

Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*)

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Summary

1. While the reasons for group-living have been studied for decades, little is known about why individuals become solitary.
2. Several previous experimental studies could demonstrate that group-living can arise as a consequence of ecological constraints.
3. It has been argued that reproductive competition between group members leads to significant costs of group-living, being a main reason of solitary-living. However, so far, no studies tested experimentally whether reproductive competition can explain solitary-living.
4. Using a socially flexible species, the African striped mouse (*Rhabdomys pumilio*), we tested experimentally in the field whether dispersal and solitary-living are more likely to occur when reproductive competition is present.
5. We investigated ecological constraints, here expressed as a function of population density, by removing groups of striped mice and creating vacant territories. To control for the effect of reproductive competition, which occurs only during the breeding season, we performed experiments during both the breeding and the non-breeding season. This is the first removal experiment performed in a species with communal breeding during the non-breeding season.
6. During the breeding season, when population density was low, more striped mice from experimental groups moved into the vacant territories and became solitary than striped mice from control groups. This is in support of the ecological constraints hypothesis.
7. During the non-breeding season, striped mice remained group-living despite the availability of free territories. Significantly, more striped mice became solitary-living during the breeding than during the non-breeding season. This is the first experimental support for the reproductive competition hypothesis explaining solitary-living.
8. Analysis of the sexual maturity of males showed that males which became solitary had a higher reproductive potential than males that remained group-living. Analysis of the body mass data of females showed that more solitary females reproduced than group-living females. These results indicate that by becoming solitary individuals of both sexes avoided costs of reproductive competition within groups.
9. Our study provides experimental evidence that reproductive competition within groups can lead to dispersal and solitary-living.

Key-words: dispersal, population density, seasonality, social flexibility, solitary-living

Introduction

Animals display highly diverse social systems, ranging from solitary species to species that form complex societies, such as

cooperative breeders with helpers at the nest (Taborsky 1994) and eusocial species (Burda *et al.* 2000). Much research has aimed to understand why social groups form and how they are maintained (Hamilton 1964; Wilson 2000). In contrast, no experimental study thus far has investigated the reasons for solitary-living, which is often simply regarded as the

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default mode of social organization. However, to understand the evolution of social organization, we also need to know why many individuals prefer a solitary life.

Social groups can form through the delayed dispersal of offspring. Such groups normally consist of dominant breeders and subordinate non-breeding offspring, which may act as helpers at the nest and gain indirect fitness benefits (Hamilton 1964; Emlen 1997). Remaining as subordinates within a social group can be costly for both sexes because of intra-group conflict, reproductive suppression and infanticide (Emlen 1982b; Brant *et al.* 1998). Thus, reproductive competition has been invoked as the main factor promoting dispersal and solitary-living in such groups (Emlen 1982a,b). Young adult individuals that delay dispersal and remain as philopatric subordinates in their natal group may incur costs: (i) by delaying onset of own reproduction; and (ii) by having to 'pay to stay' (Gaston 1978) by performing costly helping behaviour (MacColl & Hatchwell 2002; but see also Ekman, Sklepkovych & Tegelstrom 1994; Vangen *et al.* 2001; Chapple 2003) for offspring that delay dispersal but do not help. Therefore, why would an individual delay dispersal to remain at home?

Ecological constraints models (such as the 'habitat saturation hypothesis', Emlen 1982a) predict that offspring will remain philopatric when resources such as free territories or mating opportunities are scarce (Selander 1964; Pruett-Jones & Lewis 1990). Under such conditions, ecological constraints (e.g. high population density, Koenig *et al.* 1992) impose high costs on dispersal and individuals are thought to be doing 'the best of a bad job' by remaining philopatric. In other words, high dispersal costs imposed by ecological constraints increase the overall benefits of philopatry (Emlen 1982b, 1994; Stacey & Ligon 1991). Thus, the natal territory might become a 'safe haven' (Kokko & Ekman 2002) where young adult individuals have a better chance of survival by benefitting, for example, from group augmentation (Griesser, Nystrand & Ekman 2006), as well as a place where they can acquire new skills, such as parental care (Lancaster 1971; Komdeur 1996). For example, under conditions of high population density, it might pay for a young individual to delay dispersal until it is better able to compete with others for limited resources such as breeding territories (Arnold & Owens 1998).

Several removal experiments in the field have shown that the removal of ecological constraints, such as high population density, can lead to dispersal, supporting the ecological constraints hypothesis and explaining group-living (Pruett-Jones & Lewis 1990; Jacquot & Solomon 2004). For example, Komdeur (1992, 1994) showed through a manipulation experiment that habitat saturation and territory quality were important in maintaining group-living in the Seychelles warblers (*Acrocephalus sechellensis*). By experimentally providing vacant breeding sites, Bergmüller, Heg & Taborsky (2005) also demonstrated that helpers of a group-living cichlid (*Neolamprologus pulcher*) remained group-living in the presence of ecological constraints, but left and started independent breeding when ecological constraints were removed.

Further experimental evidence was provided by Lucia *et al.* (2008), who manipulated population density in prairie voles (*Microtus ochrogaster*) and demonstrated that high population density leads to delayed dispersal and group formation. However, these experiments did not explain why individuals dispersed after ecological constraints were relaxed, although it has been long argued that costs associated with reproductive competition might promote dispersal and solitary-living (Emlen 1982a). However, it is more difficult to experimentally manipulate reproductive competition than ecological constraints. One way to investigate the effect of reproductive competition on dispersal decisions and sociality would be to compare dispersal between periods with and without reproductive competition, which could be achieved by using a seasonally breeding species with year round territoriality.

