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## **Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitary than communally**

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## 1 **Summary**

2

3 1. Alternative reproductive tactics (ARTs) are discrete reproductive phenotypes  
4 governed by decision-rules called strategies. ARTs are fixed for life in species with  
5 alternative strategies, while tactic expression is plastic in species with a single  
6 strategy. ARTs have been investigated in males of many species, but few studies have  
7 tested whether the same theoretical framework applies in females.

8 2. Female striped mice (*Rhabdomys pumilio*) employ three ARTs: communal breeders  
9 give birth in a nest shared with female kin and a breeding male, and show allo-  
10 parental care; returners give birth away from the shared nest and later return to it; and  
11 solitary breeders give birth away from the shared nest and do not return to the group.

12 3. Here, studying free-living female striped mice over six breeding seasons, we tested  
13 whether ARTs arise from alternative strategies or a single strategy.

14 4. We also asked to what extent stochastic extrinsic factors explain whether individuals  
15 become solitary rather than group-living.

16 5. Females switched tactics, consistent with a single strategy, so we tested whether this  
17 represented a mixed or conditional single strategy. Only the latter predicts differences  
18 between ARTs in traits indicating competitive ability, such as body mass or age,  
19 before individuals adopt a tactic. We weighed females at conception when they were  
20 still group-living to eliminate potential confounding effects of gestation and  
21 subsequent social tactic (solitary- versus group-living) on body mass.

22 6. Females that went on to use a solitary ART were heavier than those that became  
23 communal breeders and returners, in support of a conditional strategy.

24 7. Importantly, solitary breeders also arose through extrinsic factors (mortality of all  
25 adult female group members). They weighed less than females that became solitary

26 while relatives were alive, but did not differ in body mass from communal breeders  
27 and returners.

28 8. We conclude that ART theory applies to both sexes, with female striped mice  
29 following a conditional single strategy. Future studies should consider the possibility  
30 that phenotypes that superficially resemble evolved tactics might also arise through  
31 non-adaptive extrinsic causes.

32

### 33 **Introduction**

34

35 A primary aim of life history theory is to understand the factors that influence reproductive  
36 decisions. *Alternative reproductive tactics* (ARTs) are discrete reproductive phenotypes  
37 shown by different members of the same sex and population and governed by genetically-  
38 based decision-rules called *strategies* (Dominey 1984; Gross 1996). Individuals following  
39 alternative tactics differ in behavioural, morphological, physiological and/or life history  
40 characteristics. Individuals are said to use *alternative strategies* when different tactics are  
41 controlled by different genotypes (Gross 1996), and *single strategies* when a single genotype  
42 controls different tactics (Schradin & Lindholm 2011). At the phenotypic level, ARTs are  
43 fixed for life in individuals following alternative strategies, while their expression is plastic  
44 under a single strategy (Fig. 1).

45

46 The term single strategy was introduced to describe systems where one decision-rule can  
47 produce multiple phenotypes (Fig. 1) regardless of whether fitness differences between ARTs  
48 occur (which can depend on environmental conditions) (Schradin & Lindholm 2011). Such  
49 decision-rules are traditionally divided into mixed and conditional strategies (Fig. 1). A *mixed*  
50 *strategy* occurs when tactics are expressed on a probabilistic basis rather than in response to  
51 environmental or individual-level cues (Dominey 1984). Individuals employing a *conditional*  
52 *strategy*, by contrast, are predicted to select the tactic that generates the highest fitness returns  
53 for their prevailing state or status (status-dependent selection model; Gross 1996). Individuals  
54 frequently differ in continuous traits associated with competitive ability, such as body mass  
55 or age. When the tactic that yields the highest fitness (often called the bourgeois tactic) is also  
56 the most costly to employ, only the most competitive individuals will be able to use it (Gross  
57 1996). Less competitive individuals will thus employ a different tactic that yields a lower

58 fitness but is the highest fitness they can achieve at the time, known as ‘making the best of a  
59 bad job’ (Dawkins 1980). Under a conditional strategy, individuals should express a  
60 particular tactic when they pass a threshold (*switchpoint*) for the indicator trait after which the  
61 fitness benefits for that tactic are greater than what they could achieve using an alternative  
62 tactic (Hazel, Smock & Johnson 1990). They may switch from one tactic to another, for  
63 example, when they reach a certain age or size. The environmental-threshold model predicts  
64 that selection acts upon heritable genetic variation for the position of the switchpoint, so  
65 different individuals might express a given tactic at different values of the indicator trait  
66 (reviewed in Tomkins & Hazel 2007).

67

68 ARTs have been studied extensively in males, but are less well understood in females.  
69 Female ARTs include monandry versus polyandry in horseshoe crabs (*Limulus polyphemus*)  
70 (Johnson & Brockmann 2012) and brood parasitism versus maternal care in goldeneye ducks  
71 (*Bucephala clangula*) (Åhlund & Andersson 2001). ARTs often evolve where there is  
72 pronounced intra-sexual variance in fitness and intense reproductive competition (Shuster  
73 2008). These conditions apply more frequently in males than in females, which probably  
74 explains the greater prevalence of male ARTs (Neff & Svensson 2013). However, intense  
75 reproductive competition also exists between females (Clutton-Brock 2009), and the number  
76 of studies of female ARTs has increased in recent years, suggesting that they were previously  
77 overlooked. This balance needs to be redressed to achieve a comprehensive, sex-independent  
78 understanding of ARTs.

79

80 Few studies to date have investigated the factors leading to the evolution of female ARTs and  
81 whether the theory governing male ARTs applies to females. The striped mouse (*Rhabdomys*  
82 *pumilio*) is a good species in which to address these issues because ARTs occur in both sexes,

83 with males and females either breeding solitarily or in groups. Breeding groups typically  
84 consist of 2-4 closely related females, one male and their communal offspring (Schradin &  
85 Pillay 2004). Communally-breeding females often give birth synchronously and provide allo-  
86 parental care, including allo-nursing (Schradin, Kinahan & Pillay 2009a; Schubert, Pillay &  
87 Schradin 2009). Nevertheless, reproductive competition occurs between females through  
88 aggression and infanticide (Schradin, König & Pillay 2010), and females can become solitary  
89 during the breeding season if unoccupied territories are available (Schradin, König & Pillay  
90 2010; Schoepf & Schradin 2012a). While the ratio of communal to solitary females increases  
91 with increasing population density, both solitary and group-living females co-occur under  
92 most conditions (Schradin, König & Pillay 2010; Schoepf & Schradin 2012a). In addition to  
93 these solitary and communal breeding female tactics, we report here for the first time the  
94 tactic of *returner*, where females give birth away from the natal group but later return to it.

95

96 Group-living females might become solitary as part of a strategy to optimize fitness or  
97 alternatively because of extrinsic factors that constrain them to rear young alone (Schradin  
98 2013). Groups are limited to close kin in many social species, and these groups can be  
99 reduced to a single solitary individual by natural mortality. This can occur in populations  
100 with small group sizes and high predation, such as Callitrichid primates (Anzenberger & Falk  
101 2012). In the absence of information on group history, such individuals might be mistakenly  
102 assumed to be following a solitary ART. However, in such cases, solitary-living is not the  
103 result of a strategy (an evolved set of rules), and cannot be explained by ultimate or  
104 proximate causes at the individual level (Schradin 2013). Therefore, when observing solitary  
105 versus group-living members of the same population, it is important to consider the  
106 possibility that solitary-living is not a tactic, but the result of stochastic processes. To our  
107 knowledge, this has not been considered in any previous study on ARTs.

