



HAL
open science

Geographic intra-specific variation in social organization is driven by population density

Carsten Schradin, Florian Drouard, Gildas Lemonnier, Richard Askew,
Charlotte Anaïs Olivier, Neville Pillay

► **To cite this version:**

Carsten Schradin, Florian Drouard, Gildas Lemonnier, Richard Askew, Charlotte Anaïs Olivier, et al..
Geographic intra-specific variation in social organization is driven by population density. Behavioral
Ecology and Sociobiology, 2020, 74 (9), 10.1007/s00265-020-02896-z . hal-02930773

HAL Id: hal-02930773

<https://hal.science/hal-02930773v1>

Submitted on 10 Sep 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 **Geographic intra-specific variation in social organization is driven by population density**

2
3 Published as

4 Schradin, C., Drouard, F., Lemonnier, G. *et al.* Geographic intra-specific variation in social
5 organization is driven by population density. *Behav Ecol Sociobiol* **74**, 113 (2020).

6 <https://doi.org/10.1007/s00265-020-02896-z>

7
8 Carsten Schradin^{1,2,*}, Florian Drouard², Gildas Lemonnier^{1,2}, Richard Askew², Charlotte-
9 Anaïs Olivier¹, Neville Pillay²

10
11 ¹CNRS, UMR7178, 67087 Strasbourg, France

12 ²School of Animal, Plant and Environmental Sciences, University of the Witwatersrand,
13 South Africa.

14
15 * Corresponding author carsten.schradin@iphc.cnrs.fr, + 33 (0)3 88 10 69 19

16
17 **Acknowledgments**

18 We thank P. Vuarin., C. Rochais, L. Kotze and several field assistants for help in collecting
19 the data. The comments of A. Ophir and of three anonymous referees significantly improved
20 the manuscript. We are grateful to Goegap Nature Reserve. This study was made possible by
21 the administrative and technical support of the Succulent Karoo Research Station, (registered
22 South African NPO 122-134).

25 **Abstract**

26

27 Social flexibility enables individuals to switch between group- and solitary-living, and is
28 suggested to be an adaptation to varying environments. Several previous studies on different
29 species compared two populations and hypothesized that observed differences in social
30 organization were due to differences in population density, but lacked the necessary sample
31 size to test this prediction. In a previous 8-year long-term study, we showed that one
32 population of African striped mice (*Rhabdomys pumilio*) displayed temporal social flexibility,
33 living solitarily in years when population density was low, but in groups in years when
34 population density was high. Building on this temporal variation, we now tested whether
35 geographic variation reveals the same pattern. We studied 6 populations in discrete
36 geographical locations simultaneously, predicting more solitary living in populations with
37 lower population density. Population density correlated significantly with the percentage of
38 striped mice living in groups whereas other (environmental) factors were not significant.
39 Moreover, some individuals dispersed over unoccupied habitats between these populations,
40 switching from group- to solitary living. Geographic variation in population density could
41 make social flexibility adaptive, because it allows individuals to respond quickly to the
42 prevailing conditions they experience post dispersal. Our results suggest that geographic
43 variation drives the evolution of social flexibility in our metapopulation of striped mice,
44 causing intra-specific variation in its social organization, which might also be important in
45 other species, especially in species with a fast life history.

46

47

48 **Significance statement**

49 Populations of the same species can differ in their social organization. It has often been
50 assumed that this is due to differences in population density. We studied 6 populations of the
51 African striped mice, showing that more mice were solitary living when population density
52 was low. Thus, we demonstrated that population differences in social organization were due
53 to differences in population density.

54

55 **Key words** group living; intraspecific variation; social evolution; social system; social
56 organization; solitary living

57 **Introduction**

58

59 Animal species show an interesting variety of social systems, such as solitary living, group-
60 living and even eusociality. Social systems consist of several subsystems that should be
61 studied independently. These include social organization (composition of groups), social
62 structure (social interactions), mating system, and care system (who takes care of dependent
63 offspring) (Kappeler and Schaik 2002; Kappeler et al. 2019). Most of the available data
64 concern social organization, since group composition is easy to measure. Social organization
65 can be solitary living, pair-living or living in groups of different composition (Kappeler and
66 Schaik 2002; Schradin et al. 2018). Variation in social organization is obvious between
67 different species.

68

69 Typically, only one form of social organization has been described for each species. However,
70 we have long known that many species can have several forms of social organization (Lott
71 1984, 1991; Maher and Burger 2011; Schradin et al. 2018). While different mechanisms can
72 theoretically lead to intra-specific variation in social organization (Schradin 2013), the most
73 common one is social flexibility (Schradin et al. 2018). Social flexibility is a case of
74 phenotypic plasticity, where individuals of both sexes adapt their social tactic in response to
75 the prevailing environmental conditions, enabling them to switch between different forms of
76 social organization (Schradin et al. 2012). For example, burying beetles (*Nicrophorus*
77 *vespilloides*) can form pairs or groups consisting of one male and two females, depending on
78 carrion size (Eggert and Müller 2000; Müller et al. 2006). In house mice (*Mus musculus*),
79 food availability influences whether they live solitarily, in pairs or in communal groups
80 (Latham and Mason 2004; Berry et al. 2008). Social flexibility can be an adaptation to an
81 environment varying in time but could also be an adaptation to other forms of variation.

82

83 In most species, social flexibility occurs due to changes in severity of competition, for
84 example due to changes in population density or resource availability (reviewed by (Maher
85 and Burger 2011; Schradin 2013). Dispersing individuals that migrate into a population where
86 environmental conditions differ from their natal population will benefit if they can adapt their
87 social tactics to prevailing conditions. Thus, social flexibility would be adaptive for dispersing
88 individuals if geographically isolated populations vary in ecological conditions, influencing
89 which social tactic yields the highest fitness. While geographic variation could lead to the

90 evolution of social flexibility, this is challenging to study, as multiple populations would have
91 to be monitored simultaneously.