The African striped mouse (*Rhabdomys pumilio*) represents an ideal model organism to experimentally test whether ecological constraints favour group-living while reproductive competition favours solitary-living. Striped mice are socially flexible which means that individuals can switch between a group-living and a solitary tactic (Schradin *et al.* 2011). As a result, the social organization of a striped mouse population can range from solitarily to complex family groups consisting of one breeding male, several breeding females and their adult offspring of both sexes, which remain philopatric as helpers at the nest (Schradin & Pillay 2004; Schradin, König & Pillay 2010). Previous correlative studies have shown that striped mice are solitary-living during the breeding season if population density is low, whereas they remain group-living when population density is high (Schradin, König & Pillay 2010). During the non-breeding season, when reproductive competition is absent, striped mice were found to be group-living independent of population density (Schradin, König & Pillay 2010). These conclusions were based on correlative observational data and need experimental testing to control for other environmental factors. In our study, we aimed to test experimentally whether high population density promotes group-living and reproductive competition promotes dispersal. We manipulated population density by removing neighbouring groups of mice and providing vacant territories for other individuals to move into, thus testing 'the ecological constraints hypothesis', comparing between striped mice from control and experimental groups in the same population, at the same time, and thus under identical ecological conditions. In addition, by taking advantage of the fact that striped mice are seasonal breeders (Schradin 2005), we were also able to investigate the role that reproductive competition plays on sociality by performing removal experiments both in the breeding and in the non-breeding season. This is thus the first removal study on a communally breeding species, which was performed during the non-breeding season. We predicted greater natal dispersal and decreased group sizes in experimental groups than in control groups. Further, we expected striped mice to remain group-living during the non-breeding season when reproductive competition is absent, but to disperse and become solitary in the breeding season when reproductive competition is present.

Materials and methods

STUDY AREA AND STUDY SPECIES

The study was conducted between August 2007 and August 2010 on a field site of 30 hectares located on the farm Klein Goegap (29°42'30" S–18°02'95" E) in the Northern Cape of South Africa. The vegetation type is classified as Succulent Karoo (Cowling, Esler & Rundel 1999), a semi-desert characterized by dwarf succulent shrubs. Here, striped mice typically form groups consisting of one breeding male and up to four breeding females, which are born during the previous breeding season (Schradin & Pillay 2004). Their offspring remain philopatric long after reaching adulthood (at an age of approximately four to six; Schradin, Schneider & Yuen 2009), acting as non-breeding helpers in their natal group (Schradin & Pillay 2004). In this study, we refer to individuals born during the previous breeding season as 'breeders', and to individuals born in the season during which the experiments took place as 'philopatrics' (to avoid confusion over the term 'adult' as individuals belonging to both categories could have been classified as sexually mature adults). Under low population density, philopatrics can leave their natal group when 4–6 weeks old to start independent breeding. The breeding season typically lasts for about 4 months and coincides with the flowering of the nutritious ephemerals in spring (from August/September to November; Schradin & Pillay 2005a). The non-breeding season normally lasts for 9 months and takes place from the hot dry summer (December to April) to the end of the moist cold winter (from May to August).

DETERMINATION OF SOCIAL TACTIC

All the striped mice within the study area were identified and their group affiliation determined using a combination of trapping, radiotracking and behavioural observations. Individuals were trapped directly at their nests using traps similar to Sherman's traps (26 × 9 × 9 cm). Each mouse was weighed, sexed, marked with permanent individual ear tags (National Band and Tag Co., Newport, KY, U.S.A.), and with a code-specific non-toxic hair dye (Inecto Rapido, Pinetown, South Africa). Markings were allowed for easy recognition of individuals during behavioural observations at their nests. Observations were conducted to determine group composition during the peak activity time for striped mice (i.e. in the early morning and in the late afternoon). All adult breeders and four philopatrics (two females and two males) of each group were fitted with radiocollars (Holohil, Carp, ON, Canada; 1.2–4.5 g). In total, we radiotracked 126 males and 166 females during four breeding seasons, and 81 males and 93 females during four non-breeding seasons. Striped mice were radiotracked using AOR 8000 radio-receivers (AOR USA Inc., Torrance, CA, USA) to determine home ranges and at night to determine composition of sleeping groups.

Striped mice were regarded as group-living if they shared the nest at night with the same individuals for at least 75% of the nights they were radiotracked. Individuals that were found to spend at least 75% of the nights alone were regarded as solitary. We did not find any individuals falling in between these two percentages, i.e. no individual was recorded to spend between 26% and 74% of the nights with a group or alone.

