



**HAL**  
open science

# Social flexibility and environmental unpredictability in African striped mice

Carsten Schradin, Neville Pillay, Cleo Bertelsmeier

► **To cite this version:**

Carsten Schradin, Neville Pillay, Cleo Bertelsmeier. Social flexibility and environmental unpredictability in African striped mice. Behavioral Ecology and Sociobiology, 2019, 73, pp.94. 10.1007/s00265-019-2707-7 . hal-02169668

**HAL Id: hal-02169668**

**<https://hal.science/hal-02169668>**

Submitted on 15 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 **The evolution of intra-specific variation in social organization**

2

3 **Published as**

4 **Schradin, C.**, Pillay, N. & Bertelsmeier, C. 2019. Social flexibility and environmental  
5 unpredictability in African striped mice. *Behavioral Ecology and Sociobiology*,  
6 **73**, 94.

7

8

9 Carsten Schradin<sup>1,2,\*</sup>, Neville Pillay<sup>2</sup>, & Cleo Bertelsmeier<sup>4</sup>

10 <sup>1</sup> Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

11 <sup>2</sup> School of Animal, Plant and Environmental Sciences, University of the Witwatersrand,  
12 South Africa.

13 <sup>3</sup> Department of Biology, Geology, and Environmental Sciences, University of Tennessee at  
14 Chattanooga, Chattanooga, Tennessee, USA

15 <sup>4</sup> Department of Ecology and Evolution, University of Lausanne, Switzerland.

16

17 \*[carsten.schradin@iphc.cnrs.fr](mailto:carsten.schradin@iphc.cnrs.fr)

18

19 **Keywords** phenotypic flexibility; phenotypic plasticity; intra-specific variation in social  
20 organization; alternative reproductive tactic; extrinsic factors; environmental disrupters;

21

22

23

24

25 **Abstract**

26 Many species show intra-specific variation in their social organization (IVSO), which means  
27 the composition of their social groups can change between solitary living, pair-living or living  
28 in groups. Understanding IVSO is important because it demonstrates species resilience to  
29 environmental change and can help us to study ultimate and proximate reasons for group-  
30 living by comparing solitary and group-living individuals in a single species. It has long been  
31 realized that the environment plays a key role in explaining the occurrence of IVSO. IVSO is  
32 expected to have evolved in variable environments and can thus be a key adaptation to  
33 environmental change. It has previously been shown that four different mechanisms relying  
34 on the environment exist that can lead to IVSO: environmental disrupters, genetic  
35 differentiation, developmental plasticity, and social flexibility. All four mechanisms depend  
36 on the environment such that focusing only on environmental factors alone cannot explain  
37 IVSO. Importantly, only three represent evolved mechanisms, while environmental disrupters  
38 leading to the death of important group members induce non-adaptive IVSO. Environmental  
39 disrupters can be expected to cause IVSO even in species where IVSO is also an adaptive  
40 response. Here we focus on the questions of why IVSO occurs and why it evolved. To  
41 understand IVSO at the species level it is important to conduct continuous long-term studies  
42 to differentiate between non-adaptive and adaptive IVSO. We predict that IVSO evolves in  
43 environments that vary in important ecological variables, such as rainfall, food availability,  
44 and population density. IVSO might also depend on life history factors, especially longevity.  
45 IVSO is predicted to be more common in species with a short lifespan and that breed only for  
46 one breeding season, being selected to respond optimally to the prevailing environmental  
47 situation. Finally, we emphasise the importance of accounting for IVSO when studying social  
48 evolution, especially in comparative studies, since not every species can be assigned to one  
49 single form of social organization. For such comparative studies, it is important to have  
50 reliable data-bases based on the primary literature.

51 **Introduction**

52 Formerly, it was assumed that every species has a specific social system and deviations from  
53 it were regarded as abnormal or noise. However, it has been recognized that each of the three  
54 components of a species social system (Kappeler & Schaik 2002) can vary within the species  
55 (Lott 1984; Lott 1991): i.e. its mating system (who mates with whom), its social structure  
56 (how individuals interact with each other), and its social organization (whether they are  
57 solitary, pair-living or living in groups of different composition). Most information is  
58 available for the social organization of species. The social organization can affect the social  
59 structure and the mating system, influencing the entire social system.

60 Intra-specific variation in social organization (IVSO) during breeding occurs when a  
61 species shows two or more of the following forms of social organization (Lott 1991; Schradin  
62 2013): living solitarily, in pairs, one breeding male with several breeding females, one  
63 breeding female with several breeding males, or multi-male multi-female groups. Each form  
64 of social organization must be composed of breeding individuals, not only dispersing solitary  
65 individuals or bachelor groups. Variation in group-size and optimal group size are important  
66 topics in behavioral ecology (Markham & Gesquiere 2017), but, following our definition, do  
67 not indicate IVSO if the relative numbers of breeders of each sex does not change.

68 IVSO occurs in several taxa, including insects and vertebrates. For example, burying  
69 beetles (*Nicrophorus vespilloides*) can be solitary, form pairs or communal groups with two  
70 or more breeding females (Eggert 1992), depending on the size of the carrion for which they  
71 compete, with more beetles associating at larger carrion (Müller et al. 2006). Similarly, pied  
72 kingfishers (*Ceryle rudis*) can live in pairs, in family groups with philopatric adult offspring,  
73 or in polygynous groups, depending on the availability of good nesting sites (Reyer 1980;  
74 Reyer 1984). The house mouse (*Mus musculus*) can live solitarily, in pairs or in communal  
75 groups, with resource availability modifying the intensity of intra-specific competition (intra-  
76 sexual aggression in males and female infanticide) (Latham & Mason 2004; Berry et al. 2008).

77 Dunnocks (*Prunella modularis*) also show varying forms of social organization to maximize  
78 individual fitness (Davies 1992), which was used as a model system to study the evolution of  
79 sexual conflict, mating systems, parental effort and life histories (Burke et al. 1989; Davies et  
80 al. 1996). Male and female dunnocks can change their mating system (monandry, polygyny  
81 and polyandry) and social organization (pairs, one female and several males, or multi male  
82 multi female groups). In a series of sophisticated experiments, including measuring individual  
83 fitness, it was demonstrated that IVSO is the consequence of individual dunnocks choosing  
84 the reproductive tactic with the highest fitness depending on the prevailing ecological  
85 conditions (Davies 1992).

86 To understand IVSO, it is not sufficient to study the related environmental factors.  
87 Tinbergen proposed in his four questions that behavior must be understood from the  
88 perspectives of ontogeny, causation, phylogeny and function (Tinbergen 1963), and the  
89 environment plays a crucial role in all four questions (Schradin 2018). Physiological  
90 mechanisms are evolved traits (Hofmann et al. 2014) and thus to understand why IVSO  
91 evolved, one must understand the mechanisms leading to IVSO. Thus, the first step to  
92 understand why IVSO occurs is to describe and differentiate the mechanisms of IVSO.

