



**HAL**  
open science

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

Lorène Garnier, Carsten Schradin

## ► To cite this version:

Lorène Garnier, Carsten Schradin. Pair bonding in monogamously and polygynously kept African striped mice, *Rhabdomys pumilio*. *Animal Behaviour*, 2019, 150, pp.69-76. 10.1016/j.anbehav.2019.02.001 . hal-02108362

**HAL Id: hal-02108362**

**<https://hal.science/hal-02108362>**

Submitted on 20 Jul 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Published as

5 Garnier, L. & **Schradin, C.** 2019. Pair bonding in monogamously and polygynously kept  
6 African striped mice, (*Rhabdomys pumilio*). *Animal Behaviour*, **150**, 69-76.

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

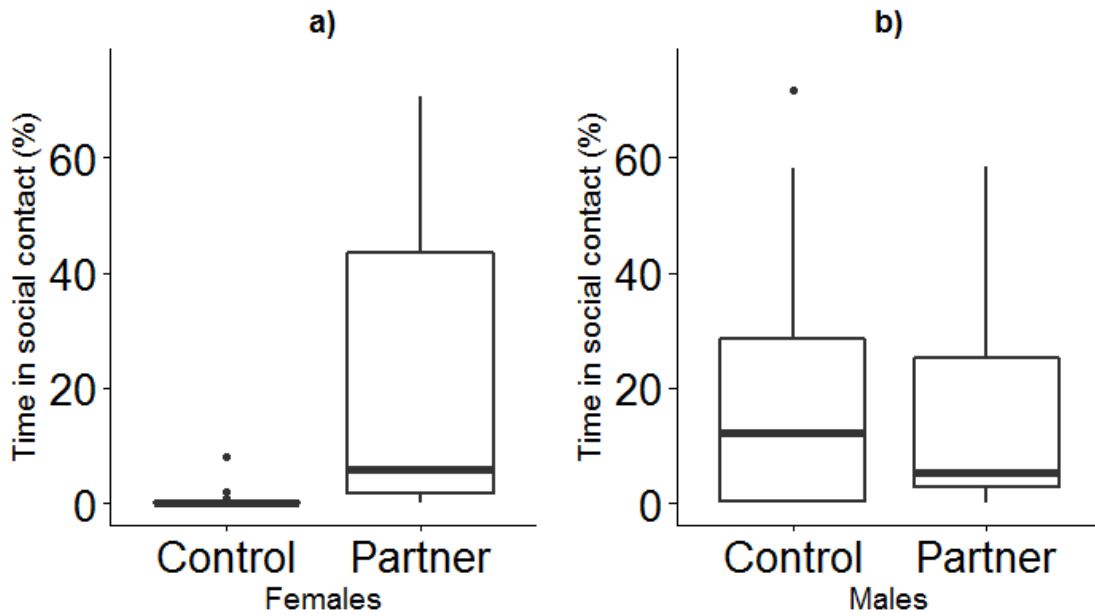
<b>Model 1 : Social contact ~ sex*stimulus*group + whatfirst + (1 ID)</b>			
Variable	Estimate (Chisq)	df	p value
sex	2.48	1	0.11
<b>stimulus</b>	<b>10.87</b>	1	<b>0.0009</b>
group	0.006	1	0.93
whatfirst	0.07	1	0.78
<b>sex*stimulus</b>	<b>4.16</b>	1	<b>0.04</b>
sex*group	0.7	1	0.4
stimulus*group	0.86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

