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Pair bonding in monogamously and polygynously kept African striped mice, *Rhabdomys pumilio*

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HAL Authorization

1 **Pair-bonding in monogamously and polygynously kept African striped mice (*Rhabdomys***
2 ***pumilio*)**

3

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7

8

9 **ABSTRACT**

10

11 Pair-bonding, i.e. individuals showing a preference for a specific opposite sex individual, has
12 been demonstrated in several socially monogamous species. However, social bonds also occur
13 in non-monogamous species, but have received less attention. Currently, we do not know
14 whether social bonds in monogamous pairs differ from social bonds in polygynous pairs. We
15 studied the socially flexible African striped mouse (*Rhabdomys pumilio*) in the laboratory,
16 conducting 3 hour partner preference tests typically used to measure pair bonds in socially
17 monogamous prairie voles. In the field, striped mice typically live in polygynous groups, but
18 socially monogamous pairs have also been observed. We compared social bonds between 12
19 monogamous pairs and 12 polygynous groups (1 male and 2 females). The social situation
20 (monogamous versus polygynous) did not influence social bonds. Female striped mice showed
21 a clear preference for their partner. While males spent more time in body contact with their
22 partner they showed a sexual preference for strange females. Polygynous males did not show a
23 preference for one of their two females. While significant preferences for partners were found
24 in striped mice, social preference was less strong than those reported for socially monogamous
25 prairie voles. In sum, our study supports that opposite sex social bonds do not only occur in

- 26 monogamous but also in species that can live in polygynous groups, but might be weaker in
- 27 polygynous species.

28 INTRODUCTION

29 Socials bonds between two or more individuals are associated with direct benefits for the
30 partners, such as an improved nest defence, a better resource gathering or an increased
31 efficiency of territory use (Bercovitch, 1988; Cords, 2001; McFarland et al., 2015; Foerster et
32 al., 2015; Kern & Radford, 2016). Socials bonds are generally described as a subset of affiliative
33 and permanent social relationships between two or more conspecifics (Carter, 2005; Sachser,
34 2005). They are characterized by social proximity (Sachser, 2005) and amicable interactions,
35 measured as a reduced physical distance between the partners (Carter & Porges, 2010). In
36 mammals, social proximity and social engagement are common between mothers and their
37 offspring, indicating that they are socially bonded (Nelson & Panksepp, 1996). Social bonds
38 are also established between partners who cooperate to breed over extended periods of time
39 (Carter et al., 1995). Socials bonds between two partners and bi-parental care often characterise
40 socially monogamous species (Kleiman, 1977). Social monogamy is defined as a long term
41 association between one adult male and one adult female covering at least one breeding season.
42 About 10% of mammals are socially monogamous, and both males and females exhibit
43 selective social behaviours, called “pair bonds” (Kleiman, 1977). Pair bonds are characterised
44 by social preference and by the male and female remaining together after mating and often even
45 during non-reproductive periods (Carter et al., 1995; Carter, 2005; Lukas & Clutton-Brock,
46 2013).

47 In mammals, pair bonds occurs in several species of primates, such as titi monkeys
48 (*Callicebus cupreus*; Carp et al., 2015), owl monkeys (*Aotus azarai*; Fernandez-Duck & Huque,
49 2013) and marmosets (*Callithrix penicillata*; Smith et al., 2010). Pair bonds also occur in
50 socially monogamous rodents such as California mice (*Peromyscus californicus*; Gubernick &
51 Nordby, 1993) and prairies voles (*Microtus ochrogaster*; Carter et al., 1995; Blocker & Ophir,
52 2016). Prairies voles are the main study model for pair bonding. They show all characteristics

53 of monogamy: they live together, co-defend their shared territory and nest, and both sexes
54 contribute to the care of the young (Johnson & Young, 2015). A recent study shows that even
55 under ideal conditions for mating with multiple receptive females, male prairies voles prefer to
56 establish a pair bond with one particular female (Blocker & Ophir, 2016). Pair bonds between
57 two individuals are measured in partner preference tests (Carter & Keverne, 2002; Young &
58 Wang, 2004; Devries et al., 1995). The criteria used to detect partner preference is the amount
59 of time spent in physical contact by the focal individual with his partner compared to a stranger
60 (Cho et al., 1999; Devries et al., 1995; Bales & Carter, 2003). While pair bonds occur between
61 the mates of a pair, similar social bonds might also occur in other social organizations such as
62 in polygynous groups.

