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Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice

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Summary

1. Social groups typically form due to delayed dispersal of adult offspring when no opportunities for independent breeding exist, or the costs of dispersal are higher than the costs of remaining philopatric. Ecological constraints are thought to be a main reason for group-living in animals.
2. Reproductive competition within groups can induce high costs of philopatry, and is thought to be a main reason for solitary living.
3. Experimental manipulation of reproductive competition is difficult. One solution is to compare sociality between periods with and without reproductive competition.
4. Here, we show empirically in a 8-year field study that striped mice (*Rhabdomys pumilio*) of both sexes were group-living during the breeding season when population density (PD) was high but solitary living when PD was low, supporting the ecological constraints model.
5. After the breeding season, in the absence of reproductive competition, the positive correlation between PD and percentage of group-living striped mice was absent. Almost all striped mice were group-living even under very low population densities. This supports the reproductive competition model.
6. Ambient temperature, food availability and predation pressure, did not influence sociality.
7. In captivity, the costs of reproductive competition in communal groups include female infanticide and aggression between females.
8. We conclude that group-living is favoured by constraints imposed through habitat saturation and by its benefits (improved thermoregulation by huddling, group-territoriality and predator avoidance), and that reproductive competition is a major force favouring solitary living in striped mice.

Key-words: communal nesting, cooperative breeding, flexibility, helper

Introduction

Reproductive competition occurs when the reproductive output of an individual is decreased due to the presence of a conspecific. As reproductive competition and conflict are inevitable in group-living species (Emlen 1982b), social groups are characterized by conflict over who reproduces (Emlen 1997). Most species solve this conflict by living solitarily (Emlen 1982a).

The idea that a low level of reproductive competition favours group-living has formed the theoretical framework for studying animal sociality (Krebs & Davies 1993; Clutton-Brock 2005). Reproductive competition can be manifested in

individuals being expelled from the group when they start breeding (Clutton-Brock 2005), in reproductive suppression through behavioural (Reyer, Dittami & Hall 1986; Brant *et al.* 1998; Wingfield & Sapolsky 2003) or olfactory cues (Faulkes & Bennett 2001), and in killing of offspring (Koenig *et al.* 1995; Reeve & Keller 2001; Clutton-Brock 2005). However, to date, there has been little empirical evidence that reproductive competition influences sociality intraspecifically.

The degree of reproductive competition in a group can be measured by reproductive skew, which quantifies the extent to which same sex group members differ in their breeding output. Low reproductive skew apparently favours philopatry, because philopatric offspring do not suffer the costs of a delayed onset of reproduction, while high reproductive skew

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should favour solitary living (Ragsdale 1999; Kokko 2003; Reeve & Shen 2006). However, reproductive skew in cooperatively breeding species differs remarkably (Sherman *et al.* 1995), ranging from species in which nearly all sexually mature individuals reproduce (plural breeders, e.g. banded mongooses, *Mungos mungo*; Gilchrist 2006), to species where dominants suppress reproduction of subordinates most of the time (meerkats, *Suricata suricatta*; Clutton-Brock 2005), to species where only the dominant breeders reproduce (female naked mole rats, *Heterocephalus glaber*; Burda *et al.* 2000). Similarly, the resolution of reproductive competition in social insects has led to the evolution of advanced animal societies with high reproductive skew (Reeve & Keller 2001).