92

93 It is well known that different populations of the same species can have different forms of
94 social organisation (Lott 1991; Agnani et al. 2018; Schradin et al. 2018). Multiple studies
95 have compared two populations of one species (reviewed in (Lott 1991; Maher and Burger
96 2011; Strier 2017). For example, pied kingfishers (*Ceryle rudis*) form pairs or family groups
97 in areas with a high abundance of high quality nesting sites, but can form polygynous groups
98 in areas where good nesting sites are rare (Reyer 1980, 1984). The comparison of two
99 populations of European badgers (*Meles meles*) in Spain lead to the hypothesis that
100 differences in population density and landscape structure might influence social organization
101 (Molina-Vacas et al. 2009). Population density has also been hypothesized to explain intra-
102 specific variation between two populations of the mountain brushtail possum (*Trichosurus*
103 *cunninghami*) (Martin and Martin 2007) and two populations of the African striped mouse
104 (*Rhabdomys pumilio*) (Schradin 2005; Schradin and Pillay 2005). A study of four populations
105 of kiwis (*Apteryx spp.*) differing in population density showed that all populations had pair-
106 living as social organization, although pairs were less stable in the population with the lowest
107 density (Taborsky and Taborsky 1999). Whereas all these studies are interesting, they lack the
108 requisite sample size to show statistically that the observed differences between two (or four)
109 populations are really due to the proposed differences in population density. An early study
110 comparing 23 populations of langurs (*Presbytis entellus*) showed that the relationship
111 between population density and group composition is complex and can be revealed only with
112 a sufficiently large number of populations (Moore 1999). Thus, many previous studies
113 comparing two populations discussed the possibility that differences in population density
114 results on variation in social organization, but this was a prediction, not a conclusion, of these
115 studies (Schradin et al. 2010a). To our knowledge, no study has compared a sufficient number
116 of populations (minimum sample size would be 6 populations), for statistical comparisons, as
117 has been proposed by (Maher and Burger 2011).

118

119 Intra-specific variation in social organization between populations of the same species could
120 be due to genetic differences caused by local adaptation of isolated populations, or due to
121 social flexibility caused by individuals changing their social tactics when immigrating into a
122 different environment (Schradin 2013). Studying whether social flexibility occurs in a
123 geographically heterogeneous habitat could best be achieved in a small animal species that

124 has a metapopulation consisting of populations connected by dispersing individuals (also
125 called sub-populations or demes (van Nouhuys 2016)). Our study population of African
126 striped mice (*Rhabdomys pumilio*) inhabits areas around seasonal riverbeds that are dry for
127 most of the time and carry water for only a few days every couple of years after high rainfall.
128 These populations are separated from each other by dry sandy flats, hills, and mountains, but
129 individuals disperse over these unoccupied areas from population to population (Solmsen et al.
130 2011), forming one large meta-population (van Nouhuys 2016).

131

132 Striped mice show social flexibility, allowing them to live solitarily or in groups of up to 30
133 adult individuals of both sexes (Schradin et al. 2010a). A correlative field study conducted for
134 8 years on one population showed that within this population, social organization depended
135 on reproductive competition and population density (Schradin et al. 2010a). Outside the
136 breeding season, when reproductive competition is absent, striped mice always formed groups
137 independent of population density, but within the breeding season, social organization was
138 density dependent (Schradin et al. 2010a; Schoepf and Schradin 2012). To avoid reproductive
139 competition in the form of female infanticide, females became solitary breeding when
140 territories became available, but remained in communally breeding groups when population
141 density was high (Schradin et al. 2010a; Schoepf and Schradin 2012; Hill et al. 2015). Male
142 social tactics followed females' tactics: more males became solitary roamers when fewer
143 groups of communally breeding females were available to be defended; instead they visited
144 solitary breeding females for mating (Schradin et al. 2010a; Schradin and Lindholm 2011).
145 Thus, temporal variation in population density explained why in this population, many striped
146 mice lived solitarily in some years, while in other years, nearly all lived in groups. The striped
147 mouse offers an ideal system to study whether social flexibility could also be an adaptation to
148 geographic (spatial) variation.

149

150 Here we tested whether geographic variation in population density is related to social
151 organization in striped mice. Thus, we tested whether the relationship described between
152 population density and the likelihood of group living that was previously described for 8
153 study years (Schradin et al. 2010a) could be replicated in a one year study of 8 populations.
154 We predicted that more striped mice would be group-living in a population with higher local
155 population density, replicating the relationship between population density and sociality
156 reported previously. In addition, we recorded any individuals dispersing between populations
157 and whether they changed their social tactics, since dispersal could make social flexibility

158 adaptive. Social flexibility would allow immigrants to follow the best alternative reproductive
159 tactic depending on the prevailing environmental conditions of the population into which they
160 immigrated.

161

162

163 **Methods**

164

165 Study area and study period

166 The study was conducted from January to October 2018 in an area covering 5540 ha of the
167 Goegap Nature Reserve in South Africa (S 29 41.56, E 18 1.60). Goegap lies within the semi-
168 desert biome of the Succulent Karoo, which is characterized by cold and moist winters
169 followed by high food abundance in spring and hot dry summers with low food abundance.
170 The landscape is dominated by short-living ephemerals (in spring) and perennial succulent
171 shrubs. The breeding season of striped mice is in spring (August – November), when
172 population density starts at its minimum.

173

174 Data were collected on 8 different sites (Fig. 1). All field sites were located along dry
175 riverbeds with perennial succulent shrubs providing a suitable habitat for striped mice. These
176 included our Main Field Site where we have continuously monitored the striped mouse
177 population since 2001 (Schradin et al. 2012), a field site where an experimental PhD study
178 was done from 2007-2010 (Schoepf and Schradin 2012) (Klein Goegap) and 6 field sites
179 where striped mice had been trapped for a population genetics study in 2008, and which found
180 dispersal among these populations (Solmsen et al. 2011). Thus, these populations form one
181 metapopulation that could be viewed as 8 sub-populations or 8 demes. We retain the term
182 “population” for each site, as there was no direct contact between them, and all were isolated
183 from each other by habitat not inhabited by striped mice (Fig. 1).

184

185 Trapping

186 Each population was trapped 4 times. Trapping during January (onset of the dry season, no
187 breeding), April (middle of the dry season, no breeding) and July (end of dry season, no
188 breeding) was done to ensure we have viable populations for our study during the breeding
189 season and to monitor potential dispersal between populations. The Gate population became
190 locally extinct in July and the Highlands population by September, leaving us with 6
191 populations in spring for study (Fig. 1). Extinction might have been associated with the very

192 dry conditions of the years 2015 to 2018, which experienced less rain than the average of
193 151mm/ year since 2005 (2015: 65mm; 2016: 85mm; 2017: 41mm; 2018: 71mm).

194

195 Data collection regarding social organization was done during the breeding season
196 (September and October). Before trapping, field sites were pre-baited for two days by casting
197 bait around trapping stations. In January, trapping was done for 3 days at 6 sites but for 5 days
198 at the field sites with lower trap success, i.e. Gate and Office. During all subsequent trapping
199 periods, all field sites were trapped for 5 days.