108

109 Here, we explored the following questions in female striped mice: (i) Do ARTs arise from  
110 alternative strategies or a single strategy? We addressed this by testing whether females  
111 switched ARTs, which would indicate a single strategy. Females did switch ARTs, and so we  
112 asked (ii) whether this represented a mixed or a conditional strategy. Under a conditional (but  
113 not mixed) strategy, females that go on to adopt different tactics are predicted to differ from  
114 each other in individual-level traits that reflect competitive ability. We examined body mass  
115 because it is associated with competitive ability (Schradin 2004) and aggression (Schoepf &  
116 Schradin 2012b) in this species, and because male striped mice following alternative tactics  
117 differ in body mass (Schradin *et al.* 2009b). To decouple the predicted effect of body mass on  
118 tactic choice from the confounding effects of following different tactics on body mass, all  
119 females were weighed when they were still group-living. We also considered age, which is  
120 related to aggression in striped mice (Schoepf & Schradin 2012b) and to rank in many co-  
121 operatively breeding species (Creel *et al.* 1992). We predicted that females that go on to  
122 breed solitarily would be heavier and/or older than communal breeders. Next, we examined  
123 breeding synchrony to test whether females leave the group to avoid reproductive  
124 competition. In communally-breeding groups, earlier-born litters suffer an increased risk of  
125 infanticide from gestating females, while later-born litters may be unable to compete with  
126 older ones (Hodge, Bell & Cant 2011). We predicted that group-living females would be  
127 more closely synchronized with nestmates than with females from other groups, and that  
128 females that were less synchronized with nestmates would be more likely to adopt a solitary  
129 or returner tactic than to breed communally. Finally, we asked (iii) whether solitary breeding  
130 is always the outcome of a strategy or if it can also arise from entirely extrinsic factors  
131 (mortality of all other adult female group members). If the latter scenario occurs, we would  
132 expect females constrained to breed solitarily by the death of relatives to be of a lower body



133 mass or age than solitary breeders with living relatives (which are predicted under ii to be  
134 subject to status-dependent selection for increased body mass or age), but to be similar in  
135 body mass and age to communal breeders.

136

137

## 138 **Materials and Methods**

139

### 140 STUDY SITE

141 Fieldwork took place every month during the years 2005 to 2010 in Goegap Nature Reserve,  
142 Northern Cape Province, South Africa (S 29 41.56, E 18 1.60). The study area is Succulent  
143 Karoo and consists of an open habitat of shrubs, grass and sandy areas. It receives 180mm  
144 precipitation *per annum*, which mostly falls between April and July. Minimum ambient  
145 temperature ( $T_a$ ) was recorded in the shade 5cm above the ground at the study site each day.

146

### 147 LIVE-TRAPPING AND BEHAVIOURAL OBSERVATIONS

148 Striped mice are diurnal and nest in shrubs at night. They rarely experience more than one  
149 breeding season, so each year of study represents a new generation. Individuals were  
150 captured using Sherman-type live-traps (26×9×9cm) baited with bran flakes, sunflower oil  
151 and salt. Traps were set in the shade close to nest sites at dawn and in the afternoon, and  
152 checked twice in the morning and once at dusk, 30-45 minutes after being set. We placed 3-  
153 20 traps (depending on group size) at several nest sites for 3-4 consecutive days throughout  
154 the year to allow each group to be monitored on rotation every two weeks. Newly-trapped  
155 individuals were provided with numbered aluminium ear-tags (National Band and Tag,  
156 Newport, KY) for identification, and marked with hair dye (Inecto, Pinetown, South Africa)  
157 so that they could be recognized during behavioural observations at nest sites (see below).

158 Adults were fitted with MD-2C radio-collars (Holohil, Canada), which weighed 2.5g,  
159 representing  $5.4 \pm 0.07\%$  of the body mass of non-gestating females ( $n=181$  records from 110  
160 females). Females were weighed to the nearest gram using an electronic balance, and nipples  
161 were classified as pink and elongated (suggestive of lactation), otherwise visible or not  
162 visible.

163

164 Juveniles (body mass  $<30\text{g}$ ) were assumed to originate from the nest where they were first  
165 trapped and observed affiliating with group members during behavioural observations. This  
166 method was validated using microsatellite markers (Schradin & Lindholm 2011).  
167 Behavioural observations took place at nest sites at dusk when striped mice were returning  
168 from the day's foraging. We observed marked individuals through binoculars for 30 minutes  
169 from a distance of  $\sim 10\text{m}$ , and recorded affiliative and aggressive interactions as described in  
170 Schradin and Pillay (2003). Observations were carried out on all focal groups on rotation  
171 throughout the year, except that a given group was not subject to both trapping and  
172 behavioural observations on the same day. As genetic data show that female group members  
173 are close kin (C. Schradin and A. K. Lindholm, unpublished data), we refer to females that  
174 nested together (or did so before becoming solitary) as 'relatives'.

175

#### 176 RADIO-TRACKING

177 Striped mice were radio-tracked 4-5 nights a week throughout the breeding season using an  
178 AR8000 wide-range receiver (AOR, Tokyo, Japan) and an H-antenna. We approached  
179 potential nest sites from different angles until we located the source of the radio-signal. We  
180 assumed that individuals were sharing a nest when their signals derived from the same  
181 position. This allowed us to determine the location of nests, the identity of all adults in a nest  
182 and the date that individuals changed nest sites. Individuals leave the nest by day to forage, so

183 we also radio-tracked them once during the day to confirm that radio-collars had not been  
184 discarded in the nest. Locations of individuals and nests were recorded using an eTrex  
185 Venture GPS (GARMIN, Olathe, KS), which was accurate to ~5m at our study site. We  
186 maintained continuity of group identities between breeding seasons by radio-tracking one  
187 female from each group during the non-breeding seasons, when group membership is stable  
188 (Schoepf & Schradin 2012; Schradin, König & Pillay 2010). Radio-collars were removed  
189 from all other group members at the end of each breeding season.

190

#### 191 DETERMINATION OF ALTERNATIVE REPRODUCTIVE TACTIC

192 Striped mice give birth in the austral spring (August to December). For each female fitted  
193 with a radio-collar, we plotted body mass records from July to January of each year against  
194 the date. We examined individual plots for the rise and sudden fall in body mass indicative of  
195 gestation and parturition. We assumed that parturition occurred on the median day within  
196 each trapping interval (the period between a female's last trapping antepartum and her first  
197 trapping postpartum) unless we could refine our estimate from observational data. We  
198 checked whether the estimated parturition date was consistent with a change in lactation  
199 status. Females were classified as *nesting communally* (sharing a nest with  $\geq 1$  adult female)  
200 or *not nesting communally* on the night before parturition. The latter category was divided  
201 into three subcategories: a) *returners*: those that nested with their original group  $\geq 1$  night  
202 after parturition; b) *solitary breeders with relatives*: those that did not nest with the group  
203 after parturition although former (female) nestmates were still alive; and c) *solitary breeders*  
204 *without relatives*: females whose female nestmates were no longer living. We refer to the four  
205 categories (communal breeder, returner, solitary breeder with relatives, solitary breeder  
206 without relatives) as *reproductive phenotypes*, and the first three of these categories (i.e. those  
207 that are not determined by mortality of all female relatives; see Introduction) as *ARTs*. We

208 ensured that solitary females were not nesting with unmonitored females by only considering  
209 groups where all adult females were wearing radio-collars when relatives gave birth, and by  
210 observing the identity of individuals returning to nests during behavioural observations.

211

## 212 ESTIMATION OF AGE AT PARTURITION AND BODY MASS AT CONCEPTION

213 *Age at parturition* (AP) was calculated as the difference between a female's estimated  
214 parturition date and her date of birth; date of birth was estimated from the population-specific  
215 growth curve in Schradin, Schneider & Yuen (2009c). We estimated the date that females  
216 conceived by subtracting 23 days (the minimum period between litters in captive striped mice  
217 (Brooks 1982)) from the estimated parturition date. To estimate *body mass of females at*  
218 *conception* (BMC) we used the closest morning body mass record available up to 10 days  
219 before or three days after the estimated conception date. We only used morning data because  
220 females weighed less in the morning than at dusk (morning:  $39.4 \pm 2.37\text{g}$ ,  $n=12,515$   
221 observations from 1917 females; dusk:  $42.6 \pm 2.37\text{g}$ ,  $n=6398$  observations from 1602 females;  
222  $\beta=3.17 \pm 0.13$ ,  $t=23.84$ ,  $P<0.001$ , controlling for individual identity and year). BMC records  
223 were considered 'missing' if no morning values were available or if females were known to  
224 be gestating. Missing values for BMC and AP were filled in using multiple imputation  
225 (Appendix S1).