93 After summarizing a previous review on IVSO (Schradin 2013), we outline three  
94 important new aspects. First, we show the importance of differentiating between adaptive and  
95 non-adaptive IVSO. Second, we focus on the questions of why IVSO occurs and why it  
96 evolved. Third, we show the importance of accounting for IVSO when studying social  
97 evolution, particularly in comparative studies. Finally, we summarise hypotheses and  
98 predications about the evolution of IVSO. Our major aim is thus to encourage more research  
99 on evolutionary reasons of IVSO and to emphasise the importance of considering IVSO in  
100 comparative studies.

101

102

103 **The four mechanisms that can lead to IVSO**

104 In a 2013 review, Schradin proposed four different mechanisms that can lead to IVSO, each  
105 mechanism depending on environmental factors (Schradin 2013): environmental disrupters  
106 (entirely extrinsic factors), genetic differentiation, developmental plasticity, and social  
107 flexibility. Environmental disrupters occur when natural mortality due to old age or predation  
108 changes the social organization, which represents a non-adaptive change imposed on the  
109 group. IVSO is thus not caused by the remaining individuals which will respond to this new  
110 situation with adaptive tactics. This is discussed in detail below. Genetic differentiation refers  
111 to the possibility that sub-populations of one species might differ genetically which could  
112 influence the resulting social organization. By genetic differences we refer to heritable  
113 differences of the genome (for behavior see (Hu & Hoekstra 2017) for social behaviors  
114 (Bendesky et al. 2017); (Dochtermann et al. 2015), which includes not only differences in  
115 genes and alleles, but also differences in genomic regions that regulate gene expression.  
116 However, while genetic differences between populations of the same species could explain  
117 the occurrence of IVSO, evidence for this process is rare to absent. The best example could be  
118 fire ants (*Solenopsis invicta*) which have two social forms (polygynous with several breeding  
119 females and monogynous with one breeding female) and it is a single polymorphism at the  
120 locus Gp-9 that determines the social organization of a colony. Queens that are homozygous  
121 BB at this locus attempt to found a colony alone, while Bb and bb queens do not fly far but  
122 attempt to join a colony (Gotzek & Ross 2007; Gotzek & Ross 2009; Keller 2009; Ometto et  
123 al. 2011). Future studies might reveal more examples where genetic differentiation could  
124 explain IVSO, but to date empirical evidence does not indicate that it is a common  
125 mechanism of IVSO.

126 IVSO can be caused by phenotypic plasticity. Non-reversible phenotypic plasticity is  
127 called developmental plasticity, depending on organizational effects during early development  
128 (Phoenix et al. 1959; West-Eberhard 2003) or puberty (Zimmermann et al. 2017). In

129 developmental plasticity, the environment determines which one of two or more alternative  
130 phenotypes develops. If the social behavioral phenotype is permanently influenced during  
131 early development, the social organization of this population could differ either from  
132 generation to generation, or compared to another population, in both cases leading to IVSO.  
133 However, to date there is no empirical evidence that developmental plasticity causes IVSO;  
134 yet, future studies might reveal species in which developmental plasticity causes IVSO.

135         Social flexibility, i.e. reversible phenotypic plasticity (Piersma & Drent 2003) of  
136 individual social tactics, is the best empirically documented mechanism leading to IVSO.  
137 Flexibility in social behavior is common, because individuals have to respond flexibly  
138 depending on the social situation. In primates, flexible dominance hierarchies enable  
139 individuals to cope with conflict, enabling them to remain in their group even if new conflict  
140 arises (Judge 2000). This is an important social ability in many obligatory group-living  
141 species, in which living solitarily is very costly and leads to increased mortality. Individuals'  
142 flexibility in social behavior stabilizes the social system including the social organization of  
143 the species, which can explain why social organization in primates is very stable (Shultz et al.  
144 2011). In social species where individuals are less flexible in their social response, alternative  
145 and reversible social tactics might exist. Therefore, social flexibility leading to IVSO might be  
146 particularly common in species with low flexibility in social behavior, while flexibility in  
147 social behavior can maintain the existing social organization. Flexibility in social tactics in  
148 both sexes can change the social organization of the entire population. This mechanism is  
149 called social flexibility (Schradin et al. 2012) and has been shown to cause IVSO in burying  
150 beetles (Eggert 1992; Müller et al. 2006), pied kingfishers (Reyer 1980; Reyer 1984), house  
151 mice (Latham & Mason 2004; Berry et al. 2008), great gerbil (*Rhombomys opimus*; (Randall  
152 et al. 2005) and African striped mice (*Rhabdomys pumilio*; Schradin et al. 2012).

153         Schradin (2013) identified that for all four possible mechanisms, the environment  
154 plays a critical role. Thus, to understand which mechanism is at play, it is not sufficient to

155 study the environmental factors. One must also establish whether the underlying physiological  
156 mechanisms are genetically determined, organizational, or activational (Table 2 in Schradin,  
157 2013). In accordance with Piersma & Gils (2011), Schradin (2013; Table 2) hypothesized that  
158 the predictability of the environment will determine which mechanism evolved such that: (i)  
159 genetic differentiation evolves in predictable environments (two or more populations with  
160 different but predictable environments); (ii) developmental plasticity occurs in short-term,  
161 predictable environments (the individual can predict from the environment in which it grows  
162 up the environment in which it will breed); and (iii) social flexibility evolves in unpredictable  
163 environments. As environmental disrupters do not represent an evolved mechanism of IVSO,  
164 it is also not associated to a specific physiological mechanisms nor a specific environment  
165 (Schradin 2013).