200

201 At each population, we trapped along transects of 580m consisting of 30 trapping stations,
202 one every 20m under shrubs providing sufficient shelter or where signs of striped mice
203 activity were apparent (feces, tracks). Two traps were set at each trapping station (60 traps in
204 total for each field site). In the morning, we set traps 20min before sunlight was incident on
205 the field site because activity of striped mice is dependent on the onset of direct sunlight
206 (Schradin et al. 2007). Traps were checked twice, first 30min after the sun started shining on
207 the first stations and again approx. 40min later. Traps were then unset (locked open) for the
208 hot period of the day. In the evening, we set traps 45min before sundown and checked traps
209 once after the sunlight was no longer incident on the field site. Striped mice never spent more
210 than one hour in traps. Trapped striped mice were weighed, sexed, and permanently marked
211 with ear tags (National Band and Tag Co., USA) (Schradin and Pillay 2004; Schradin 2006).
212 Striped mice were also temporarily marked with hair dye (Inecto Rapido, Pinetown, South
213 Africa) only during the breeding season in September / October to allow for individual
214 identification during direct observations at their sleeping sites (Schradin and Pillay 2004).

215

216

217 Determination of social tactic

218 It was not possible to record data blind because our study involved focal animals in the field.
219 The social tactic was determined during the breeding season in September/ October to
220 establish whether individuals were living solitarily or in groups. For this, each trapped
221 individual weighing ≥ 30 g received a radio-transmitter (MD-2C transmitters from Holohil,
222 Canada) weighing 2.0 to 3.5g. We radio-tracked striped mice using an AOR 8000 wide-range
223 receiver once during their activity period in the afternoon before trapping and a second time at
224 night to determine sleeping sites.

225

226 Radio-tracking started on the same day the radio-collar was fitted. The sleeping site was
227 determined at night and we also placed 4 to 6 traps at the nesting site and started trapping
228 there the next morning for the rest of the study. Any additional striped mice trapped were
229 marked and received a radio-collar; trapping at nesting sites continued, with more traps being
230 set if necessary. Some sleeping sites were also observed during mornings and afternoons to
231 determine whether striped mice not carrying transmitters were present. We prioritized
232 sleeping sites where only one mouse was radio-tracked (assumed to be solitary) over sleeping
233 sites where several mice were radio-tracked (known to be group living) to verify that an
234 individual was solitary. If after the original five days of trapping, the social organization was
235 not apparent for every individual, radio-tracking, trapping and observations continued for up
236 to another seven days. We did not have to spend any extra days at the Main Field Site, since
237 we knew the social tactics of all trapped mice there, nor on the two field sites where no striped
238 mice were trapped within 5 days (regarded as extinct: Gate and Highland). In total we spent 6
239 days at Office, 10 days at Tourist Road, 11 days at Riverbed End and Klein Goegap, and 12
240 days at Mountains. We determined group- versus solitary living by using the following
241 definitions from our previous studies (Schradin et al. 2009; Schradin and Yuen 2011). 1.
242 Group-living: two or more adult mice sleep together in the same nest for a minimum of three
243 consecutive nights. Groups consisted either only of adult females, a pair, or adults of both
244 sexes. 2. Solitary living female (with or without pups): a female sleeps alone for a minimum
245 of three consecutive nights and we either trapped no other adult individual at the same nest(s)
246 for at least three days, or other adult individuals trapped there were radio-tracked at night at
247 another nest. 3. Solitary living male (roamer): a male sleeps alone for a minimum of three
248 consecutive nights and we either trapped no other adult individual at the same nest(s) for at
249 least three days, or other adult individuals trapped there were radio-tracked at night at another
250 nest. Altogether we determined the social tactics of 39 males and 48 females (sex ratio: 0.81).

251

252 Population density

253 Population density was estimated for the breeding season only. The habitat in Goegap is
254 heterogenous and many areas are not inhabited by striped mice, as they do not provide the
255 necessary resources, such as food and shelter (Schradin and Pillay 2006; Solmsen et al. 2011).
256 While we chose our trapping transects in areas suitable for striped mice, the long transects
257 often also included unoccupied areas, especially sandy areas without vegetation providing
258 food and cover. To calculate population density as an indicator of competition for scarce
259 resources, we thus only included the areas used by striped mice. For this, we used the GPS

260 points of all sleeping sites, all trapping sites where striped mice were trapped, and of all radio-
261 tracking data collected during afternoons. Using the minimum polygon method, we then
262 determined the size of the area in hectares using the software QGIS 3.6. For individual home
263 ranges of striped mice, convex polygons correlated highly and significantly with Kernel
264 estimates (Schradin and Pillay 2006; Schradin et al. 2010b), but as Kernel contours would be
265 more affected by single individuals with small home ranges, we used convex polygons. Visual
266 inspection of the polygons did not indicate any outliers having a huge impact on field site
267 estimate. For each population, population density was then calculated as the number of adult
268 striped mice (body mass ≥ 30 g) per hectare.

269

270 Statistical analyses

271 Data were analyzed using R v. 3.6.1 (The R foundation for statistical computing,
272 <http://www.r-project.org/>), GraphPad InStat 3.05 and CurveExpert 1.4. Data are reported as
273 means \pm standard deviation. Because we had data from only 6 populations, restricting the
274 statistical power of our analysis, we could not include co-variables into the statistical analysis
275 and we thus focused on population density, the variable of interest in our study. However, we
276 measured food availability, rainfall and the percentage of cover and report that they had no
277 influence on sociality with the given sample size (see electronic supplement). Population
278 density was log transformed for statistical analysis since the relationship with sociality was
279 non-linear.

280

281

282 Results

283

284 Due to extremely dry conditions during the years 2015-2018, population density was
285 generally low, and two populations had become extinct by the onset of the study. For the
286 remaining 6 populations, population density ranged from 1.1 striped mice/ha to 22.4 mice/ha,
287 with a mean of 5.1 ± 8.5 (SD) mice/ha (Fig. 2). In one population (Riverbed End), no striped
288 mice lived in groups, while in another population (Office), all striped mice lived in groups.

289

290 There was a significant regression between the percentage of striped mice living in groups
291 and log transformed population density ($r^2=0.821$, $p=0.01$; Fig. 2A). At lower population
292 density in a population, more striped mice lived solitarily. For females alone, the regression
293 was also significant ($r^2=0.73$, $p=0.03$), and also for males ($r^2=0.91$, $p=0.004$). Significantly

294 more females ($66.5 \pm 36.8\%$) than males ($50.0 \pm 33.9\%$) lived in groups (paired $t_5=2.75$,
295 $p=0.04$).