63 In polygynous groups, individuals might develop social bonds with several non-related
64 partners from the opposite sex (Parker et al. 2001; Karelina 2010). Prairie voles, which are
65 considered monogamous, can also switch to a polygynous mating system under high population
66 density (Getz et al., 1987). While the social system changes, social bonds between individuals
67 still occur, even with multiple non-related partners of the opposite sex (Young, 1999). In
68 another rodent species, the meadow vole (*Microtus pennsylvanicus*), females are territorial
69 during summer but show high social tolerance to conspecifics during colder months in winter
70 (McShea & Madison, 1984). In winter, meadow voles form stable groups composed of several
71 females and at least one male (Madison et al., 1984). Voles form opposite-sex pair bonds in
72 these groups (Parker et al., 2001). While social bonds can occur in polygynous groups, it has
73 never been tested whether the strength of social relationships differs between polygynous
74 groups and monogamous pairs. The comparison of social bonds between two species with a
75 different social systems could be biased. However, within some species, individuals can show
76 different forms of social organization, often depending on the environmental conditions and
77 period. This is the case for several rodents' species such as prairies voles (Getz & Carter, 1996),
78 house mice (*Mus musculus*, Latham & Mason, 2004) and African striped mice (*Rhabdomys*

79 *pumilio*, Schradin, 2013). These species are called socially flexible, as individuals can switch
80 their social tactics resulting in a change of the social system (Schradin, 2013). Consequently,
81 individuals of the same species can be polygynous while other individuals might be
82 monogamous. These socially flexible species are good candidates to investigate differences in
83 social relationships between monogamous and polygynous groups.

84 The African striped mouse, a diurnal murid rodent, has been described as a socially flexible
85 species (Schradin et al., 2010; Schradin et al., 2012). Striped mice can live in polygynous
86 groups, in pairs, or solitarily (Schradin et al., 2010; Schradin et al., 2012; for pair living:
87 Schradin, unpubl. data). Females often remain philopatric and breed in their natal group, such
88 that breeding females of one group are closely related, typically sisters, half-sisters, or cousins
89 (Schradin & Pillay, 2004; Schradin et al. 2010; genetic comparison: Schradin & Lindholm,
90 unpubl. data). Individuals of one group show amicable behaviour towards each other, such as
91 grooming and sitting in body contact, but they are aggressively territorial towards individuals
92 from other groups (Schradin & Pillay, 2004). However, whether partners of striped mice groups
93 form affiliative bonds is so far unknown. A recent study indicating individual recognition in
94 striped mice makes it likely that social bonds occur (Brunner et al., 2016). The first aim of this
95 study was therefore to determine whether captive male and female striped mice from
96 polygynous and monogamous groups form selective opposite-sex partner preferences, and
97 whether the strength of social bonds differ between monogamously and polygynously kept
98 groups. We then compared our results to results from prairie voles that used similar
99 methodology, comparing the percentage of time spent in physical contact by the focal individual
100 with their partner in contrast to an unfamiliar individual (Blocker & Ophir, 2016). Our third
101 aim was to determine whether males from polygynous groups show preference toward one
102 particular female or if they bond equally with both females.

103 **MATERIAL AND METHODS**

104 *Study animals and housing conditions*

105 Striped mice were kept and bred at the animal facility of the IPHC-DEPE. The founders of this
106 colony originated from a captive colony kept at the Succulent Karoo Research Station in South
107 Africa, which arose from individuals trapped in 2003 and in 2016 in the Goegap Nature Reserve
108 where a long term study about this specie is done. All animals used in the study were born at
109 the IPHC-DEPE.

110 Breeding pairs were housed in two tanks (each 40 x 30 x 30 cm) connected by a tube.
111 Tanks were provided with litter of crushed corn cobs and water was available ad libitum. To
112 avoid obesity (leading to infertility and diabetes in this species) and thus to increase welfare of
113 animals, animals were not fed ad libitum. In the mornings animals were fed with a mix of
114 cereals, fruits and seeds (“Nager Krokant”, ZG Raiffeisen) with approximately 4.25 gram/adult.
115 In the afternoon one pinch (less than 2 grams) of food supplementation, consisting of a mix of
116 seeds for tropical finches, was given for 4 adults. Juveniles were considered as half an adult for
117 food quantity. With this diet, animals grew fast and reached a body mass typical for the heaviest
118 individuals in the field during the moist season with highest food availability. To enhance the
119 welfare of individuals, as enrichments, a shelter (10cm x 8cm x 12cm long) was provided in
120 one of the two tanks, and in the second tank one wooden tunnel (20cm long) was provided, with
121 6 holes (3.5cm diameter) per tunnel (7.0cm diameter). Furthermore, the two tanks functioned
122 to reduce stress during cleaning, as only one tank per week was cleaned, keeping one familiar
123 tank for individuals at all times, and individuals were not handled during cleaning. The tanks
124 were maintained in a room under 11:13 hour light-dark cycle. The light was turned on at 8 a.m.
125 and off at 7 p.m., starting at 10% light at 8 a.m. increasing to 100% light at 12 p.m and
126 decreasing slowly until 6 p.m., mimicking natural lighting conditions during the breeding
127 season. The ambient temperature was maintained at 18°C during the night and rose to 25°C

128 during the day. Study animals were separated from their parents at an age of 21-30 days
129 (weaning occurs at day 16) and housed in same-sex siblings groups (from two to six
130 individuals). Sibling groups were kept in two connected tanks under the same conditions as
131 described above.