166

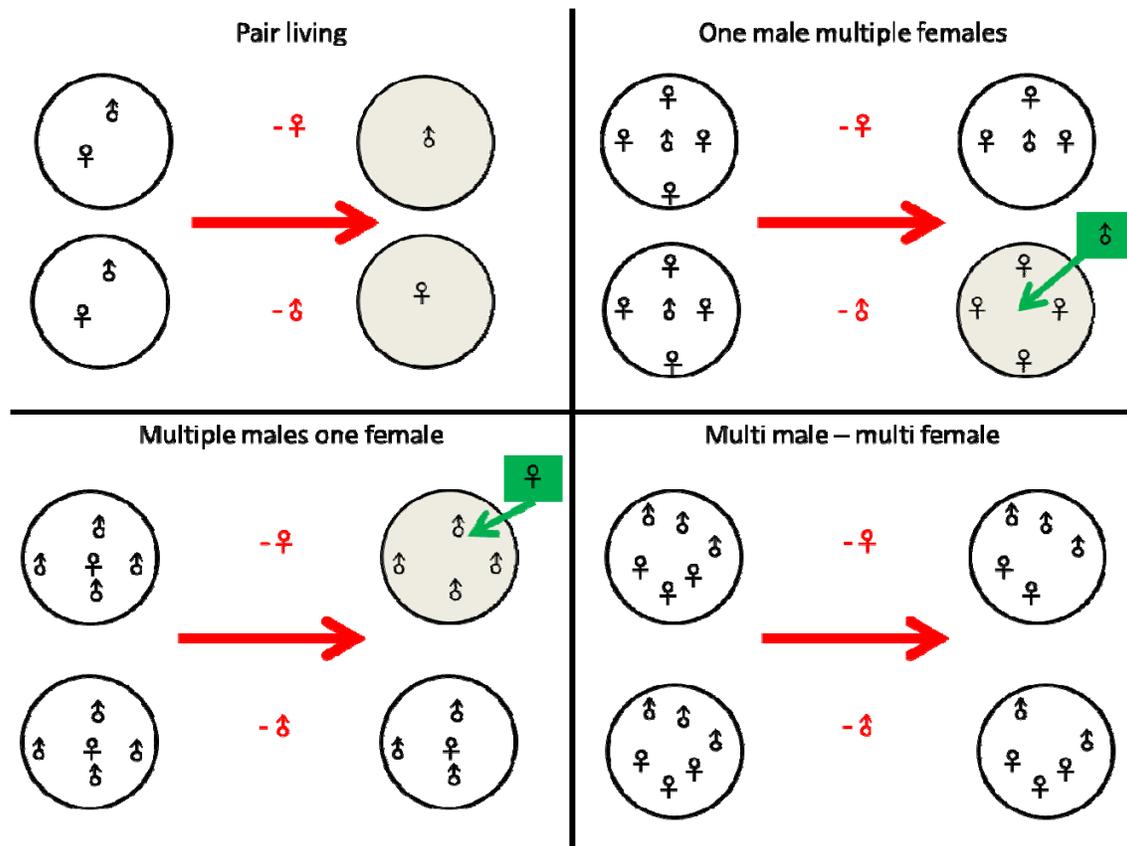
#### 167 **How to recognize the different mechanisms?**

168 Schradin (2013) identified two questions one needs to answer to show which one of the four  
169 mechanisms explains an observed IVSO (Table 3 and 4 in Schradin 2013). 1. Does IVSO  
170 occur within or between individuals? This differentiates between genetic variation and  
171 developmental plasticity (IVSO between individuals) on the one hand and entirely extrinsic  
172 factors and social flexibility on the other (IVSO occurs within individuals). 2. If IVSO occurs  
173 between individuals, to differentiate between genetic variation and developmental plasticity  
174 one would have to answer the question ‘to what extent does the genotype or the environment  
175 determine the social tactics shown by individuals? If IVSO occurs within individuals, one has  
176 to (i) establish whether the environment induces changes in individual behavior which in turn,  
177 leads to a new form of social organization (social flexibility), or (ii) whether the social  
178 organization is changed due to one (or more) individuals disappearing (environmental  
179 disrupters).

180

181 **IVSO can be non-adaptive**

182 Environmental disrupters are common reasons of IVSO but do not represent an adaptation,  
183 but a case where a change in social organization is imposed on the individuals by the  
184 environment. If an important group member dies, the social organization of the entire group  
185 might change (Fig. 1). For example, in pair-living species, if one of the two breeders dies, the  
186 other individual automatically becomes solitary living (Fig. 1). The death of a single  
187 individual in pair-living Scandinavian wolves often results in temporarily solitary individuals  
188 (Milleret et al. 2017). Individuals might then respond adaptively to this imposed change, such  
189 as by re-pairing as reported in beavers (*Castor fiber*; (Mayer et al. 2017). In pair-living  
190 species where the offspring remain in their natal family after reaching adulthood and help in  
191 raising their younger siblings, the death of one of the two breeders often leads to reproductive  
192 conflicts between the adult non-breeders, which can lead to several forms of social  
193 organization. For example, cooperatively breeding callitrichid primates reportedly show  
194 considerable IVSO, which has been typically interpreted as an adaptive strategy (Garber 1997;  
195 Garber et al. 2016). However, IVSO in callitrichids is often induced by the disappearance of a  
196 dominant breeder, for example a breeding male in Goeldi's monkeys (*Callimico goeldii*)  
197 (Porter et al. 2001), in black faced lion tamarins (*Leontopithecus caissara*) (Martins et al.  
198 2015), or in mustached tamarins (*Saguinus mystax*) (Löttker et al. 2007). In these examples,  
199 the changes in social behavior observed in the remaining individuals can be regarded as  
200 adaptive, since each individual attempted to optimize its fitness under the new social  
201 conditions and to obtain a breeding position. However, the observed IVSO itself was not  
202 caused by the individuals. IVSO due to environmental disrupters therefore seems to be very  
203 common.



204

205 **Fig. 1**

206 Mortality of a single individual (indicated by a red arrow and red sex specific symbol) can change the  
 207 social organization if there is no other breeding individual of the same sex in the group (indicated in  
 208 grey). This is especially the case in pair-living species (top left), but not in species living in multi-male  
 209 multi-female groups (bottom right). In species where groups typically consist of only one individual of  
 210 one sex and multiple individuals of the other sex, mortality of only the individual of the rarer sex  
 211 changes the social organization (one male multi female groups top right, and multiple males one  
 212 female groups bottom left). However, in these species, often the vacant breeding position is taken over  
 213 very quickly (for example from males in bachelor groups), such that no IVSO might be observed  
 214 (green insets). Note that pair-living species often have groups that also contain adult non-breeders,  
 215 for example in cooperatively breeding species such as wolves and callitrichids. In these species,  
 216 mortality of a dominant breeder typically leads to conflict between the remaining group members about who  
 217 will become a breeder.  
 218

219 It is important to know whether the observed IVSO is due to an environmental  
 220 disrupter or due to the adaptive choice of individuals. In facultative group-living African  
 221 striped mice, solitary breeding in females has been described as an adaptive tactic to avoid  
 222 reproductive competition within groups (Schradin et al. 2010). However, long-term studies  
 223 revealed that solitary breeding in female striped mice could be the result of two alternative

224 mechanisms: 1. females leaving the communal group to become solitary breeders, indicating  
225 an individual choice; or 2. females becoming solitary breeders because all other females of  
226 their group have disappeared, probably due to predation (Hill et al. 2015a). This difference in  
227 mechanisms is also represented in differences between females, with solitary females that left  
228 the group having a higher body mass and lower corticosterone levels than females that  
229 remained in the group, whereas females that became solitary due to environmental disrupters  
230 did not differ from group-living females in body size or hormonally (Hill et al. 2015a; Hill et  
231 al. 2015b). However, females that chose to become solitary differed significantly in body  
232 mass and in hormone levels from females that became solitary due to environmental  
233 disrupters (Hill et al. 2015a; Hill et al. 2015b). Thus, to understand the proximate mechanisms  
234 and ultimate consequences of solitary breeding, it is important to know whether solitary  
235 breeding has been caused by an environmental disrupter or by adaptive individual choices.