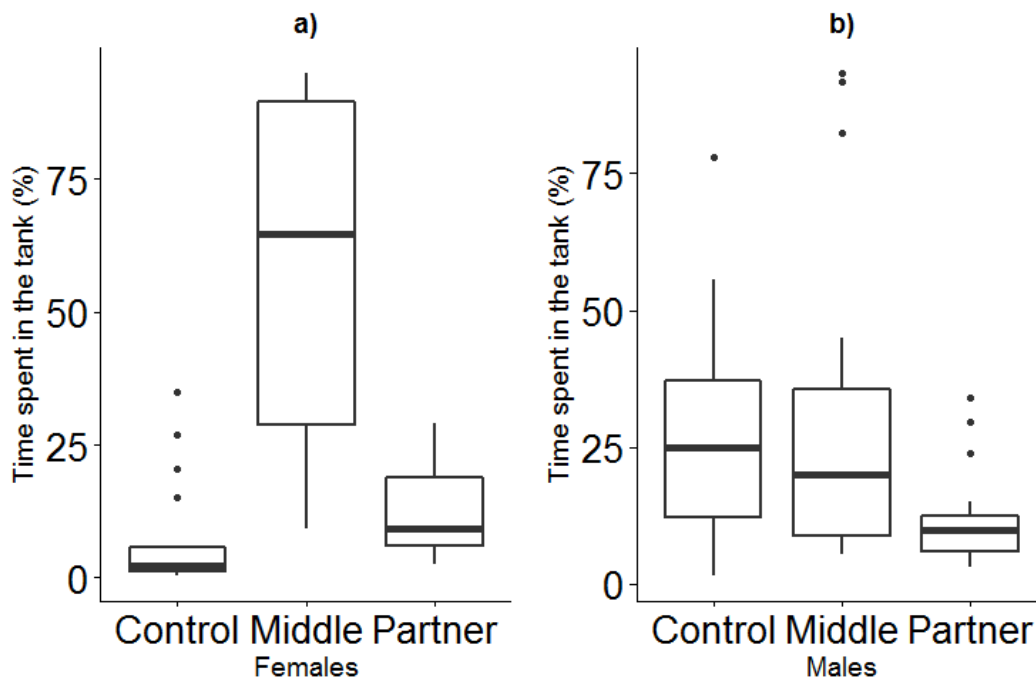
284



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

<b>A) Model 3 : Grooming ~ sex*stimulus*group + (1  ID)</b>			
Variable	Estimate (Chisq)	df	p value
<b>sex</b>	<b>6.15</b>	<b>1</b>	<b>0.013</b>
<b>stimulus</b>	<b>3.96</b>	<b>1</b>	<b>0.046</b>
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>B) Model 4 : Body contact ~ sex*stimulus*group + (1  ID)</b>			
Variable	Estimate (Chisq)	df	p value
sex	0.93	1	0.33
<b>stimulus</b>	<b>11.42</b>	<b>1</b>	<b>0.0007</b>
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

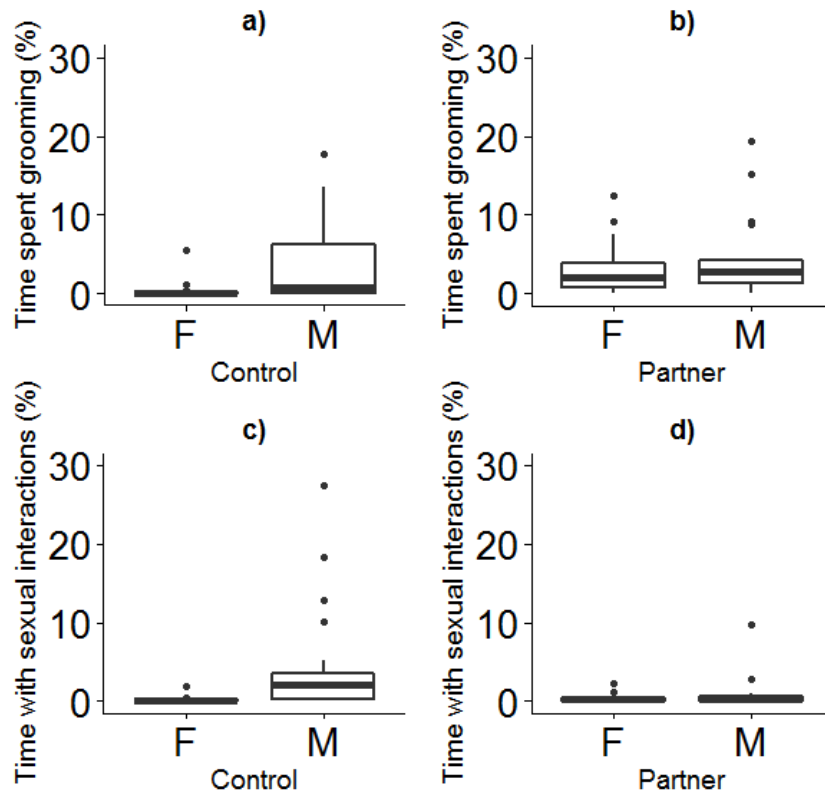
C) **Model 5 : Sexual ~ sex\*stimulus\*group + (1| ID)**

