



# Social flexibility and environmental unpredictability in African striped mice

Carsten Schradin<sup>1,2</sup> · Neville Pillay<sup>2</sup> · Cleo Bertelsmeier<sup>3</sup>

Received: 8 November 2018 / Revised: 27 May 2019 / Accepted: 31 May 2019  
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## Abstract

The resilience of an individual to environmental change depends on its ability to respond adaptively. Phenotypic flexibility, i.e., reversible phenotypic plasticity, is such an adaptive response, which has been predicted to evolve in unpredictable environments. We present data on the environmental predictability for 17 generations of socially flexible African striped mice *Rhabdomys pumilio*, which can switch from group living to solitary living and back to group living. Population density during the breeding season is the main predictor of social organization in striped mice, which become solitary breeding when population density is low and plural breeding when population density is high. Using time series analysis, we could not reject randomness for the variation in population density and found a 6-year cycle for food availability. However, food availability when individual females grew up did not predict the environmental conditions during which they bred in the next year, their only breeding season. Group size was predictable and most females bred plurally in communal groups. However, single breeding is the preferred tactic to avoid infanticide but for single breeding females, it was not predictable from the environment in which they grew up whether they would become single breeders in the next breeding season. Our study indicates unpredictability in the factors most important for determining the optimal breeding tactics for 322 female striped mice. In sum, striped mice exhibit social flexibility in an unpredictable environment, making it an adaptive trait.

## Significance statement

It has long been assumed that the evolution of different forms of sociality depends on the environment. Social flexibility, i.e., the ability of individuals to switch from group living to solitary living and back to group living, has been predicted to be an adaptation to unpredictable environments. However, the extent to which unpredictability influences sociality has never been studied previously. For female African striped mice, population density is the main factor determining whether they live alone or in groups. Here, we show that females cannot predict from the population density under which they grew up the population density under which they will reproduce, making social flexibility adaptive.

**Keywords** Phenotypic flexibility · Phenotypic plasticity · Intra-specific variation in social organization · Alternative reproductive tactic

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Communicated by E. Korpimäki

✉ Carsten Schradin  
carsten.schradin@iphc.cnrs.fr

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

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

<sup>3</sup> Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

## Introduction

While current anthropogenic environmental change happens faster than genetic adaptation in most species (IPCC 2014; Rymer et al. 2016), phenotypic plasticity might provide a quick adaptive response to such rapid change (Piersma and Drent 2003; West-Eberhard 2003; Ashander et al. 2016; Maille and Schradin 2016; Rymer et al. 2016). Two forms of phenotypic plasticity have been described (Piersma and Drent 2003): non-reversible developmental plasticity occurs when one of several alternative developmental pathways occurs early in life, determining the adult phenotype, and reversible phenotypic

plasticity, also called flexibility, occurs when the phenotype changes as a response to environmental change, changing back and forth depending on prevailing environmental conditions. The two different forms of phenotypic plasticity might represent adaptations to different environments.

If the environment is variable but predictable for an individual, developmental plasticity allows individuals to develop a specific phenotype during ontogeny that is adaptive in the future environment. A well-studied example is plasticity in tadpoles (*Rana temporaria*), which have been found to change both morphologically and behaviorally to the presence of specific predators (Steiner and Buskirk 2008). Developmental plasticity is not reversible, since one of several alternative ontogenetic pathways occurs depending on specific environmental cues. If the environment is variable but not predictable, reversible phenotypic flexibility has been predicted to evolve. An example is the reversible morphological change in the digestive tract of snakes after food uptake (Lignot et al. 2005). Phenotypic plasticity is predicted to evolve in variable environments, and the degree of predictability might determine whether this plasticity is fixed or flexible. Although this argument has received a lot of theoretical attention (Steiner and Buskirk 2008; Piersma and van Gils 2011; Schradin 2013), few empirical studies have tested this prediction.

Many behaviors represent plastic phenotypic traits. Permanent organizational effects during development can non-reversibly modify social behavior, such as aggression and parental care, while reversible activational effects can produce flexible behaviors (Phoenix et al. 1959; Wallen 2009; Blumstein et al. 2010). Plasticity in social behavior can lead to intra-specific variation in social organization (Schradin 2013).

Social flexibility describes a phenomenon where the social system of an entire population can change reversibly as individuals of both sexes change their reproductive and social tactics in response to environmental change (Schradin et al. 2012). Social flexibility occurs in several species, including burying beetles (*Nicrophorus vespilloides*) (Müller et al. 2006), pied kingfishers (*Ceryle rudis*) (Reyer 1980, 1984), dunnocks (*Prunella modularis*) (Davies 1992), and house mice (*Mus musculus*) (Latham and Mason 2004; Berry et al. 2008). It has been hypothesized that social flexibility evolved to cope with unpredictable environmental change (Schradin et al. 2012, 2018; Schradin 2013).

Variation in population density can drive changes in social organization because it influences the availability of breeding territories (Koenig and Pitelka 1981; Emlen 1982). Population density has been associated with variation in social organization in several small mammal species (Latham and Mason 2004; Randall et al. 2005; Lucia et al. 2008; Schradin et al. 2010). Whether developmental plasticity or social flexibility evolves in varying environments depends on the predictability

of variation in population density. For developmental plasticity, the environment in which an individual grows up would have to contain reliable and predictable information for the individual about the future population density (Piersma and Drent 2003). In this case, the individual could develop an alternative phenotype via developmental plasticity leading to the highest possible reproductive success in the future environment. If the population density is not predictable, social flexibility could evolve to offer an immediate response to changing environmental conditions (Schradin et al. 2018). Environmental variability has been identified as an important factor for social evolution (Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2017) but the predictability of variation for the individual has not been investigated. While it is known that variation in social organization occurs in variable environments (Latham and Mason 2004; Randall et al. 2005; Lucia et al. 2008; Schradin et al. 2010), it is not known whether or not this variability is predictable, possibly because it is statistically impossible to demonstrate unpredictability. One can search for patterns in a time series using different tests to reject the null hypothesis of randomness. If all of these tests fail, such that no predictability is found in the used dataset, unpredictability of the measured variable for the given study period is a parsimonious explanation.