236

### 237 **The importance of long—term field studies with continuous monitoring**

238 Identifying IVSO is challenging, especially for long-lived species. It requires long-term field  
239 studies (Hayes & Schradin 2017) which are difficult to initiate and sustain (Schradin & Hayes  
240 2017). The history of the group must be known for an extended period of time to identify  
241 whether changes in social organization are the result of individual choices, indicating adaptive  
242 IVSO, or due to environmental disrupters changing the group organization. Thus, long-term  
243 field studies must contain continuous observations over several years, not just several  
244 extended field trips to the same field site over a few years. This is in contrast to many projects,  
245 which are typically funded for only three years, with periods between study years when no  
246 field data are collected, and when important members of the study population might disappear  
247 for then unknown reasons (Porter et al. 2001). While it is easy to provide adaptive  
248 interpretations to explain the observed IVSO, whether or not it is really adaptive or the  
249 consequence of environmental disrupters remains unknown. It is important to be aware that

250 cases of non-adaptive IVSO due to environmental disrupters can also occur in species where  
251 adaptive IVSO occurs, as was demonstrated in the case of solitary breeding in African striped  
252 mice (Hill et al. 2015b).

253

#### 254 **Why did IVSO evolve?**

255 Regarding the evolution of IVSO, one can ask several questions. 1. Which environmental  
256 factors lead to the evolution of IVSO? 2. How do environmental factors differ between the  
257 three described adaptive mechanisms? 3. Which life history traits are related to the evolution  
258 of IVSO?

259 IVSO may represent an adaptive response to spatio-temporal variation in  
260 environmental conditions (Table 1). Accordingly, stable social organizations can be expected  
261 in stable or predictable environments. Such social stability is beneficial because all forms of  
262 phenotypic plasticity have costs such as gathering the correct information to decide which  
263 phenotype to develop, costs of nervous system tissue to make fitness-enhancing decisions  
264 (e.g., dispersal vs. natal philopatry), the risk of developing the wrong phenotype, and the time  
265 cost to change (for reviews see (VanBuskirk & Steiner 2009; Auld et al. 2010; Piersma & Gils  
266 2011). To avoid these costs, having a stable social organization might be the optimal solution  
267 for species evolving in stable or predictable environments. However, if the costs and benefits  
268 of social stability differ between sexes (Ebensperger et al. 2016), inter-sexual conflict could  
269 facilitate changes in social organization within populations. IVSO might be expected in  
270 species that have large geographical ranges encompassing very different environments.  
271 Variation in ecological conditions between populations could lead to genetic differentiation  
272 affecting the social system and thus IVSO between populations. This could be the starting  
273 point of speciation (Meynard et al. 2012; Rymer et al. 2013; Nonaka et al. 2015).

274 Adaptive phenotypic plasticity within populations, including IVSO, can evolve in  
275 environments that are variable (Table 1). For an adaptive response to evolve, this variation

276 must be repeatable in different generations. For example, IVSO could evolve in environments  
 277 characterized by repeated, predictable environmental disrupters resulting in periods of high  
 278 and low availability of resources, such as periodic El Niño-Southern Oscillation (ENSO)  
 279 events (Zabel & Taggart 1989; Dickman et al. 2010). Any given ENSO cannot be predicted  
 280 precisely, but it is predictable that ENSO will occur again in the future. Thus, animals that  
 281 evolved in areas where ENSOs occur experience periodic but predictable variation, to which  
 282 IVSO could be an adaptation (Zabel & Taggart 1989; Dickman et al. 2010).

283 Variation in population density may drive IVSO as it influences the availability of  
 284 breeding territories (habitat saturation hypothesis: (Emlen 1982; Koenig et al. 1992). For  
 285 example, the social organization of striped mice in the Succulent Karoo is mainly dependent  
 286 on population density, with solitary living occurring in generations experiencing low  
 287 population density and communal breeding in generations experiencing high population  
 288 density (Schradin et al. 2010). Whether developmental plasticity or social flexibility evolves  
 289 in varying environments would then depend on the predictability of this variation. For  
 290 developmental plasticity, the environment in which an individual grows up must contain  
 291 reliable (predictable) information about the environment in which it will breed. In this case,  
 292 the individual could develop an alternative phenotype via developmental plasticity with the  
 293 highest reproductive success occurring in the future environment.

294 **Table 1**

295 Environmental conditions under which the four mechanisms leading to IVSO are predicted to  
 296 evolve. Predictability can occur within generations (i.e., early and later life of an individual)  
 297 or between generations (i.e., conditions experienced by adults and their offspring).

<b>Mechanisms for IVSO</b>	<b>Environmental conditions under which it is predicted to evolve</b>
Environmental disrupter	It is not an evolved trait but enforced and thus occurs in all environments
Genetic differentiation	Environmental variation between populations. Environment is predictable for the individual.
Developmental plasticity	Re-occurring variation within populations which the individuals can predict.
Social flexibility	Non-predictable but re-occurring variation within populations.

298

299           If the environment is not predictable but differs significantly from generation to  
300 generation, social flexibility enabling an adaptive response at a later life history stage and not  
301 during early development should evolve. Social flexibility offers the potential to respond  
302 immediately in a number of ways to changing environmental conditions. In most cases of  
303 developmental plasticity, such as a response to prevailing predation pressure (Steiner &  
304 Buskirk 2008; Lind et al. 2015), there is no or only a very short time lag between the reliable  
305 information and the fitness benefit of the alternative phenotype. In contrast, the time lag  
306 between the juvenile stage and the breeding stage is often much longer. This could explain  
307 why many examples exist of social flexibility explaining IVSO, but not for developmental  
308 plasticity (Schradin, 2013). We therefore predict that developmental plasticity as the  
309 mechanism for IVSO is most likely to occur in species where the juvenile and the breeding  
310 life history stage follow shortly after one another. For example, in common voles (*Microtus*  
311 *arvalis*), precocious fertile mating of non-weaned 14 days old females occurs (Tkadlec &  
312 Zejda 1995), being an extreme example of overlap between the juvenile and the breeding  
313 stage. Future studies will have to test whether developmental plasticity is the mechanism  
314 leading to IVSO in some species and whether this is related to a short time lag between  
315 development and reproduction. In sum, all three adaptive mechanisms leading to IVSO are  
316 predicted to have evolved as a response to environmental variation (Table 1).