132 Striped mice were paired when fully adult (90-120 days old). For the pairs, one male
133 and one female were removed from two sibling groups and housed together in two cages
134 connected by a tube, in the same conditions as previously mentioned. The female and the male
135 were unrelated and had approximately the same age (99 days +/- 12 days). For the polygynous
136 groups, one male was housed with two females that were unrelated to the male, but which were
137 full sisters of the same age (originated from the same litter) and kept together in one sibling
138 group. In the field, breeding females of a group are closely related and can be full sisters. The
139 male and the two females had approximately the same age (97days +/- 14 days).

140

141 *Experiment 1: Partner preference test*

142 In total, individuals from twelve pairs (N= 24 individuals) and twelve trios (N= 24) were tested
143 (12 females from trios were not tested). Our aim was to study social bonds independent of
144 sexual motivation. After pairing, striped mice typically mate within 3-7 days and then females
145 are not receptive anymore. Therefore, tests started seven days after pairing. This duration would
146 have been sufficient, as it was longer than in previous studies on rodents (prairie voles, Carter
147 et al., 1995; Wang & Aragona, 2004; Blocker & Ophir, 2016; and meadow voles, Parker et al.,
148 2001), to allow the formation of social bonds between individuals. Receptiveness of females
149 was then determined in retrospect from pregnancy and parturition. In total 19 females were
150 pregnant during the preference test and 5 were not, of which only one had a perforated vagina
151 potentially allowing for mating. These 5 females behaved the same as the other females with

152 no obvious differences. One female was excluded from the study because she did not move
153 through the tunnels of the three cages (figure. 1).

154



155

156 **Figure 1:** Setup used for preference test as well as polygynous tests, composed of three tanks
157 connected with two tubes. The mice at the two sides were tethered with a collar to which a
158 fishing line was attached to the lids. Here the line was taut and the mice could move until the
159 middle of their respective tanks but not further. The focal individual (in the right tube
160 connecting two tanks) was free to move through the entire device.

161

162 During the partner preference tests, a focal individual was presented with two mice from
163 the opposite sex, one being his partner and the other being a stranger (i.e. control individual),
164 and the interactions with both were recorded. Partner preference tests were running during 3h
165 the mornings between 9h30 to 12h30. Each test was video recorded with a camcorder (SONY,
166 HDR-CX405). In total, 48 individuals were tested for the partner preference tests, including 24
167 males and 24 females coming from 12 trios and 12 pairs. The partner preference tests were
168 conducted in a three tank apparatus (each tank 30 x 30 x 40 cm) with a central tank being
169 connected to the other two tanks by two tubes (figure 1). All mice used were weighted before

170 the experiment, and their reproductive status was noted. All males were scrotal. For females, it
171 was recorded whether the vagina was closed or perforated. Pregnant females, as well as females
172 with a closed vagina, were not sexually receptive. Two striped mice of the same sex with similar
173 body mass ($\text{mean}_{\text{control}} = 46.6 \pm 5.9$; $\text{mean}_{\text{partner}} = 46.3 \pm 5.4$; Paired t test: $t_{44}=0.24$, $p>0.05$)
174 and reproductive status were used for the partner preference test. One striped mouse was the
175 partner of the focal mouse, with which it had cohabited during at least one week, and the second
176 was a stranger, coming from another pair. The partner, as well as the stranger, were tethered by
177 a fishing line (diameter of 0.4 mm) connected to a collar made of a cable-tie (2.5 x 98 mm).
178 Each of them was placed in one of the two opposite tanks of the device, one on the left tank,
179 one on the right (figure 1). For half of the experiments, the partners were one the right, and for
180 the other half on the left. The line was attached to the lids of the tanks and was long enough to
181 allow individuals to move normally in the cage, but too short for them to reach the connecting
182 tube. After tethering the mice in the tanks, 20min acclimation was given to allow them to get
183 used to the collars. After this period, the focal individual was released in the middle tank and it
184 was free to move through all three tanks. Among the 48 tests realized, 22 experiments were
185 shorter than 3h (mean 2h 14min \pm 8min, range 1h 23min – 2 h 48 min) because the mice chewed
186 through the cable and got free. Data from shorter videotaping did not differ from data obtained
187 from videotaping for 3 hours (see Fig. 1 in electronic supplement). As data were analysed as
188 percentage of total time (see below), these experiments could still be used. These cases were
189 recognised quickly as experiments were monitored from outside via a video screen; mice never
190 fought and never got injured. Two tests could not be analysed, one because the focal mouse did
191 not jump through the tubes to move freely through the device, and the second because of a SD
192 card problem leading to data loss.

193 All males from pairs and trios, as well as all females from pairs and one designated
194 female per trio, were included in a maximum of three tests: once as the focal, once as the partner,
195 and once as the control individual. Eight out of 48 mice were tested only twice (as the focal and

196 the partner). The mice were chosen to have randomized tests (between control, partner and
197 focus) to allow independent statistical analysis between the different tests. Between each
198 experiment, the tanks were cleaned with water, dried, and clean litter was provided.