EXPERIMENTAL DESIGN

Removal experiments consisted of a replicated 2 × 2 factorial design with treatment (control, removal) and season (breeding, non-

breeding) as factors. Each season we conducted two replicates of controls and two replicates of treatments. Local population density was manipulated by removing mice to create vacant territories for neighbouring striped mice to move into. All the experiments were performed in a valley, with the removal groups being the closest to the valley walls, such that these groups had neighbours only on one side. At the time of the experiments, all the territories within the study areas were occupied by striped mice groups and no open space remained between the different territories (for more information on how group enlarge their home ranges see Schradin *et al.* 2010). Two replicates, separated by groups not used in the experiment, were carried out at the same time. Six groups were used in each replicate: two groups were removed; two groups were used as experimental groups and two groups were used as control groups (Fig. 1). Experimental groups directly neighbored removed groups and control groups, whereas control groups only neighbored experimental groups and additional non-observed groups. In this way, striped mice from experimental groups directly experienced a local reduction in population density, while striped mice from control groups only experienced a reduction in population density when some of their neighbours from experimental groups dispersed into the newly available territories. Whereas each year different groups were used for experiments, within the same year the same groups were observed for both the breeding and the non-breeding season. Before removal, home range size and group affiliation were determined by radiotracking mice six times per day for a period of 2 weeks (see Schradin & Pillay 2005b for details on the method used). Removal of groups took place immediately after radiotracking for home ranges had ended. Using a combination of trapping, radiotracking and nest observation, we were able to establish with precision to which group each mouse belonged to, and we were thus able to successfully remove all the mice belonging to the 'removal groups'. Removed striped mice were used for breeding in a captive colony or in other studies (brain immunohistochemistry; *unpublished data*). Trapping was continued in the vacant territories and if striped mice of unknown origin (three individuals of 16 replicates) immigrated into the area, they were removed.

Striped mice from experimental and control groups were radiotracked for an additional 4 weeks after removal, which from our experience is a period of time long enough to allow dispersal in this species (i.e. individuals will take between one and 3 weeks to disperse

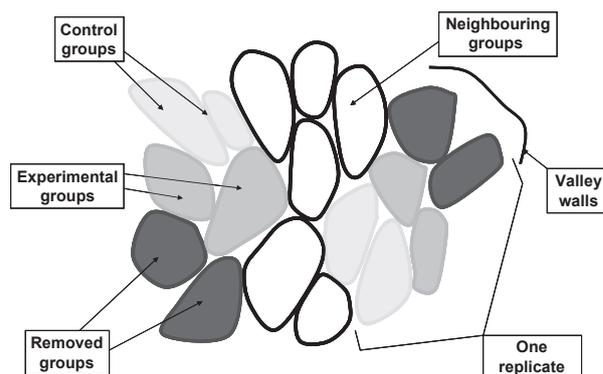


Fig. 1. Experimental design, with each polygon representing a group's home range. Each removal experiment consisted of two replicates of six groups each. Of these, two were removed (R1 and 2), two were monitored as experimental groups (E1 and 2) and two were used as control groups (C1 and 2). The white polygons separating the two replicates represent non-focal neighbouring groups, which were monitored only by trapping.

at the beginning of the breeding season, unpublished data). In total, eight replicates were carried out during the breeding season and eight replicates during the non-breeding season.

Local population density was measured separately for each replicate after removal of striped mice. For striped mice from experimental groups, local population density was calculated as the total number of individuals of control and experimental groups divided by the area occupied by removal, experimental and control groups. For striped mice from control groups, local population density was calculated as the total number of individuals of control and experimental groups divided by the area occupied by experimental and control groups. As local population density was influenced by group size of the studied control and experimental groups (local population density embeds group size), we did not include group size as a separate variable.

Males were regarded as potentially reproductively active when they were scrotal (i.e. their testes were fully descended; see Schradin & Pillay 2005a). Females were regarded as potentially reproductively active when they had a perforated vagina or showed signs of lactation (Schradin & Pillay 2005a). Parturition was determined by changes in females' body mass over a short period: a loss of > 10 g indicated that a female gave birth (Schubert, Pillay & Schradin 2009). A female was considered reproductively successful when she had given birth to at least one litter.

DATA ANALYSIS AND STATISTICS

Data analysis was performed using the statistical software R (version 2.11.0; R Development Core Team 2006, Vienna, Austria). All statistical tests were two-tailed. Data were tested for normality using the Shapiro–Wilk Normality test and are presented as mean \pm SD. To test the predictions that relaxed ecological constraints and the presence of reproductive competition would lead to greater natal dispersal and solitary-living, we first used a Wilcoxon sign-rank test (with exact *P*-value calculations in R to correct for the small sample size). When the standard deviation was zero, we used the sign test instead. We used a generalized linear model (GLM) with a binomial error family to analyse the proportion of group-living striped mice ($N = 32$; 16 experiments and 16 controls during both seasons), including relative population density, season (breeding and non-breeding) and treatment (experiment and control) as factors. Lines of best fit were fitted to the data for the breeding and the non-breeding season. We also used a GLM with a poisson error family to test for significant differences in the likelihood of individuals from four different social classes to become solitary: breeding males, breeding females, philopatric males and philopatric females. We first fitted a saturated model with a three-way interaction between dispersal (group and solitary), reproductive status (breeder and philopatric) and gender (male and female). We then tested for the significance of this interaction by deleting it from a second model and comparing between the two models. Fisher's exact tests were used to compare: (i) the number of reproductively mature philopatric and solitary females at time of dispersal; (ii) the number of reproductively successful solitary and philopatric females at the end of the breeding season; and (iii) the number of males that became scrotal among solitary and philopatric males before and after dispersal took place.

Results

During the breeding season and before removal, group size was 9.75 ± 3.45 individuals for control groups and

10.3 ± 5.34 individuals for experimental groups. During the non-breeding season and before removal, group size was 7.9 ± 2.99 individuals for control and 8.5 ± 2.94 individuals for experimental groups. Local population density was 11.10 ± 6.75 individuals/hectare for control groups and 12.71 ± 6.63 individuals/hectare for experimental groups during the breeding season, and 8.67 ± 7.29 individuals/hectare for control and 7.56 ± 4.06 individuals/hectare for experimental groups during the non-breeding season.