The African striped mouse (*Rhabdomys pumilio*) is well known for its social flexibility (Schradin et al. 2012). Striped mice breed during the austral spring. Male and female offspring remain in their natal group throughout the following summer dry season, during which all of the previous breeders typically disappear. During the subsequent spring, individuals of both sexes can either live solitarily, in pairs, or in groups consisting of one breeding male and up to four breeding females (Schradin and Pillay 2004). Females prefer single breeding (i.e., solitary or pair living) over communal breeding (two or more breeding females in a group) because it enables them to avoid reproductive competition in the form of female-female aggression and female infanticide (Schradin et al. 2010). The singly breeding tactic is possible only when population density is low and suitable territories are available (Schoepf and Schradin 2012) while plural (communal) breeding is the optimal tactic when population density is high and it is impossible for most females to occupy a territory alone (Schradin et al. 2010). Population density is mainly influenced by food availability (Nater et al. 2018) and by predation pressure (Vuarin et al. 2019). These studies indicate that variation in environmental conditions, especially population density (i.e., availability of free territories for solitary breeding), makes social flexibility adaptive.

Here, we tested the hypothesis that social flexibility in striped mice occurs in a highly variable and unpredictable environment. We focused on females, whose reproductive tactics determine male tactics (Schradin et al. 2010). For this, we assessed whether population density, food availability, and

group composition (number of breeding females) that female striped mice experienced when growing up (first spring of their life) predicted the environmental and social conditions in which they bred (second—and the last—spring of their life). Additionally, we assessed whether the social conditions under which single breeding females had grown up were different to those of plural breeding females.

## Methods

### Study area and study period

The study was conducted in Goegap Nature Reserve in South Africa (S 29 41.56, E 18 1.60). Goegap lies within the semi-desert biome of the Succulent Karoo, which is characterized by cold and moist winters followed by spring with high food abundance and hot dry summers with low food abundance. The landscape is dominated by short-lived ephemerals in spring and by long-lived succulent shrubs. Trapping and behavioral data were collected from September 2001 to September 2017, and plant survey data from September 2005 to September 2017.

### Study species

The striped mouse is an omnivorous annual species: they are born in one spring, then have to survive the following dry summer, before reproducing in the following spring, with less than 1% of striped mice surviving to reproduce in a second spring (Schradin et al. 2012). There are thus three major live history phases: (1) pups and juveniles in spring (September–December), (2) young adults that need to survive the dry season (January–April) and cold moist winter (May–July), to become (3) breeders in the following breeding season in spring (August to November), when females have 2–3 litters. Long-distance dispersal is male-biased but also occurs in females (Solmsen et al. 2011). Females regularly immigrate into our study area although most of the study females originate from our study population. Females typically stay with their natal group from birth until the next breeding season. If population density is low, the largest females can leave their group and start solitary breeding (Hill et al. 2015a, 2015b). For this, they typically disperse to an unoccupied nest at the edge of the group territory and occupy a part of the former group territory and additional surrounding areas. They might also travel as far as several hundred meters into areas that do not provide food and cover in the dry season, but which become covered by vegetation that provides food after the winter rains (Schradin and Pillay 2006).

### Determination of reproductive tactic (single versus plural breeding)

We permanently monitor our study populations, trapping each group at their nest for three consecutive days, once or twice per month, doing direct behavioral observations for two consecutive days once or twice per month, and radio-tracking at least one individual per group 5 days a week. Juveniles are trapped and individually marked soon after they left the nest for the first time, such that we know the natal group of individuals. Reproductive tactics were determined by a combination of trapping, behavioral observations, and radio-tracking (Schradin et al. 2009; Schradin and Yuen 2011). Trapped striped mice were weighed, sexed, and permanently marked with ear tags (8 mm long, 2.4 mm wide, National Band and Tag Co., USA) and temporarily with hair dye (Inecto Rapido, Pinetown, South Africa) for individual recognition during behavioral observations (Schradin and Pillay 2005, 2006). All solitary-living and most group-living females were fitted with radio collars (Holohil, Canada) and were radio-tracked to determine their sleeping site locations (Schradin and Pillay 2005; Schradin and Pillay 2006). In total, 318 out of 414 females carried a radio collar weighing between 2 and 4 g, typically not more than 5% of an individual's body mass. Individuals were radio-tracked once per day during the activity period and once at night, to determine sleeping sites. The natal group was determined by trapping striped mice there as juveniles (body mass < 30 g) and them being trapped there subsequently. Females which showed signs of breeding (lactating, open vagina, and loss of body mass indicating parturition, or high body mass indicating pregnancy) were regarded as breeding females. Breeding females that remained in a group with at least one more breeding female at the start of the breeding season in September were regarded as plural breeders, while solitary and pair-living females were regarded as single breeders (Hayes 2000). It was not possible to record data using a blind protocol because our study involved focal animals in the field.

### Estimating population density

Population density was calculated as the number of adult mice/size of the study area in hectares (Table 1). Population density was calculated for September of every year, representing the start of the breeding season. Juveniles born in August or September were not considered, since they were not competing for breeding or territories with the adult female striped mice of our study.

### Plant surveys

Striped mice feed on several plant species (Schradin and Pillay 2006). Plant surveys were carried out on the 15th of

**Table 1** Data for the reproductive tactic and the conditions under which females reproduced

Year	Size study area (ha)	Population density (mice/ha)	<i>N</i> of singly breeding females	<i>N</i> of plural breeding females
2003	16.0	1.5	12	0
2004	9.7	3.2	4	12
2005	6.7	19.0	1	10
2006	6.9	30.5	1	38
2007	9.9	6.5	10	18
2008	9.7	5.5	5	29
2009	6.6	15.7	4	36
2010	5.6	8.3	5	20
2011	13.2	5.7	6	27
2012	6.8	18.9	4	52
2013	5.5	11.2	9	15
2014	6.8	9.7	7	32
2015	7.0	7.6	2	20
2016	10.1	6./	5	11
2017	6.5	4.8	4	10
Total			79	330