Variable	Estimate (Chisq)	df	p value
<b>sex</b>	<b>5.27</b>	<b>1</b>	<b>0.021</b>
stimulus	0.14	1	0.7
group	0.013	1	0.9
<b>sex*stimulus</b>	<b>5.1</b>	<b>1</b>	<b>0.023</b>
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

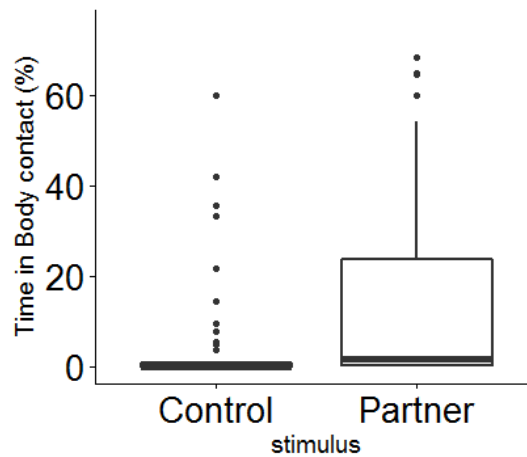


326

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

#### 438 **Acknowledgments**

439 This study was supported by the CNRS. We are grateful for comments by R. Rimbach and N.  
440 Pillay that significantly improved the manuscript. The study obtained ethical clearance from  
441 the CREMEAS Committee (reference n° 2016121213346905).

442

#### 443 **References**

444 Bales, K. L., & Carter, C. S. (2003). Developmental exposure to oxytocin facilitates partner preferences  
445 in male prairie voles (*Microtus ochrogaster*). *Behavioral Neuroscience*, *117*(4), 854–859.

446 Beery, A. K., Christensen, J. D., Lee, N. S. & Blandino, K. L. 2018. Specificity in Sociality: Mice and  
447 Prairie Voles Exhibit Different Patterns of Peer Affiliation. *Frontiers in Behavioral Neuroscience*,

448 **12**.Bercovitch, F. B. (1988). Coalitions, cooperation and reproductive tactics among adult male  
449 baboons. *Animal Behaviour*, *36*(4), 1198–1209.

450 Blocker, T. D., & Ophir, A. G. (2016). A preference to bond? Male prairie voles form pair bonds even  
451 in the presence of multiple receptive females. *Animal Behavior*, *122*, 89–97.

452 Brunner, P., I. Schoepf, C. H. Yuen. B. König and C. Schradin. (2016). Does a mouse have a friend?  
453 Mixed evidence for individual recognition in the African striped mouse (*Rhabdomys pumilio*).  
454 *Journal of Zoology*, *299*, 142-149.

455 Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews*, *78*(4), 575–595.Carp,  
456 S. B., Rothwell, E. S., Bourdon, A., Freeman, S. M., Ferrer, E. & Bales, K. L. 2016. Development  
457 of a partner preference test that differentiates between established pair bonds and other

458 relationships in socially monogamous titi monkeys (*Callicebus cupreus*). *American Journal of*  
459 *Primatology*, **78**, 326-339.

460 Carter, C. S., DeVries, A. C., & Getz, L. L. (1995). Physiological substrates of mammalian monogamy:  
461 the prairie vole model. *Neuroscience and Biobehavioral Reviews*, *19*(2), 303–314.

462 Carter, C. S., & Keverne, E. B. (2002). The neurobiology of social affiliation and pair bonding.  
463 *Hormones and Behavior*, *1*, 299–337.

464 Carter, C. S. (2005). Biological perspectives on social attachment and bonding. *Attachment and*  
465 *Bonding: A New Synthesis*. (Bowlby 1969), 85–100.

466 Carter, C. S. S., & Porges, S. W. S. (2010). Social bonding and attachment. *Encyclopedia of Behavioral*  
467 *Neuroscience*, 257–262.