226

## 227 STATISTICAL ANALYSIS

228 We retained for statistical analysis all parturitions occurring between 1<sup>st</sup> August and 31<sup>st</sup>  
229 December in 2005 to 2010 where parturition date and reproductive phenotype could be  
230 determined ( $n=243$  parturitions from 132 females from 33 groups; Table 1). Four females  
231 gave birth in two consecutive breeding seasons (two in 2005-06 and two in 2007-08); the  
232 remaining 128 individuals bred in a single season. Variation in monitoring effort is likely to

233 be a common feature of longitudinal field studies like ours, but is rarely reported. We present  
234 annual survey effort in Table 1. *Parturition trapping interval* (PTI) and *radio-tracking effort*  
235 were not associated with reproductive phenotype (Generalized and General Linear Mixed  
236 effects Models, respectively, controlling for individual identity, group identity and year: PTI  
237  $P \geq 0.059$ ; radio-tracking effort  $P \geq 0.128$ , adjusted for multiple comparisons). Mean annual  
238 breeding synchrony was not correlated with PTI ( $r_s = 0.49$ ,  $P = 0.356$ ,  $n = 6$ ).

239

240 **Table 1.** The numbers of groups and ‘focal’ females (i.e. females that gave birth while they and all  
 241 female relatives were fitted with radio-collars), the number of parturitions for which radio-tracking  
 242 data were available, adult population density at the start of the breeding season (Sept), the mean  
 243 trapping interval within which females gave birth, and mean radio-tracking effort (the number of  
 244 nights a female was tracked as a percentage of the number of nights she wore a radio-collar). Each  
 245 year represents a new generation. Means are given ( $\pm 1$  SE)

<b>Year</b>	<b>No. focal groups</b>	<b>No. focal females</b>	<b>No. parturitions</b>	<b>Population density (adults/ha)</b>	<b>PTI (days)</b>	<b>Radio-tracking effort (%)</b>
2005	8	14	17	19.0	12.1 $\pm$ 2.44	32.9 $\pm$ 2.05
2006	7	19	31	30.5	10.2 $\pm$ 1.13	52.1 $\pm$ 1.00
2007	12	29	59	6.5	7.2 $\pm$ 0.96	67.1 $\pm$ 0.70
2008	15	33	68	7.7	7.6 $\pm$ 0.75	59.8 $\pm$ 0.52
2009	9	23	43	10.4	6.5 $\pm$ 0.73	50.9 $\pm$ 0.65
2010	9	18	25	4.7	5.2 $\pm$ 0.93	65.6 $\pm$ 0.74

246 PTI is parturition trapping interval

247

248 *(i) Do ARTs arise from alternative strategies or a single strategy?* We determined whether  
249 female striped mice switch tactic (consistent with a single strategy), and estimated the  
250 probabilities of females moving from one tactic to another ('transition probabilities') in  
251 continuous time using a general multi-state Markov model. We considered all females with  
252 living relatives and >1 parturition, and assumed that individuals could move from any of the  
253 three states (communal, returner, solitary) to any other state in either direction or retain a  
254 single state. Transition probabilities for each state were modelled with 95% confidence  
255 intervals, accounting for individual identity and parturition date. We used the msm package  
256 (Jackson 2014) in R version 3.1.1. (R Development Core Team 2014).

257

258 *(ii) Do ARTs represent a mixed or a conditional strategy?* We tested for differences in  
259 individual-level traits between females that subsequently use alternative tactics, as expected  
260 under a conditional strategy. We used a multinomial Generalized Linear Mixed effects model  
261 because this allowed us to fit female ART as a nominal response variable with three levels  
262 (communal breeder, solitary breeder and returner) and BMC and AP as fixed effects. We  
263 focused on females whose relatives were alive when they bred because the aim was to  
264 understand tactic choice. We only considered females that were group-living when body  
265 mass was recorded (conception) to determine whether differences in body mass induce  
266 females to adopt different tactics, which can otherwise be confounded by the effects of  
267 employing a given ART on body mass. We controlled for  $T_a$  and the interaction between  
268 BMC and  $T_a$  because environmental conditions might affect females differently depending on  
269 their size or body reserves. We fitted random intercepts for individual identity, natal group  
270 identity and year to control for repeated measures. Considering natal group identity also  
271 allowed us to control for potential effects of territory quality and genetic relatedness between  
272 members of the same group, while 'year' allowed us to account for potential variation in

273 population density, predation, food availability and other unknown variables that might  
274 influence tactic choice between breeding seasons. The model was executed using the package  
275 MCMCglmm (Hadfield 2010; Hadfield 2012) in R; specifications and diagnostics are given  
276 in Appendix S2.

277

278 To evaluate breeding synchrony, we calculated the absolute number of days between all  
279 possible pairs of parturitions by different individuals up to a maximum of 23 days apart (the  
280 estimate of gestation length used in our study). Where a given parturition by female A  
281 occurred  $\pm 23$  days from two parturitions by female B (i.e. where B gave birth  $\leq 23$  days  
282 before A and again  $\leq 23$  days after A), only the record yielding the smaller date difference  
283 between the pair was retained in the dataset. We noted whether each pair of females shared a  
284 nest when they conceived ('nestmates'), originated in the same group but no longer shared a  
285 nest when they conceived ('related non-nestmates') or originated in different groups ('non-  
286 relatives'). We focused on females that were group-living when they conceived to test  
287 whether breeding asynchrony is associated with females leaving the group; records  
288 comparing related non-nestmates were discarded. For all records from nestmates, we  
289 determined the tactics used for each pair of parturitions. This produced a categorical variable  
290 ('pair category') with three levels for females that shared a nest when they conceived  
291 (communal vs communal, communal vs returner, communal vs solitary), and a fourth level  
292 for unrelated pairs where at least one female bred communally. Breeding synchrony data  
293 were analysed in a single Generalized Linear Mixed effects Model (GLMM) with Poisson  
294 errors using the lme4 package (Bates *et al.* 2014). The absolute number of days between two  
295 parturitions was the response variable, year and natal group identity were random factors and  
296 pair category was a fixed factor with four levels. We carried out a Dunnett multiple  
297 comparison test based on this model to compare synchrony within communal breeders (i.e.



298 pairs where both individuals were communally-breeding nestmates) with synchrony between  
299 communal breeders and the other three levels (returners, solitary breeders, non-relatives).

300

301 To investigate changes in the distribution of reproductive phenotypes over the breeding  
302 season we fitted a Linear Mixed effects Model (LMM) to data from all four reproductive  
303 phenotypes (including those that were already solitary at conception). BMC, AP,  $T_a$  and  
304 reproductive phenotype were fitted as fixed effects to ordinal parturition date (i.e. where 1<sup>st</sup>  
305 January of any year is day 1), controlling for female identity, group identity and year (random  
306 intercepts only). This allowed us to compare parturition dates among the different  
307 phenotypes.

308

309 *(iii) Is solitary breeding always the outcome of a strategy or can it also arise from entirely*  
310 *extrinsic factors?* Solitary-breeding phenotypes produced by extrinsic factors (mortality of all  
311 other adult female group members) occurred in the population, and so we tested whether they  
312 differed in individual-level traits from females using ARTs. BMC and AP were normally-  
313 distributed response variables in separate LMMs, and we fitted reproductive phenotype as a  
314 fixed factor with four levels. We controlled for fixed effects of  $T_a$  and random intercepts of  
315 female identity, group identity and year.