317

### 318 **Testing predictions at the species level**

319           Testing for the adaptive value of IVSO requires a comparison of the fitness of  
320 individuals living in different types of social organizations under different environmental  
321 conditions. For example, male striped mice have alternative reproductive tactics, being either  
322 the breeding males of communally breeding groups (called breeding males) or solitary  
323 roamers attempting to copulate with females of several groups (Schradin et al. 2009). In

324 striped mice, IVSO occurs within populations. Striped mice of both sexes live solitarily when  
325 population density is low, but live in communally breeding groups when population density is  
326 high. However, solitary roaming males occur even under high population densities (because  
327 the sex ratio at birth is equal but there is only one breeding male per communal group), but  
328 have a lower body mass (= competitive ability) than breeding males (Schradin et al. 2009).  
329 Breeding males have 10 times higher reproductive success than roamers (Schradin &  
330 Lindholm 2011). However, when only roaming males occur, many of them have very high  
331 reproductive success (Schradin & Lindholm 2011). Importantly, under intermediate  
332 population density, males (and also females) can be solitary or group-living, and the  
333 reproductive success of roamers equals the reproductive success of breeding males (Schradin  
334 & Lindholm 2011). This indicates that IVSO in this species is the result of selection having  
335 acted on individuals to maximize reproductive success.

336         If adaptive IVSO has been identified in a species, the main expectation would be that  
337 the species showing IVSO lives in a variable environment (Table 1). In striped mice,  
338 population density is the main predictor of social organization, determining whether  
339 individuals live in groups or solitarily (Schradin et al. 2010; Schoepf & Schradin 2012).  
340 Population density is highly variable from year to year. This indicates that African striped  
341 mice live in a variable and unpredictable environment, favoring the evolution of social  
342 flexibility.

343         Statistically testing whether or not IVSO in a single species is due the variability in its  
344 environment can be challenging. If genetic differentiation has been identified as the  
345 mechanism of IVSO, one could measure selected environmental factors and compare these  
346 between populations with social organization type A with populations showing the different  
347 social organization type B. For this, an appropriate sample size is needed in the different  
348 populations showing the two forms of social organization. If the identified mechanism is

349 developmental plasticity, it could be shown statistically that the environmental factors are  
350 predictable for the individuals by doing autocorrelations or other time series analyses.

351 Social flexibility is characterized by environmental factors that are unpredictable, such  
352 that no significant autocorrelation of the factors determining social organization would be  
353 expected. For example, the population density experienced as juveniles would not predict  
354 (correlate with) the population density when the individual is breeding. Thus, the  
355 environmental factor measured at time<sub>(breeding-x)</sub> does not predict the same factor at time<sub>(breeding)</sub>,  
356 which would be the case if an identified cycle (for example 7 years) does not correspond with  
357 the life history cycle (e.g. 2 year) of a species, or if no cycles exist at all, indicating  
358 environmental unpredictability that results in non-significant statistical relationships. This  
359 would be statistically problematic as one would expect the null hypothesis to be true (the  
360 variable factor cannot be predicted). There are no tests demonstrating unpredictability, but  
361 there are statistical tools such as time series tests to detect structure in a dataset. This can be  
362 applied to a time series of environmental data and the absence of any signal at the time scales  
363 of the animal's lifetime would indicate that the variable is unpredictable for the individual of  
364 this study period. Potential methods include wavelet analysis which generates complementary  
365 wavelets with different periodicities to decompose data without gaps. The wavelets are then  
366 used to detect periodicity in the environmental time series at different time scales. Another  
367 approach is to use a test for autocorrelation (Moran's test, Portmanteau test's, Box-Pierce,  
368 Ljung-Box Q test) to detect a structure in the time series (Diggle 1990).

369

### 370 **Testing predictions in comparative studies**

371 The comparative method relies on large datasets of many species. Comparative studies  
372 could be used to establish whether variation in key environmental factors such as rainfall and  
373 food availability or life history are associated with the occurrence of IVSO over a large  
374 number of species. There are three important issues we want to address about how to improve

375 future comparative studies. First, despite evidence that IVSO has been observed in mammals  
376 (Dalerum 2007; Valomy et al. 2015; Garber et al. 2016; Mann & Karniski 2017), existing  
377 databases on the social organization of mammals and other taxa typically do not consider  
378 IVSO but assign one form of social organization to each species. Ignoring IVSO in  
379 comparative studies can lead to spurious conclusions about social evolution (Silvestro et al.  
380 2015; Sandel et al. 2016). For example, it was previously believed that social carnivores  
381 evolved from a solitary ancestor, but taking IVSO into account indicated that the ancestor  
382 might rather have been socially flexible (Dalerum 2007). Thus, it is crucial that IVSO is  
383 considered in comparative studies of factors influencing social diversity in animals.

384         Second, to achieve maximum taxonomic breadth, some databases are populated with  
385 information from the secondary literature and some data are based on the assumption that  
386 closely related species have the same form of social organization, even if only one species has  
387 been studied in detail. We advocate for a different approach in which scientists build a smaller  
388 dataset based on the most reliable information from the primary literature (Schradin 2017) and  
389 that includes IVSO (Valomy et al. 2015). Conclusions from comparative studies using high  
390 quality primary data can differ significantly from comparative studies of large databases of  
391 low quality data from the secondary and tertiary literature (Kappeler & Fichtel 2016). For  
392 example, one database for comparative studies included 90% (399/445) of Eulipotyphla in their  
393 dataset with >99% assigned a solitary social organization, often based on secondary literature  
394 (Lukas & Clutton-Brock 2013). In contrast, Valomy et al. (2015) using only primary literature  
395 determined that reliable information was only available for 16 species, of which 56% of  
396 species (n=9/16) were social (living in pairs or in groups). Interestingly, IVSO was found in 7  
397 Eulipotyphla species (Valomy et al. 2015). Detailed long-term studies can change our  
398 understanding animal social systems even in well studied taxa (Elbroch et al. 2017).  
399 Databases used in future comparative studies of IVSO and social evolution should be built  
400 from data collected from the primary literature and not include assumptions about the social

401 organization of an entire genus based on observations in a single or a few species (Schradin  
 402 2017). This will require that the social organizations of more species are studied in their  
 403 natural environment (Valomy et al. 2015; Schradin 2017).

404 Third, the next major challenge with comparative studies is the restriction of analyses  
 405 to adaptive forms of IVSO. This is difficult because environmental disrupters are a frequent  
 406 cause of non-adaptive IVSO. Thus, it would be beneficial if databases on the social  
 407 organization of a taxon do not only include whether IVSO occurs, but also whether it is  
 408 adaptive or non-adaptive. Unfortunately, this information is normally not available.

409

410 **Predictions about the factors favouring the evolution of adaptive IVSO**

411 **Table 2**

412 Predictions regarding IVSO to be tested in comparative studies.

<b>Hypothesis</b>	<b>Prediction &amp; mechanisms</b>
Non-adaptive	IVSO is more common in species that are typically characterised by one dominant breeding pair, indicating that environmental disrupters (death of one dominant breeder) cause the observed variation.
Benefits under environmental heterogeneity	IVSO occurs more frequently in species that occur in areas of the world characterized by high inter-annual (among) year variation (coefficient of variation) in rainfall and ambient temperature. This can for example induce significant variation in population density and thus competition for reproduction (and resources).  A positive relationship between IVSO and increasing diet breadth and greater IVSO is expected in species found in regions with high within-year and inter-annual variation in rainfall and food availability.
Benefits to short lived species	IVSO is more common in species with a short lifespan and that breed only for one breeding season; these species are selected to respond optimally to the prevailing environmental situation.
Responsiveness to changing environments over a long lifetime	IVSO is greater in species with long lifespans and that reproduce during multiple years than species with short lifespans and that do not produce offspring during multiple breeding seasons and that IVSO is positively associated with habitat breadth.