468 Carp, S. B., Rothwell. E. S., Bourdon. A., Freeman. S. M., Ferrer. E., & Bales. K. L. (2016).  
469 Development of a partner preference test that differentiates between established pair bonds and  
470 other relationships in socially monogamous titi monkeys (*Callicebus cupreus*). *American Journal*  
471 *of Primatology*, *78*(3), 326–339.

472 Cho, M. M., DeVries, A. C., Williams, J. R., & Carter. C. S. (1999). The effects of oxytocin and  
473 vasopressin on partner preferences in male and female prairie voles (*Microtus ochrogaster*).  
474 *Behavioral Neuroscience*, *113*(5), 1071–1079.

475 Cords, M. (2001). Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour*, *139*,  
476 291–314.

477 Cushing, B. S., & Carter, C. S. (2000). Peripheral pulses of oxytocin increase partner preferences in  
478 female but not male prairie voles. *Hormones and Behavior*, *37*, 49–56.



- 479 DeVries, A. C., DeVries, M. B., Taymans, S., & Carter, C. S. (1995). Modulation of pair bonding in  
480 female prairie voles (*Microtus ochrogaster*) by corticosterone. *Proceedings of the National*  
481 *Academy of Sciences of the United States of America*, 92(17), 7744–8.
- 482 Dewsbury, D. A. (1975). Diversity and adaptation in rodent copulatory behavior. *Science*, 190, 947–  
483 954.
- 484 Dufour, C. M., Pillay, N., & Ganem, G. (2015). Ventro – ventral copulation in a rodent : a female  
485 initiative? *Journal of Mammalogy*, 96(5), 1017–1023.
- 486 Edgar, J., Held, S., Paul, E., Pettersson, I., Anson, R. I., & Nicol, C. (2015). Social buffering in a bird.  
487 *Animal Behaviour*, 105, 11–19.
- 488 Fernandez-duque, E., & Huck, M. (2013). Till death (or an intruder) do us part : intrasexual- competition  
489 in a monogamous primate. *PLoS ONE*, 8(1), 1–5.
- 490 Fernández-Vargas, Tang-Martinez, Z., & Phelps, S. (2011). Singing, allogrooming and allomarking  
491 behaviour during inter- and intra-sexual encounters in the Neotropical short-tailed singing mouse  
492 (*Scotinomys teguina*). *Behaviour*, 148, 945–965.
- 493 Foerster, S., McLellan, K., Schroepfer-walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey,  
494 A. E. (2015). Social bonds in the dispersing sex : partner preferences among adult female  
495 chimpanzees. *Animal Behaviour*, 105, 139–152.
- 496 Friard, O., & Gamba, M. (2016). BORIS : a free versatile open-source event-logging software for video  
497 / audio coding and live observations.
- 498 Getz, L.L., Hofmann, J.E., & Carter, C.S. (1987). Mating system and population fluctuations of the  
499 prairie vole, *Microtus ochrogaster*. *American Zoologist*, 27, 909–920.
- 500 Getz, L. L., & Carter, C. S. (1996). Prairie-vole partnerships. *American Scientist*, 84(1), 56–62.