199

200 *Experiment 2: Male preference test in polygynous groups*

201 The goal of this experiment was to determine whether polygynously mated males show a
202 preference for one of their two females. Polygynous preference tests were done in the same
203 room as experiment 1 and under the same conditions in the three tank apparatus, with both
204 females being tethered and the male moving freely in the apparatus. The tests were conducted
205 in the afternoons between 2 p.m. to 6 p.m. during 30min per trio and each trio was tested eight
206 times. For 4 trios only 6 videos were recorded because one female gave birth. Two trios had to
207 be excluded from the analysis, one because a female gave birth before the sixth test and the
208 second one because one mouse died of unknown reasons in the home tank (not during
209 experiment). Only one test per day per trio was done. Each day, the side where each female was
210 tethered was alternated compared to the previous day, one day to the left and the next one to
211 the right.

212

213 *Video analysis*

214 Videos were analysed with the software BORIS (version 3.48; Friard & Gamba, 2016). Four
215 categories of behaviours were distinguished: 1. sexual behaviours (mounting, sniffing genitals
216 and lordosis), 2. sociopositive behaviours (grooming and sitting in body contact), 3. aggressive
217 behaviours (standing upright, charge), and 4. presence, i.e. the presence of the focal mouse in
218 the middle tank or in the same tank as another mouse but without interacting with it. Aggressive

219 behaviour was very rare and biting never occurred (see results) and no individual was injured.
220 Sexual behaviours and sociopositive behaviours were in some cases analysed together as “social
221 contact”. All behaviours were recorded as states (duration) and they were all exclusive, i.e. the
222 start of one behaviour stopped the previous one. A first set of modifiers, “Partner”, “Control”
223 and “Alone”, was added to record in which tank the focal mouse was for each expressed
224 behaviour. For the polygynous test, the modifiers were “Left” or “Right” instead of
225 Partner/Control. We also recorded whether the focal mouse initiated or received the behaviour.
226 When one mouse initiated a behaviour, we also noticed if the other mouse tried to avoid this
227 behaviour.

228

229 *Welfare note*

230 We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. All experiments
231 conducted received ethical clearance from the CREMEAS Committee (reference n°
232 2016121213346905). Mice were checked in their home cages twice a day in the morning and
233 afternoon for their well-being. The welfare of animals was improved by using highly enriched
234 cages, and by only changing one cage per week, such that animals had not to be handled for
235 cleaning and always had one familiar cage. After tethering, mice which were left alone in the
236 experimental room for a 20minute acclimation phase. During this entire period they were
237 watched from outside on a monitor via a webcam to ensure that they were not in distress. After
238 experiments, individuals were either euthanized or remained as breeding stock in the colony.

239

240 *Statistical analysis*

241 All analyses were made in Rstudio using R (version 3.1.1). Data are presented as mean \pm SD.
242 To test for partner preference, a Linear Mixed-Effects Model (LMM) was used with the
243 percentage of time the focal individual spent in social interactions with the partner or the
244 stranger as dependant variable. The tested model was: social contact \sim sex*group*stimulus +
245 whatfirst + (1|ID). “Social contact” was the proportion of time spent by the focal mouse in
246 social contact with a conspecific (socio-positive and sexual behaviours combined), either with
247 the partner or with the stranger, such that each individual had two data points. ID of the focal
248 individual was thus added as a random factor. “Sex” was the sex of the focal individual.
249 “Category” represented whether the focal mouse came from a monogamous pair or a
250 polygynous group. “Stimulus” was the role of the conspecific tested, “Partner” or “Control”.
251 As individuals were often used in two tests, as stimulus or as focal individual, which could
252 influence their behaviour, we included this as the categoric factor “what first” into the model.
253 Tukey Contrasts were used as post-hoc tests. To test whether males and females spent the same
254 amount of time in the three tanks of the apparatus, a second Linear Mixed-Effects Model
255 (LMM) was used. The tested model was: time \sim sex * stimulus + (1|ID). Here, “stimulus”
256 represented the tank where the focal was present (“Partner”, “Control”, or “Middle”).
257 Therefore, one Kruskal-Wallis test per sex was used to test for a difference in the time spent in
258 the different tanks. To compare the results between sexes, Conover tests were used. In order to
259 see which component of social contact (sexual, grooming, and body contact) could influence
260 the choice of individuals, three additional LMMs were run. The tested models were for each
261 component: Grooming \sim sex*stimulus*group + (1| ID), Body Contact \sim sex*stimulus*group +
262 (1| ID), and Sexual \sim sex*stimulus*group + (1| ID). To test for a preference of the males for
263 one of female in the polygynous groups, we used paired t test per trio. For this, each female of
264 each trio received randomly the status “female A” or “female B”. Therefore, for each trio, we
265 compared the proportion of time the focal male spent in physical contact with female A *versus*

266 female B. In order to correct for multiple comparisons, sign tests were used where each trio
267 contributed one data point (categorical: significant preference yes or no).

268

269 **Results**

270 **Table 1:** Results of the LMM investigating which variables relate to the time spent in social
271 contact by the focal mice. The four variables tested are the sex of focal individual (male or
272 female), whether they were kept in monogamous or polygynous “group”, and the stimulus
273 (control or partner). Significant variables are indicated in bold.