413

414 The main prediction is that environmental factors important for fitness vary more in species  
415 with than without IVSO (Table 2). Important factors are variation in rainfall and food  
416 availability, which influence population density. Population density in combination with  
417 resource availability can influence both the degree of competition within populations and the  
418 extent to which ecological constraints limit reproductive and social options (Emlen 1982;  
419 Koenig et al. 1992; Schradin 2013). Other environmental factors such as ambient temperature  
420 and changes in predation pressure or parasite / infectious disease prevalence could also be  
421 important for the evolution of IVSO.

422         The adaptive value of IVSO may depend on both environmental conditions and life  
423 history (Table 2). This is expected when environmental variation has different effects on long-  
424 lived versus short-lived species and those with many versus few breeding attempts during a  
425 lifetime. Short-lived species will experience less environmental variation during a lifetime  
426 and thus must breed in the prevailing environment rather than wait to breed until the  
427 environmental conditions have improved. If an individual of a short-lived species chooses a  
428 reproductive and social tactic that leads to a comparatively low reproductive success during  
429 its only breeding opportunity, its lifetime reproductive success will be below average. In  
430 contrast, an individual of a long-lived species that breeds during many breeding seasons can  
431 have a relatively high lifetime reproductive success even if its tactic leads to low success in  
432 one breeding season. As an extreme example, consider a reproductive tactic that leads to very  
433 high reproductive success during years in which multiple preferred foods are abundant but to  
434 no reproductive success in years when food availability is restricted. In a long-lived species  
435 where individuals breed in many years, this reproductive tactic could still be advantageous.  
436 However, in a short-lived species where every generation breeds for only one year and is then  
437 replaced by the next generation, individuals with this reproductive tactic would die without  
438 having reproduced, resulting in a shift in the frequency of an alternative tactic. In sum, we  
439 predict that IVSO is more likely to evolve in short-lived species, particularly species where

440 individuals only breed during one single breeding season. This prediction should be compared  
441 to the alternative prediction: long-lived species from heterogeneous environments evolved  
442 IVSO as a tactic to cope with inter-annual variation in environmental conditions, thereby  
443 using the best strategy for current conditions, while short-lived species are constrained to one  
444 social tactic (Table 2).

445

## 446 **Conclusions**

447 The fact that a species shows IVSO is no evidence that it is an evolved trait of this species.  
448 Environmental disrupters can be expected to cause IVSO even in species where IVSO is also  
449 an adaptive response (Hill et al. 2015a; Hill et al. 2015b). Adaptive IVSO is expected to have  
450 evolved in variable environments. To understand IVSO at the species level it is important to  
451 conduct continuous long-term studies to differentiate between non-adaptive and adaptive  
452 IVSO. In addition, it is necessary to measure variation in the environment, and statistical tools  
453 such as time series analyses can be used test for structure in the data. One problem is that such  
454 statistical analyses mainly demonstrate significant relationships such as cycles, but not non-  
455 existing cycles, which would represent unpredictability. Thus, unpredictability is difficult to  
456 demonstrate statistically, but an important factor for the evolution of social flexibility causing  
457 IVSO.

458 IVSO is an important consideration when studying social evolution (evolution of  
459 monogamy, cooperative breeding, paternal care, group versus solitary living), as not every  
460 species can be assigned to one single form of social organization (Lott 1984; Lott 1991). For  
461 such comparative studies, it is important to have reliable data based on the primary literature.  
462 IVSO is an interesting phenomenon that needs scientific explanation. Understanding IVSO is  
463 important because it demonstrates species resilience against environmental change and it can  
464 help us to study ultimate and proximate reasons of group-living by comparing between  
465 solitary and group-living individuals in a single species (Schradin et al. 2012). Finally, social

466 organization can influence both social structure and mating system, but does not determine  
467 these. Thus, once adaptive IVSO has been identified, future studies should investigate its  
468 effects on social structure and mating system.

469

#### 470 **Acknowledgments**

471 CS is thankful to Gustl Anzenberger who made him aware of the important mechanism of  
472 environmental disruptor leading to non-adaptive IVSO. Studies in IVSO by CS were  
473 supported by the Swiss National Science Foundation, the University of Zurich, Vontobel  
474 Foundation, the Holcim Foundation, the Baumgarten Stiftung, the Helene-Bieber Fonds, the  
475 University of Strasbourg Institute of Advanced Studies (USIAS) and the CNRS. LDH was  
476 supported by National Science Foundation grant no. 1261026, a Summer Faculty Fellow  
477 from the University of Tennessee at Chattanooga, and USIAS Visiting Scholar program.

478

#### 479 **Literature cited**

- 480 Auld, J. R., Agrawal, A. A. & Relyea, R. A. 2010: Re-evaluating the costs and limits of  
481 adaptive phenotypic plasticity. *Proc. R. Soc. B-Biol. Sci.* **277**, 503-511.
- 482 Bendesky, A., Kwon, Y.-M., Lassance, J.-M., Lewarch, C. L., Yao, S., Peterson, B. K., He, M.  
483 X., Dulac, C. & Hoekstra, H. E. 2017: The genetic basis of parental care evolution in  
484 monogamous mice. *Nature* **544**, 434-439.
- 485 Berry, R. J., Tattersall, F. H. & Hurst, J. 2008: Genus *Mus*. In: *Mammals of the British Isles*  
486 *Handbook*, 4th edn. (Harris, S. & Yalden, D. W., eds). The Mammal Society,  
487 Southampton, U.K.
- 488 Burke, T., Davies, N. B., Bruford, M. W. & Hatchwell, B. J. 1989: Parental care and mating  
489 behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA  
490 fingerprinting. *Nature* **338**, 249-250.
- 491 Dalerum, F. 2007: Phylogenetic reconstruction of carnivore social organizations. *Journal of*  
492 *Zoology* **273**, 90-97.
- 493 Davies, N. B. 1992: *Dunnock Behaviour and Social Evolution*. Oxford University Press,  
494 Oxford.
- 495 Davies, N. B., Hartley, I. R., Hatchwell, B. J. & Langmore, N. E. 1996: Female control of  
496 copulations to maximize male help: a comparison of polygynandrous alpine accentors,  
497 *Prunella collaris*, and dunnocks, *P. modularis*. *Animal Behaviour* **51**, 27-47.
- 498 Dickman, C. R., Greenville, A. C., Beh, C.-L., Tamayo, B. & Wardle, G. M. 2010: Social  
499 organization and movements of desert rodents during population “booms” and “busts”  
500 in central Australia. *J. Mammal.* **91**, 798-810.
- 501 Diggle, P. J. 1990: *Time Series, A Biostatistical Introduction*. Clarendon Press, Oxford.