316

317 For all tests, significant effects are denoted by  $P < 0.05$  or a credible interval (CrI hereafter) or  
318 confidence interval (CoI) that does not include zero. Continuous fixed effects were mean-  
319 centred to assist model convergence. LMMs were fitted by Restricted Maximum Likelihood  
320 using lme4 (Bates et al. 2014) and lmerTest (Kuznetsova, Brockhoff & Christensen 2014).  
321 Tukey or Dunnett contrasts allowed us to determine which levels of factors differed from  
322 each other, and  $P$ -values were adjusted using a single-step method (multcomp package:

323 Hothorn, Bretz & Westfal 2014). Statistical tests are two-tailed and means are least squares  
324 means  $\pm$  1 SE.

325

326

## 327 **Results**

328

### 329 **Did female striped mice switch ARTs, consistent with a single strategy?**

330 Female striped mice with living relatives bred communally (40.7% of parturitions), as  
331 returners (42.7%) or solitarily (17.3%). Multiple breeding attempts within a single season  
332 were recorded for 55.0% of females with relatives ( $n=120$  females with relatives:  $1.8\pm 0.08$   
333 (range 1-4) litters), of which 57.6% switched ARTs at least once (Table 2). For females that  
334 bred more than once and did not switch tactic while relatives were living, the majority  
335 (46.4%) bred communally, 28.6% bred as returners and 25.0% bred solitarily (Table 2).

336

337 **Table 2.** The numbers of female striped mice that showed a single reproductive phenotype (RP:  
 338 communal breeder, returner, solitary breeder with living relatives, solitary breeder without living  
 339 relatives) and those that changed from one RP to another in a single breeding season. All females  
 340 shown ( $n=75$ ) produced at least two litters in a breeding season

RP	No. females
<i>Did not switch ARTs, female relatives alive</i>	
Communal	13
Returner	8
Solitary	7
<i>Switched ARTs, female relatives alive</i>	
communal → returner <sup>a</sup>	16
returner → solitary <sup>b</sup>	8
returner → communal <sup>a</sup>	6
communal → solitary	1
communal → returner → communal	3
returner → communal → returner	3
communal → returner → solitary	1
<i>RP caused by extrinsic factor: death of female relatives</i>	
returner → solitary <sup>b</sup>	3
communal → solitary	1
solitary	7

341 <sup>a</sup>One female produced multiple litters in two consecutive seasons and is presented for the two seasons  
 342 separately.

343 <sup>b</sup>One female belongs to both these categories because she bred as a returner then twice solitarily (once before  
 344 and once after her relatives died).

345

346

347 Females that had living relatives and bred more than once were no more likely to switch  
348 tactic than to use the same tactic throughout the breeding season (probability of switching  
349 tactic: 0.58, 95% CoI=0.45 to 0.70,  $P=0.268$ ,  $n=66$ ; exact binomial test). A female's  
350 subsequent tactic depended on her previous tactic (likelihood ratio  $\chi^2_4 = 44.60$ ,  $P<0.001$ ; Fig.  
351 S1, Supporting information). Communal breeders were more likely to continue breeding  
352 communally ( $\beta=0.013$ , 95% CoI=0.0190 to 0.0087) or become returners ( $\beta=0.012$ ,  
353 CoI=0.0078 to 0.0178) than to breed solitarily ( $\beta=0.001$ , CoI=0.0003 to 0.0041) on their next  
354 breeding attempt. Returners were no more likely to continue breeding as returners ( $\beta=0.014$ ,  
355 CoI=0.0091 to 0.0209) than to switch to communal ( $\beta=0.008$ , CoI=0.0047 to 0.0140) or  
356 solitary ( $\beta=0.006$ , CoI=0.0029 to 0.0108) breeding. Among those that switched tactic,  
357 communal breeders were 11.5 times more likely to become returners (92 (CoI=82 to 103) %)  
358 than to become solitary breeders (8 (CoI=2 to 30) %).

359

### 360 **Did individual-level traits influence ARTs, as expected under a conditional strategy?**

361 BMC was associated with ARTs in female striped mice with living relatives (Fig. 2; Table 3),  
362 while AP,  $T_a$  and the interaction between BMC and  $T_a$  were not (Table 3). Solitary breeders  
363 with relatives were heavier at conception than females that bred communally and returners,  
364 but there was no difference in BMC between communal breeders and returners (Fig. 2).  
365 Among females that had living relatives and went on to breed solitarily, body mass did not  
366 differ between females that were group-living at conception ( $51.3\pm 1.87$ ,  $n=18$  observations  
367 from 18 females that became solitary after conception), and those that were already solitary  
368 when they conceived ( $47.8\pm 1.90$ ,  $n=19$  observations from 16 females;  $\beta=3.52\pm 2.04$ ,  $t=1.72$ ,  
369  $P=0.099$ , controlling for AP and  $T_a$ ).

370

371 **Table 3.** Multinomial Mixed effects Model to test for the effects of body mass at conception (BMC),  
 372 age at parturition (AP), minimum ambient temperature ( $T_a$ ) and the interaction between  $T_a$  and BMC  
 373 on ARTs in female striped mice with living relatives ( $n=195$  records from 112 individuals that were  
 374 group-living when they conceived). We fitted unique variance and co-variance structures for each  
 375 ART ('communal breeder', 'solitary breeder', 'returner') interacted with each random term  
 376 (individual identity, group identity and year; not shown). Parameter estimates ( $\beta$ ) are modes from the  
 377 posterior distribution with 95% credible intervals. Non-significant fixed effects were eliminated  
 378 sequentially to reach the final model. Significant effects are in bold.

Fixed effects	$\beta$	$p$ MCMC
communal breeder intercept	2.524 (0.603 to 4.586)	<b>0.007</b>
returner intercept	2.738 (1.147 to 4.535)	<b>0.001</b>
BMC <sup>a</sup> (communal)	-0.157 (-0.274 to -0.047)	<b>0.003</b>
BMC <sup>a</sup> (returner)	-0.121 (-0.230 to -0.016)	<b>0.021</b>
$T_a^a$ (communal)	0.066 (-0.174 to 0.314)	0.605
$T_a^a$ (returner)	0.132 (-0.099 to 0.369)	0.246
AP <sup>a</sup> (communal)	0.005 (-0.004 to 0.015)	0.290
AP <sup>a</sup> (returner)	0.005 (-0.004 to 0.014)	0.296
$T_a \times \text{BMC}^a$ (communal)	-0.024 (-0.052 to 0.003)	0.078
$T_a \times \text{BMC}^a$ (returner)	-0.023 (-0.049 to 0.003)	0.080

379 <sup>a</sup> 'solitary breeder' is the baseline level of the response (reference group)

380

381

382 The returner tactic was more likely to occur because returners moved to a new nest ( $n=69$   
383 parturitions from 53 individuals) than because they stayed behind when their nestmates  
384 moved away ( $n=18$  parturitions from 18 individuals; probability of returner tactic arising  
385 through movement of focal female versus relatives: 0.75, 95% CoI=0.63 to 0.84,  $P<0.001$ ,  
386 exact binomial test). There was no difference between returners that moved and those that  
387 stayed behind in AP ( $\beta=-0.005\pm 0.003$ ,  $Z=1.60$ ,  $P=0.110$ ), BMC ( $\beta=-0.02\pm 0.04$ ,  $Z=0.54$ ,  
388  $P=0.589$ ) or the number of females they shared a nest with before parturition ( $\beta=0.25\pm 0.17$ ,  
389  $Z=1.48$ ,  $P=0.138$ ; GLMM with binomial errors controlling for individual and group identities  
390 and year). Groups were more likely to reunite because the returner moved back ( $n=58$   
391 parturitions from 46 individuals) than because the returners' relatives moved to join her at her  
392 new nest ( $n=29$  parturitions by 27 individuals; probability of re-joining group owing to  
393 movement of returner versus relatives: 0.67 (0.56 to 0.76),  $P=0.002$ ).