274

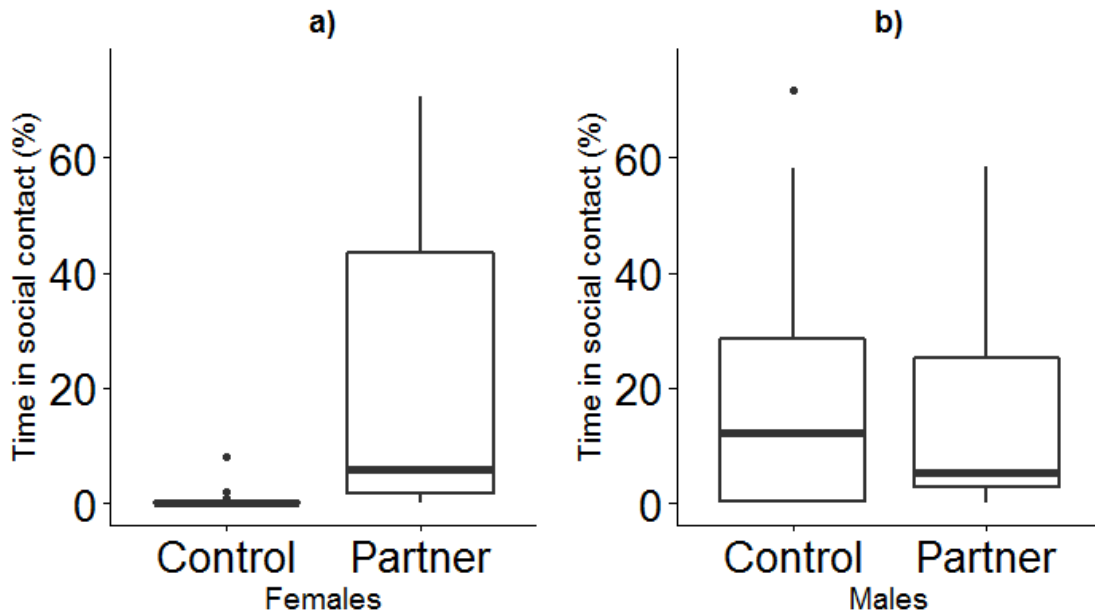
Model 1 : Social contact ~ sex*stimulus*group + whatfirst + (1 ID)			
Variable	Estimate (Chisq)	df	p value
sex	2.48	1	0.11
stimulus	10.87	1	0.0009
group	0.006	1	0.93
whatfirst	0.07	1	0.78
sex*stimulus	4.16	1	0.04
sex*group	0.7	1	0.4
stimulus*group	0.86	1	0.35
sex*stimulus*group	0.1	1	0.74

275

276 *Experiment 1: Partner preference test*

277 Stimulus and the interaction between sex and stimulus were significantly related to the
278 time focal mice spent in social contact with other mice, while there was no significant difference
279 in preference between individuals coming from monogamous or polygynous groups, nor was
280 there an effect whether an individual was first tested as stimulus or focal individual (whatfirst)
281 (table 1). Females spent significantly more time with their partner than the control, while there
282 was no significant difference for males (Multiple Comparison of Means: Tukey contrasts;
283 Figure 2).

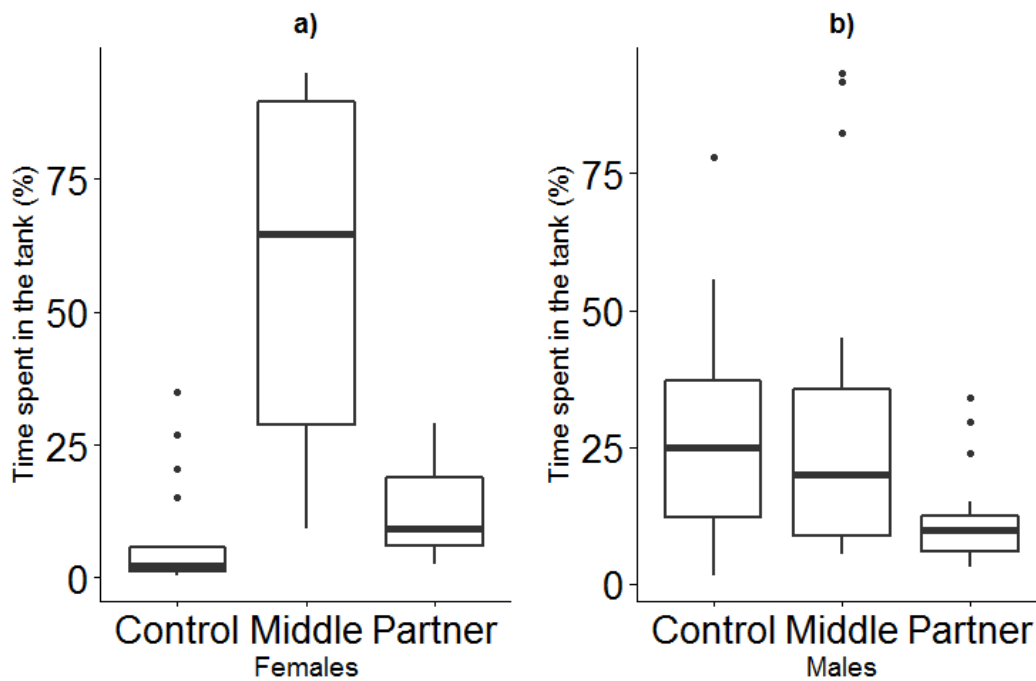
284



285

286 **Figure 2:** Percentage of time spent in social contact (+/- Standard deviation) by the focal
 287 individual with the control and the partner individual for a) females (N=23) and b) males
 288 (N=23). The bold line represents the median.