502 Dochtermann, N. A., Schwab, T. & Sih, A. 2015: The contribution of additive genetic  
503 variation to personality variation: heritability of personality. *Proceedings of the Royal*  
504 *Society B: Biological Sciences* **282**.

505 Ebensperger, L. A., Correa, L. A., León, C., Ramírez-Estrada, J., Abades, S., Villegas, Á. &  
506 Hayes, L. D. 2016: The modulating role of group stability on fitness effects of group  
507 size is different in females and males of a communally rearing rodent. *Journal of*  
508 *Animal Ecology* **85**, 1502-1515.

509 Eggert, A.-K. 1992: Alternative male mate-finding tactics in burying beetles. *Behav Ecol* **3**,  
510 243-254.

511 Elbroch, L. M., Levy, M., Lubell, M., Quigley, H. & Caragiulo, A. 2017: Adaptive social  
512 strategies in a solitary carnivore. *Science Advances* **3**.

513 Emlen, S. T. 1982: The evolution of helping. I. An ecological constraints model. *Am Nat* **119**,  
514 29-39.

515 Garber, P. A. 1997: One for all and breeding for one: cooperation and competition as a  
516 tamarin reproductive strategy. *Evol Anthropol* **3**, 187-199.

517 Garber, P. A., Porter, L. M., Spross, J. & Di Fiore, A. 2016: Tamarins: Insights into  
518 monogamous and non-monogamous single female social and breeding systems. *Am. J.*  
519 *Primatol.* **78**, 298-314.

520 Gotzek, D. & Ross, K. G. 2007: Genetic regulation of colony social organization in fire ants:  
521 An integrative overview. *Quarterly Review of Biology* **82**, 201-226.

522 -. 2009: Current Status of a Model System: The Gene Gp-9 and Its Association with Social  
523 Organization in Fire Ants. *PLOS ONE* **4**.

524 Hayes, L. D. & Schradin, C. 2017: Long-term field studies in mammals: what the short-term  
525 study cannot tell us. *J Mammal.*

526 Hill, D. L., Pillay, N. & Schradin, C. 2015a: Alternative reproductive tactics in female striped  
527 mice: heavier females are more likely to breed solitarily than communally. *Journal of*  
528 *Animal Ecology* **84**, 1497-1508.

529 -. 2015b: Alternative reproductive tactics in female striped mice: Solitary breeders have lower  
530 corticosterone levels than communal breeders. *Horm. Behav.* **71**, 1-9.

531 Hofmann, H. A., Beery, A. K., Blumstein, D. T., Couzin, I. D., Earley, R. L., Hayes, L. D.,  
532 Hurd, P. L., Lacey, E. A., Phelps, S. M., Solomon, N. G., Taborsky, M., Young, L. J.,  
533 Rubenstein, D. R., Nescent Working Group on Integrative Models of Vertebrate  
534 Sociality: Evolution, M. & Emergent, P. 2014: An evolutionary framework for  
535 studying mechanisms of social behavior. *Trends in Ecology & Evolution* **29**, 581-589.

536 Hu, C. K. & Hoekstra, H. E. 2017: *Peromyscus* burrowing: A model system for behavioral  
537 evolution. *Seminars in Cell and Developmental Biology* **61**, 107-114.

538 Judge, P. G. 2000: Coping with crowded conditions. In: *Natural conflict resolution*. (Aureli, F.  
539 & De Waal, F., eds). University of California Press.

540 Kappeler, P. M. & Fichtel, C. 2016: The evolution of eulemur social organization.  
541 *International Journal of Primatology* **37**, 10-28.

542 Kappeler, P. M. & Schaik, C. P. v. 2002: Evolution of primate social systems. *Int J Primatol*  
543 **23**, 707-740.

544 Keller, L. 2009: Adaptation and the genetics of social behaviour. *Philos. Trans. R. Soc. Lond.*  
545 *B. Biol. Sci.* **364**, 3209-3216.

546 Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. & Stanback, M. T. 1992: The  
547 evolution of delayed dispersal in cooperative breeders. *Quart Rev Biol* **67**, 111-150.

548 Latham, N. & Mason, G. 2004: From house mouse to mouse house: the behavioural biology  
549 of free-living *Mus musculus* and its implications in the laboratory. *Applied Animal*  
550 *Behaviour Science* **86**, 261-289.