The main reason that offspring remain philopatric, even when they cannot breed in their natal group, is believed to be ecological constraints. Offspring stay at home when opportunities for independent breeding are absent as no territories or only territories of suboptimal quality are available (Emlen 1982a; Koenig *et al.* 1992). The importance of suitable territories has been demonstrated experimentally by removal of breeding individuals and thus providing free territories, causing philopatric offspring to disperse from their natal territory and start independent breeding (Pruett-Jones & Lewis 1990; Komdeur 1992; Bergmüller, Heg & Taborsky 2005). In small mammals such as prairie voles (*Microtus ochrogaster*), sociality is density dependent (Lucia *et al.* 2008). Habitat saturation, however, cannot explain why delayed dispersal occurs in some species but not in others that live under similar ecological conditions (Koenig *et al.* 1992; Hatchwell & Komdeur 2000; Baglione *et al.* 2005). Furthermore, even suitable territories are not used if they are of low quality (Heg *et al.* 2008), and it is difficult to determine whether a habitat is 'saturated', or what constitutes an acceptable territory into which an individual can disperse (Koenig *et al.* 1992; Komdeur 1992). Thus, most studies have investigated the influence of population density (PD), a correlate of habitat saturation, on sociality. Population density influences the availability and quality of territories, which determine relative fitness payoffs of independent breeding. Therefore, offspring are more likely to remain philopatric when PD is high, resulting in the formation of families, while dispersal and independent breeding is preferred when PD is low, suitable breeding territories are available, and costs of dispersal are low.

Evidence that reproductive competition acts against group-living is surprisingly rare. One reason for this may be the difficulty of manipulating reproductive competition experimentally. One approach would be to compare intraspecifically periods when reproductive competition occurs (breeding season) with periods when reproductive competition is absent (non-breeding season). Here, we studied African striped mice (*Rhabdomys pumilio*), which defend territories both within the 4-month breeding season in spring and the 8-month non-breeding season for the remainder of the year (Schradin & Pillay 2004).

In striped mice, group-living is beneficial due to reduced energy expenditure by huddling in the nest (Scantlebury

et al. 2006), increased vigilance for predators in communal nests (Schradin 2005b) and group defence of limiting resources (Schradin & Pillay 2004). Nevertheless, this species shows high social flexibility, ranging from solitary living to extended family groups with 2–4 communally breeding females and helpers at the nest (Schradin & Pillay 2004). Competition between female striped mice occurs in the form of infanticide (Schradin & Pillay 2003; Schradin, Kinahan & Pillay 2009a) and could be a main cost of group-living, counteracting sociality. Apart from reproductive competition, several other factors might favour solitary vs. group-living in striped mice. If resources such as food are scarce, individuals might be forced to have larger home ranges that support only a single individual (Schradin 2005b). In fact, the availability of protein rich food plants is important in determining the breeding season and home range sizes (Schradin & Pillay 2006a; Schradin *et al.* in press). On the other hand, the benefits of group-living might vary seasonally. Thermoregulatory benefits due to huddling promote group-living in many small mammals, especially in winter (i.e. non breeding season; Canals, Rosenmann & Bozinovic 1989). Predator avoidance can also favour group-living (Schradin 2000), and seasonal variation in predation pressure could influence group-living vs. solitary living. Thus, when testing whether reproductive competition influences sociality, it is important to control for such co-factors.

In the present study, we focussed on the two mutually non-exclusive hypotheses that explain why animals live in groups or are solitary, and aimed to test the following predictions:

- 1 The ecological constraints model predicts that animals remain philopatric and form groups if opportunities for independent breeding are limited (Emlen 1982a). Thus, we predicted a positive correlation between PD and the percentage of striped mice living in groups, as high PD constrains dispersal due to a lack of unoccupied territories.
- 2 The reproductive competition model states that competition for reproduction within groups leads to significant costs of group-living, one main reason for social groups being inherently unstable (Emlen 1995). We therefore tested for reproductive competition within groups, and predicted that groups are unstable under conditions of reproductive competition (breeding season: groups break up and mice become solitary) but not when reproductive competition is absent (non-breeding season).

Materials and methods

STUDY AREA AND PERIOD

The study was conducted from 2001 to 2009 in Goegap Nature Reserve near Springbok, South Africa (S29 41.56, E18 1.60). We collected data in December 2001, September to November 2002, July 2003 to January 2004, July 2004 to April 2005, August 2005 to April 2006 and August 2006 to September 2009. The vegetation type is classified as Succulent Karoo (Cowling, Esler & Rundel 1999); the locality is arid, with an average rainfall of 160 mm p.a.