394  
395 Returners gave birth  $1.7\pm 0.35$  (range 0-28) days after becoming temporarily solitary ( $n=84$   
396 parturitions by 63 females), and re-joined the group after  $6.4\pm 0.61$  (range 1-35) days alone.  
397 On average, they re-joined the group after their communally-breeding nestmates had given  
398 birth (mean difference= $7.7\pm 1.95$  days;  $t_{89}=3.82$ ,  $P<0.001$ , paired t-test). The interval between  
399 leaving the group and parturition was not influenced by BMC ( $\beta=0.00002\pm 0.01$ ,  $Z=0.001$ ,  
400  $P=0.999$ , GLMM with poisson errors controlling for individual and group identities and year)  
401 or AP ( $\beta=-0.0006\pm 0.001$ ,  $Z=0.53$ ,  $P=0.600$ ). Those that moved to a new nest stayed away for  
402 longer than those that stayed behind when their relatives moved away (changed nest:  
403  $6.8\pm 0.72$  nights; stayed:  $4.0\pm 0.65$  nights;  $\beta=0.40\pm 0.18$ ,  $Z=2.27$ ,  $P=0.023$ ; GLMM with  
404 poisson errors). The number of nights that returners spent away was not related to BMC  
405 ( $\beta=0.01\pm 0.01$ ,  $Z=1.41$ ,  $P=0.158$ ) or AP ( $\beta=-0.0002\pm 0.001$ ,  $Z=0.22$ ,  $P=0.823$ ).

406

407 Females with living relatives were more likely to become solitary by moving to a new nest  
408 ( $n=18$  individuals) than by remaining at the nest when their nestmates moved away ( $n=7$ ;  
409 probability of becoming solitary by moving away: 0.72, 95% CoI=0.51 to 0.88,  $P=0.043$ ). All  
410 seven females in the latter category had only one female relative, while those that moved to a  
411 new nest came from larger groups ( $1.9\pm 0.31$  female nestmates, range 1-5;  $Z=2.05$ ,  $P=0.040$ ,  
412 asymptotic Wilcoxon Rank Sum Test). There was no difference between solitary females that  
413 moved to a new nest and those whose nestmates moved in age ( $\beta=0.001\pm 0.003$ ,  $Z=0.25$ ,  
414  $P=0.806$ ) or BMC ( $\beta=0.009\pm 0.056$ ,  $Z=0.16$ ,  $P=0.876$ , GLMM with binomial errors  
415 controlling for year and group identity) with regard to their first solitary breeding attempt.  
416 Solitary breeders left the group before their communally-breeding nestmates gave birth  
417 (mean difference= $-19.35\pm 4.45$  days;  $t_{20}=6.39$ ,  $P<0.001$ , paired t-test).

418

419 The interval between leaving the group and giving birth was longer for solitary breeders with  
420 relatives ( $12.9\pm 3.7$  days,  $n=25$ ) than for returners ( $\beta=1.28\pm 0.18$ ,  $Z=6.99$ ,  $P<0.001$ , GLMM  
421 with poisson errors controlling for individual and group identities and year). Among solitary  
422 breeders ( $n=25$ ), 56% gave birth within six (median 0) days of leaving the nest, while 28%  
423 did not appear to be gestating when they left the nest (26-37 day interval between leaving the  
424 nest and parturition). The interval between becoming solitary and giving birth increased with  
425 AP ( $\beta=0.002\pm 0.001$ ,  $Z=2.2$ ,  $P=0.025$ ;  $n=25$ , GLMM with poisson errors controlling for group  
426 identities and year) and the number of female nestmates ( $\beta=0.146\pm 0.002$ ,  $Z=66.3$ ,  $P<0.001$ )  
427 and decreased with increasing BMC ( $\beta=-0.065\pm 0.02$ ,  $Z=29.7$ ,  $P<0.001$ ).

428

#### 429 **Was breeding synchrony associated with ARTs?**

430 Communally-breeding females from the same group were more synchronized with each other  
431 in giving birth ( $5.8\pm 0.49$  days apart,  $n=61$  pairs of observations from 44 individuals) than

432 females from different groups were with each other ( $9.0\pm 0.57$  days apart,  $n=1938$  pairs from  
433 132 individuals;  $\beta=0.43\pm 0.06$ ,  $Z=7.68$ ,  $P<0.001$ ). Communally-breeding nestmates were also  
434 more synchronized with each other than with returners from their own group ( $7.1\pm 0.56$  days  
435 apart,  $n=63$  pairs from 54 individuals;  $\beta=0.19\pm 0.07$ ,  $Z=2.70$ ,  $P=0.018$ ), but synchrony within  
436 communal breeders did not differ from synchrony between communal and solitary breeders  
437 from the same group ( $5.1\pm 0.70$  days apart,  $n=12$  pairs from 16 individuals;  $\beta=0.13\pm 0.13$ ,  
438  $Z=1.06$ ,  $P=0.622$ ). Returners were no more likely to give birth before communally-breeding  
439 nestmates ( $n=31$  pairs from 33 individuals) than after them ( $n=31$  pairs from 37 individuals;  
440  $P=1.000$ , exact binomial test; 1 pair of observations in which a communal breeder and a  
441 returner gave birth on the same day excluded), nor were solitary breeders more likely to give  
442 birth before communally-breeding nestmates ( $n=5$  pairs from 8 individuals) than after them  
443 ( $n=7$  pairs from 10 individuals;  $P=0.774$ ).

444

#### 445 **Did the distribution of reproductive phenotypes change over the breeding season?**

446 Communal breeders gave birth earlier in the season than females of any other category  
447 (Tukey contrasts based on LMM:  $P\leq 0.004$ ; Fig. 3); solitary females with and without  
448 relatives and returners did not differ in the timing of their parturitions ( $P\geq 0.297$ ; Fig. 3),  
449 controlling for  $T_a$  ( $\beta=2.44\pm 0.34$ ,  $t=7.28$ ,  $P<0.001$ ) and BMC ( $\beta=0.66\pm 0.18$ ,  $t=3.60$ ,  $P<0.001$ ),  
450 which were positively related to parturition date. Age did not influence parturition date ( $\beta=-$   
451  $0.01\pm 0.01$ ,  $t=0.95$ ,  $P=0.342$ ).

452



**453 Solitary breeding as a consequence of extrinsic factors**

454 Of the 45 females that bred solitarily, 57.8% had surviving female relatives in the population.  
455 The rest were constrained to breed solitarily because their female relatives died, and they did  
456 not join another group with unrelated females. Females that became solitary because their  
457 relatives died did not differ in BMC from communal breeders ( $\beta=2.48\pm 1.59$ ,  $Z=1.56$ ,  
458  $P=0.242$ ; LLM with Dunnett contrasts; Fig. 2) or returners ( $\beta=1.28\pm 1.52$ ,  $Z=0.84$ ,  $P=0.680$ ).  
459 However, females that were group-living at conception and became solitary while their  
460 relatives were living weighed more than females whose relatives died ( $\beta=4.81\pm 2.01$ ,  $Z=2.39$ ,  
461  $P=0.040$ ; Fig. 2). BMC did not differ before and after females' relatives died (before relatives  
462 died:  $48.22\pm 3.50$ g,  $n=4$  records from 4 females, after:  $48.50\pm 1.37$ g,  $n=17$  observations from  
463 25 females;  $\beta=-0.28\pm 3.71$ ,  $t=0.07$ ,  $P=0.941$ ), controlling for AP ( $\beta=0.03\pm 0.01$ ,  $t=2.25$ ,  
464  $P=0.033$ ). Solitary females without relatives did not differ in AP ( $299.5\pm 21.87$  days) from  
465 communal breeders ( $297.2\pm 16.24$  days;  $\beta=2.32\pm 21.79$ ,  $Z=0.11$ ,  $P=0.999$ ; LMM with Dunnett  
466 contrasts) or returners ( $298.4\pm 15.86$  days;  $\beta=1.14\pm 20.93$ ,  $Z=0.06$ ,  $P=0.999$ ). There was a  
467 tendency for solitary females with living relatives to be younger ( $245.4\pm 20.71$  days) than  
468 those whose relatives had died ( $\beta=54.15\pm 24.06$ ,  $Z=2.25$ ,  $P=0.056$ ).