- 551 Lind, M. I., Yarlett, K., Reger, J., Carter, M. J. & Beckerman, A. P. 2015: The alignment  
552 between phenotypic plasticity, the major axis of genetic variation and the response to  
553 selection. *Proceedings of the Royal Society of London B: Biological Sciences* **282**.
- 554 Lott, D. F. 1984: Intraspecific variation in the social systems of wild vertebrates. *Behaviour*  
555 **88**, 266-325.
- 556 -. 1991: *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge  
557 University Press, New York.
- 558 Löttker, P., Huck, M., Zinner, D. P. & Heymann, E. W. 2007: Grooming relationships  
559 between breeding females and adult group members in cooperatively breeding  
560 moustached tamarins (*Saguinus mystax*). *Am. J. Primatol.* **69**, 1159-1172.
- 561 Lukas, D. & Clutton-Brock, T. H. 2013: The evolution of social monogamy in mammals.  
562 *Science* **341**, 526-530.
- 563 Mann, J. & Karniski, C. 2017: Diving beneath the surface: long-term studies of dolphins and  
564 whales. *J. Mammal.* **98**, 621-630.
- 565 Markham, A. C. & Gesquiere, L. R. 2017: Costs and benefits of group living in primates: an  
566 energetic perspective. *Philosophical Transactions of the Royal Society B: Biological*  
567 *Sciences* **372**.
- 568 Martins, M. M., Nascimento, A. T., Nali, C., Velastin, G. O., Mangini, P. B., Valladares-  
569 Padua, C. B. & Galetti Jr, P. M. 2015: A test for sex-biased dispersal in the black-  
570 faced lion tamarin (*Leontopithecus caissara*): inferences from microsatellite markers.  
571 *Studies on Neotropical Fauna and Environment* **50**, 14-20.
- 572 Mayer, M., Künzel, F., Zedrosser, A. & Rosell, F. 2017: The 7-year itch: non-adaptive mate  
573 change in the Eurasian beaver. *Behav Ecol Sociobiol* **71**, 32.
- 574 Meynard, C. N., Pillay, N., Perrigault, M., Caminade, P. & Ganem, G. 2012: Evidence of  
575 environmental niche differentiation in the striped mouse (*Rhabdomys sp.*): inference  
576 from its current distribution in southern Africa. *Ecology and Evolution* **2**, 1008-1023.
- 577 Milleret, C., Wabakken, P., Liberg, O., Åkesson, M., Flagstad, Ø., Andreassen, H. P. & Sand,  
578 H. 2017: Let's stay together? Intrinsic and extrinsic factors involved in pair bond  
579 dissolution in a recolonizing wolf population. *Journal of Animal Ecology* **86**, 43-54.
- 580 Müller, J. F., Braunisch, V., Hwang, W. & Eggert, A.-K. 2006: Alternative tactics and  
581 individual reproductive success in natural associations of the burying beetle,  
582 *Nicrophorus vespilloides*. *Behav Ecol* **18**, 196-203.
- 583 Nonaka, E., Svanbäck, R., Thibert-Plante, X., Englund, G. & Brännström, Å. 2015:  
584 Mechanisms by which phenotypic plasticity affects adaptive divergence and  
585 ecological speciation. *The American Naturalist* **186**, E126-E143.
- 586 Ometto, L., Shoemaker, D., Ross, K. G. & Keller, L. 2011: Evolution of Gene Expression in  
587 Fire Ants: The Effects of Developmental Stage, Caste, and Species. *Mol. Biol. Evol.*  
588 **28**, 1381-1392.
- 589 Phoenix, C. H., Goy, R. W., Gerall, A. A. & Young, W. C. 1959: Organizing action of  
590 prenatally administered testosterone propionate on the tissue mediating mating  
591 behavior in the female guinea pig. *Endocrinology* **65**, 369-382.
- 592 Piersma, T. & Drent, J. 2003: Phenotypic flexibility and the evolution of organismal design.  
593 *Trends in Ecology & Evolution* **18**, 228-233.
- 594 Piersma, T. & Gils, J. A. v. 2011: *The flexible Phenotype*. Oxford University Press, Oxford.
- 595 Porter, L. M., Hanson, A. M. & Bercera, E. N. 2001: Group demographics and dispersal in a  
596 wild group of Goeldi's monkeys (*Callimico goeldii*). *Folia Primatol* **72**, 108-110.
- 597 Randall, J. A., Rogovin, K., Parker, P. G. & Eimes, J. A. 2005: Flexible social structure of a  
598 desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints.  
599 *Behav Ecol* **16**, 961-973.
- 600 Reyer, H.-U. 1984: Investment and relatedness: a cost/benefit analysis of breeding and  
601 helping in the pied kingfisher (*Ceryle rudis*). *Anim. Behav.* **32**, 1163-1178.

- 602 Reyer, H. U. 1980: Flexible helper structure as an ecological adaptation in the pied kingfisher  
603 (*Ceryle rudis rudis* L.). Behav Ecol Sociobiol **6**, 219-227.
- 604 Rymer, T., Pillay, N. & Schradin, C. 2013: Extinction or survival? Behavioral flexibility in  
605 response to environmental change in the African striped mouse *Rhabdomys*.  
606 Sustainability **5**, 163-186.
- 607 Sandel, A. A., Miller, J. A., Mitani, J. C., Nunn, C. L., Patterson, S. K. & Garamszegi, L. Z.  
608 2016: Assessing sources of error in comparative analyses of primate behavior:  
609 Intraspecific variation in group size and the social brain hypothesis. Journal of Human  
610 Evolution **94**, 126-133.
- 611 Schoepf, I. & Schradin, C. 2012: Better off alone! Reproductive competition and ecological  
612 constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*).  
613 Journal of Animal Ecology **81**, 649-656.
- 614 Schradin, C. 2013: Intraspecific variation in social organization by genetic variation,  
615 developmental plasticity, social flexibility or entirely extrinsic factors. Philos. Trans.  
616 R. Soc. B-Biol. Sci. **368**.
- 617 Schradin, C. 2017: Comparative studies need to rely both on sound natural history data and on  
618 excellent statistical analysis. R. Soc. Open Sci. .
- 619 Schradin, C. & Hayes, L. D. 2017: A synopsis of long-term field studies in mammals:  
620 achievements, future directions, and some advice J Mammal.
- 621 Schradin, C., König, B. & Pillay, N. 2010: Reproductive competition favours solitary living  
622 while ecological constraints impose group-living in African striped mice. Journal of  
623 Animal Ecology **79**, 515-521.
- 624 Schradin, C. & Lindholm, A. K. 2011: Relative fitness of alternative male reproductive tactics  
625 in a mammal varies between years. Journal of Animal Ecology **80**, 908-917.
- 626 Schradin, C., Lindholm, A. K., Johannesen, J., Schoepf, I., Yuen, C.-H., König, B. & Pillay,  
627 N. 2012: Social flexibility and social evolution in mammals: a case study of the  
628 African striped mouse (*Rhabdomys pumilio*). Molecular Ecology **21**, 541-553.
- 629 Schradin, C., Scantlebury, M., Pillay, N. & König, B. 2009: Testosterone levels in dominant  
630 sociable males are lower than in solitary roamers: physiological differences between  
631 three male reproductive tactics in a sociably flexible mammal. Am Nat **173**, 376-388.
- 632 Shultz, S., Opie, C. & Atkinson, Q. D. 2011: Stepwise evolution of stable sociality in  
633 primates. Nature **479**, 219-222.
- 634 Silvestro, D., Kostikova, A., Litsios, G., Pearman, P. & Salamin, N. 2015: Measurement  
635 errors should always be incorporated in phylogenetic comparative analysis. Methods  
636 of Ecol Evol **6**, 340-346.
- 637 Steiner, U. K. & Buskirk, J. V. 2008: Environmental stress and the costs of whole-organism  
638 phenotypic plasticity in tadpoles. J. Evol. Biol **21**, 97- 103.
- 639 Tinbergen, N. 1963: On aims and methods of ethology. Z Tierpsychol **20**, 410-433.
- 640 Tkadlec, E. & Zejda, J. 1995: Precocious Breeding in Female Common Voles and Its  
641 Relevance to Rodent Fluctuations. Oikos **73**, 231-236.
- 642 Valomy, M., Hayes, L. D. & Schradin, C. 2015: Social organization in Eulipotyphla: evidence  
643 for a social shrew. Biology Letters **11**.
- 644 VanBuskirk, J. & Steiner, U. K. 2009: The fitness costs of developmental canalization and  
645 plasticity. J. Evol. Biol **22**, 852- 860.
- 646 West-Eberhard, M. J. 2003: Developmental Plasticity and Evolution. Oxford University Press,  
647 Oxford.
- 648 Zabel, C. J. & Taggart, S. J. 1989: Shift in red fox, *Vulpes vulpes*, mating system associated  
649 with El Niño in the Bering Sea. Animal Behaviour **38**, 830-838.
- 650 Zimmermann, T. D., Kaiser, S., Hennessy, M. B. & Sachser, N. 2017: Adaptive shaping of  
651 the behavioural and neuroendocrine phenotype during adolescence. Proceedings of the  
652 Royal Society B: Biological Sciences **284**.

653  
654