296

297 Using CurveExpert, the relationship was best described by a non-linear regression with the
298 formula $y = 98.89 * (1-(\exp(-0.516x)))$, with y representing the percentage of group-living
299 striped mice in the population, and x the population density in striped mice/ha (Fig. 2B). The
300 correlation coefficient was 0.942 (SE=14.74) indicating very high model fit. For females and
301 males alone, the best fit curves were very similar (females: $y=97.77*(1-(\exp(-0.76x)))$,
302 SE=15.91, correlation coefficient=0.938; males: $y=97.87*(1-(\exp(-0.34x)))$, SE=11.14,
303 correlation coefficient=0.960). In comparison, the best fit model from the data published in
304 2010 was $y = 91.3 - (136/x)$, the correlation coefficient was 0.984 (SE=5.82) (Schradin et al.
305 2010a); inserted in Fig. 2B for comparison). Our small sample size did not allow us to include
306 additional environmental co-factors into the analysis; in any case, from the start of the project
307 planning, we focused on the effect of population density as main effect. In the electronic
308 supplement we show that all regressions between the dependent variable (% group-living
309 striped mice) and several environmental co-factors (number of food plants, plant cover and
310 rainfall) were non-significant, indicating that population density, the a priori chosen main
311 factor, was the most important.

312

313 During the entire study, we observed seven individuals (five males and two females)
314 originating from Main Field Site that immigrated into three other populations (Table 1). Of
315 those, three dispersal events occurred during the breeding season (last trapped on main field
316 site after 1st of July and trapped on new field site in September; Table 1). For three males that
317 dispersed during the breeding season, we established that they had changed their social tactic
318 from group-living philopatric male at Main Field Site to solitary living roamer at the new
319 population (Table 1).

320

321

322 **Discussion**

323

324 Social flexibility has been interpreted as an adaptation to changing environments. Change
325 occurs not only in time but also in space. Here we showed for the first time that geographic
326 variation in population density is significantly related to social flexibility, a prediction that
327 emerged from many field studies on multiple species where differences between two

328 populations were observed (Schradin and Pillay 2005; Martin and Martin 2007; Molina-Vacas
329 et al. 2009). We showed that 6 populations of a larger meta-population differed in their degree
330 of sociality, depending on population density. Thus, within this metapopulation, individuals
331 being able to switch from group- to solitary living and back might benefit from this flexibility
332 not only when the environment changes over time (Schradin et al. 2010a), but also when they
333 disperse into another environment.

334

335 Dispersal is adaptive when there is a chance that a dispersing individual ends up in an
336 environment which differs sufficiently from its original environment to generate higher fitness.
337 A previous study using molecular markers showed that striped mice disperse several
338 kilometers over unoccupied habitats between populations (Solmsen et al. 2011). When
339 populations of the same species differ in social organization, this can either be due to them
340 being isolated and having evolved different social tactics fixed between populations, or due to
341 social flexibility of individuals (Schradin 2013). Genetic studies (Solmsen et al. 2011) and our
342 limited observations indicate that dispersal between populations occurs and that dispersing
343 striped mice changed their social tactics, indicating that population differences in social
344 organization are due to social flexibility rather than genetic differentiation. We found
345 dispersal throughout the year, with most events in July, which corresponds to previous
346 findings of the same population using a large sample size (Vuarin et al. 2019). While more
347 exhaustive studies are needed to understand the fitness consequences of dispersal, here we
348 demonstrate dispersal of individuals over several kilometers between populations that differed
349 in population density and social organization and associated reproductive tactic change in
350 some dispersers.

351

352 Striped mice are well known for their social flexibility, i.e. individuals being able to switch
353 from group- to solitary living and back to group-living (Schradin et al. 2012). This has been
354 demonstrated first with long-term data collected during 8 years from our field site, where
355 more striped mice were group-living at a higher population density (Schradin et al. 2010a), in
356 agreement with the habitat saturation hypothesis (Koenig and Pitelka 1981; Emlen 1982;
357 Komdeur 1992). Female tactics drive male sociality, since for males it is beneficial to join
358 groups of communally breeding females and defend them as the only breeding male against
359 other males. However, when many females live solitarily, solitary living males visiting
360 several single females can also have high reproductive success (Schradin and Lindholm 2011).
361 Importantly, single breeding females have much larger home ranges than communal groups,

362 making it impossible for single males to defend the home ranges of multiple solitary females
363 (Schradin et al. 2010b). Reproductive competition between males is high, and single males
364 defending groups of communally breeding females can explain why we found more solitary
365 males than females in every population. Our current study extends our previous findings,
366 demonstrating that striped mice of different populations can either live solitarily (one
367 population), in groups (one population) or that within an area both solitary and group-living
368 can occur (4 populations). Thus, social flexibility is a key characteristic of striped mice both
369 in time and space.

370

371 Here we showed that 6 populations of a meta-population of striped mice differed both in
372 population density and sociality. The relationship between population density and sociality
373 causing intra-specific variation in social organization has been hypothesized by comparing
374 two populations in several different species (e.g. brushtail possums (Martin and Martin 2007),
375 Europeans badgers (Molina-Vacas et al. 2009), including striped mice (Schradin and Pillay
376 2005). However, comparing only two populations (N=2) reduces statistical validity. Thus,
377 such studies are useful to make predictions, but not to draw conclusions, and it has been
378 suggested that more populations need to be studied in the future (Maher and Burger 2011).
379 We found within the metapopulation studied that the lower the population density, the more
380 likely striped mice were solitary. Our six populations were studied within 1.5 months in the
381 same nature reserve and under similar ecological conditions (electronic supplement 1). The
382 relationship was not linear, indicating that solitary living is favored at very low population
383 density, but then group-living becomes more quickly common and reaches a plateau at which
384 nearly all striped mice are living in groups (Fig. 2). Our study indicates that some female
385 striped mice prefer to breed solitarily when free territories are available, and that more males
386 follow a solitary roaming tactic when more solitary females can be visited. Female striped
387 mice in communal groups suffer from reproductive competition in the form of female-female
388 aggression and female infanticide (Schradin et al. 2010a). In this context, solitary living is a
389 beneficial alternative tactic (Hill et al. 2015). Social flexibility thus allows striped mice to
390 respond to prevailing conditions. These studies help us to understand the reasons for animals
391 living solitarily, a point often missed in behavioral research that normally focuses on the
392 contrary point of why animals live in groups (Krause and Ruxton 2002; Hill et al. 2015;
393 Kappeler 2019).