289



290

291 **Figure 3:** Percentage of time the focal individual spent in each tank (+/- Standard deviation) of
 292 the three-chamber apparatus without interacting with the other mice for (a) females (N=23) and
 293 (b) males (N=23). The bold lines are the median.

294 The time spent in the three different compartments (middle/partner/control) was
 295 significantly influenced by the interaction between sex and tank (LMM, $p < 0.001$). The time
 296 spent in the three different tanks differed both for females (Kruskal Wallis $\text{Chisq}^2 = 41.20$,
 297 $P < 0.001$) and for males (Kruskal Wallis $\text{Chisq}^2 = 10.87$, $P < 0.01$). Females spent more time
 298 alone in the middle tank than with their partner, and they spent more time in their partner's tank
 299 than in the control's tank (Conover test, $P_{\text{Middle-Control}} < 0.001$, $P_{\text{Middle-Partner}} < 0.001$, $P_{\text{Partner-Control}}$
 300 < 0.001 , Figure 3a). Males spent significantly less time in the tank with the partner, with no
 301 difference in time spent in the control and the middle tank (Conover test, $P_{\text{Middle-Control}} = 0.49$,
 302 $P_{\text{Middle-Partner}} < 0.01$, $P_{\text{Partner-Control}} < 0.01$ Figure 3b).

303
 304
 305
 306
 307

308 **Table 2:** Results of the three LMMs investigating which variables influence the time spent by
 309 the focal mice with the two stimulus “control” and “partner” in A) grooming interaction B) in
 310 body contact, and C) sexual interaction. The variables tested are the sex of focal individual
 311 “males” or “females”, their group “monogamous” or “polygynous” and their identity “ID”
 312 added as a random factor. Significant variables are in bold.

313

A) Model 3 : Grooming ~ sex*stimulus*group + (1 ID)			
Variable	Estimate (Chisq)	df	p value
sex	6.15	1	0.013
stimulus	3.96	1	0.046
group	1.2	1	0.27
sex*stimulus	2.54	1	0.11
sex*group	0.46	1	0.49
stimulus*group	0.13	1	0.71
sex*stimulus*group	0.04	1	0.82

B) Model 4 : Body contact ~ sex*stimulus*group + (1 ID)			
Variable	Estimate (Chisq)	df	p value
sex	0.93	1	0.33
stimulus	11.42	1	0.0007
group	0	1	0.99

sex*stimulus	3.24	1	0.07
sex*group	0.53	1	0.46
stimulus*group	1.05	1	0.3
sex*stimulus*group	0.1	1	0.74

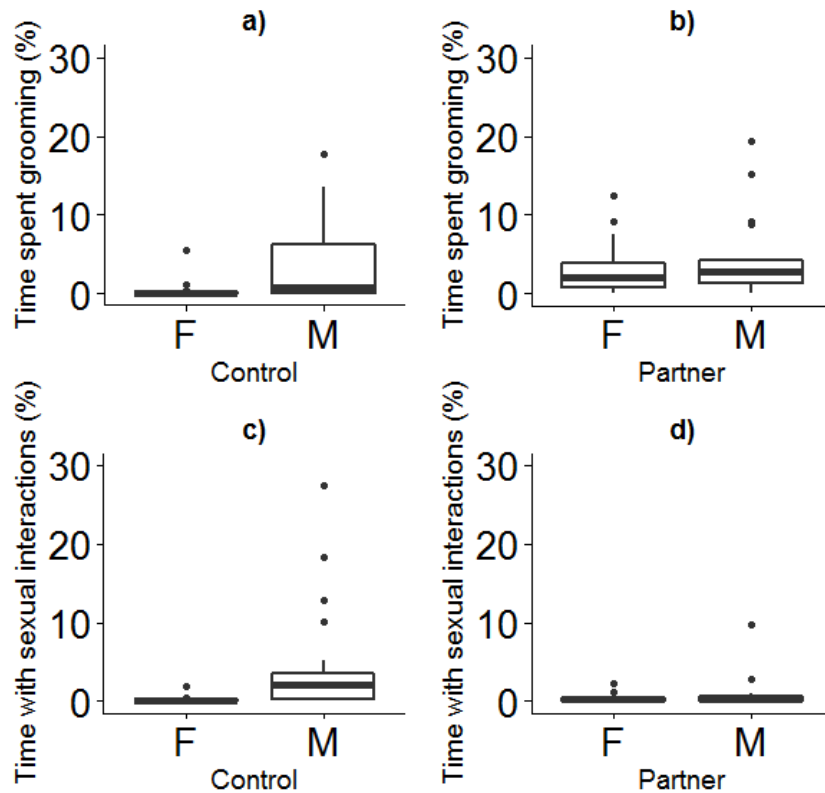
C) **Model 5 : Sexual ~ sex*stimulus*group + (1| ID)**