STUDY SPECIES

Striped mice are diurnal, inhabit an open habitat and are readily habituated to the presence of observers, which allows for direct behavioural observations in the field (Schradin & Pillay 2004). The breeding season of 3–4 months (2–3 litters per female) begins in spring, typically in August/September, depending on the rainfall (Schradin & Pillay 2005a). The striped mouse is an 'annual' species. Between 1% and 20% of individuals that are born in one breeding season survive until the next breeding season, when they breed themselves, but individuals do not survive for another year (Schradin & Pillay 2005a). Thus, every year represents another generation. Groups consist of close kin (Schradin & Lindholm, unpublished data) and are stable during the non-breeding season, but can break up at the start of the new breeding season. When no kin are available (low PD due to high mortality), unrelated striped mice form huddling groups during winter (Schradin, Schubert & Pillay 2006b). Apart from these specific conditions, unrelated mice do not form groups, but groups form by offspring remaining philopatric.

DETERMINATION OF SOCIAL TACTIC

On average, 12.4 ± 4.1 (range: 8–20) striped mouse groups were observed per year. The size of the study area varied from 1.3 to 16.0 ha (average: 7.9 ± 4.7 ha) depending on PD. Trapping was done around nesting sites, at least 3 days per month, as described elsewhere (Schradin & Pillay 2004). Trapped striped mice were weighed, sexed and permanently marked with ear tags (National Band and Tag Co., Newport, KY, USA) and temporarily with hair dye (Rapido, Pinetown, South Africa) for individual recognition during behavioural observations (Schradin 2006). All solitary living individuals and one to four striped mice from each group were fitted with radio-collars (Holohil, Ontario, Canada). Striped mice were radio-tracked as described elsewhere (Schradin & Pillay 2005c) to determine the sleeping sites of the groups. On average, 45.8 ± 18.9 striped mice were radio-tracked each year (range: 23–75). We observed all nests at the field site to determine individual group affiliation (Schradin & Pillay 2004).

The striped mouse offers an easy way to determine whether they are solitary or live in groups: group-living striped mice share one nest at night. Thus, by radio-tracking the diurnal striped mice at night and determining their nesting sites, one can determine whether individuals sleep in groups or alone. We determined sleeping sites five times a week for the entire study period. We defined social individuals as mice living in groups of 2 or more adult individuals for more than 50% of the time. This included 11 pairs with juvenile offspring during the breeding seasons (2 in 2005, 1 in 2006, 4 in 2007, 1 in 2008 and 3 in 2009). These pairs originated from polygynous groups of which one or more females disappeared due to predation. Individuals that were sleeping alone or with different partners for more than 70% of the time were regarded as solitary. This included females and their immature offspring as well as roaming males that spent some nights with females but otherwise slept alone, as well as single females visited by roaming males.

We determined the percentage of group-living striped mice during the pre-breeding season, breeding season and post-breeding season. The pre-breeding season typically covered 2 months before the onset of breeding and included August 2003, July 2004, June 2007, July 2008 and June 2009. No data were available for 2001, 2002. For 2005 and 2006, we used data from April and March respectively, as no data were available for May to July. For the breeding season, we used data collected in September, with the exception of 2003, when we

used data collected in October due to the delayed onset of breeding. For the post-breeding season, we used data from January 2004 to 2009, 2–3 months after breeding had terminated, when all individuals in the population were adults. For 2001, data were only available for December, and for 2002 only for the end of November.

POPULATION DENSITY

The PD of adults was estimated from the number of sexually mature individuals (body mass > 30 g) trapped divided by total study area size. Population density varied over the years due to differences in food abundance, drought and predation. In good years, 27% of the adults survived from the post-breeding season to the next breeding season (Schradin & Pillay 2005a), but mortality increased to 99% during the non-breeding season in 2003 due to an extreme drought (Schradin 2005a; Schradin *et al.* 2006b). During the dry season in 2005 and 2009, unexpected rainfall led to a short additional breeding season (February–April) and thus an increase in PD. In 2007 and 2008, PD declined steeply due to high predation pressure by African wildcats, jackals and raptors.

POTENTIAL CO-FACTORS OF SOCIALITY

Data on possible co-factors were recorded from the 2004 breeding season onwards (five pre-breeding, six breeding and five post-breeding seasons).