During the breeding season, more striped mice from experimental groups became solitary ($18.81 \pm 13.08\%$) than striped mice from control groups ($3.49 \pm 7.59\%$; Wilcoxon sign-rank test, $V = 0$, $N = 8$; $P = 0.008$; Fig. 2). During the non-breeding season, nearly all striped mice remained group-living (experimental groups: $99.31 \pm 1.96\%$; control groups: $100 \pm 0\%$; sign test, $\chi = 1$, $N = 8$, $P > 0.70$; Fig. 2). Significantly, more striped mice from experimental groups dispersed and became solitary in the breeding ($18.81 \pm 13.08\%$) than in the non-breeding season ($0.69 \pm 1.96\%$; Wilcoxon sign-rank test; $V = 35$, $N = 8$; $P = 0.016$; Fig. 2).

For all 32 replicates combined (experimental and control groups during both seasons), the proportion of group-living striped mice was significantly influenced by season (i.e. more mice became solitary during the breeding season: GLM: $F_{1,29} = 50.32$, $P < 0.001$), treatment (i.e. more mice from experimental groups became solitary: GLM: $F_{1,28} = 46.13$, $P < 0.001$) and by the interaction between season and local population density (population density played a role only during the breeding season but not during the non-breeding season; GLM: $F_{1,27} = 7.91$, $P = 0.009$), while local population density alone did not have an effect (GLM: $F_{1,30} = 1.21$, $P = 0.28$). The best fit for the relationship between population density (PD) and percentage of group-living striped mice (%GL) during the breeding season for the

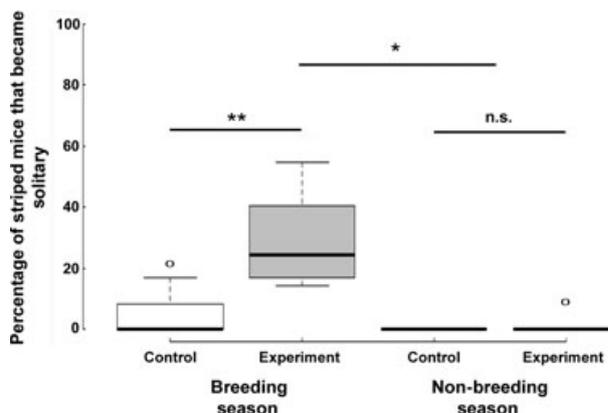


Fig. 2. During the breeding season, more mice from experimental groups became solitary than mice from control groups. During the non-breeding season, mice from experimental and control groups did not differ in their likelihood of becoming solitary. Mice were more likely to become solitary in the breeding season (time with reproductive competition) than during the non-breeding season. (* $P < 0.05$, ** < 0.01 , n.s. = not significant).

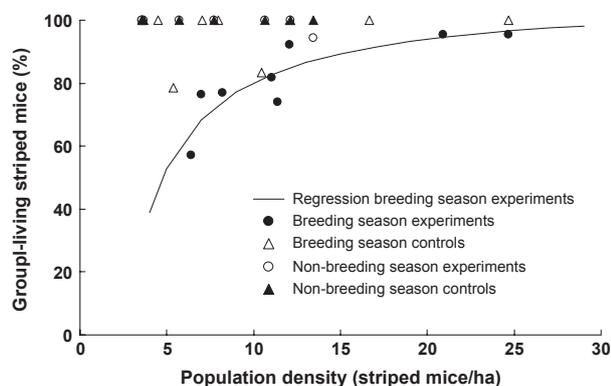


Fig. 3. Hyperbolic regression curve of the relationship between population density and group-living striped mice of experimental groups during the breeding season (black circles, black line, $N = 8$; $P < 0.001$). The hyperbolic regression curve was only fitted to the data of experimental groups during the breeding season (i.e. the black line only runs through the black dots). Data for experimental groups during the non-breeding season (white circles) and for control groups during the breeding (black triangles) and the non-breeding season (white triangles) were not significant. During the non-breeding season, many data overlap, thus not all the 16 points are clearly visible.

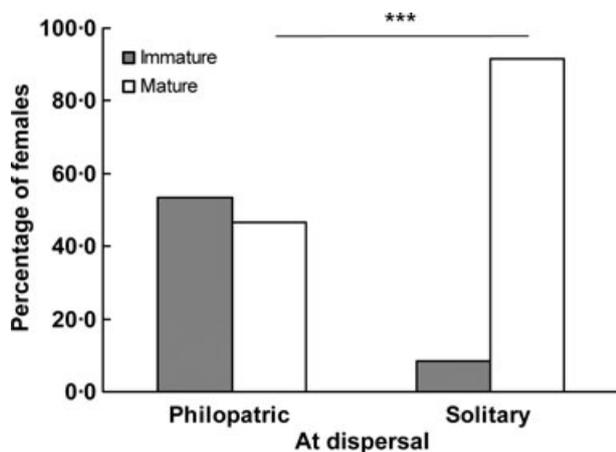


Fig. 4. At time of dispersal, significantly more females that became reproductively mature than females that philopatric ($***P < 0.001$).

experimental groups ($N = 8$) was obtained from a hyperbolic curve ($R = 0.87$, $F_{2,7} = 574.01$, $P < 0.001$, Fig. 3), resulting in $y = a + (b/x)$, with $y = \%GL$; $a = 107.65$; $b = -274.65$ and $x = PD$ (Fig. 3).