469

470

**471 Discussion**

472

473 We tested whether the theoretical framework developed to explain strategies governing male  
474 ARTs also applies to females. Among female striped mice, three ARTs occurred  
475 simultaneously in the population: most females bred communally in a nest shared with  
476 relatives (communal breeders) or left the group temporarily to give birth (returners). A  
477 smaller proportion became solitary and did not return to the group after producing young,

478 even though relatives were still living (solitary breeders with relatives). Females switched  
479 between ARTs, which can occur under single but not alternative strategies, and so we tested  
480 whether this represented a conditional or mixed single strategy. Studies of conditional  
481 strategies in free-living individuals are often unable to measure potential cues (e.g. body  
482 mass) before individuals switch tactic, and are thus often confounded by environmental  
483 effects that occur after the switch. We addressed this by investigating body mass records  
484 collected before females became solitary. Females that went on to breed solitarily were  
485 heavier than communal breeders and returners, which suggests that body mass influences  
486 tactic choice. We could differentiate between two kinds of solitary breeder: those that became  
487 solitary while their relatives were alive and those that were forced by stochastic external  
488 factors (mortality of relatives) to rear young alone. We did not find an association between  
489 female reproductive phenotype and either parturition trapping interval and radio-tracking  
490 effort, which suggests that variation in survey effort did not bias our results towards a  
491 particular phenotype. Our results show that both phenotypic plasticity and extrinsic factors  
492 can produce intra-specific variation in social organization, and that evolutionary theory  
493 developed for ARTs in males also applies in females.

494

495 *(i) Do ARTs arise from alternative strategies or a single strategy in female striped mice?*

496 The majority of female striped mice that bred more than once switched reproductive tactics.  
497 The ability to switch ARTs has been described in females of several species of birds, fish and  
498 insects (Warner 1985; Åhlund & Andersson 2001; Zink 2003). This behaviour is consistent  
499 with a single strategy, where different tactics arise from one decision-rule (Schradin &  
500 Lindholm 2011). It is worth noting, however, that several females that bred more than once  
501 did not switch tactics. Instead they showed a single phenotype of solitary breeder, communal  
502 breeder or returner. Those females could be following i) alternative strategies with fixed

503 tactics or ii) a single strategy in the absence of (or without responding to) cues that elicit  
504 switching between tactics. Strategic models show that alternative and plastic strategies can  
505 coexist within a single population and be evolutionarily stable under a range of conditions  
506 (Lively 1986; Plaistow et al. 2004). This idea has received further theoretical support from a  
507 quantitative genetics perspective (Hazel, Smock & Lively 2004). Indeed, empirical work has  
508 described coexistence of conditional and unconditional strategies in barnacles (Lively et al.  
509 2000), mites (Buzatto, Simmons & Tomkins 2012) and sailfin mollies (Fraser et al. 2014). In  
510 our study, many females that switched tactics had previously maintained one tactic for  
511 multiple breeding attempts before the switch. It therefore seems likely that at least some of  
512 the females that did not switch tactic were capable of doing so. In striped mice, high  
513 population density can constrain females to remain group-living (the best tactic under these  
514 conditions; Schradin et al 2010), while experimentally easing these constraints by decreasing  
515 local population density induces a switch to solitary-living (Schoepf & Schradin 2012a). The  
516 decision not to switch tactics can therefore represent an adaptive response to stable  
517 environmental conditions. While we cannot exclude the possibility that females that  
518 maintained the same tactic throughout the breeding season were using alternative strategies,  
519 we present evidence for the existence of a plastic strategy that is used by most females in the  
520 population.

521

522 A female's reproductive tactic was a predictor of her subsequent tactic, with individuals often  
523 following the same tactic for more than one consecutive breeding attempt. Females that  
524 switched tactics generally proceeded from communal breeder to returner to solitary. The  
525 relative distribution of ARTs changed over the breeding season, with communal breeding  
526 occurring earlier in the season than the other ARTs. Tactic switches between communal  
527 breeders and returners were often reversible. Solitary breeders, by definition, do not re-join

528 their former group, but can make the transition to communal breeder (or returner) by forming  
529 plural breeding groups with adult daughters. One female established a new group after her  
530 relatives died, and she and her daughters bred communally the following year. Females  
531 whose nestmates died did not join other groups, indicating the importance of genetic kinship  
532 in the formation of breeding groups. Although non-relatives can form transient overnight  
533 huddling groups in winter (Schradin, Schubert & Pillay 2006), aggression towards non-kin  
534 during the breeding season (Schradin 2004) probably constrains the direction of tactic  
535 switching.

536

537 *(ii) Do ARTs represent a mixed or a conditional strategy?*

538 Mixed and conditional strategies are two types of single strategy (Schradin & Lindholm  
539 2011). When individuals follow a conditional strategy, ARTs can be determined by  
540 differences in traits that reflect competitive ability (Gross 1996). No such association is  
541 predicted under a mixed strategy, which assumes that tactics are stochastically assigned  
542 (Dominey 1984). We found that solitary breeders with relatives were heavier than communal  
543 breeders and returners before leaving the group, consistent with a conditional strategy (Fig.  
544 4). Body mass or size is an important cue governing the switchpoint between ARTs in males  
545 (e.g. Tomkins & Brown 2004; Schradin et al. 2009b) and females (Warner 1985) of various  
546 taxa. This probably reflects its reliability as an indicator of competitive ability (Wada et al.  
547 2005) and/or energy reserves (Nunes et al. 1999) in species with alternative life histories.  
548 Male and female Belding's ground squirrel (*Spermophilus beldingi*), for example, do not  
549 disperse until they reach a threshold body mass, and dispersing males have more fat reserves  
550 than males of the same age that delay dispersal (Nunes et al. 1999). Thermoregulation is  
551 more energetically expensive in solitary than group-living striped mice (Scantlebury et al.  
552 2006), and solitary breeders must also meet the energetic requirements of nursing pups and

553 defending a territory alone. We therefore propose that female striped mice remain group-  
554 living until they have amassed enough body reserves to support the energetic demands of  
555 solitary breeding. Together these results show that body mass is a key trait underlying the  
556 evolution of conditional strategies in many species.

557

558 Leaving the group temporarily to give birth may allow females to avoid reproductive  
559 competition without foregoing the long-term benefits of group-living. Female lions (*Panthera*  
560 *leo*) become less gregarious during the first weeks postpartum and hide cubs from pridemates  
561 (Packer, Pusey & Eberly 2001). Breeding synchrony is thought to have evolved to reduce the  
562 risk of infanticide by co-breeding females (Lambin 1993; Poikonen *et al.* 2008), which stop  
563 being infanticidal after their own offspring are born (e.g. McCarthy & Saal 1985). In  
564 addition, asynchronous births are associated with higher pup mortality for later-born litters in  
565 some cooperatively breeding mammals because younger pups are outcompeted by older ones  
566 or suffer physical trauma from being crushed by them (Mennella *et al.* 1990; Hodge, Bell &  
567 Cant 2011). Indeed, we found that the degree of within-group breeding synchrony was lower  
568 for returners than communal breeders. This suggests that the returner tactic might have  
569 evolved as a counter-measure against infanticide and/or offspring competition with older  
570 litters. Interestingly, females that left the group without returning did not differ in synchrony  
571 from communal breeders, which suggests that synchrony did not underlie their decision to  
572 breed solitarily.

