



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

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## Abstract

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

## Significance statement

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

**Keywords** Group living · Intra-specific variation · Social evolution · Social system · Social organization · Solitary living

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## Introduction

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

2018). Variation in social organization is obvious between different species.

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

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

It is well known that different populations of the same species can have different forms of social organization (Lott 1991; Agnani et al. 2018; Schradin et al. 2018). Multiple studies have compared two populations of one species (reviewed in Lott 1991; Maher and Burger 2011; Strier 2017). For example, pied kingfishers (*Ceryle rudis*) can form pairs in or family groups in areas with a high abundance of high-quality nesting sites but can form in polygynous groups in areas where good nesting sites are rare (Reyer 1980, 1984). The comparison of two populations of European badgers (*Meles meles*) in Spain lead to the hypothesis that differences in population density and landscape structure might influence social organization (Molina-Vacas et al. 2009). Population density has also been hypothesized to explain intra-specific variation between two populations of the mountain brushtail possum (*Trichosurus cunninghami*) (Martin and Martin 2007) and two populations of the African striped mouse (*Rhabdomys spp.*) (Schradin 2005; Schradin and Pillay

2005). A study of four populations of kiwis (*Apteryx spp.*) differing in population density showed that all populations had pair living as social organization, although pairs were less stable in the population with the lowest density (Taborsky and Taborsky 1999). Whereas all these studies are interesting, they lack the requisite sample size to show statistically that the observed differences between two (or four) populations are due to the proposed differences in population density. An early study comparing 23 populations of langurs (*Presbytis entellus*) showed that the relationship between population density and group composition is complex and can be revealed only with a sufficiently large number of populations (Moore 1999). Thus, many previous studies comparing two populations discussed the possibility that differences in population density results in variation in social organization, but this was a prediction, not a conclusion, of these studies. To our knowledge, no study has compared a sufficient number of populations for statistical comparisons, as has been proposed by (Maher and Burger 2011).

Intra-specific variation in social organization between populations of the same species could be due to genetic differences caused by local adaptation of isolated populations, or due to social flexibility caused by individuals changing their social tactics when immigrating into a different environment (Schradin 2013). Studying whether social flexibility occurs in a geographically heterogeneous habitat could best be achieved in a small animal species that have a metapopulation consisting of populations connected by dispersing individuals (also called sub-populations or demes (van Nouhuys 2016)). Our study population of African striped mice (*Rhabdomys pumilio*) inhabits areas around seasonal riverbeds that are dry for most of the time and carry water for only a few days every couple of years after high rainfall. These populations are separated from each other by dry sandy flats, hills, and mountains, but individuals disperse over these unoccupied areas from population to population (Solmsen et al. 2011), forming one large metapopulation (van Nouhuys 2016).

Striped mice show social flexibility, allowing them to live solitarily or in groups of up to 30 adult individuals of both sexes (Schradin et al. 2010a). A correlative field study conducted for 8 years on one population showed that within this population, social organization depended on reproductive competition and population density (Schradin et al. 2010a). Outside the breeding season, when reproductive competition is absent, striped mice always formed groups independent of population density, but within the breeding season, social organization was density-dependent (Schradin et al. 2010a; Schoepf and Schradin 2012). To avoid reproductive competition in the form of female infanticide, females became solitary breeding when territories became available, but remained in communally breeding groups when population density was high (Schradin et al. 2010a; Schoepf and Schradin 2012; Hill et al. 2015). Male social tactics followed females' tactics:

more males became solitary roamers when fewer groups of communally breeding females were available to be defended; instead, they visited solitary breeding females for mating (Schradin et al. 2010a; Schradin and Lindholm 2011). Thus, temporal variation in population density explained why in this population, many striped mice lived solitarily in some years, while in other years, nearly all lived in groups. The striped mouse offers an ideal system to study whether social flexibility could also be an adaptation to geographic (spatial) variation.