Breeding males (three of 28), breeding females (three of 27), philopatric males (19 of 76) and philopatric females (12 of 86) did not differ in their likelihood of becoming solitary (i.e. there were similar sex-by-reproductive status interactions, GLM: Df Residuals = 0.62, $P = 0.43$).

At the time of dispersal, more females that would become solitary were reproductively mature (11 of 12 females) than females that remained philopatric (48 of 103 females; Fisher exact test, $P < 0.000$, Fig. 4). No females reproduced before dispersal. At the end of the breeding season, we found that more females that had become solitary had produced at least



Fig. 5. Significantly more solitary females reproduced during the breeding season than philopatric females ($**P < 0.01$).

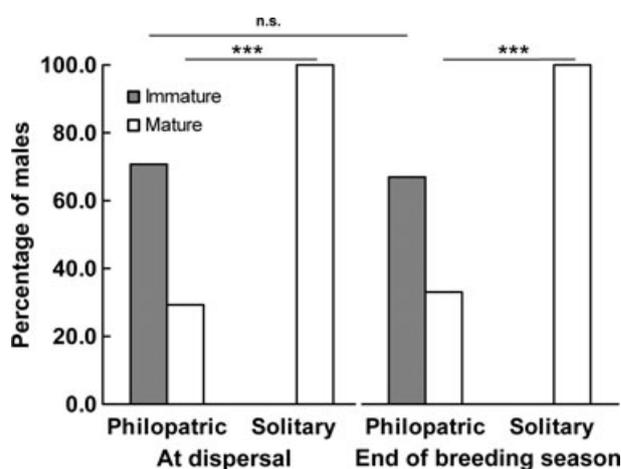


Fig. 6. Percentage of males that were scrotal with fully descended tests and thus regarded as sexually mature. Left: at the time of dispersal, a significantly higher percentage of solitary males was scrotal than philopatric males ($***P < 0.001$). Right: at the end of the breeding season, a significantly higher percentage of solitary males was scrotal than philopatric males ($***P < 0.001$). Philopatric males were not more likely to be scrotal at the end of the breeding season than at dispersal ($P = 0.66$, not significant).

one litter (nine of 12 females), while very few females that remained philopatric had reproduced (13 of 103 females; Fisher exact test, $P = 0.004$, Fig. 5).

At the time of dispersal, more males that would become solitary were scrotal (19 of 19 males) than males that remained philopatric (32 of 109 males; Fisher exact test, $P < 0.000$, Fig. 6). At the end of the breeding season, more solitary males (19 of 19) were scrotal than philopatric males (36 of 109; Fisher exact test, $P < 0.000$, Fig. 6). Philopatric males did not differ in scrotality at dispersal and at the end of the breeding season (Fisher exact test, $P = 0.66$, Fig. 6).

Discussion

Striped mice became solitary and moved into the vacant territories as they became available, but only during the breeding

season when reproductive competition was present. During the non-breeding season, striped mice remained group-living, even when vacant territories were available. Striped mice that became solitary had a higher reproductive capacity (males) or success (females), indicating that they were successful in avoiding reproductive competition. This is the first experimental field study providing evidence that reproductive competition can cause solitary-living when ecological constraints are relaxed.

Population density affected sociality in striped mice, but only during the breeding season. When population density was high and all the territories were occupied, striped mice remained group-living, supporting the habitat saturation hypothesis (Emlen 1982a; Hatchwell & Komdeur 2000). In contrast, more individuals dispersed and became solitary when local population density was low and vacant territories were available, providing an important resource for striped mice (Schradin, König & Pillay 2010). It has been suggested that not only the availability but also the quality of the resources available may affect the decision of an individual to disperse (Komdeur 1992). In our study, we did not measure territories quality; however, the territories from which we removed groups were directly adjacent the territories of experimental groups and were of similar size, supported a similar number of individuals as neighbouring experimental territories and striped mice belonging to experimental groups readily moved into the removed territories and took them over. This indicates that differences in territory quality did not play a significant role in our study. Our study thus indicates that breeding territories are a limiting resource for striped mice when population density is high.

The results of our study concur with correlative results obtained from an 8-year-long field study on a neighbouring population of striped mice, living only three kilometres away from our experimental field site (Schradin, König & Pillay 2010). Similarly to the observations of Schradin, König & Pillay (2010), our experiment showed that population density influences sociality, but only during the breeding season. In both studies, it was found that a hyperbolic curve is the best fit for the relationship between population density and percentage of group-living striped mice during the breeding season, while outside the breeding season, no relationship exists between population density and sociality (compare our Fig. 3 with Fig. 2 in Schradin, König & Pillay 2010). Previous experiments performed during the breeding season in fish (Bergmüller, Heg & Taborsky 2005; Stiver *et al.* 2006; Wong 2010), birds (Pruett-Jones & Lewis 1990; Walters 1991; Komdeur 1992) and mammals (Jacquot & Solomon 2004) already confirmed predictions of the ecological constraints hypothesis especially that groups form when resources are limited (Koenig *et al.* 1992; Kokko & Ekman 2002; Baglione *et al.* 2005). Ours is the first experiment in a mammal under natural conditions (vs. experiments in enclosures: Jacquot & Solomon 2004; Lucia *et al.* 2008), demonstrating the importance of territory availability on sociality.