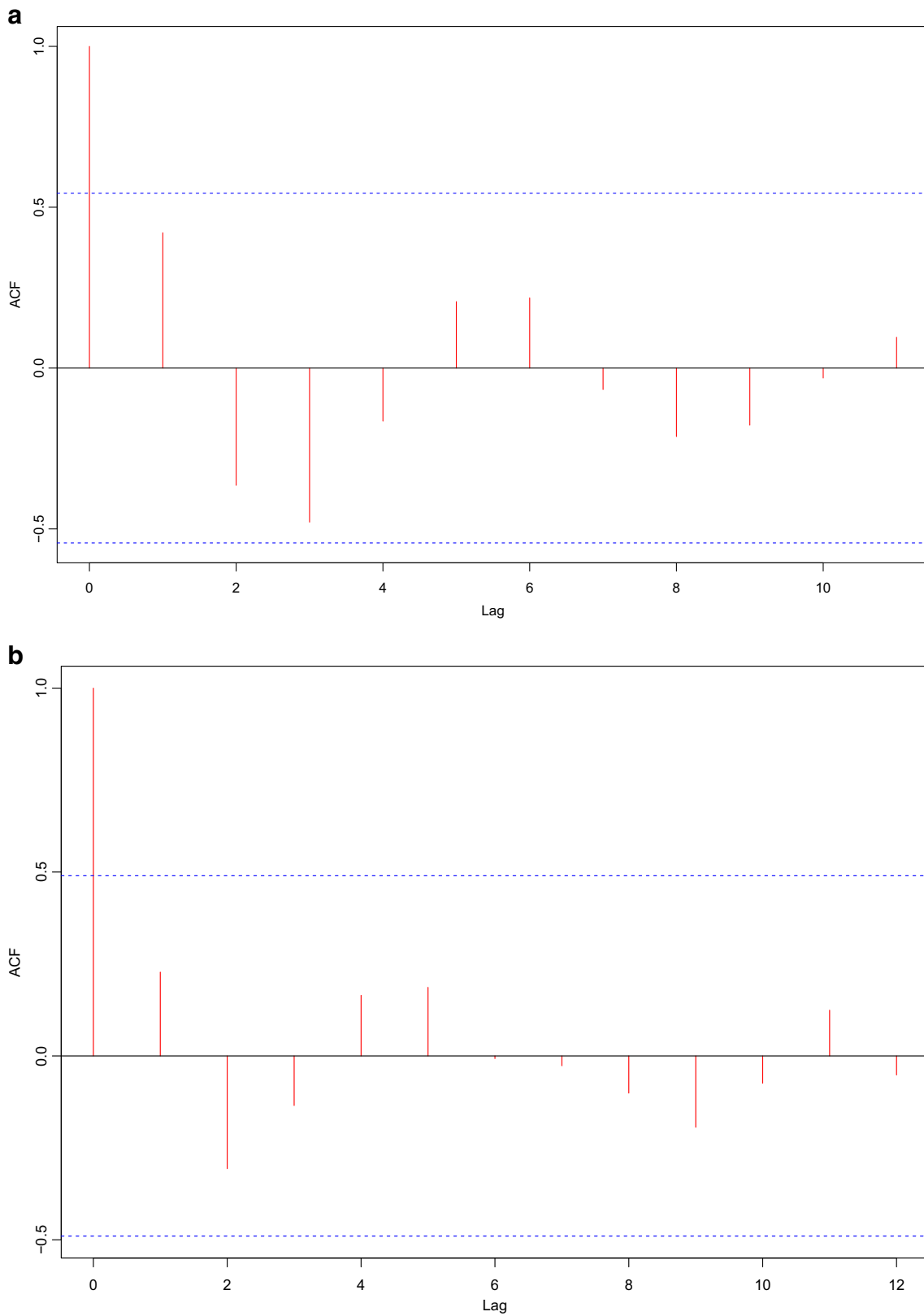
each month on eight monitoring plots located within the home ranges of eight different striped mouse groups. Each plot covered an area of  $2 \times 2$  m and was sampled using standard protocols (Braun-Blanquet method; Werger 1974), previously employed in other striped mouse studies (Keller and Schradin 2008; Schradin et al. 2014). Briefly, the number and palatability of each food plant contained within each monitoring plot were recorded, and we took the means of the eight plots for September of each year, representing the start of the breeding season. For the summer dry season, we calculated the mean from January to April.

## Data analysis

Population density data were available for the 17 generations living from 2001 to 2017. Plant survey data were available for 13 generations from 2005 to 2017. Data for the reproductive tactic were available for 409 females from 15 generations (2003–2017; Table 1), and the social conditions under which females grew up and later reproduced were available for 322 of them; the remaining females were either immigrants or not studied previously since we had to enlarge the field site in years of low population density. The size of the study area changed from year to year depending on population density, such that enough groups were monitored (Table 1).

To test whether the time series data (Diggle 1990) of food availability, population density, and percentage of single breeding females deviated from random, we performed a two-sided non-parametric turning point test of randomness using the function `turning.point.test` in the R package `randtests` test (Mateus and Caeiro 2013). Additionally, we

tested for a spatial structure in the time series using Moran's *I* test and Geary's *C* randomization test (Thioulouse et al. 1995), with the function `gearymoran` in the R package `ade4`. To visualize the structure in the time series data and to test for temporal autocorrelation at different scales (time lags), we estimated the autocorrelation function using the function `afc..` Refining the findings of the ACF, we computed a periodogram to identify any intrinsic periodic signals in the time series data. We first computed a series of eigenvectors based on the neighborhood between the 17 data points of the time series on a circular neighboring graph, using the function `orthobasis.circ(17)` in the `ade4` R package (Dray and Dufour 2007). Then, we decomposed the variance of the variable (yearly food availability or population density) using a linear polynomial regression on these eigenvectors. For the social data, we used a paired approach, since for each female, we had data about its group composition both for when it grew up and when it bred. Thus, we performed Spearman correlations and compared ratios using Fisher's exact test. To test whether the single breeding tactic depends on population density, we correlated the percentage of single breeding females in September with population density for the years 2003–2017. A subset of these data, the years 2003–2009, was already used for a similar analyses in a previous study (Schradin et al. 2010), which was replicated here using a larger dataset (2003–2017). Single breeding is the preferred tactic by females if environmental conditions allow them to occupy a territory on their own to avoid reproductive competition within plural breeding groups (Schradin et al. 2010; Schoepf and Schradin 2012). We tested whether the group composition in which single breeding females grew up differed from plurally breeding females.



**Fig. 1** Autocorrelation function (ACF) of food availability (a) and population density (b). Dotted blue lines, 95% confidence interval; red lines that are beyond this interval represent significant lags

## Data availability

All data generated or analyzed during this study are included in the supplementary information file.

## Results

### Time series (predictability) of food availability

The time series of food availability was not random (turning point test, statistic =  $-3.01$ ,  $n = 13$ ,  $p < 0.01$ ; Moran's  $I$  and Geary's  $C$ ,  $I$  and  $C = 0.476$ ,  $p = 0.023$ ). The autocorrelation function showed a tendency for cyclical variation in food availability at a 3-year lag (Fig. 1a). This was confirmed by the periodogram, showing that the neighborhood eigenvector number 3 with a periodicity of 6 years was a significant predictor of the variability in food availability ( $F(1,10) = 24.5$ ,  $p < 0.001$ , Fig. 2).