Here, we tested whether geographic variation in population density is related to social organization in striped mice. Thus, we tested whether the relationship described between population density and the likelihood of group living that was previously described for 8 study years (Schradin et al. 2010a) could be replicated in a one year study of 8 populations. We predicted that more striped mice would be group living in a population with higher local population density, replicating the relationship between population density and sociality reported previously. In addition, we recorded any individuals dispersing between populations and whether they changed their social tactics, since dispersal could make social flexibility adaptive. Social flexibility would allow immigrants to follow the best alternative reproductive tactic depending on the prevailing environmental conditions of the population into which they immigrated.

## Methods

### Study area and study period

The study was conducted from January to October 2018 in an area covering 5540 ha of the 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 high food abundance in spring and hot dry summers with low food abundance. The landscape is dominated by short-living ephemerals (in spring) and perennial succulent shrubs. The breeding season of striped mice is in spring (August–November), when population density starts at its minimum.

Data were collected on 8 different sites (Fig. 1). All field sites were located along dry riverbeds with perennial succulent shrubs providing a suitable habitat for striped mice. These included our main field site where we have continuously monitored the striped mouse population since 2001 (Schradin et al. 2012), a field site where an experimental PhD study was done from 2007 to 2010 (Schoepf and Schradin 2012) (Klein Goegap), and 6 field sites where striped mice had been trapped for a population genetics study in 2008, and which found dispersal among these populations (Solmsen et al. 2011). Thus, these populations form one metapopulation that could

be viewed as 8 sub-populations or 8 demes. We retain the term “population” for each site, as there was no direct contact between them, and all were isolated from each other by habitat not inhabited by striped mice (Fig. 1).

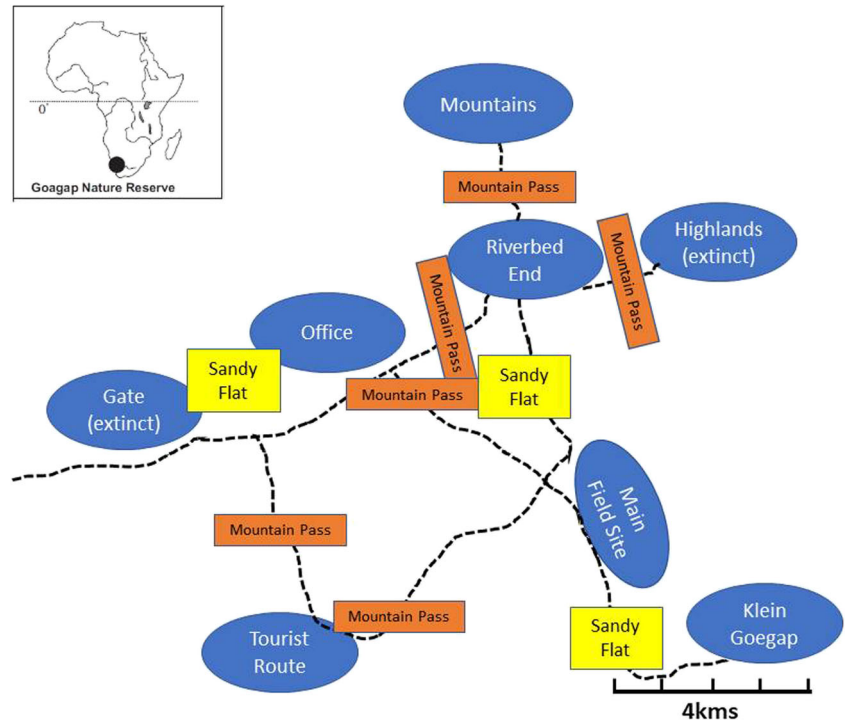
### Trapping

Each population was trapped 4 times. Trapping during January (onset of the dry season, no breeding), April (middle of the dry season, no breeding), and July (end of dry season, no breeding) was done to ensure we have viable populations for our study during the breeding season and to monitor potential dispersal between populations. The gate population became locally extinct in July and the Highlands population by September, leaving us with 6 populations in spring for study (Fig. 1). Extinction might have been associated with the very dry conditions of the years 2015 to 2018, which experienced less rain than the average of 151 mm/year since 2005 (2015: 65 mm; 2016: 85 mm; 2017: 41 mm; 2018: 71 mm).