While ecological constraints could explain why striped mice remained natally philopatric when population density was high, they cannot explain why they did not disperse when vacant territories were available in the non-breeding season. Reproductive competition can be high in striped mice of both sexes. In each group, a single breeding male monopolizes several communally breeding females (Schradin *et al.* 2009) and reproductively suppresses the adult philopatric males of the group (Schradin, Schneider & Yuen 2009). Female striped mice show intra-sexual aggression and infanticide towards the pups of other females within the group (Schradin, König & Pillay 2010). Thus, we attribute the difference in the results obtained between the breeding and non-breeding seasons to the role of reproductive competition which only occurs during the breeding season.

If reproductive competition is the reason for becoming solitary-living in striped mice, then solitary striped mice should be reproductively more successful than group-living ones. In support of this, we found that solitary males were scrotal and thus fully sexually mature, while many philopatric males (of the same age and body mass as solitary males) were not scrotal. In several cooperative-breeding species, subordinates are reproductively suppressed by dominant breeders (Blumstein & Armitage 1999; Saltzman *et al.* 2006; for male striped mice see Schradin, Schneider & Yuen) or may delay reproductive maturity to avoid aggressive expulsion by the dominant breeders (Hamilton 2004). In our study, most of the male striped mice that remained philopatric also remained unscrotal during the entire breeding season, suggesting that they were unable to escape reproductive suppression. While we could not measure reproductive success of males, our data indicate that solitary males, which were all scrotal, might have reproduced, while most of the philopatric males could not reproduce, as they were not scrotal. For females, our data gave even better support: females that dispersed were more reproductively mature than group-living philopatrics, and 75% of solitary females reproduced, but only 13% of philopatric females. Our results indicate that striped mice that became solitary reduced costs of reproductive competition within groups, which were significant for striped mice that remained philopatric.

While reproductive competition is one cost of group-living, remaining within the natal group may also offer considerable advantages. Benefits of group-living include enhanced protection against predation, better resource defence and energy savings (Krause & Ruxton 2002). Predation pressure, mainly from many-horned adders (*Bitis cornuta*), jackal buzzards (*Buteo rufofuscus*) and African wildcats (*Felis silvestris lybica*), was significant at our field site, with > 40% of radiocolared striped mice lost before the end of our experiment. Increased group vigilance has been suggested as one of the potential advantages of communal nesting and has been reported for several species (Gagliardo & Guildford 1993; Krebs & Davies 1993). Striped mice sleeping in groups might benefit from increased vigilance against potential predators at night (Schradin 2005). Additionally, groups may be better able to defend territories than single individuals, as all group

members participate in territorial defence (Schradin 2004). Territories contain essential feeding and nesting areas during periods of scarcity, such as during the dry season. Most importantly, by remaining within the group, striped mice can obtain thermoregulatory benefits from huddling together at night, significantly reducing energy expenditure and water consumption: benefits are particularly important for a species that lives in a semi-desert environment (Scantlebury *et al.* 2006). Costs of group-living can include intra-group competition for limited resources such as food, and transmission of parasites (Danchin, Giraldeau & Wagner 2008). Significant benefits of group-living exist in striped mice, which are predicted to be higher than costs of group-living during the non-breeding season, leading to group-living. However, when the extra costs of reproductive competition arise during the breeding season, such as reproductive suppression and infanticide, the costs seem to be higher than the benefits, leading to solitary-living if costs of dispersal (= benefits of philopatry) are low.

Dispersal and resulting solitary-living of striped mice can thus be explained as a tactic to avoid reproductive competition and, in the case of young adult philopatrics, to start independent breeding. While most of the individuals that dispersed were young philopatrics, we also observed breeding adults born during the previous breeding season dispersing and becoming solitary, and there was no significant difference between breeders and philopatrics. Striped mice are socially flexible, i.e. individuals of both sexes can follow alternative reproductive tactics (Schradin *et al.* 2011). Male striped mice have the following tactics: (i) to remain as philopatric helpers in their natal group; (ii) to disperse and become solitary roamers with defined home ranges; or (iii) to become group-living territorial breeders (Schradin *et al.* 2009). Female striped mice have the following options: (i) to remain as philopatric helpers in their natal group; (ii) to disperse and breed singly; or (iii) to breed communally (Schradin, Schneider & Lindholm 2010). When population density is high, being a territorial breeding male is the most successful tactic, but when population density is low and resources, such as females, are not clumped (i.e. females breed solitarily and not communally), being a roamer is the preferred tactic (Schradin & Lindholm 2011). Our results concur with previous correlative studies demonstrating that at the beginning of the breeding season, striped mice of both sexes that were born during the previous breeding season leave huddling groups and follow a solitary tactic, if vacant territories are available (Schradin, König & Pillay 2010).

Whereas several previous experimental studies demonstrated the importance of ecological constraints in maintaining group-living (Jacquot & Solomon 2004; Dickinson & McGowan 2005; Griesser *et al.* 2008), no experimental studies thus far tested the reasons for solitary-living. This is peculiar as reproductive competition within groups has often been used as a plausible explanation for why individuals disperse and become solitary (Emlen 1982a, 1997). In our study, we were able to show that free-living striped mice leave com-

munal groups and become solitary if vacant territories are provided experimentally, but they do so only during the breeding season. Population density alone could not explain this, and as our controls during the non-breeding season were performed during both the hot dry summer when food availability is low and the moist cold winter, when food availability is high, neither temperature nor food *per se* is likely to explain our results (see also Schradin, König & Pillay 2010). Thus, the main difference between the breeding and the non-breeding season is the presence or absence of reproductive competition, which is the most parsimonious explanation for the differences in sociality we found. Further, we found evidence for both sexes that striped mice were able to avoid reproductive competition by becoming solitary. This is to our knowledge so far the best experimental evidence that reproductive competition within groups is responsible for dispersal and can lead to solitary-living.