### Time series (predictability) of population density

We could not reject randomness in the temporal structure of population density, using the turning point test (statistic =  $-1.83$ ,  $n = 16$ ,  $p = 0.068$ ) as well as Moran's  $I$  and Geary's  $C$  ( $I$  and  $C = 0.133$ ,  $p = 0.169$ ). The autocorrelation function showed no significant time lag (Fig. 1b), and the periodogram revealed no significant neighborhood eigenvector predictive of the variation.

### Population density and single breeding

Population density and adult group size at the start of the breeding season in September correlated significantly with each other ( $r_s = 0.50$ ,  $N = 178$  groups,  $p < 0.0001$ ). The lower

the population density, the higher the percentage of single breeding female striped mice in the population ( $r_s = -0.69$ ,  $N = 15$  years,  $p = 0.004$ ; Fig. 3a).

### Time series (predictability) of female breeding tactic

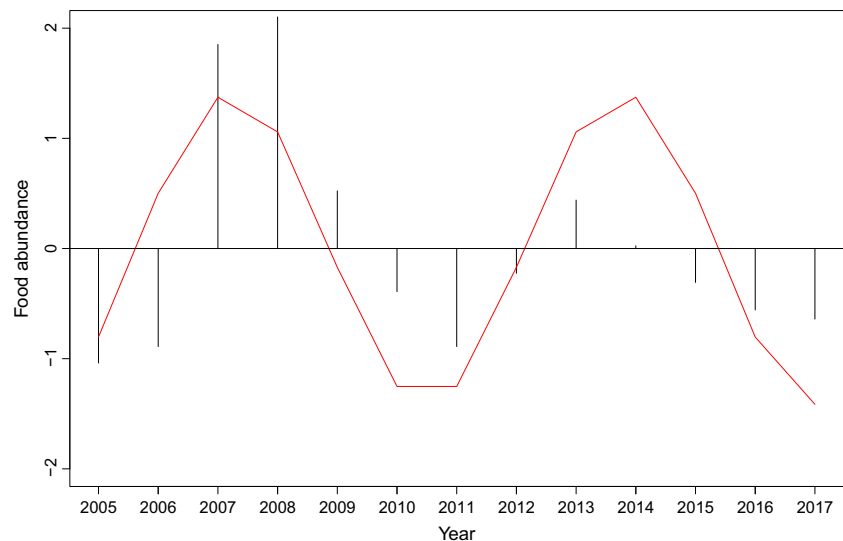
We could not reject randomness in the temporal structure in the proportion of female single breeders, using the turning point test (statistic =  $-0.435$ ,  $n = 15$ ,  $p = 0.66$ ) as well as Moran's  $I$  and Geary's  $C$  ( $I$  and  $C = 0.049$ ,  $p = 0.23$ ). The autocorrelation function showed no significant time lag (Fig. 3b), and the periodogram revealed no significant neighborhood eigenvector predictive of the variation.

### Predictability of group composition

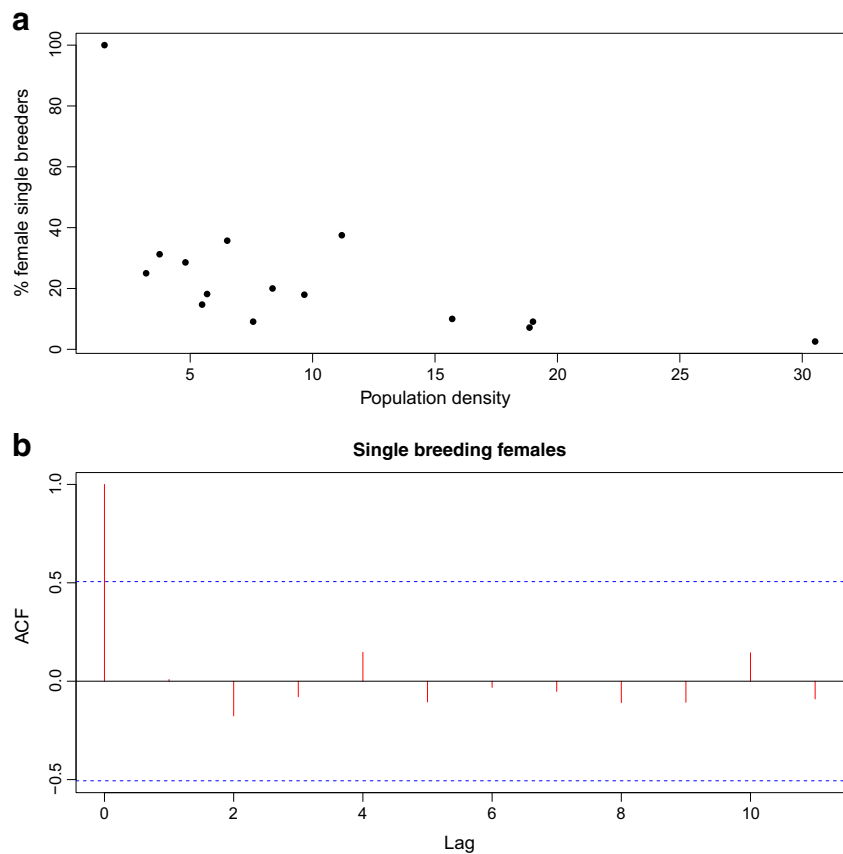
The size of groups in which females lived just before the onset of the dry season in December correlated significantly positively with the size of the group in which they bred at the beginning of the next breeding season in September ( $r_s = 0.34$ ,  $N = 322$  females,  $p < 0.0001$ ). The number of breeding females present in the natal group when a female was born correlated significantly with the number of breeding females present 1 year later in the group in which that female bred ( $r_s = 0.29$ ,  $N = 258$  females,  $p < 0.0001$ ).

Most females that grew up in a plural breeding group also bred plurally later (152 out of 173 females, with the remaining 21 becoming single breeders). However, females that grew up in a group with a single breeding female also often bred in a group with plural breeders later (71 out of 86, with 15 females becoming solitary breeders). Thus, it was significantly more likely for females growing up in plural breeding groups to also breed under the same conditions (become a plural breeder, ratio of 152:21) than it was for females that grew up in a group with a single breeding female to also breed under the same

**Fig. 2** Normalized food abundance (gray bars) and 6-year periodicity of the periodogram eigenvector no. 3 (red line), a significant predictor of variation in food abundance



**Fig. 3** **a** Significant relationship between population density and the percentage of females in the population that were single breeders. The lower the population density, the more females bred singly. **b** Autocorrelation function (ACF) of percentage of single breeding females. Dotted blue lines, 95% confidence interval; red lines that are beyond this interval represent significant lags.



conditions (become a single breeder, ratio of 15:71; Fisher's exact test,  $p < 0.0001$ , Fig. 4a). Plural breeding females did not grow up more often in plural groups than single breeding females. We knew the conditions under which 36 of the 79 singly breeding females grew up (other females were immigrants or we had to increase the field site size due to low population density such that their groups were not studied in the previous year). The ratio of single breeding females that originated from plural groups (21 out of 173) did not differ from the ratio of single breeding females that originated from a single breeding female (15 out of 86; Fisher's exact test,  $p = 0.35$ , Fig. 4b).