Data collection regarding social organization was done during the breeding season (September and October). Before trapping, field sites were pre-baited for 2 days by casting bait around trapping stations. In January, trapping was done for 3 days at 6 sites but for 5 days at the field sites with lower trap success, i.e., gate and office. During all subsequent trapping periods, all field sites were trapped for 5 days.

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

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



### Determination of social tactic

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

Radio-tracking started on the same day the radio-collar was fitted. The sleeping site was determined at night and we also placed 4 to 6 traps at the nesting site and started trapping there the next morning for the rest of the study. Any additional striped mice trapped were marked and received a radio-collar; trapping at nesting sites continued, with more traps being set if necessary. Some sleeping sites were also observed during mornings and afternoons to determine whether striped mice not carrying transmitters were present. We rather observed sleeping sites where one mouse was radio-tracked than sleeping sites where several mice were radio-tracked (known to be group living) to verify that an individual was solitary. If after the original 5 days of trapping, the social organization was not apparent for every individual, radio-tracking, trapping, and observations continued for up to another seven days. We did not have to spend any extra days at the main field site, since we knew the social tactics of all trapped mice there, nor on the two field sites where no striped mice were trapped

within 5 days (regarded as extinct: gate and highland). In total, we spent 6 days at office, 10 days at tourist road, 11 days at riverbed end and Klein Goegap, and 12 days at mountains. We determined group versus solitary living by using the following definitions from our previous studies (Schradin et al. 2009; Schradin and Yuen 2011).

1. Group living: two or more adult mice sleep together in the same nest for a minimum of three consecutive nights. Groups consisted either only of adult females, a pair, or adults of both sexes.
2. Solitary living female (with or without pups): a female sleeps alone for a minimum of three consecutive nights and we either trapped no other adult individual at the same nest(s) for at least 3 days, or other adult individuals trapped there were radio-tracked at night at another nest.
3. Solitary living male (roamer): a male sleeps alone for a minimum of three consecutive nights and we either trapped no other adult individual at the same nest(s) for at least 3 days, or other adult individuals trapped there were radio-tracked at night at another nest.

Altogether we determined the social tactics of 39 males and 48 females (sex ratio: 0.81).

### Population density

Population density was estimated for the breeding season only. The habitat in Goegap is heterogeneous and many areas are not inhabited by striped mice, as they do not provide the

necessary resources, such as food and shelter (Schradin and Pillay 2006; Solmsen et al. 2011). While we chose our trapping transects in areas suitable for striped mice, the long transects often also included unoccupied areas, especially sandy areas without vegetation providing food and cover. To calculate population density as an indicator of competition for scarce resources, we thus only included the areas used by striped mice. For this, we used the GPS points of all sleeping sites, all trapping sites where striped mice were trapped, and of all radio-tracking data collected during afternoons. Using the minimum polygon method, we then determined the size of the area in hectares using the software QGIS 3.6. For individual home ranges of striped mice, convex polygons correlated highly and significantly with Kernel estimates (Schradin and Pillay 2006; Schradin et al. 2010b), but as Kernel contours would be more affected by single individuals with small home ranges, we used convex polygons. Visual inspection of the polygons did not indicate any outliers having a huge impact on field site estimates. For each population, population density was then calculated as the number of adult striped mice (body mass  $\geq 30$  g) per hectare.