- 501 Gubernick, D. J., & Nordby, J. C. (1993). Mechanisms of sexual fidelity in the monogamous California  
502 mouse, *Peromyscus californicus*. *Behavioral Ecology and Sociobiology*, 32(3), 211–219.
- 503 Haunhorst, C. B., Heesen, M., Ostner, J., & Schülke, O. (2017). Social bonds with males lower the costs  
504 of competition for wild female Assamese macaques. *Animal Behaviour*, 125, 51–60.
- 505 Hill, D. L., N. Pillay, and C. Schradin. (2015). Alternative reproductive tactics in female striped mice:  
506 heavier females are more likely to breed solitarily than communally. *Journal of Animal Ecology*,  
507 84, 1497–1508.
- 508 Insel, T.R., Preston, S., & Winslow, T. (1995). Mating in the monogamous male: behavioral  
509 consequences. *Physiology & Behavior*, 57(4), 615–627.
- 510 Insel, T. R., & Hulihan, T. J. (1995). A gender-specific mechanism for pair bonding: oxytocin and  
511 partner preference formation in monogamous voles. *Behavioral Neuroscience*, 109(4), 782–789.
- 512 Johnson, Z. V. & Young, L. J. (2015). Neurobiological mechanisms of social attachment and pair  
513 bonding. *Current Opinion in Behavioral Sciences*, 3, 38–44.
- 514 Kappeler, P., & Kappeler, P. M. (2016). Lemur behavior informs the evolution of social monogamy.  
515 *Trends in Ecology & Evolution*, 29(11), 591–593.
- 516 Karelina, K., Walton, J. C., Weil, Z. M., Norman, G. J., Nelson, R. J., & Devries, A. C. (2010).  
517 Hormones and behavior estrous phase alters social behavior in a polygynous but not a  
518 monogamous *Peromyscus species*. *Hormones and Behavior*, 58(2), 193–199.
- 519 Kern, J. M., & Radford, A. N. (2016). Social-bond strength influences vocally mediated recruitment to  
520 mobbing. *Biology Letters*, 1–4.
- 521 Kiyokawa, Y., Ishida, A., Takeuchi, Y., & Mori, Y. (2016). Sustained housing-type social buffering  
522 following social housing in male rats. *Physiology & Behavior*, 158, 85–89.
- 523 Kleiman, D. G. (1977). Monogamy in mammals. *The Quarterly Review of Biology*, 52(1), 39–69.

- 524 Kowalczyk, A. S., Davila, R. F. & Trainor, B. C. 2018. Effects of social defeat on paternal behavior and  
525 pair bonding behavior in male California mice (*Peromyscus californicus*). *Hormones and*  
526 *Behavior*, **98**, 88-95.
- 527 Latham, N., & Mason, G. (2004). From house mouse to mouse house: the behavioural biology of free-  
528 living *Mus musculus* and its implications in the laboratory. In *Applied Animal Behaviour Science*  
529 (Vol. 86. pp. 261–289).
- 530 Lazarus, S. R., and Folkman, S. (1984). *Stress, appraisal and coping*. Springer, New York.
- 531 Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*,  
532 *341*(6145), 526–530.
- 533 Madison, D. M., Fitzgerald, R. W., & Mcshea, W. J. (1984). Dynamics of social nesting in overwintering  
534 meadow voles possible consequences for population cycling. *Behavioral Ecology and*  
535 *Sociobiology*, *15*(1), 9–17.
- 536 Madison, D. M., & Mcshea, W. J. (1987). Seasonal-changes in reproductive tolerance, spacing, and  
537 social-organization in meadow voles - a microtine model. *American Zoologist*, *27*(3), 899–908.
- 538 McFarland, R. Fuller, A., Hetem, R. S., Mitchell, D, Maloney, S.K., Henzi, S. P., Barrett, L. (2015).  
539 Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology*,  
540 *84*(3), 871–878.
- 541 McGraw, L., Skékely. T., & Young, L.J. (2010). Pairs bonds and parental behaviour. In *Social*  
542 *Behaviour: Genes, Ecology and Evolution* (pp. 270-301). Cambridge University Press.
- 543 McNeal, N., Scotti, M. L., Wardwell, J., Chandler, D. L., Bates, S. L., Larocca, M., Grippo, A. J. (2014).  
544 Basic and clinical disruption of social bonds induces behavioral and physiological dysregulation  
545 in male and female prairie voles. *Autonomic Neuroscience: Basic and Clinical*, *180*, 9–16.

546 McShea, W. J. Madison, D. M. (1984). Communal nesting between reproductively active females in a  
547 spring population of *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, 62, 344–346.

548 Mikami, K., Kiyokawa, Y., Takeuchi, Y., & Mori, Y. (2016). Social buffering enhances extinction of  
549 conditioned fear responses in male rats. *Physiology & Behavior*, 163, 123–128.

550 Nelson, E. & Panksepp, J. (1996). Oxytocin and infant-mother bonding in rats. *Behavioral*  
551 *Neuroscience*, 110, 583–592.

552 Numan, M., & Young, L. J. (2015). Neural mechanisms of mother – infant bonding and pair bonding :  
553 similarities, differences, and broader implications. *Hormones and Behavior*, 77, 98–112.