## Discussion

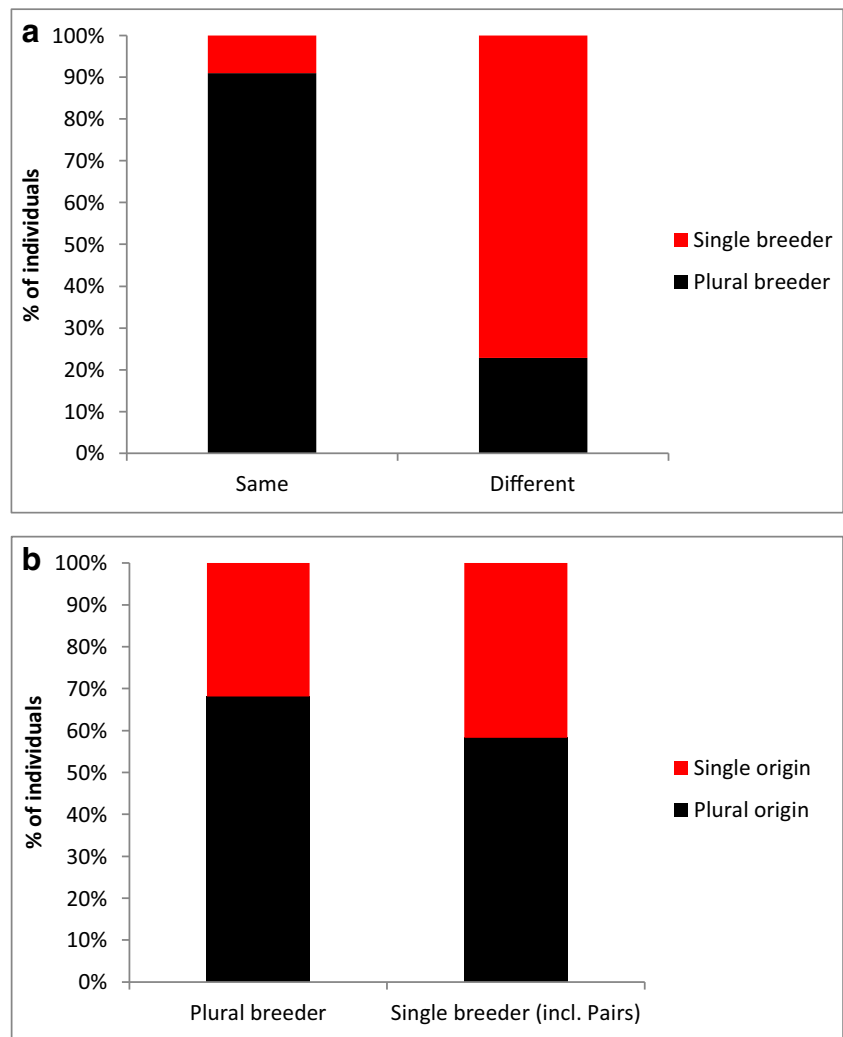
We did not find predictability for important factors known to determine the optimal social and reproductive tactics for female African striped mice. Population density, the most important factor influencing social tactics (Schradin et al. 2010; Schoepf and Schradin 2012), did not show significant cyclicality. For female striped mice, which live for less than 2 years, food availability was not predictable, since food availability did not correlate between years. While it was most likely for females to become communal breeders, it was not predictable

which of the 322 females would be able to follow the favored single breeding tactic.

Here, we showed in one case study that social flexibility occurs in an unpredictable environment. To test whether the evolution of social flexibility is associated with unpredictability, a comparative approach with many species would be needed. This is not possible currently since other case studies are missing. While several comparative studies used environmental variability as an important factor in social evolution (Jetz and Rubenstein 2011; Chak et al. 2017; Lukas and Clutton-Brock 2017; Guindre-Parker and Rubenstein 2018), no information exists about whether this variability is predictable.

Interestingly, both social flexibility and cooperative breeding are predicted to occur in environments characterized by high variability. In comparative studies of social evolution, intra-specific variation in social organization has been evident to the researchers (Chak et al. 2017; Cornwallis et al. 2017) but has not been included in their analyses (Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2013). As outlined above, it is currently not possible to address the predictability of variation in a comparative study. This is a shortcoming because it is not variation per se but unpredictability for the individuals which is expected to favor the evolution of social flexibility (Schradin et al. 2018). Here, unpredictable variation means, for example, that very dry years can be

**Fig. 4** **a** The probability for females breeding under the same condition in which they grew up was significantly higher for plurally breeding than for singly breeding females, because most females bred plurally. **b** Females that became single breeders did not originate more often from single breeding females than from plurally breeding groups



