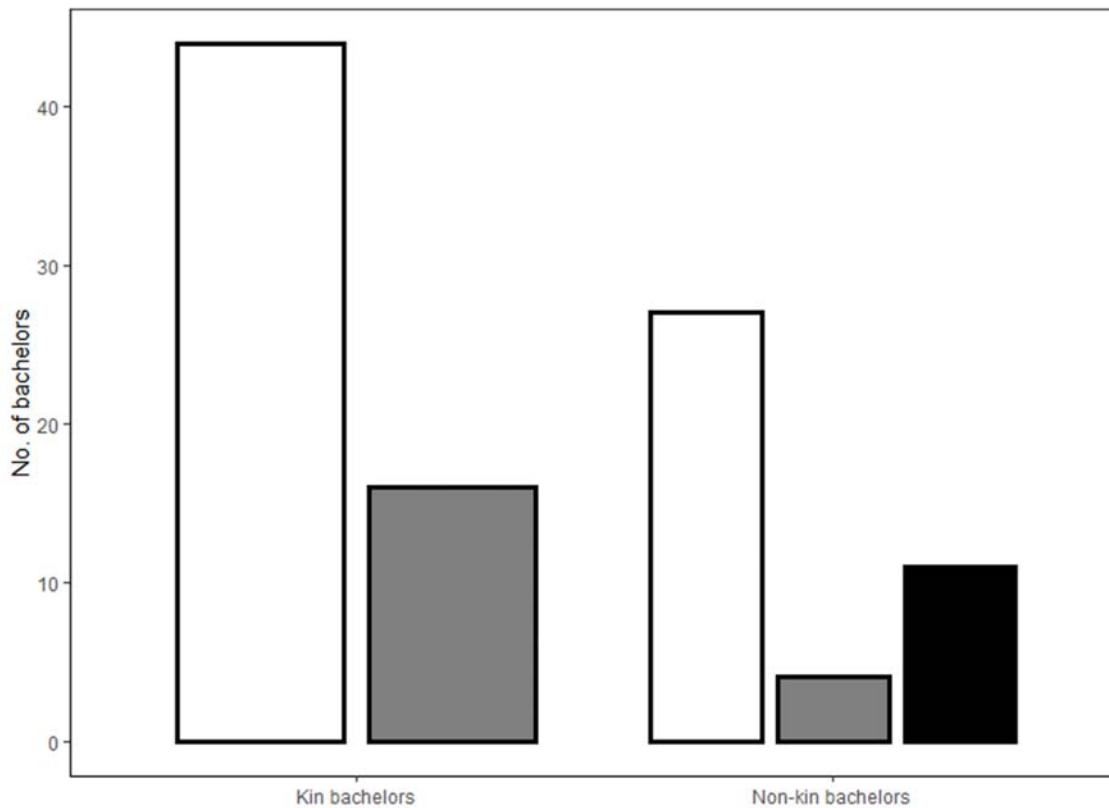
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524 **Table 1:** Results of post-hoc pairwise comparisons of body mass (g) and age (months) across different
 525 male tactic in *Rhabdomys pumilio* using the Wilcoxon rank sum test for multiple comparisons, with
 526 the Benjamini Hochberg p-adjustment method. Significant differences between tactics appear in
 527 bold.

		Philopatric	Breeder	Roamer	Kin bachelor	Non-kin bachelor
Philopatric	Mass	-	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> > 0.05	<i>P</i> < 0.05
	Age	-	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> > 0.05	<i>P</i> < 0.05
Breeder	Mass	<i>P</i> < 0.05	-	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> < 0.05
	Age	<i>P</i> < 0.05	-	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> > 0.05
Roamer	Mass	<i>P</i> < 0.05	<i>P</i> < 0.05	-	<i>P</i> < 0.05	<i>P</i> > 0.05
	Age	<i>P</i> < 0.05	<i>P</i> < 0.05	-	<i>P</i> > 0.05	<i>P</i> > 0.05
Kin bachelor	Mass	<i>P</i> > 0.05	<i>P</i> < 0.05	<i>P</i> < 0.05	-	<i>P</i> < 0.05
	Age	<i>P</i> > 0.05	<i>P</i> < 0.05	<i>P</i> > 0.05	-	<i>P</i> > 0.05
Non-kin bachelor	Mass	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> > 0.05	<i>P</i> < 0.05	-
	Age	<i>P</i> < 0.05	<i>P</i> > 0.05	<i>P</i> > 0.05	<i>P</i> > 0.05	-