573

### 574 *(iii) Solitary breeding as a consequence of extrinsic factors*

575 Group-living females can become solitary of their own volition or because of external  
576 constraints. Among the females that bred solitarily in our study, 57.8% had surviving female  
577 relatives in the population and the rest became solitary because their relatives had died.

578 Importantly, the latter group weighed less than solitary breeders with living relatives, but did  
579 not differ from group-living females in body mass. This suggests that solitary breeders  
580 without relatives would have usually remained group-living if their relatives had survived.  
581 The trend towards females with no relatives being older than solitary females with relatives  
582 may be a consequence of the former having outlived their relatives. In summary, extrinsic  
583 factors can produce a solitary-breeding phenotype that differs in individual-level traits from  
584 females that become solitary through choice.

585

#### 586 *Potential fitness outcomes*

587 Alternative phenotypes can persist within a population when relative fitness rankings reverse  
588 across different spatial or temporal units (Moran 1992). Relative fitness varies between years  
589 in male striped mice: in years with high population density dominant breeding males sired  
590 more pups than roamers and philopatric males, whereas all males were roamers in years with  
591 low population density (Schradin & Lindholm 2011). It is not yet known whether fitness  
592 differs between ARTs in female striped mice, and whether relative fitness rankings vary  
593 under different ecological conditions (e.g. population density). In our study, communal  
594 breeders gave birth ~11 days earlier than returners and ~16 days before solitary breeders. The  
595 abundance of food plants at our study site decreased linearly over the breeding season (D.L.  
596 Hill, Pillay, N. & Schradin, C., unpublished data). This raises the possibility that communal  
597 breeders' offspring could experience greater food availability. This may be traded-off with  
598 the greater risk of infanticide in communally-breeding groups (Schradin et al. 2010).  
599 Comparisons of fitness correlates between solitary and communally-breeding female rodents  
600 have yielded mixed results (e.g. Boyce & Boyce 1988, Manning et al. 1995). Whether free-  
601 living offspring born in communal and solitary nests differ in growth trajectories, condition  
602 or survival remains to be tested in female striped mice.

603

604 *Conclusions and implications*

605 Male ARTs usually evolve where investment by dominant resource-holding ('bourgeois')  
606 males can be exploited by other males (Taborsky, Oliveira & Brockmann 2008). However,  
607 owing to anisogamy, and gestation in viviparous species, all breeding females must make a  
608 substantial investment in reproduction, resulting in smaller asymmetries in effort and fitness  
609 between females compared to males (Taborsky, Oliveira & Brockmann 2008). Consequently,  
610 ARTs are usually more subtle in females than in males and more likely to occur after  
611 fertilisation. Female striped mice show three ARTs whose expression is controlled by a single  
612 strategy (Fig. 4) in at least the majority of the population. This strategy may enable females to  
613 avoid reproductive competition when certain individual-level and environmental conditions  
614 are met. Male and female ARTs share many similarities in striped mice, but also differ in  
615 certain respects. Males, like females, follow three ARTs that differ in body mass; they can  
616 breed solitarily (as roamers) or in a group (as dominant breeders or philopatrics; Schradin et  
617 al. 2009b). Philopatric males differ in age from dominant breeders and roamers (Schradin et  
618 al. 2009b), but age did not influence female ARTs in our study. At a proximate level, males  
619 following alternative tactics differ in corticosterone and testosterone levels (Schradin et al.  
620 2009b), whereas female ARTs differ in corticosterone and oestrogen levels but not in  
621 testosterone (Hill, Pillay & Schradin 2015). These differences and the occurrence of the  
622 returner tactic in females suggest that ARTs in female striped mice are unlikely to simply  
623 reflect a correlated response to selection for ARTs in males.

624

625 An important feature of populations in which reproductive and social tactics occur in both  
626 sexes is the potential for the entire social system to change facultatively as a result of  
627 decisions made at the individual level (Schradin et al 2012). Social flexibility has been

628 described in various taxa, including dunnocks (*Prunella modularis*), burying beetles  
629 (*Nicrophorus vespilloides*) and humans (*Homo sapiens*, reviewed in Schradin et al. 2012). It  
630 is particularly prevalent in species where individuals need to respond quickly to  
631 unpredictable, fluctuating environmental conditions that might differ substantially from those  
632 experienced by previous and subsequent generations (Schradin et al. 2012). Improving our  
633 understanding of the evolution of phenotypic plasticity and how it facilitates resilience to  
634 environmental change is an important and timely goal.



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636

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647

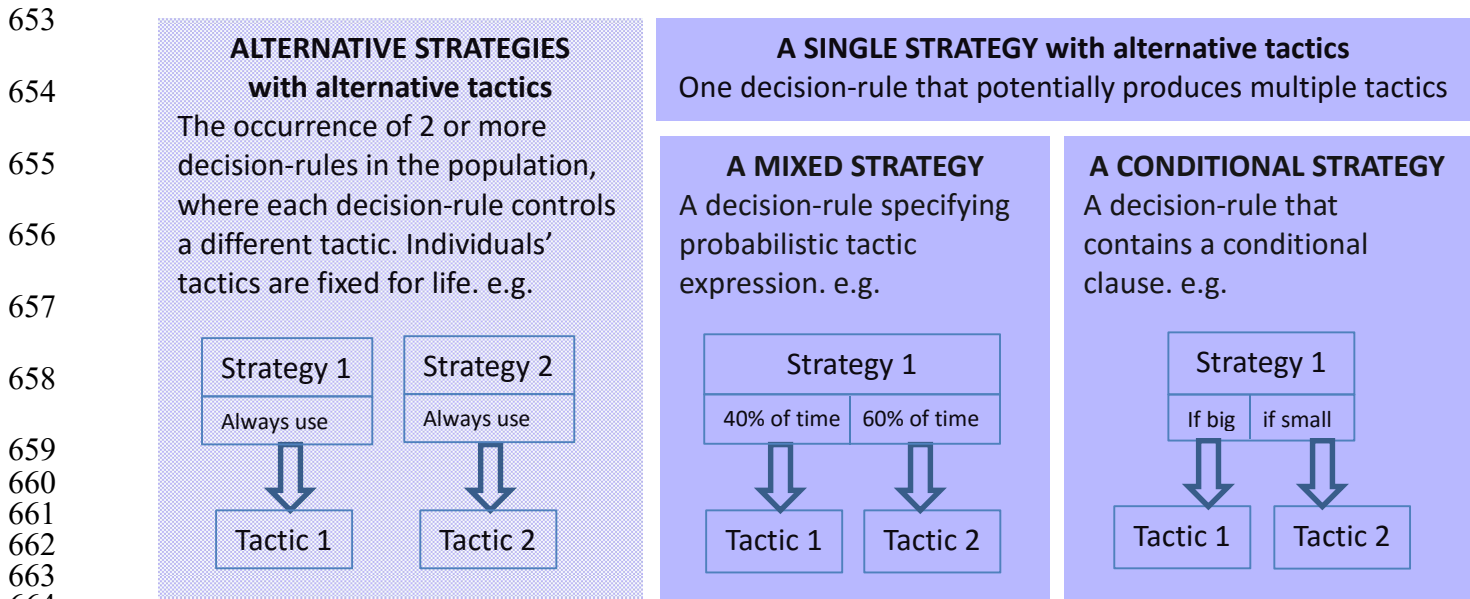
648 **Data accessibility**

649

650 Data to be made available from the Dryad Digital Repository (Hill, Pillay & Schradin

651 unpublished).