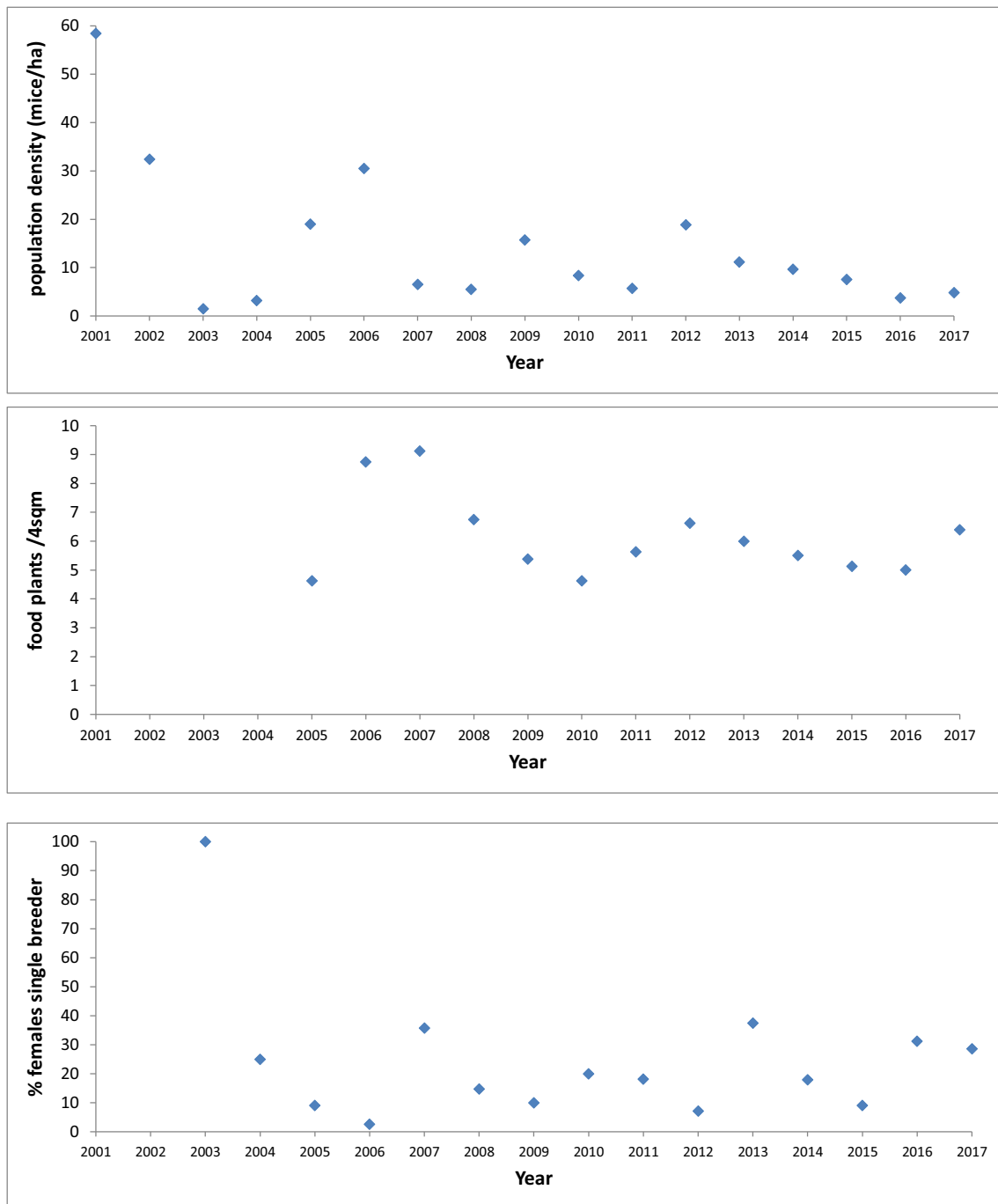
expected to occur, but the individual cannot predict when the next dry year will be. In contrast to variability, for example of climate, predictability cannot be easily added to existing databases, since it depends on the species' life history. The predictability of one specific environment can differ between species living in the same environment, as species differ in seasonality of breeding, life expectancy, age when reaching sexual maturity, and the number of breeding seasons experienced. In sum, future studies should not only address variability but also predictability as an important factor in social evolution.

For female striped mice, the conditions under which they live are not totally unpredictable. In fact, the life history of female striped mice contains two highly predictable phases. First, striped mice are always group living during the dry season and winter (9 months), which represents their longest life history stage (Schradin et al. 2010; Schradin 2013). Second, most females become plural breeders, independent of whether they grew up with a single breeding mother or in a communally breeding group. Thus, female striped mice

must be able to live in groups and to become plural breeders. Importantly, this in contrast to their preferred tactic, which is single breeding (Schradin et al. 2010).

Single breeding in female striped mice is most likely associated with increased reproductive success due to reduced risk of infanticide by other females (Schradin et al. 2010; Schoepf and Schradin 2012; Hill et al. 2015a, 2015b). Here, we found that more females were single breeding when population density was lower, replicating a previous study with a smaller sample size (7 of the 15 years considered in the current analysis, (Schradin et al. 2010). This provides further support to the previous conclusion that female striped mice become solitary breeders when free territories make this possible but are constrained to plural breeding when population density is high (Schradin et al. 2010; Schoepf and Schradin 2012). While we focused on the effect of predictability in our current but not in earlier studies, it is important that our earlier studies were replicated and validated with a much larger sample size. That single breeding is a choice is indicated by the fact that 11 of the 12 singly breeding females in September 2013 were





**Fig. 5** Visualizing predictability for female African striped mouse from the year they were born to the next year when they were breeding, for population density (top, data for the years 2001–2017), food availability start of the breeding season (middle, data for the years 2005–2017), and for the percentage of females that could follow the preferred tactic of

single breeding (bottom, data for the years 2003–2017). From 1 year to the next (year born to breeding year), it was not predictable for the females of the current study whether the value would remain similar, decrease, or increase

still living in groups 1 month earlier (Schradin et al. 2010), before heavy rainfall ended the dry season and started the breeding season. In sum, our long-term dataset and experimental field studies (Schoepf and Schradin 2012) indicate that single breeding is the preferred tactic and that population

density is an important factor that determines whether single breeding is possible.

Population density was highly variable between years. We did not find a significant periodicity or structure in the time series since all tests failed to reject randomness. Our data

indicate that predictability was extremely low for the striped mice. Indeed, a year with high population density, making plural breeding the main reproductive tactic, could be followed by a year when population density was still high or a year with low population density, when single breeding is the best tactic (Fig. 5). However, group size correlated from year to year, and groups were larger when population density was higher. Do these correlations contradict the unpredictability of the social conditions from year to year? No, because these correlations simply indicate that when there was an unpredicted decline in population density, small groups declined in a similar way to large groups, and if survival was high, large groups (with many offspring) remained larger than smaller groups. Therefore, these correlations demonstrate that unpredictable changes affected small and large groups similarly. In sum, population density was highly variable and unpredictable.

Food availability followed a 6-year cycle, and thus a given year was correlated negatively with food availability 3 years later. However, this does not offer predictability for female striped mice for two reasons: (1) Food availability in the year of birth did not correlate with food availability in the year of breeding, i.e., the following year (Fig. 5), and (2) female striped mice do not live long enough to be able to estimate where in the prevailing cycle they occur. For example, a female growing up under intermediate food availability (2005 and 2009) cannot predict whether food availability will be higher (2006) or lower (2010) in the next year when it experiences its only breeding season (see Fig. 5). Thus, even though a 6-year cycle was evident, the predictability of future food availability was very low for female striped mice.