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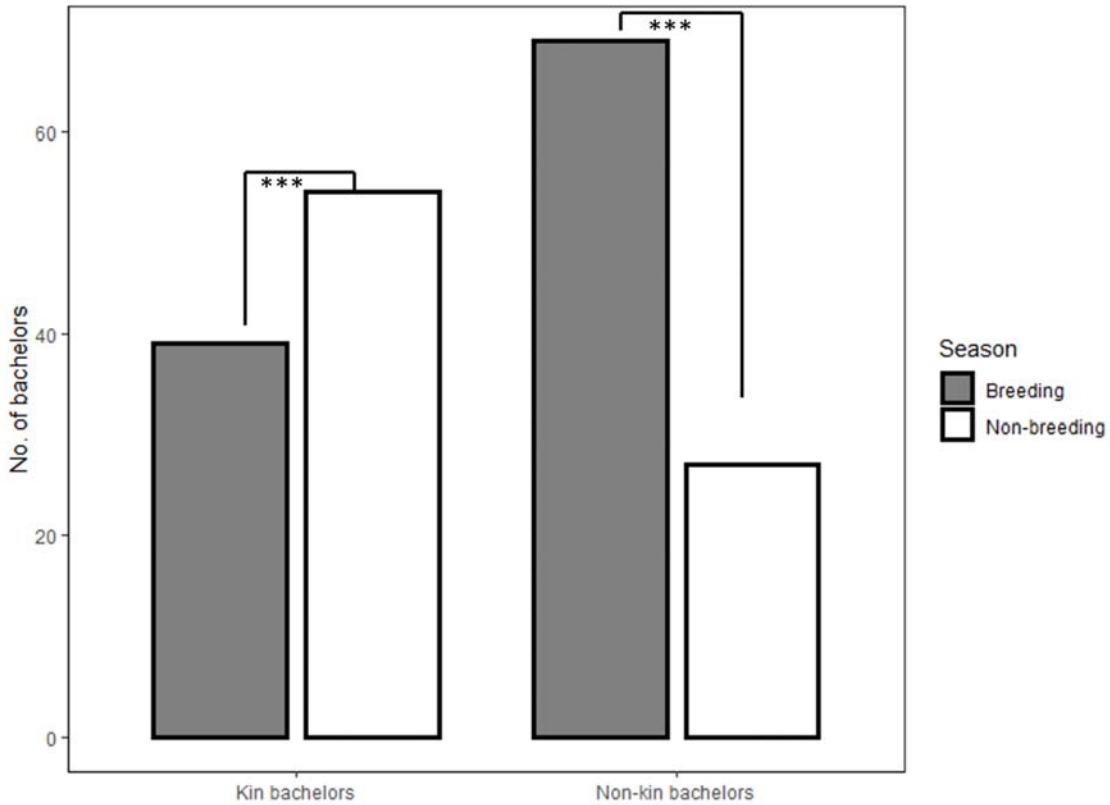
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531 **Figure 1: The number of bachelor males in each origin category.** Bachelor groups formed when all
 532 females of a breeding group disappeared, leaving behind only males (kin bachelors) or when unrelated
 533 males that had dispersed from their natal groups formed a bachelor group (non-kin bachelors). The
 534 pre-tactics of bachelor males are indicated. Bar width indicates group sample size.

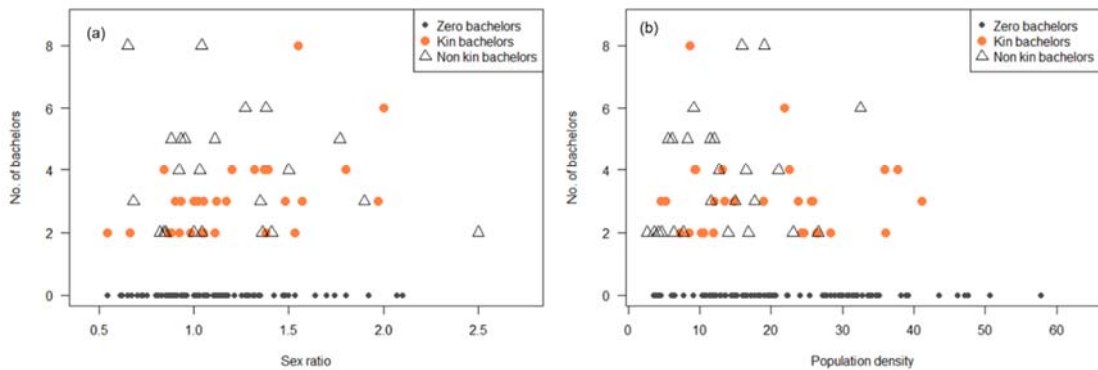
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537 **Figure 2: The number of kin and non-kin bachelors that occurred during the breeding season and**
 538 **the non-breeding season. *** denote statistically significant differences between the seasons.**