394

395 Experimental manipulation of population density has resulted in changes in social
396 organisation in the cichlid *Neolamprologus pulcher* in captivity (Bergmüller et al. 2005),
397 prairie voles (*Microtus ochrogaster*) kept in enclosures (Lucia et al. 2008), and free-living
398 populations of striped mice (Schoepf and Schradin 2012) and Seychelles warblers
399 (*Acrocephalus sechellensis*) (Komdeur 1992, 1994). Whereas these studies focussed on one
400 population, a multitude of previous studies comparing two populations showed that intra-
401 specific variation in social organisation between populations is widespread (Taborsky and
402 Taborsky 1999; Martin and Martin 2007; Molina-Vacas et al. 2009) and can be related to
403 population density (Schradin 2013), for example in prairie voles (Streatfeild et al. 2011).
404 Variation in social organisation between two populations has typically been discussed to be
405 adaptive, but these studies lacked statistical power to test this assumption, creating hypotheses
406 but not reaching conclusions. In caviomorph rodents, intra-specific variation in social systems
407 is common and apparently related to ecological factors (but in degus, at least, it is not related
408 to population density (Ebensperger et al. 2011)). However, most studies on caviomorphs were
409 purely observational, suffering from low sample size and short study periods, such that
410 conclusions could not be drawn with confidence, again leading to predictions rather than
411 conclusions (Maher and Burger 2011). Maher and Burger (2011) recommended for the future
412 to compare several populations of the same species, which is what we have done here. Thus,
413 multiple previous studies suggested that IVSO between populations is related to population
414 density, and here we showed this for the first time statistically.

415

416 In many primate species, individual flexibility in social behavior stabilises the social
417 organisation, for example by changing dominance hierarchies and coalitions, such that the
418 main form of social organisation can be maintained (Schradin et al. 2018). In comparison,
419 some other species, such as striped mice, cannot respond to conflict by adjusting their social
420 hierarchy and groups might instead break up, leading to intra-specific variation in social
421 organisation (Schradin et al. 2018). Nevertheless, variation in social organisation is also
422 common in primates (Strier 2017; Agnani et al. 2018) and explained by socio-ecological
423 models focussing on resource abundance (Dunbar 1988; Kappeler and Schaik 2002; Kappeler
424 et al. 2013, 2017; Koenig et al. 2013) and demography (Moore 1999; Strier 2017). Comparing
425 multiple populations of the same species helped to understand the adaptive significance of
426 infanticide in langurs independent of population density (Moore 1999). For primates, it has
427 been suggested that intra-specific variation must be taken into account in comparative studies
428 (Sandel et al. 2016) because it significantly changes our understanding of primate social

429 evolution (Kappeler and Fichtel 2016). Similar claims have been made in the studies
430 regarding cooperative breeding in birds, where the importance of variation within species has
431 been ignored (Griesser and Suzuki 2016).

432

433 Individuals of both sexes changing their social tactics (individual trait) can change the social
434 system of an entire population, which is called social flexibility (observed at the population
435 level; (Schradin et al. 2012). It has been hypothesized that the variation in social organization
436 observed between two populations of a species might be due to differences in population
437 density (Taborsky and Taborsky 1999; Schradin and Pillay 2005; Martin and Martin 2007;
438 Molina-Vacas et al. 2009) but more populations must be studied simultaneously to test this
439 hypothesis (Maher and Burger 2011). To date, this phenomenon had been studied in relation
440 to environmental change over time in one population (Schradin et al. 2018, 2019). Here we
441 showed that, for the meta-population studied, intra-specific variation in social organization
442 can be related to geographic variation in population density. Thus, social organization can
443 differ at different localities simultaneously in time depending on population density. How
444 individual dispersal tactics and associated changes in social tactics benefit individual fitness
445 will require further studies. Our study emphasizes the importance of considering intra-specific
446 variation in social tactics in both a spatial and temporal context.

447

448

449 **Compliance with Ethical Standards**

450 Funding

451 This work was supported by the National Research Foundation (South Africa), the University
452 of Witwatersrand (South Africa), and the CNRS (France) under the framework of the
453 International Research Project DROUGHT (Response to Drought, Climate Change and
454 Climate Unpredictability: Social Flexibility, Adaptation, and Species Range Shifts)–
455 Laboratoire International Associé (IRP / LIA).

456

457 Conflict of Interest

458 We declare that we have no conflict of interest.

459

460 Ethical approval

461 All animal experimentation met the ABS/ASAB guidelines for ethical treatment of animals.
462 Animal ethics clearance was provided by the University of the Witwatersrand (AESC
463 2007/40/01), following the guidelines for the use and care of animals in teaching and research
464 of the University of the Witwatersrand which complies with the University's ethical and legal
465 practices and with the National Code.

466

467 Data availability

468 All data generated or analysed during this study are included in the supplementary
469 information files of this published article.

470

471 **References**

- 472 Agnani P, Kauffmann C, Hayes LD, Schradin C (2018) Intra - specific variation in social
473 organization of Strepsirrhines. *Am J Primatol* 80:e22758
- 474 Bergmüller R, Heg D, Taborsky M (2005) Helpers in a cooperatively breeding cichlid stay
475 and pay or disperse and breed, depending on ecological constraints. *Proc R Soc Lond*
476 *B* 272:325-331
- 477 Berry RJ, Tattersall FH, Hurst J (2008) Genus *Mus*. In: Harris S, Yalden DW (eds) *Mammals*
478 *of the British Isles Handbook*, 4th edn. The Mammal Society, Southampton, UK, pp
479 141-149
- 480 Dunbar RIM (1988) Socio-ecological systems. In: Dunbar RIM (ed) *Primate Social Systems*.
481 Cornell University Press, New York, pp 262-291
- 482 Eggert A-K, Müller JK (2000) Timing of oviposition and reproductive skew in cobreeding
483 female burying beetles (*Nicrophorus vespilloides*). *Behav Ecol* 11:357-366
- 484 Emlen ST (1982) The evolution of helping. I. An ecological constraints model. *Am Nat*
485 119:29-39
- 486 Griesser M, Suzuki TN (2016) Occasional cooperative breeding in birds and the robustness of
487 comparative analyses concerning the evolution of cooperative breeding. *Zool Lett* 2:7
- 488 Hill DL, Pillay N, Schradin C (2015) Alternative reproductive tactics in female striped mice:
489 heavier females are more likely to breed solitarily than communally. *J Anim Ecol*
490 84:1497-1508
- 491 Kappeler PM (2019) A framework for studying social complexity. *Behav Ecol Sociobiol*
492 73:13
- 493 Kappeler PM, Barrett L, Blumstein DT, Clutton-Brock TH (2013) Constraints and flexibility
494 in mammalian social behaviour: introduction and synthesis. *Phil Trans R Soc B*
495 368:20120337
- 496 Kappeler PM, Clutton-Brock T, Shultz S, Lukas D (2019) Social complexity: patterns,
497 processes, and evolution. *Behav Ecol Sociobiol* 73:5
- 498 Kappeler PM, Cuzzo FP, Fichtel C et al (2017) Long-term field studies of lemurs, lorises,
499 and tarsiers. *J Mammal* 98:661-669
- 500 Kappeler PM, Fichtel C (2016) The evolution of eulemur social organization. *Int J Primatol*
501 37:10-28
- 502 Kappeler PM, Schaik CPv (2002) Evolution of primate social systems. *Int J Primatol* 23:707-
503 740