554 Ophir, A. G., Phelps, S. M., Sorini, A. B., & Wolff, J. (2008). Social but not genetic monogamy is  
555 associated with greater breeding success in prairie voles. *Animal Behaviour*, 75, 1143–1154.

556 Parker, K. J., Phillips, K. M., & Lee, T. M. (2001). Development of selective partner preferences in  
557 captive male and female meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, 61(6), 1217–  
558 1226.

559 Parker, K. J., & Lee, T.M. 2003. Female meadow voles (*Microtus pennsylvanicus*) demonstrate same-  
560 sex partner preference. *Journal of Comparative Psychology*, 117, 283-289. Pizzuto, T., & Getz, L.  
561 L. (1998). Female prairie voles (*Microtus ochrogaster*) fail to form a new pair after loss of mate.  
562 *Behavioural Processes*, 43, 79–86.

563 Polechová, J., & Stopka, P. (2002). Geometry of social relationships in the Old World wood mouse.  
564 *Apodemus sylvaticus*. *Canadian Journal of Zoology*, 80, 1383–1388.

565 Reite, M. & Boccia, M. L. (1994) Physiological aspects of adult attachment. In: Sperling, M. B. and  
566 Berman, W. H. (Eds.). *Attachment in Adults*. Guilford Press, New York.

- 567 Sanchez-Macouzet, O., Rodriguez. C., & Drummond. H. (2014). Better stay together: pair bond duration  
568 increases individual fitness independent of age-related variation. *Proceedings of the Royal Society*  
569 *B: Biological Sciences*, 281(1786), 20132843.
- 570 Sachser, N. (2005) Adult social bonding insights from studies in nonhuman mammal's species. In  
571 Attachment and Bonding: a New Synthesis (pp. 120-135). MIT Press. Cambridge: England.
- 572 Sachser, N., Dürschlag, M., & Hirzel, D. (1998). Social relationships and the management of stress.  
573 *Psychoneuroendocrinology*, 23(8), 891–904.
- 574 Sauer, E. G. F. (1973). Zum Sozialverhalten der Kurzohrigen Elefantenspitzmaus, *Macroscelides*  
575 *proboscideus*. *Z Säugetierkunde* 38, 65–97.
- 576 Schradin, C. (2004). Territorial defense in a group-living solitary forager : who, where, against whom ?  
577 *Behavioral Ecology and Sociobiology*, 55, 439–446.
- 578 Schradin, C., König, B., & Pillay, N. (2010). Reproductive competition favours solitary living while  
579 ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology*,  
580 79(3), 515–521.
- 581 Schradin, C. & Pillay, N. (2004b). The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of  
582 South Africa: a territorial group living solitary forager with communal breeding and helpers at the  
583 nest. *Journal of Comparative Psychology*, 118, 37–47.
- 584 Schradin, C. & Pillay, N. (2005). Intraspecific variation in the spatial and social organization of the  
585 African striped mouse. *Journal of Mammalogy*, 86, 99–107.
- 586 Schradin, C., Lindholm, A. K., Johannesen, J. E. S., Schoepf, I., Yuen, C., & Ko, B. (2012). Social  
587 flexibility and social evolution in mammals : a case study of the African striped mouse (*Rhabdomys*  
588 *pumilio*). *Molecular Ecology*, 21, 541–553.