Variable	Estimate (Chisq)	df	p value
sex	5.27	1	0.021
stimulus	0.14	1	0.7
group	0.013	1	0.9
sex*stimulus	5.1	1	0.023
sex*group	0.43	1	0.5
stimulus*group	0.043	1	0.83
sex*stimulus*group	0.0046	1	0.94

314

315 There was a sex difference concerning the time spent grooming the stimulus individual
316 (LMM sex difference: $P=0.04$; stimulus difference $P=0.01$; Table 2A). Males spent
317 significantly more time grooming control individuals compared to females but males and
318 females did not differ in the amount of time spent grooming their partner (Figure 4 a,b). Time
319 spent in body contact differed according to the stimulus animal (Table 2C) but not between
320 sexes. Striped mice from both sexes spent significantly more time in body contact with their
321 partner than with the control (Figure 5). Model 5 found a significant interaction between sex
322 and stimulus for sexual behaviour (LMM, $P=0.023$, Table 2B). Mice from both sexes spent a
323 similar amount of time in sexual interactions with their partner (Figure 4d) but males spent
324 more time in sexual interactions with strangers than females (Figure 4c).

325

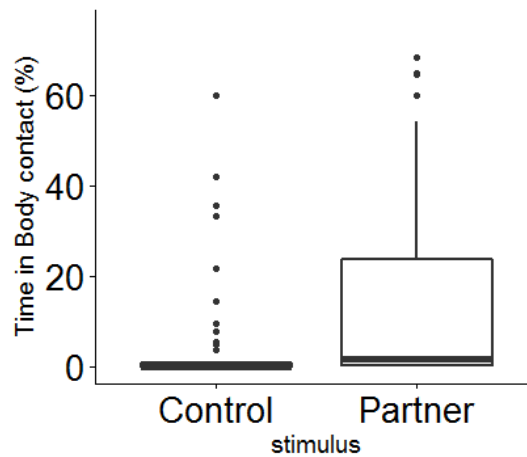


326

327 **Figure 4:** Percentage of time spent by the focal mice in grooming interactions with a control
 328 (a) or with its partner (b) for both sexes (F: females. M: males, each N=23). Percentage of time
 329 spent by the focal mice in sexual interaction with a control (c) or with its partner (d) for both
 330 sexes (F: females. M: males, each N=23). The median is represented by the bold horizontal line.

331

332



333

334 **Figure 5:** Percentage of time spent by the focal mice from both sexes in body contact with a
 335 control or with their partner (N=46). The median is represented by the bold horizontal line.

336

337 *Comparison with prairies vole published data*

338 Males did not show a partner preference (see above) and were not analysed here. Females spent
339 on average 22.62% +/- 26.7; range [0.14; 70.47] of their time with their partner. Only 3 out of
340 23 female striped mice reached the criteria of 66% reported for female prairie voles (Devries
341 1995). Females striped mice spent significantly less time in social contact with their partner
342 compared to an expectation based on data reported from female prairie voles (one sample t test
343 with $\mu=0.66$, $t_{22}=-7.73$. $p<0.001$).

344

345 *Experiment 2: Male preference in polygynous groups*

346 Only two out of ten males showed a significant preference for one particular female (Trio 4, $t_7=$
347 -4.34 ; $p<0.01$; and Trio 6, $t_7=-4.61$; $p<0.01$). After correction for multiple comparisons, these
348 differences did not remain significant. Male striped mice did not significantly prefer one of their
349 females over their other female (sign test, $p>0.1$).

350

351 **DISCUSSION**

352 Understanding social bonds between sex partners is important to understand the variety of
353 social systems we observe. However, so far the focus on studying social bonds was only on one
354 specific social system, social monogamy. This is not sufficient to understand social evolution.
355 Here we studied social bonds in a socially flexible species that can live in pairs, but typically
356 lives in polygynous groups. We found that female striped mice form selective partner
357 preferences, independently whether they lived in a monogamous or a polygynous group. In
358 contrast, males did not show social preferences. Males showed a sexual preference for a strange
359 female over their partner female. Interestingly, males and females did not differ in the amount

360 of social interactions with their partner, but males interacted more than females with the
361 unfamiliar individual. Thus, the preference of males for an unfamiliar individual might not
362 indicate that they are less bonded to their female partner than females are bonded to their male
363 partner. There was no difference between monogamously and polygynously kept striped mice
364 regarding their preference for familiar versus strange partners. Finally, there was little evidence
365 that polygynous males prefer one female over the other. Our study shows that social bonds
366 similar to pair bonds can occur in polygynous species, though these bonds seem to be less
367 strong.