- 504 Koenig A, Scarry CJ, Wheeler BC, Borries C (2013) Variation in grouping patterns, mating
505 systems and social structure: what socio-ecological models attempt to explain. *Phil*
506 *Trans R Soc B* 368:20120348
- 507 Koenig WD, Pitelka FA (1981) Ecological factors and kin selection in the evolution of
508 cooperative breeding in birds. In: Alexander RD, Tinkle DW (eds) *Natural Selection*
509 *and Social Behavior: Recent Research and New Theory*. Chiron Press, New York, pp
510 261-280
- 511 Komdeur J (1992) Importance of habitat saturation and territory quality for evolution of
512 cooperative breeding in the Seychelles warbler. *Nature* 358:493-495
- 513 Komdeur J (1994) Experimental evidence for helping and hindering by previous offspring in
514 the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behav Ecol*
515 *Sociobiol* 34:175-186
- 516 Krause J, Ruxton GD (2002) *Living in Groups*. Oxford University Press, Oxford
- 517 Latham N, Mason G (2004) From house mouse to mouse house: the behavioural biology of
518 free-living *Mus musculus* and its implications in the laboratory. *Appl Anim Behav Sci*
519 86:261-289
- 520 Lott DF (1984) Intraspecific variation in the social systems of wild vertebrates. *Behaviour*
521 88:266-325
- 522 Lott DF (1991) *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge
523 University Press, New York
- 524 Lucia KE, Keane B, Hayes LD, Lin YK, Schaefer RL, Solomon NG (2008) Philopatry in
525 prairie voles: an evaluation of the habitat saturation hypothesis. *Behav Ecol* 19:774-
526 783
- 527 Maher CR, Burger JR (2011) Intraspecific variation in space use, group size, and mating
528 systems of caviomorph rodents. *J Mammal* 92:54-64
- 529 Martin JK, Martin AA (2007) Resource distribution influences mating system in the bobuck
530 (*Trichosurus cunninghami*: Marsupialia). *Oecologia* 154:227-236
- 531 Molina-Vacas G, Bonet-Arboli V, Rafart-Plaza E, Rodriguez-Teijeiro JD (2009) Spatial
532 ecology of European badgers (*Meles meles*) in mediterranean habitats of the north-
533 eastern Iberian peninsula. I: Home range size, spatial distribution and social
534 organisation. *Vie Milieu* 59:223-232
- 535 Moore J (1999). Population density, social pathology, and behavioral ecology. *Primates* 40:1-
536 22
- 537 Müller JF, Braunisch V, Hwang W, Eggert A-K (2006) Alternative tactics and individual
538 reproductive success in natural associations of the burying beetle, *Nicrophorus*
539 *vespilloides*. *Behav Ecol* 18:196-203
- 540 Reyer H-U (1980) Flexible helper structure as an ecological adaptation in the pied kingfisher
541 (*Ceryle rudis rudis* L.). *Behav Ecol Sociobiol* 6:219-227
- 542 Reyer H-U (1984) Investment and relatedness: a cost/benefit analysis of breeding and helping
543 in the pied kingfisher (*Ceryle rudis*). *Anim Behav* 32:1163-1178
- 544 Sandel AA, Miller JA, Mitani JC, Nunn CL, Patterson SK, Garamszegi LZ (2016) Assessing
545 sources of error in comparative analyses of primate behavior: Intraspecific variation in
546 group size and the social brain hypothesis. *J Hum Evol* 94:126-133
- 547 Schoepf I, Schradin C (2012) Better off alone! Reproductive competition and ecological
548 constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*). *J*
549 *Anim Ecol* 81:649-656
- 550 Schradin C (2005) When to live alone and when to live in groups: ecological determinants of
551 sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784). *Belg J*
552 *Zool* 135 (suppl):77-82
- 553 Schradin C (2006) Whole day follows of the striped mouse. *J Ethol* 24:37-43

- 554 Schradin C (2013) Intraspecific variation in social organization by genetic variation,
555 developmental plasticity, social flexibility or entirely extrinsic factors. *Phil Trans R*
556 *Soc B* 368:20120346
- 557 Schradin C, Hayes LD, Pillay N, Bertelsmeier C (2018) The evolution of intraspecific
558 variation in social organization. *Ethology* 124:527-536
- 559 Schradin C, König B, Pillay N (2010a) Reproductive competition favours solitary living while
560 ecological constraints impose group-living in African striped mice. *J Anim Ecol*
561 79:515-521
- 562 Schradin C, Krackow S, Schubert M, Keller C, Schradin B, Pillay N (2007) Regulation of
563 activity in desert-living striped mice: The importance of basking. *Ethology* 113:606-
564 614
- 565 Schradin C, Lindholm AK (2011) Relative fitness of alternative male reproductive tactics in a
566 mammal varies between years. *J Anim Ecol* 80:908-917
- 567 Schradin C, Lindholm AK, Johannesen J, Schoepf I, Yuen C-H, König B, Pillay N (2012)
568 Social flexibility and social evolution in mammals: a case study of the African striped
569 mouse (*Rhabdomys pumilio*). *Mol Ecol* 21:541-553
- 570 Schradin C, Pillay N (2004) The striped mouse (*Rhabdomys pumilio*) from the succulent
571 karoo of South Africa: A territorial group living solitary forager with communal
572 breeding and helpers at the nest. *J Comp Psychol* 118:37-47
- 573 Schradin C, Pillay N (2005) Intraspecific variation in the spatial and social organization of the
574 African striped mouse. *J Mammal* 86:99-107
- 575 Schradin C, Pillay N (2006) Female striped mice (*Rhabdomys pumilio*) change their home
576 ranges in response to seasonal variation in food availability. *Behav Ecol* 17:452-458
- 577 Schradin C, Pillay N, Bertelsmeier C (2019) Social flexibility and environmental
578 unpredictability in African striped mice. *Behav Ecol Sociobiol* 73:94
- 579 Schradin C, Scantlebury M, Pillay N, König B (2009) Testosterone levels in dominant
580 sociable males are lower than in solitary roamers: physiological differences between
581 three male reproductive tactics in a sociably flexible mammal. *Am Nat* 173:376-388
- 582 Schradin C, Schmohl G, Rödel HG, Schoepf I, Treffler SM, Brenner J, Bleeker M, Schubert
583 M, König B, Pillay N (2010b) Female home range size is regulated by resource
584 distribution and intraspecific competition: a long-term field study. *Anim Behav*
585 79:195-203
- 586 Schradin C, Yuen C-H (2011) Hormone levels of male African striped mice change as they
587 switch between alternative reproductive tactics. *Horm Behav* 60:676-680
- 588 Solmsen N, Johannesen J, Schradin C (2011) Highly asymmetric fine-scale genetic structure
589 between sexes of African striped mice and indication for condition dependent
590 alternative male dispersal tactics. *Mol Ecol* 20:1624-1634
- 591 Streatfeild CA, Mabry KE, Keane B, Crist TO, Solomon NG (2011) Intraspecific variability
592 in the social and genetic mating systems of prairie voles, *Microtus ochrogaster*. *Anim*
593 *Behav* 82:1387-1398
- 594 Strier KB (2017) What does variation in primate behavior mean? *Am J Phys Anthropol*
595 162:4-14
- 596 Taborsky B, Taborsky M (1999) The mating system and stability of pairs in kiwi *Apteryx* spp.
597 *J Avian Biol* 30:143-151
- 598 van Nouhuys S (2016) Metapopulation Ecology. In: *Encyclopedia of Life Sciences (eLS)*.
599 John Wiley & Sons Ltd, Chichester, pp 1-9
- 600 Vuarin P, Pillay N, Schradin C (2019) Elevated basal corticosterone levels increase
601 disappearance risk of light but not heavy individuals in a long-term monitored rodent
602 population. *Horm Behav* 113:95-102
- 603
- 604
- 605