- 589 Schradin, C., C. Schneider, & A. Lindholm. (2010). The nasty neighbour in the striped mouse  
590 (*Rhabdomys pumilio*) steals paternity and elicits aggression. *Frontiers in Zoology* 7:19.
- 591 Schradin, C. (2013). Intraspecific variation in social organization by genetic variation, developmental  
592 plasticity, social flexibility or entirely extrinsic factors. *Philosophical Transactions of the Royal*  
593 *Society B: Biological Sciences*, 368(1618), 20120346.
- 594 Schradin, C., Kenkel, W., Krackow, S., & Carter, C. S. (2013). Staying put or leaving home : endocrine,  
595 neuroendocrine and behavioral consequences in male African striped mice. *Hormones and*  
596 *Behavior*, 63(1), 136–143.
- 597 Schoepf, I., & Schradin, C. (2012). Better off alone! Reproductive competition and ecological  
598 constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*). *Journal of*  
599 *Animal Ecology*, 81(3), 649–656.
- 600 Schoepf, I., & Schradin, C. (2014). Arginine vasopressin plasma levels change seasonally in African  
601 striped mice but do not differ between alternative reproductive tactics. *General and Comparative*  
602 *Endocrinology*, 204, 43–48.
- 603 Smith, A. S., Agmo, A., Birnie, A.K., & J. A. French. (2010). Manipulation of the oxytocin system alters  
604 social behavior and attraction in pair-bonding primates, *Callithrix penicillata*. *Hormones and*  
605 *Behavior*, 57, 255–262.
- 606 Smith, A. S., & Wang, Z. (2014). Hypothalamic oxytocin mediates social buffering of the stress  
607 response. *Biological Psychiatry*, 76(4), 281–288.
- 608 Stopka, P., & Graciasová, R. (2001). Conditional allogrooming in the herb-field mouse. *Behavioral*  
609 *Ecology*, 12(5), 584–589.
- 610 Wang, Z., Ferris, C. F., and De Vries, G, J, (1994). Role of septal vasopressin innervation in paternal  
611 behavior in prairie voles (*Microtus ochrogaster*). *Proceedings of the National Academy of*  
612 *Sciences*, 91, 400–404.

- 613 Wang, Z., & De Vries, G. J. (1993). Testosterone effects on paternal behavior and vasopressin  
614 immunoreactive projections in prairie voles (*Microtus ochrogaster*). *Brain Research*, 631(1), 156–  
615 160.
- 616 Wang, Z., & Insel, T. (1996). Parental behavior in voles. *Advances in the Study of Behavior*, 25, 361–  
617 384.
- 618 Wang, Z., Young, L. J., De Vries, G. J., Insel, T. R., Vries, G. J. De. & Insel, T. R. (1998). Voles and  
619 vasopressin: a review of molecular, cellular, and behavioral studies of pair bonding and paternal  
620 behaviors. *Progress in Brain Research*, 119, 483–499.
- 621 Wiley, R.H & Poston, J. (1996). Indirect mate choice, competition for mates and coevolution of the  
622 sexes. *Evolution*, 50(4), 1371–1381.
- 623 Willan, B. R. (1982). Social ecology of *Otomys irroratus*, *Rhabdomys pumilio* and *Mastomys natalensis*.  
624 University of Natal, Pietermaritzburg, South Africa.
- 625 Winslow, J.T., Hastings, A., Carter, C.S., Harbaugh, C.R., Insel, T. R. (1993). A role for central  
626 vasopressin in pair bonding in monogamous prairie voles. *Nature Publishing Group*, 365, 545–  
627 548.
- 628 Young, L. J., Winslow, J. T., Nilsen, R., & Insel, T. R. (1997). Species differences in V1a receptor gene  
629 expression in monogamous and non-monogamous voles: Behavioral consequences. *Behavioural*  
630 *Neuroscience*, 111, 599–605.
- 631 Young, L. J. (1999). Oxytocin and vasopressin receptors and species-typical social behaviors. *Hormones*  
632 *and Behavior*, 36, 212–221.
- 633 Young, L. J., Nilsen, R., Waymire, K. G., MacGregor, G. R., & Insel, T. R. (1999). Increased affiliative  
634 response to vasopressin in mice expressing the vasopressin receptor from a monogamous vole.  
635 *Nature*, 400, 766–768.

- 636 Young, L. J., Lim, M. M., Gingrich, B., & Insel, T. R. (2001). Cellular mechanisms of social attachment.  
637 *Hormones and Behavior*, 40(2), 133–138.
- 638 Young, L. J., & Wang, Z. (2004). The neurobiology of pair bonding. *Nature Neurosciences*, 7(10),  
639 1048–1054.
- 640 Young, K. A., Liu, Y., & Wang, Z. (2008). The neurobiology of social attachment: A comparative  
641 approach to behavioral, neuroanatomical, and neurochemical studies. *Comparative Biochemistry  
642 and Physiology, Part C*, 148(4), 401–410.
- 643 Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and  
644 environmental stress are attenuated by strong male bonds in wild macaques. *Proceedings of the  
645 National Academy of Sciences of the United States of America*, 1–6.
- 646