The social conditions under which these females grew up did not predict that they would become single breeders. About as many single breeding females originated from a single breeding mother (15) as from a plurally breeding mother (21). Seventeen percent of all females that grew up under a single breeding condition became single breeders, and 12% of females that grew up in plurally breeding groups became single breeders. This shows that a mother's tactic did not predict her daughter's tactic, indicating that neither genetic nor maternal effects were determining female striped mice reproductive tactics. Thus, single breeding females could not predict, from the environment in which they grew up, that they would breed singly later. Instead, the prevailing population density rather than previous population density and group size determined whether the single breeding reproductive tactic could be adopted by specific females. These conditions occur late in adult life which would favor the evolution of social flexibility allowing an adaptive response of adults rather than the evolution of non-reversible developmental plasticity in early life.

The unpredictability of whether a female will be able to choose the preferred single breeding tactic would have selected for the ability of female striped mice to respond flexibly to their

environmental conditions, instead of investing in tactic specific ontogenetic pathways, as would be the case under developmental plasticity (two pathways: plural or single breeding) or specialization (one pathway leading to plural breeding). In cases of adaptive developmental plasticity, there is typically no or only a very short time lag between the reliable information and the fitness benefit of the alternative phenotype (Steiner and Buskirk 2008; Lind et al. 2015). In contrast, the time lag between the juvenile stage and the breeding stage is often much longer; approximately 9 months in our study, representing more than 50% of the entire lifespan of striped mice. The long time lag between the juvenile and the breeding stage might explain why many examples exist of social flexibility explaining intra-specific variation in social organization, but not for developmental plasticity (Schradin et al. 2018).

We predicted that social flexibility of striped mice evolved in an unpredictable environment. There are no tests demonstrating unpredictability, but our different time series tests did not detect structure in a dataset that would have permitted female striped mice to predict population density or food availability from the season when they were born to the season they bred. While a larger dataset could allow us to identify statistically significant cycles, this would not provide predictability for the more than 300 female striped mice we studied.

We showed that it is predictable that female striped mice will be group living in the dry season. Further, plural breeding is the most common and consequently the most likely, but not preferred, tactic. Indeed, when population density declined, more females were able to choose the single breeding tactic, but the percentage of single breeding females varied unpredictably from year to year (Fig. 5). Using a time series analysis, we showed a 6-year food availability cycle. Yet, this food cycle could not be detected by striped mice because most live for less than 2 years, and food availability is not predictable annually. Population density, the main determinant of social organization (Schradin et al. 2010; Schoepf and Schradin 2012), did not show significant cyclicity in our time series analyses, indicating unpredictability for this factor. It is possible that females could detect other factors, unknown to us, that could provide predictable information long before onset of the breeding season. However, it is parsimonious to assume that they used the available information of prevailing population density and their group composition at the onset of the breeding season to decide whether or not to leave their group and start solitary breeding (Schoepf and Schradin 2012; Hill et al. 2015a, 2015b).

In conclusion, we showed for the first time for one species that unpredictably changing environmental conditions are associated with social flexibility, making it likely that social flexibility evolved in such an unpredictably changing environment. Social flexibility might be a key trait allowing individuals to cope with climate change, protecting populations from extinction (Rymer et al. 2013). Future research is needed in

other species to determine the extent to which their phenotypic plasticity allows them to cope with change (Rymer et al. 2016), and flexibility in social organization might be a key factor here (Valomy et al. 2015; Agnani et al. 2018).

**Acknowledgments** We thank Ivana Schoepf, Ed Yuen, Jörg Jäger, Milena Zduniak, Jessica Mulvey, Davina Hill, Audrey Maille, Rebecca Rimbach, several master students, and more than 80 field assistants for the help in collecting the data. We are grateful for the very helpful comments from two referees. We are grateful to Goegap Nature Reserve. This study was made possible by the administrative and technical support of the Succulent Karoo Research Station (registered South African NPO 122-134). Comments by L. Hayes significantly improved the manuscript.

**Author contributions** CS and NP designed the study. CS collected the data. CS and CB analysed the data. All authors contributed to writing the manuscript.

**Funding** Financial support was provided by the Swiss National Science Foundation, the Claude-Leon Foundation, the German Science Foundation, the National Research Foundation, the University of the Witwatersrand, the University of Zurich, the CNRS, the University of Lausanne, the University of Strasbourg Institute of Advanced Study, the Vontobel Stiftung, the Holcim Stiftung, the Promotor Stiftung, and the Helene Biber Fonds.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** Animal ethics clearance was provided by the University of the Witwatersrand (AESC 2007/40/01), following the guidelines for the use and care of animals in teaching and research of the University of the Witwatersrand which complies with the University's ethical and legal practices and with the National Code.