606
607

Table 1
Individual striped mice that dispersed from Main Field site to a different population

Sex	Last trapped on main field site	New population	First trapped at new population	Last trapped at new population	Social tactic at main field site	Social tactic at new population
Male	27.03.2018	Klein Goegap	25.04.2018	25.04.2018	Group-living	Tactics not determined in April
Female	11.04.2018	Klein Goegap	27.04.2018	27.04.2018	Group-living	Tactics not determined in April
Male	09.06.2018	Mountain	18.07.2018	10.09.2018	Group-living	Solitary living
Male	02.02.2018	Riverbed End	07.09.2018	13.09.2018	Group-living	Solitary living
Female	18.07.2018	Riverbed End	14.09.2018	14.09.2018	Group-living	Not determined because it were trapped on last day
Male	27.07.2018	Klein Goegap	24.09.2018	03.10.2018	Group-living	Solitary living
Male	08.09.2018	Klein Goegap	05.10.2018	05.10.2018	Floater? (Only trapped once)	Floater? (Only trapped once at each site)

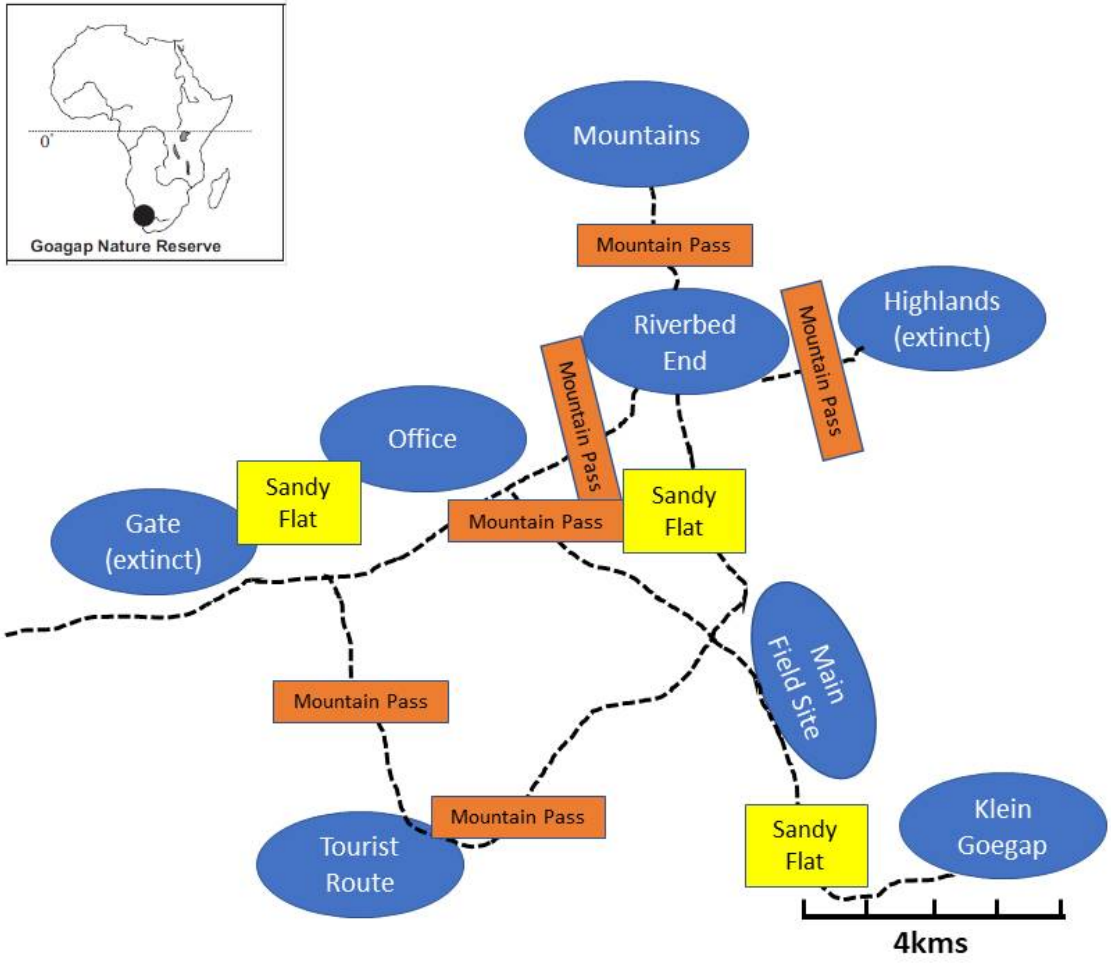
608
609

610 **Figure captions**

611

612 **Fig. 1** Schematic representation of the 8 populations studied in Goegap Nature Reserve, South
613 Africa. Dashed lines represent roads and tracks, which are often along dry riverbeds. All
614 populations were separated by areas not inhabited by striped mice such as sandy flats or
615 mountain passes. While striped mice were trapped at all localities in April, the Gate
616 population had become locally extinct by July and the Highlands population by September
617

618 **Fig. 2** A) Relationship between log population density and the percentage of striped mice
619 living in groups. B) Raw data. Black: data from 6 populations studied simultaneously in 2018
620 at 6 distinct geographic locations. Grey: published data from 8 different years in the
621 population Main Field Site (Schradin et al. 2010a), which provided the predictions for the
622 current study. Best fit curves on the raw data were fitted using CurveExpert
623
624