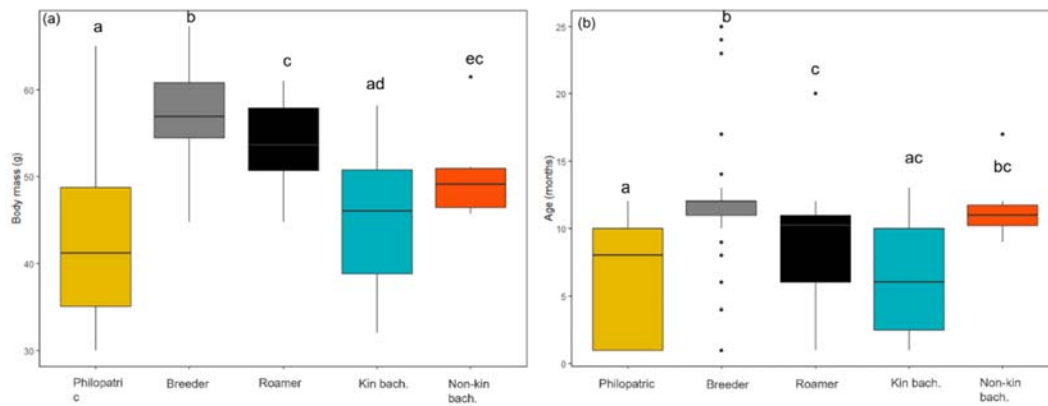
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541 **Figure 3: Body mass (a) and age (b) of philopatric, breeding, roaming, kin bachelors and non-kin**
 542 **bachelors at the start of the breeding season (September).** Horizontal lines inside the box show the
 543 median, whiskers show minimum and maximum values. Black circles show the outliers. Different
 544 letters above box plots depict statistically significant differences following the Wilcoxon pairwise
 545 comparisons adjusted for multiple comparison with the Benjamini Hochberg method.

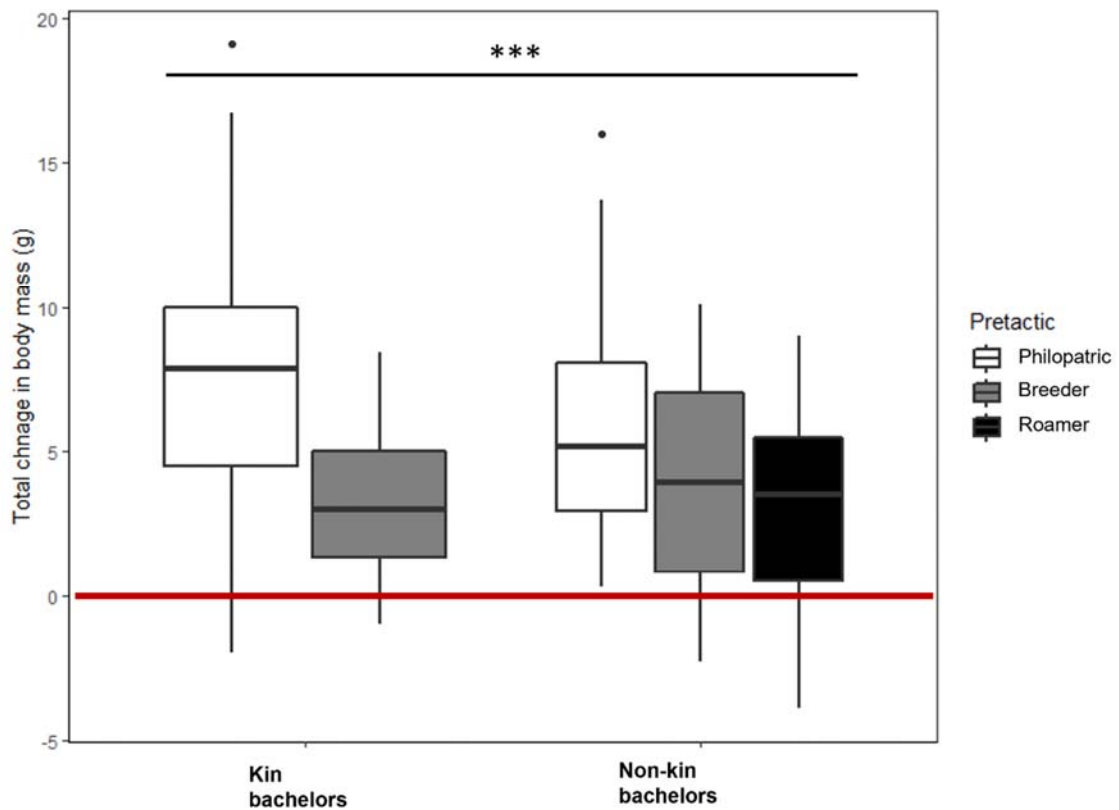
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548 **Figure 4: (a) Number of kin and non kin bachelors that occurred at different sex ratios (number of**
 549 **adult males/number of adult females) and (b) Number of kin and non-kin bachelors that occurred at**
 550 **different population densities (total number of adult mice per hectare).**