652



665 **Fig. 1.** Genetically-based decision-rules called strategies govern alternative reproductive tactics in

666 members of the same sex and population. In species with *alternative strategies*, each strategy controls

667 a different tactic with canalized expression (i.e. phenotypes are robust to environmental or genetic

668 perturbations). In species with a *single strategy*, individuals use one decision-rule that controls the

669 expression of multiple phenotypes (Schradin et al. 2012). Single strategies can be divided into mixed

670 or conditional strategies. Mixed strategies specify that individuals switch tactics according to a

671 particular probability distribution or are assigned permanently-adopted tactics probabilistically

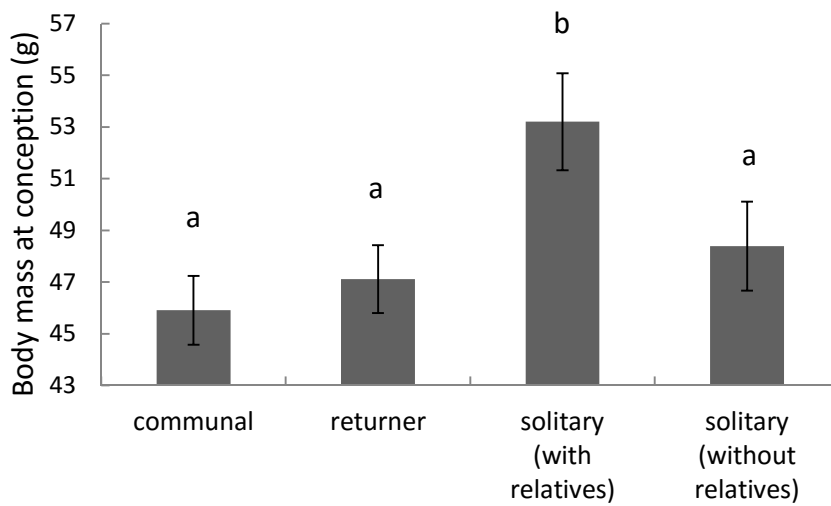
672 (Dominey 1984). Conditional strategies occur when each individual selects the tactic that generates

673 the highest fitness returns for its prevailing circumstances (Gross 1996). The scenarios represented

674 above are not necessarily mutually exclusive within a population (e.g. Plaistow et al. 2004)

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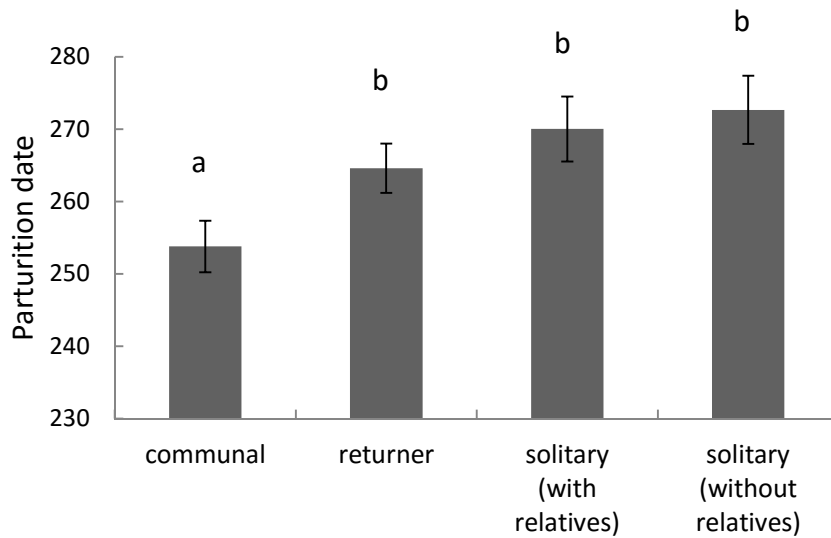
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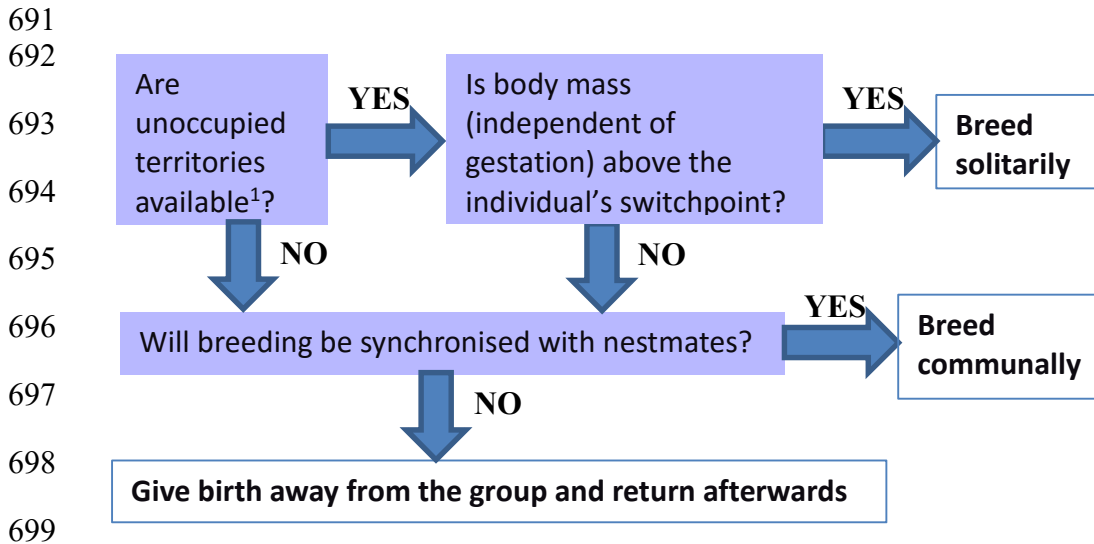
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**Fig. 2.** Mean body mass at conception  $\pm 1$ SE in communal breeders ( $n=87$  parturitions by 64 individuals), returners ( $n=90$  parturitions from 66 females) and solitary breeders with living relatives ( $n=18$  parturitions by 18 females that were still group-living when body mass was measured) and without living relatives ( $n=29$  parturitions by 20 females). Different letters above bars represent significant differences adjusted for False Discovery Rate. Note that the y-axis is truncated



684  
685 **Fig. 3.** Mean parturition date  $\pm 1$ SE (1 Jan of any year=day 1) in communal breeders ( $n=87$   
686 parturitions by 64 individuals), returners ( $n=90$  parturitions by 66 individuals) and solitary breeders  
687 with living relatives ( $n=37$  parturitions by 26 individuals) and without relatives ( $n=29$  parturitions by  
688 20 individuals). Different letters above bars represent significant differences adjusted for multiple  
689 testing  
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700 **Fig. 4.** The strategy (evolved set of decision-rules) predicted to govern the expression of the three  
 701 alternative reproductive tactics used by female striped mice with living relatives. This ties together  
 702 results from the present study and <sup>1</sup>Schradin, König & Pillay (2010). Females switched tactic upon  
 703 reaching thresholds of body mass or breeding asynchrony with nestmates. Those that became solitary  
 704 breeders were heavier when they conceived than communal breeders and returners, which did not  
 705 differ in body mass. Females that were less closely synchronized with nestmates were more likely to  
 706 use a returner tactic than to give birth communally. Selection is thought to act upon heritable genetic  
 707 variation for the position of the switchpoint, so different individuals might change tactics at different  
 708 values of the underlying traits (Tomkins & Hazel 2007). Solitary-breeding phenotypes can arise either  
 709 from this strategy or as a consequence of extrinsic stochastic processes (mortality of all adult female  
 710 relatives)  
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## Supporting Information

The following Supporting Information is available for this article online:

Appendix S1. Methods for multiple imputation of missing body mass and age values

Appendix S2. Specifications for multinomial mixed effects model

Figure S1. Correspondence between 97 consecutive pairs of alternative reproductive tactics

(ARTs) represented by  $\chi^2$  distances between points in female striped mice