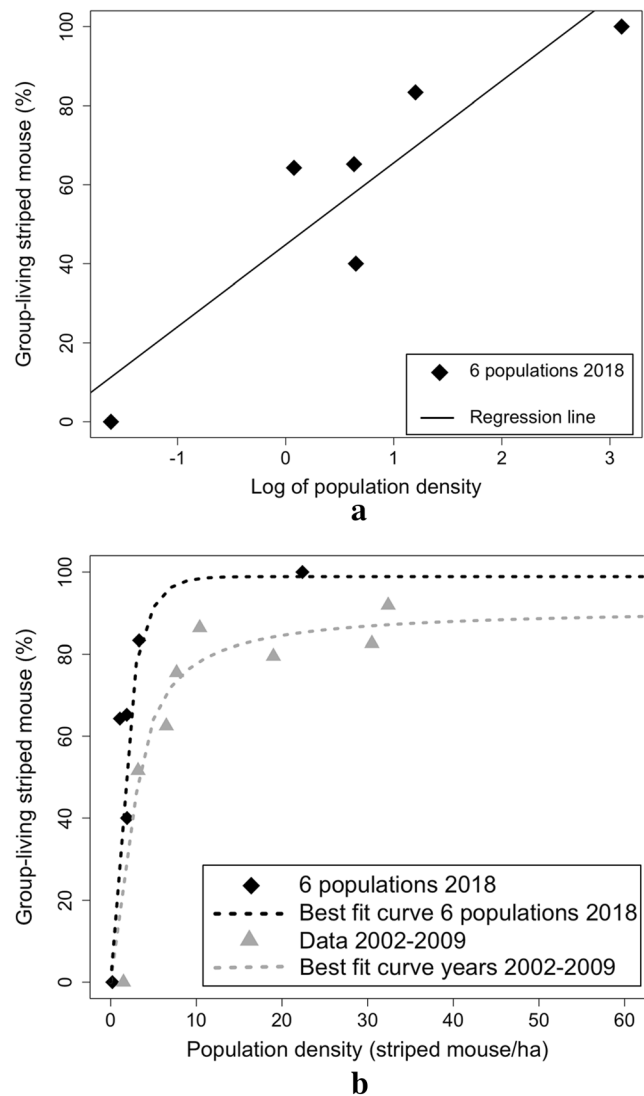
### Statistical analyses

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

### Results

Due to extremely dry conditions during the years 2015–2018, population density was generally low, and two populations had become extinct by the onset of the study. For the remaining 6 populations, population density ranged from 1.1 striped mice/ha to 22.4 mice/ha, with a mean of  $5.1 \pm 8.5$  (SD) mice/ha (Fig. 2). In one population (riverbed end), no striped mice lived in groups, while in another population (office), all striped mice lived in groups.

There was a significant regression between the percentage of striped mice living in groups and log-transformed population density ( $r^2 = 0.821$ ,  $p = 0.01$ ; Fig. 2a). At lower population density in a population, more striped mice lived solitarily.



**Fig. 2** a Relationship between log population density and the percentage of striped mice living in groups. **b** Raw data. Black: data from 6 populations studied simultaneously in 2018 at 6 distinct geographic locations. Gray: published data from 8 different years in the population main field site (Schradin et al. 2010a), which provided the predictions for the current study. Best-fit curves on the raw data were fitted using CurveExpert

For females alone, the regression was also significant ( $r^2 = 0.73$ ,  $p = 0.03$ ), and also for males ( $r^2 = 0.91$ ,  $p = 0.004$ ). Significantly more females ( $66.5 \pm 36.8\%$ ) than males ( $50.0 \pm 33.9\%$ ) lived in groups (paired  $t_5 = 2.75$ ,  $p = 0.04$ ).

Using CurveExpert, the relationship was best described by a non-linear regression with the formula  $y = 98.89 x (1 - (\exp(-0.516x)))$ , with  $y$  representing the percentage of group-living striped mice in the population, and  $x$  the population density in striped mice/ha (Fig. 2b). The correlation coefficient was 0.942 (SE = 14.74) indicating a very high model fit. For females and males alone, the best-fit curves were very similar (females:  $y = 97.77 x (1 - (\exp(-0.76x)))$ , SE = 15.91, correlation coefficient = 0.938; males:  $y = 97.87 x (1 - (\exp(-$

0.34x)), SE = 11.14, correlation coefficient = 0.960). In comparison, the best-fit model from the data published in 2010 was  $y = 91.3 - (136/x)$  and the correlation coefficient was 0.984 (SE = 5.82) (Schradin et al. 2010a; inserted in Fig. 2b for comparison). Our small sample size did not allow us to include additional environmental co-factors into the analysis; in any case, from the start of the project planning, we focused on the effect of population density as the main effect. In the electronic supplement, we show that all regressions between the dependent variable (% group-living striped mice) and several environmental co-factors (number of food plants, plant cover and rainfall) were non-significant, indicating that population density, the a priori chosen main factor, was the most important.