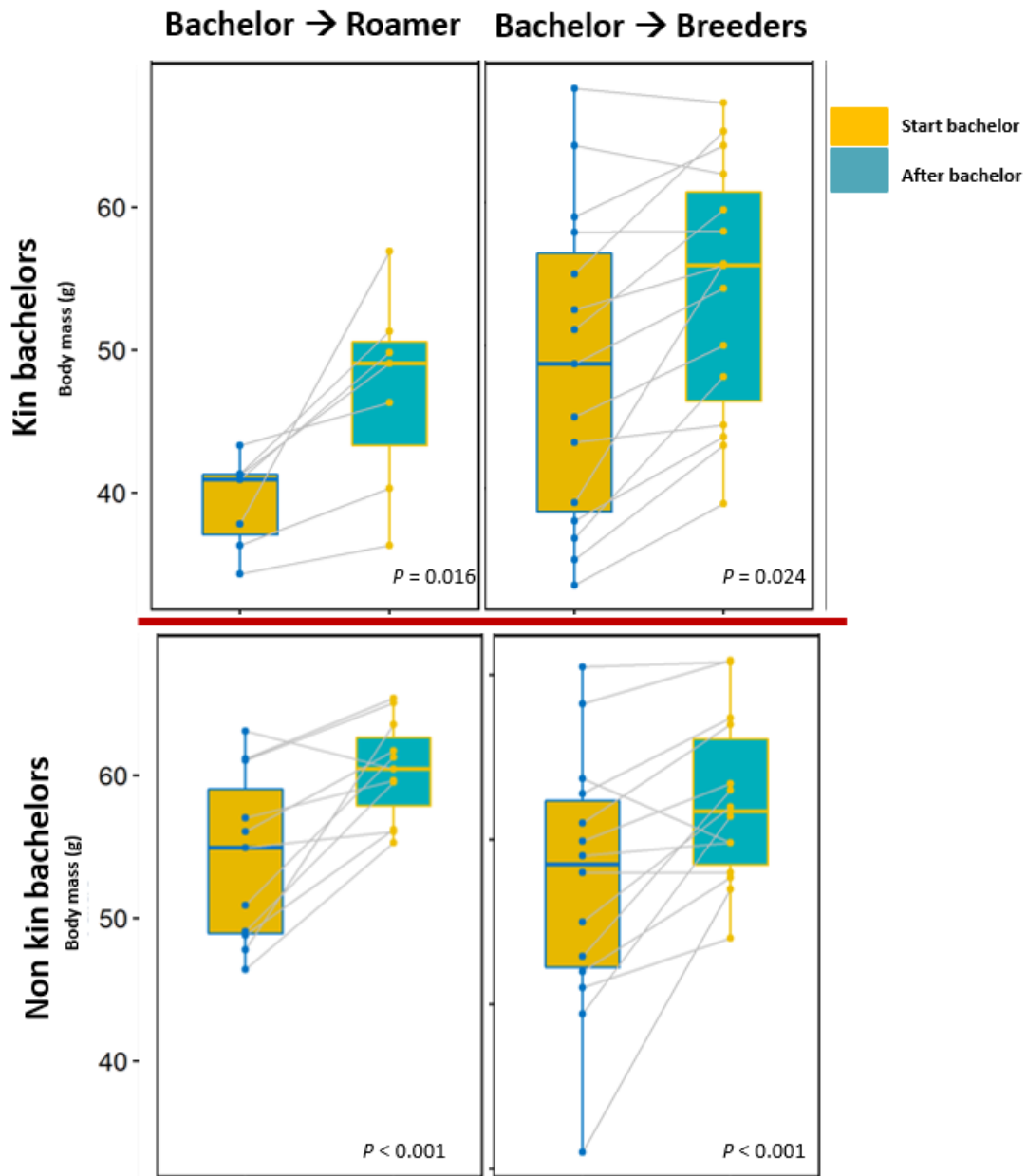
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553 **Figure 5: Total change in body mass (g/full period) in kin and non-kin bachelors during time spent**
 554 **(tenure) as bachelors depending on their previous tactic. Kin and non kin philopatrics showed the**
 555 **highest increase in body mass amongst all bachelors ($P < 0.001$).**