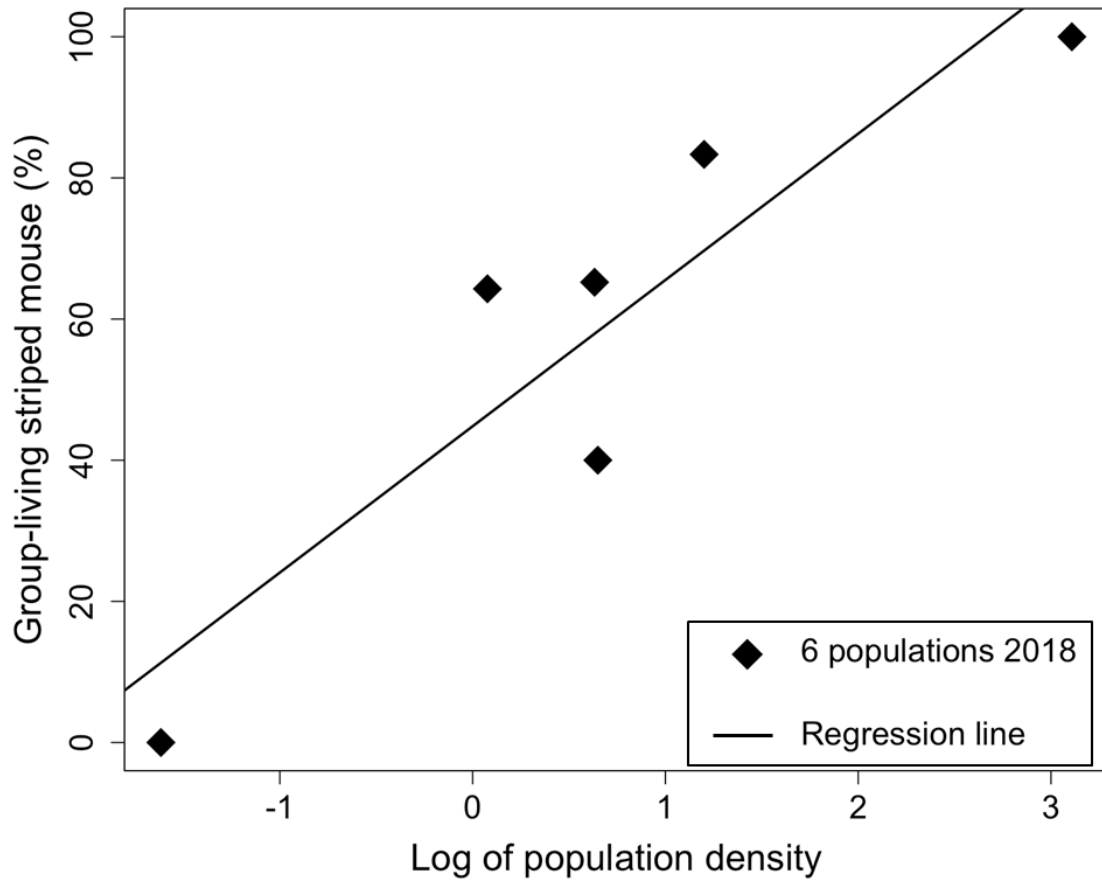
625

626 **Figure 1**

627

628

629



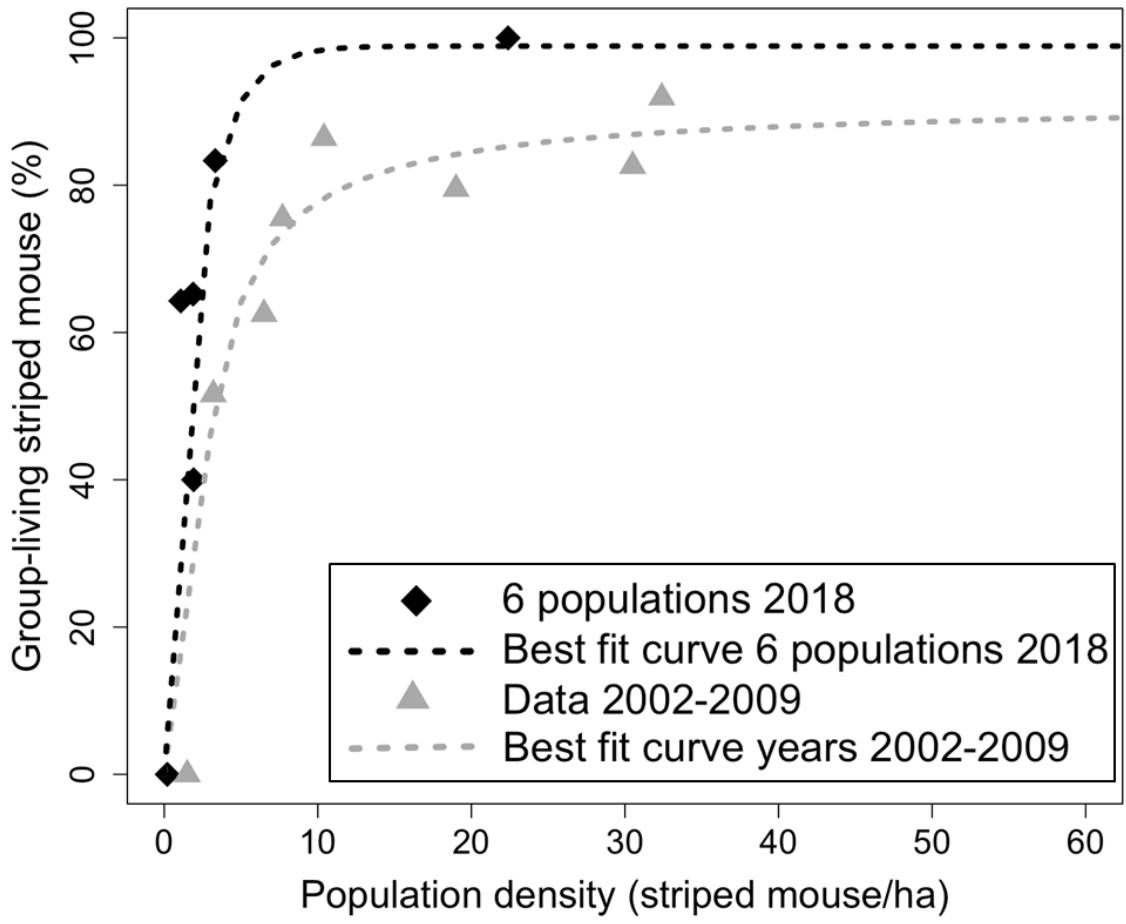
630

631

632 **Figure 2 A**

633

634



635

636 **Figure 2 B**

637