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

## Discussion

Social flexibility has been interpreted as an adaptation to changing environments. Change occurs not only in time but also in space. Here, we showed for the first time that geographic variation in population density is significantly related to social flexibility, a prediction that emerged from many field studies on multiple species where differences between two populations were observed (Schradin and Pillay 2005; Martin and Martin 2007; Molina-Vacas et al. 2009). We showed that 6 populations of a larger metapopulation differed in their degree of sociality, depending on population density.

Thus, within this metapopulation, individuals being able to switch from group to solitary living and back might benefit from this flexibility not only when the environment changes over time (Schradin et al. 2010a) but also when they disperse over space.

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

Striped mice are well known for their social flexibility, i.e., individuals being able to switch from group to solitary living and back to group living (Schradin et al. 2012). This has been demonstrated first with long-term data collected during 8 years from our field site, where more striped mice were group living at a higher population density (Schradin et al. 2010a), in agreement with the habitat saturation hypothesis (Koenig and Pitelka 1981; Emlen 1982; Komdeur 1992). Female tactics drive male sociality, since for males, it is beneficial to join groups of communally breeding females and defend them as

**Table 1** Individual striped mice that dispersed from main field site to a different population

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

the only breeding male against other males. However, when many females live solitarily, solitary living males visiting several single females can also have high reproductive success (Schradin and Lindholm 2011). Importantly, single breeding females have much larger home ranges than communal groups, making it impossible for single males to defend the home ranges of multiple solitary females (Schradin et al. 2010b). Reproductive competition between males is high, and single males defending groups of communally breeding females can explain why we found more solitary males than females in every population. Our current study extends our previous findings, demonstrating that striped mice of different populations can either live solitarily (one population), in groups (one population), or that within an area both solitary and group living can occur (4 populations). Thus, social flexibility is a key characteristic of striped mice in both time and space.

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

Experimental manipulation of population density has resulted in changes in social organization in the cichlid *Neolamprologus pulcher* in captivity (Bergmüller et al.

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

In many primate species, individual flexibility in social behavior stabilizes the social organization, for example by changing dominance hierarchies and coalitions, such that the main form of social organization can be maintained (Schradin et al. 2018). In comparison, some other species, such as striped mice, cannot respond to conflict by adjusting their social hierarchy and groups might instead break up, leading to intra-specific variation in social organization (Schradin et al. 2018). Nevertheless, variation in social organization is also common in primates (Strier 2017; Agnani et al. 2018) and explained by socio-ecological models focusing on resource abundance (Dunbar 1988; Kappeler and Schaik 2002; Kappeler et al. 2013, 2017; Koenig et al. 2013) and demography (Moore 1999; Strier 2017). Comparing multiple populations of the same species helped to understand the adaptive significance of infanticide in langurs (Moore 1999). For primates, it has been suggested that intra-specific variation must be taken into account in comparative studies (Sandel et al. 2016) because it significantly changes our understanding of primate social evolution (Kappeler and Fichtel 2016). Similar claims have been made in the studies regarding cooperative breeding in birds, where the importance of variation within species has been ignored (Griesser and Suzuki 2016).

Individuals of both sexes changing their social tactics (individual trait) can change the social system of an entire population, which is called social flexibility (observed at the

population level; Schradin et al. 2012). It has been hypothesized that the variation in social organization observed between two populations of a species might be due to differences in population density (Taborsky and Taborsky 1999; Schradin and Pillay 2005; Martin and Martin 2007; Molina-Vacas et al. 2009) but more populations must be studied simultaneously to test this hypothesis (Maher and Burger 2011). To date, this phenomenon had been studied in relation to environmental change over time in one population (Schradin et al. 2018, 2019). Here, we showed that, for the metapopulation studied, intra-specific variation in social organization can be related to geographic variation in population density. Thus, social organization can differ at different localities simultaneously in time depending on population density. How individual dispersal tactics and associated changes in social tactics benefit individual fitness will require further studies. Our study emphasizes the importance of considering intra-specific variation in social tactics in both a spatial and temporal context.

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**Data availability** All data generated or analyzed during this study are included in the supplementary information files of this published article.

## Compliance with ethical standards

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

**Ethical approval** All animal experimentation met the ABS/ASAB guidelines for the ethical treatment of animals. 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.

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