Acknowledgements

We wish to thank the manager and staff of the Goegap Nature Reserve for their support and the Department of Tourism, Environment and Conservation of the Northern Cape for research permits. We are also thankful to Steyn Jacobson, owner of the Farm Klein Goegap, for permitting us to conduct our experiments on his property. We are grateful to the research station manager C.H. Yuen, J. Raynaud and G. Schmol as well as the many field assistants who contributed to the project. We are grateful to Y. Auclair, C. Bousquet, L. Hayes, A. K. Lindholm and M. B. Manser for their comments and N. Pillay for comments and assistance with the statistical analysis. The Swiss National Science Foundation (grant 3100A0-120194 to CS), the Swiss Academy of Natural Sciences and the Swiss South African Joint Research Programme provided the funding. The study obtained ethical clearance from the University of the Witwatersrand (AESC: 2007/38/04).

References

- Arnold, K.E. & Owens, I.P.F. (1998) Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London, Series B*, **265**, 739–745.
- Baglione, V., Marcos, J.M., Canestrari, D., Griesser, M., Andreotti, G., Bardini, C. & Bogliani, G. (2005) Does year-round territoriality rather than habitat saturation explain delayed natal dispersal and cooperative breeding in the carrion crow? *Journal of Animal Ecology*, **74**, 842–851.
- Bergmüller, R., Heg, D. & Taborsky, M. (2005) Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society of London, Series B*, **272**, 325–331.
- Blumstein, D.T. & Armitage, K.B. (1999) Cooperative breeding in marmosets. *Oikos*, **84**, 369–382.
- Brant, C.L., Schwab, T.M., Vandenberg, J.G., Schaefer, R.L. & Solomon, N.G. (1998) Behavioural suppression of female pine voles after replacement of the breeding male. *Animal Behaviour*, **55**, 615–627.
- Burda, H., Honeycutt, R.L., Begall, S., Locker-Grutjen, O. & Scharff, A. (2000) Are naked and common mole-rats eusocial and if so, why? *Behavioral Ecology and Sociobiology*, **47**, 293–303.
- Chapple, D.G. (2003) Ecology, life-history, and behavior in the Australian Scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs*, **17**, 145–180.
- Cowling, R.M., Esler, K.J. & Rundel, P.W. (1999) Namaqualand, South Africa – an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology*, **142**, 3–21.
- Danchin, E., Giraldeau, L.A. & Wagner, R.H. (2008) Animal aggregations: hypothesis and controversies. *Behavioural Ecology* (eds E. Danchin, L.A. Giraldeau & F. Cézilly), pp. 503–545. Oxford University Press, Oxford, United Kingdom.
- Dickinson, J.L. & McGowan, A. (2005) Winter resource wealth drives delayed dispersal and family-group living in western bluebirds. *Proceedings of the Royal Society of London, Series B*, **272**, 2423–2428.