## References

- Agnani P, Kauffmann C, Hayes LD, Schradin C (2018) Intra-specific variation in social organization of strepsirrhines. *Am J Primatol* 80:e22758
- Ashander J, Chevin L-M, Baskett ML (2016) Predicting evolutionary rescue via evolving plasticity in stochastic environments. *Proc R Soc B* 283:20161690
- Berry RJ, Tattersall FH, Hurst J (2008) Genus *Mus*. In: Harris S, Yalden DW (eds) *Mammals of the British Isles handbook*, 4th edn. The Mammal Society, Southampton, pp 141–149
- Blumstein DT, Ebensperger LA, Hayes LD et al (2010) Toward an integrative understanding of social behavior: new models and new opportunities. *Front Behav Neurosci* 4:34
- Chak STC, Duffy JE, Hultgren KM, Rubenstein DR (2017) Evolutionary transitions towards eusociality in snapping shrimps. *Nat Ecol Evol* 1:0096
- Cornwallis CK, Botero CA, Rubenstein DR, Downing PA, West SA, Griffin AS (2017) Cooperation facilitates the colonization of harsh environments. *Nat Ecol Evol* 1:0057
- Davies NB (1992) *Dunnock behaviour and social evolution*. Oxford University Press, Oxford
- Diggle PJ (1990) *Time series, a biostatistical introduction*. Clarendon Press, Oxford
- Dray S, Dufour A-B (2007) The ade4 package: implementing the duality diagram for ecologists. *J Stat Softw* 22:1–20
- Emlen ST (1982) The evolution of helping. I. An ecological constraints model. *Am Nat* 119:29–39
- Guindre-Parker S, Rubenstein DR (2018) Multiple benefits of alloparental care in a fluctuating environment. *R Soc Open Sci* 5: 172406
- Hayes LD (2000) To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Anim Behav* 59: 677–688
- Hill DL, Pillay N, Schradin C (2015a) Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitarily than communally. *J Anim Ecol* 84:1497–1508
- Hill DL, Pillay N, Schradin C (2015b) Alternative reproductive tactics in female striped mice: solitary breeders have lower corticosterone levels than communal breeders. *Horm Behav* 71:1–9
- IPCC (2014) *Climate change 2014: synthesis report*. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva
- Jetz W, Rubenstein DR (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr Biol* 21:72–78
- Keller C, Schradin C (2008) Plant and small mammal richness correlate positively in a biodiversity hotspot. *Biodivers Conserv* 17:911–923
- Koenig WD, Pitelka FA (1981) Ecological factors and kin selection in the evolution of cooperative breeding in birds. In: Alexander RD, Tinkle DW (eds) *Natural selection and social behavior: recent research and new theory*. Chiron Press, New York, pp 261–280
- Latham N, Mason G (2004) From house mouse to mouse house: the behavioural biology of free-living *Mus musculus* and its implications in the laboratory. *Appl Anim Behav Sci* 86:261–289
- Lignot JH, Helmstetter C, Secor SM (2005) Postprandial morphological response of the intestinal epithelium of the Burmese python (*Python molurus*). *Comp Biochem Physiol A* 141:280–291
- Lind MI, Yarlett K, Reger J, Carter MJ, Beckerman AP (2015) The alignment between phenotypic plasticity, the major axis of genetic variation and the response to selection. *Proc R Soc B* 282:20151651
- Lucia KE, Keane B, Hayes LD, Lin YK, Schaefer RL, Solomon NG (2008) Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behav Ecol* 19:774–783
- Lukas D, Clutton-Brock TH (2013) The evolution of social monogamy in mammals. *Science* 341:526–530
- Lukas D, Clutton-Brock T (2017) Climate and the distribution of cooperative breeding in mammals. *R Soc Open Sci* 4:160897
- Maille A, Schradin C (2016) Ecophysiology of cognition: how do environmentally induced changes in physiology affect cognitive performance? *Biol Rev* 20160346
- Mateus A, Caeiro F (2013) Comparing several tests of randomness based on the difference of observations. *AIP Conf Proc* 1558:809–812
- Müller JF, Braunsch V, Hwang W, Eggert A-K (2006) Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*. *Behav Ecol* 18:196–203
- Nater CR, Benthem KJ, Canale CI, Schradin C, Ozgul A (2018) Density feedbacks mediate effects of environmental change on population dynamics of a semidesert rodent. *J Anim Ecol* 87:1534–1546
- Phoenix CH, Goy RW, Gerall AA, Young WC (1959) Organizing action of prenatally administered testosterone propionate on the tissue mediating mating behavior in the female guinea pig. *Endocrinology* 65: 369–382
- Piersma T, Drent J (2003) Phenotypic flexibility and the evolution of organismal design. *Trends Ecol Evol* 18:228–233
- Piersma T, van Gils JA (2011) *The flexible phenotype*. Oxford University Press, Oxford
- Randall JA, Rogovin K, Parker PG, Eimes JA (2005) Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behav Ecol* 16:961–973

- Reyer H-U (1980) Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis rudis* L.). *Behav Ecol Sociobiol* 6: 219–227
- Reyer H-U (1984) Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim Behav* 32:1163–1178
- Rymer T, Pillay N, Schradin C (2013) Extinction or survival? Behavioral flexibility in response to environmental change in the African striped mouse *Rhabdomys*. *Sustainability* 5:163–186
- Rymer TL, Pillay N, Schradin C (2016) Resilience to droughts in mammals: a conceptual framework for estimating vulnerability of a single species. *Q Rev Biol* 91:133–176
- Schoepf I, Schradin C (2012) Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*). *J Anim Ecol* 81:649–656
- Schradin C (2006) Whole day follows of the striped mouse. *J Ethol* 24: 37–43
- Schradin C (2013) Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philos Trans R Soc B* 368:20120346
- Schradin C, Pillay N (2004) The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of South Africa: a territorial group living solitary forager with communal breeding and helpers at the nest. *J Comp Psychol* 118:37–47
- Schradin C, Pillay N (2005) Intraspecific variation in the spatial and social organization of the African striped mouse. *J Mammal* 86: 99–107
- Schradin C, Pillay N (2006) Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behav Ecol* 17:452–458
- Schradin C, Yuen C-H (2011) Hormone levels of male African striped mice change as they switch between alternative reproductive tactics. *Horm Behav* 60:676–680
- Schradin C, Scantlebury M, Pillay N, König B (2009) Testosterone levels in dominant sociable males are lower than in solitary roamers: physiological differences between three male reproductive tactics in a sociably flexible mammal. *Am Nat* 173:376–388
- Schradin C, König B, Pillay N (2010) Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *J Anim Ecol* 79:515–521
- Schradin C, Lindholm AK, Johannesen J, Schoepf I, Yuen C-H, König B, Pillay N (2012) Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Mol Ecol* 21:541–553
- Schradin C, Raynaud J, Arrivé M, Blanc S (2014) Leptin levels in free ranging striped mice (*Rhabdomys pumilio*) increase when food decreases: the ecological leptin hypothesis. *Gen Comp Endocrinol* 206:139–145
- Schradin C, Hayes LD, Pillay N, Bertelsmeier C (2018) The evolution of intraspecific variation in social organization. *Ethology* 124:527–536
- Solmsen N, Johannesen J, Schradin C (2011) Highly asymmetric fine-scale genetic structure between sexes of African striped mice and indication for condition dependent alternative male dispersal tactics. *Mol Ecol* 20:1624–1634
- Steiner UK, Buskirk JV (2008) Environmental stress and the costs of whole-organism phenotypic plasticity in tadpoles. *J Evol Biol* 21: 97–103
- Thioulouse J, Chessel D, Champely S (1995) Multivariate analysis of spatial patterns: a unified approach to local and global structures. *Environ Ecol Stat* 2:1–14
- Valomy M, Hayes LD, Schradin C (2015) Social organization in Eulipotyphla: evidence for a social shrew. *Biol Lett* 11:20150825
- Vuarin P, Pillay N, Schradin C (2019) Elevated basal corticosterone levels increase disappearance risk of light but not heavy individuals in a long-term monitored rodent population. *Horm Behav* (published online). <https://doi.org/10.1016/j.yhbeh.2019.05.001>
- Wallen K (2009) Commentary: The organizational hypothesis: reflections on the 50th anniversary of the publications of Phoenix, Goy, Gerall, and Young (1959). *Horm Behav* 55:561–565
- Werger MJA (1974) On concept and techniques applied in the Zürich-Montpellier method of vegetation survey. *Bothalia* 11:309–323
- West-Eberhard MJ (2003) *Developmental plasticity and evolution*. Oxford University Press, Oxford

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