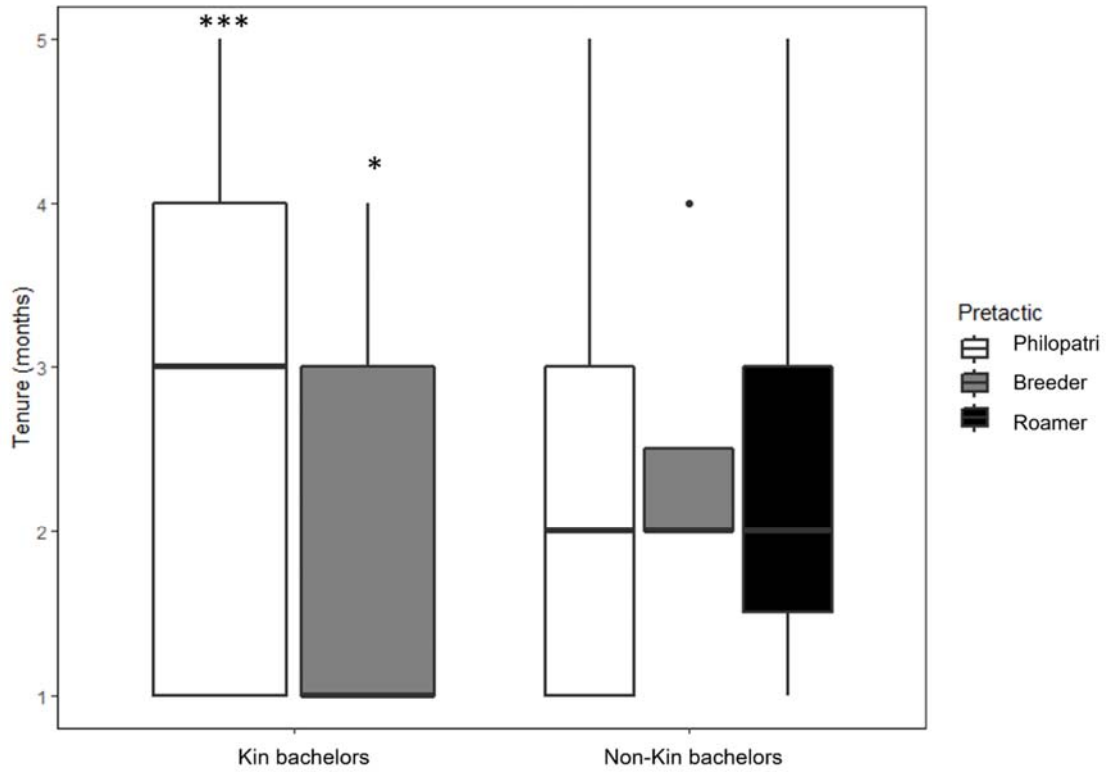
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558 **Figure 6: Change in body mass during tenure as bachelors.** The boxplots compare the mean body mass
 559 of males when they switched to the bachelor tactic (yellow boxes) and when they switched from
 560 bachelor (blue boxes) to breeding or roaming tactic. Horizontal lines inside the box show the median,
 561 whiskers show minimum and maximum values. Grey lines depict changes in body mass before and
 562 after becoming bachelors for individual males. P -values are indicated inside frames for each
 563 comparison following Wilcoxon rank sum tests.

564



565

566 **Figure 7: The tenure (in months) that males remained in bachelor groups before switching to another**
 567 **tactic (or disappearing from the study site).** Horizontal lines inside the box show the median, whiskers
 568 show minimum and maximum values. Asterisks (*) show the variables that significantly influenced the
 569 duration spent as bachelors (GLM; *p < 0.05; **p < 0.01; ***p < 0.001).