- Ekman, J., Sklepkovych, B. & Tegelstrom, H. (1994) Offspring retention in the Siberian Jay (*Perisoreus infaustus*) – the prolonged Brood Care Hypothesis. *Behavioral Ecology*, **5**, 245–253.
- Emlen, S.T. (1982a) The evolution of helping. I. An ecological constraints model. *American Naturalist*, **119**, 29–39.
- Emlen, S.T. (1982b) The evolution of helping. II. The role of behavioral conflict. *American Naturalist*, **119**, 40–53.
- Emlen, S.T. (1994) Benefits, constraints and the evolution of family. *Trends in Ecology & Evolution*, **9**, 282–285.
- Emlen, S.T. (1997) Predicting family dynamics in social vertebrates. *Behavioral Ecology* (eds J.R. Krebs & N.B. Davies), Vol. 4, pp. 228–253. Blackwell Science, Oxford, United Kingdom.
- Gagliardo, A. & Guildford, T. (1993) Why do aposematic prey live gregariously? *Proceedings of the Royal Society of London, Series B*, **251**, 69–74.
- Gaston, A.J. (1978) Evolution of group territorial behavior and cooperative breeding. *American Naturalist*, **112**, 1091–1100.
- Griesser, M., Nystrand, M. & Ekman, J. (2006) Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society of London, Series B*, **273**, 1881–1886.
- Griesser, M., Nystrand, M., Eggers, S. & Ekman, J. (2008) Social constraints limit dispersal and settlement decisions in a group-living bird species. *Behavioral Ecology*, **19**, 317–324.
- Hamilton, W.D. (1964) The genetical evolution of social behaviour I and II. *Journal of Theoretical Biology*, **7**, 1–16 and 17–52.
- Hamilton, I.M. (2004) A commitment model of reproductive inhibition in cooperatively breeding groups. *Behavioral Ecology*, **15**, 585–591.
- Hatchwell, B.J. & Komdeur, J. (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, **59**, 1079–1086.
- Jacquot, J.J. & Solomon, N.G. (2004) Experimental manipulation of territory occupancy: effects on immigration of female prairie voles. *Journal of Mammalogy*, **85**, 1009–1014.
- Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L. & Standback, M.T. (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology*, **67**, 111–150.
- Kokko, H. & Ekman, J. (2002) Delayed dispersal as a route to breeding: territorial inheritance, safe havens and ecological constraints. *American Naturalist*, **160**, 468–484.
- Komdeur, J. (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, **358**, 493–495.
- Komdeur, J. (1994) Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behavioral Ecology and Sociobiology*, **34**, 175–186.
- Komdeur, J. (1996) Influence of helping and breeding experience on reproductive performance in the Seychelles warbler a translocation experiment. *Behavioral Ecology*, **7**, 326–333.
- Krause, J. & Ruxton, G.D. (2002) *Living in Groups*. Oxford University Press, Oxford, United Kingdom.
- Krebs, J.R. & Davies, N.B. (1993) *An Introduction to Behavioural Ecology*. Oxford Blackwell Scientific, Oxford, United Kingdom.
- Lancaster, J.B. (1971) Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica*, **15**, 161–182.
- Lucia, K.E., Keane, B., Hayes, L.D., Lin, Y.K., Schaefer, R.L. & Solomon, N.G. (2008) Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behavioral Ecology*, **19**, 774–783.
- MacColl, A.D.C. & Hatchwell, B.J. (2002) Temporal variation in fitness pay-offs promotes cooperative breeding in long-tailed tits (*Aegithalos caudatus*). *American Naturalist*, **160**, 186–194.
- Pruett-Jones, S.G. & Lewis, M.J. (1990) Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature*, **348**, 541–542.
- Saltzman, W., Ahmed, S., Fahimi, A., Wittwer, D.J. & Wegner, F.H. (2006) Social suppression of female reproductive maturation and infanticidal behavior in cooperatively breeding Mongolian gerbils. *Hormones and Behavior*, **49**, 527–537.
- Scantlebury, M., Bennett, N.C., Speakman, J.R., Pillay, N. & Schradin, C. (2006) Huddling in groups leads to daily energy savings in free-living African Four-Striped Grass Mice, *Rhabdomys pumilio*. *Functional Ecology*, **20**, 166–173.
- Schradin, C. (2004) Territorial defense in a group-living solitary forager: who, where, against whom? *Behavioral Ecology and Sociobiology*, **55**, 439–446.
- Schradin, C. (2005) When to live alone and when to live in groups: ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784). *Belgian Journal of Zoology*, **135**, 77–82.
- Schradin, C., König, B. & Pillay, N. (2010) Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology*, **79**, 515–521.
- Schradin, C. & Lindholm, A.K. (2011) Relative fitness of alternative male reproductive tactics in a mammal varies between years. *Journal of Animal Ecology*, **80**, 908–917.
- Schradin, C. & Pillay, N. (2004) The striped mouse (*Rhabdomys pumilio*) from the Succulent Karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology*, **118**, 37–47.
- Schradin, C. & Pillay, N. (2005a) Demography of the striped mouse (*Rhabdomys pumilio*) in the Succulent Karoo. *Mammalian Biology*, **70**, 84–92.
- Schradin, C. & Pillay, N. (2005b) Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy*, **86**, 99–107.
- Schradin, C., Schneider, C. & Lindholm, A. (2010) The nasty neighbour in the striped mouse (*Rhabdomys pumilio*) steals paternity and elicits aggression. *Frontiers in Zoology*, **7**, 19.
- Schradin, C., Schneider, C. & Yuen, C.H. (2009) Age at puberty in male African striped mice: the impact of food, population density and the presence of the father. *Functional Ecology*, **23**, 1004–1013.
- 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. *American Naturalist*, **173**, 376–388.
- Schradin, C., Schmohl, G., Rodel, H.G., Schoepf, I., Treffler, S.M., Brenner, J., Bleeker, M., Schubert, M., König, B. & Pillay, N. (2010) Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. *Animal Behaviour*, **79**, 195–203.
- Schradin, C., Lindholm, A.K., Johannesen, J., Schoepf, I., Yuen, C.H., König, B. & Pillay, N. (2011) Social flexibility as a tool to understand social evolution in mammals: the case of the African striped mouse (*Rhabdomys pumilio*). *Molecular Ecology*, doi: 10.1111/j.1365-294X.2011.05256.x.
- Schubert, M., Pillay, N. & Schradin, C. (2009) Parental and alloparental care in a polygynous mammal. *Journal of Mammalogy*, **90**, 724–731.
- Selander, R.K. (1964) Speciation in wrens of the genus *Campylorhynchus*. *University of California Publications in Zoology*, **74**, 1–305.
- Stacey, P.B. & Ligon, J.D. (1991) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *American Naturalist*, **137**, 831–846.
- Stiver, K.A., Fitzpatrick, J., Desjardins, J.K. & Balshine, S. (2006) Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. *Animal Behaviour*, **71**, 449–456.
- Taborsky, M. (1994) Sneakers, satellites, and helpers – parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, **23**, 1–100.
- Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerstrom, P. (2001) Characteristics of dispersal in wolverines. *Canadian Journal of Zoology*, **79**, 1641–1649.
- Walters, J.R. (1991) Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. *Annual Review of Ecology and Systematics*, **22**, 505–523.
- Wilson, O.E. (2000) *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, Massachusetts, USA.
- Wong, M.Y.L. (2010) Ecological constraints and benefits of philopatry promote group-living in a social but non-cooperatively breeding fish. *Proceedings of the Royal Society of London, Series B*, **277**, 353–358.

Received 22 August 2011; accepted 19 November 2011
 Handling Editor: Stan Boutin