368 Monogamously and polygynously kept striped mice did not differ in the social bonds
369 they formed with their opposite sex partner(s). Whether striped mice lived in pairs or
370 polygynous groups was determined by the experiment and did not represent a choice of the
371 individuals. Therefore, the imposed mating system could explain the absence of differences
372 obtained between monogamous and polygynous mice. Importantly, female striped mice showed
373 a partner preference by spending twice as much time with their partner compared to the stranger,
374 independent from the social situation (monogamous or polygynous) under which they were
375 living. In contrast, male striped mice showed a sexual preference for control individuals, even
376 though the females in our study were not sexually receptive. This might explain why sexual
377 behaviour was shown very rarely by males and why females showed very little if any sexual
378 interest in any male (Fig. 4d). Our experimental setup aimed at only measuring social preference
379 and avoiding any sexual motivation and a different set of experiments using receptive females
380 would have to be used to measure sexual preference. Importantly, in our study males did not
381 show less interest (social contact, grooming, body contact) in their female partners than did
382 females show for their male partners. Thus, the difference between the sexes in partner
383 preference might not be due to differences in the strength of social bonding towards their
384 partner. Instead, a higher sexual attractiveness for potential extra-group mates in males can

385 explain the results, and this would indicate an adaptive strategy, as male fitness is to one fifth
386 (21%) determined by extra-group paternity (Schradin et al., 2010).

387 Striped mice spent less time with their partners (22%) compared to what has been reported
388 for prairie voles (66%) by Devries et al (1995). Only three out of 23 female striped mice reached
389 the mean of 66% reported for prairie voles and male striped mice showed a sexual preference
390 for control individuals. While there have been differences between our study and studies on
391 prairie voles (our test apparatus did not allow mice to see the other two compartments, focal
392 individuals also acted as tethered partners, and duration of cohabitation before testing was
393 longer), these results indicate that these two species differ in social bonding.

394 Social bonds between opposite sex members do exist in polygynous species but might be
395 weaker than in some monogamous species. However, socially monogamous species without
396 pair-bonds also exist (Macroscelididae, elephant shrews; Sauer 1973) and some socially
397 monogamous species prefer a stranger over their own partner (marmosets *Callithrix penicillata*;
398 Smith et al., 2010), while other polygynous species have also been reported to form pair-bonds
399 (meadow voles, Parker et al. 2001). Partner preference tests might fail to demonstrate a
400 preference even in species with pair bonds. For example in socially monogamous California
401 mice, males do not show a preference for their partner under normal conditions, but do so if
402 they are stressed (Kowalczyk et al. 2018). Additionally, social preferences can also exist
403 between familiar same sex individuals, as reported for prairie voles (but not laboratory mice;
404 Beery et al. 2018), meadow voles (Parker & Lee 2003), and titi monkeys (*Callicebus moloch*;
405 Carp et al. 2016) using partner preference tests in captivity, and also for non-reproductive adult
406 striped mice observed in the field (Brunner et al. 2016). This variety offers an important source
407 to study the mechanisms underlying social-bonding, independent of the social system of the
408 species. Research measuring the fitness consequences of variation in pair-bond strength is then
409 needed to explain the variation in bonding pattern over different forms of social organisation.

410 Prairie voles are typically monogamous (DeVries et al., 1995; Getz & Carter, 1996), while
411 free-living striped mice generally form polygynous groups of one male and up to four breeding
412 females (Schradin & Pillay, 2004). It has recently been demonstrated that even in the presence
413 of two receptive females, male prairie voles prefer to establish a pair bond with one particular
414 female and do not try to mate with the other (Blocker & Ophir, 2016). In prairie voles, when
415 the male from a pair dies, eighty percent of the females do not form a new bond with another
416 male (Pizzuto & Getz, 1998). Whether selective social bonds exist in polygynous species is so
417 far unknown. Striped mice have recently been shown to be capable of individual recognition
418 (Brunner et al., 2016) and polygynous males could thus have a favourite female partner. Instead,
419 polygynous male striped mice seemed to bond equally with their two females in our study.
420 Communal groups of striped mice consist of closely related breeding females such as sisters,
421 half-sisters, and cousins (Schradin et al. 2010; Schradin & Lindholm, unpublished genetic data).
422 In our study, females were full siblings from the same litter, i.e. of the same age and body mass.
423 Thus, their fecundity and reproductive value for the male might have been equal, which – from
424 an ultimate point of view - could explain why males did not show a preference towards one
425 particular female. Under natural conditions, where females differ in body mass (Hill et al.,
426 2015) and thus probably fecundity, and are genetically more diverse (Schradin et al. 2010),
427 male preference for a particular female might be adaptive and might occur.

428 In conclusion, we found indication for pair bonding in the form of proximity between
429 partners in socially flexibly African striped mice. Female striped mice showed a stronger
430 partner preference while males had a sexual preference for strangers. The imposed mating
431 system (i.e. polygyny or monogamy) had no impact on individual's preference. Thus, social
432 bonds between mating partners occur in monogamous and in polygynous species but they seem
433 to be less strong in polygynous species. To understand the evolution of sociality it will be
434 important to study social bonds in more species with a variety of social systems, which will

435 then enable us to come to a better understanding of the physiological mechanisms of social
436 bonding, and whether different mechanisms exist.

437

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442

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