Food availability

We sampled eight plots each of 2×2 m within the home ranges of eight groups on the 15th of each month, using standard protocols (Braun-Blanquet Method; Werger 1974), recording the number of food plant species in each plot (palatability was known from a previous study; Schradin & Pillay 2006a). For analysis, we used the monthly mean values of the eight plots.

Ambient temperature

Daily minimum temperatures were recorded at the research station in the shade, 5 cm above ground (i.e. in the area used by striped mice). Monthly averages were used for analysis.

Estimation of relative predation pressure

Whenever we found a transmitter in the field of a collared striped mouse that had disappeared, we recorded the most likely cause of disappearance. When the transmitter was in the pellet of a bird of prey, detected inside a snake, covered by blood, or next to fur remains, death due to predation was assumed to be the cause of disappearance. We calculated the percentage of radio-tagged striped mice that were lost due to predation for each season. This gave us a value of relative predation pressure, which is an underestimation of total predation pressure, as we did not find all lost transmitters and not all mice were carrying transmitters.

REPRODUCTIVE COMPETITION BETWEEN FEMALES OF COMMUNAL GROUPS IN CAPTIVITY

We kept groups of striped mice in a captive colony at our research station in the study area under semi-natural conditions, as described elsewhere (Schradin & Pillay 2005b). We collected data from 54 communal groups and 37 monogamous pairs from 2005 to 2008.

Communal groups consisted of two, same-litter full sisters and one unrelated male. Monogamous pairs were used to test whether conflict between males and females could be a cost of group-living, leading to solitary living. Communal groups were kept in two glass tanks ($49 \times 34 \times 40$ cm) connected by a tube, while monogamous pairs were housed in a single cage. Cages were checked weekly when females were weighed. When pups were born, we used data from female body mass to ascribe maternity in communal groups. We recorded any indications of infanticide, i.e. killed or partly eaten pups. We also recorded any incidence of aggression within groups.

DATA ANALYSIS

The software packages SAS 9.1.3, INSTAT 3.05 and CURVEEXPERT were used. Data are presented as mean \pm SD. To obtain maximum independence, data were analysed at the levels of year and season, with all striped mice from a single year and season representing one data point. Correlations were done using Spearman correlations (r_s). We used a General Linear Model (GLM) to explain the percentage of group-living striped mice using type III (simultaneous) modelling; PD, food availability, average minimum ambient temperatures and percentage of predated striped mice were covariates, and season (1 = breeding season, 2 = non-breeding season) a categorical effect. The only variables that correlated significantly with each other were food availability and temperature ($r = -0.51$, $P = 0.04$), because more food was available during the cold rainy season. Due to the high number of predictive variables and low sample size ($n = 16$ seasons in 6 years; see above) we only considered interactions that were predicted to be significant on theoretical grounds, i.e. season \times PD (PD was predicted to only play a role during the breeding, but not during the non-breeding season). Data from the captive study were compared using the Fisher's exact test.

Results

FIELD DATA

During the pre-breeding season, nearly all striped mice were group-living, independent of PD ($r_s = 0.27$, $n = 7$ years, $P = 0.56$; Fig. 1a). During the breeding season, PD correlated positively and significantly with the percentage of group-living striped mice ($r_s = 0.93$, $n = 8$ years, $P = 0.002$, Bonferroni corrected $P = 0.006$; Fig. 1b). This correlation disappeared after the breeding season in summer, when striped mice were again almost always group-living, independent of PD ($r_s = 0.16$, $n = 8$ years, $P = 0.70$; Fig. 1c).

The GLM revealed that PD ($F_{1,15} = 5.34$, $P = 0.046$) and season ($F_{1,15} = 26.77$, $P = 0.0006$) had a significant effect, with more striped mice being solitary during the breeding season and when PD was low. Their interaction was also statistically significant ($F_{1,15} = 5.12$, $P < 0.05$), indicating that PD only played a role during the breeding season, but not during the non-breeding season. In contrast, food abundance ($F_{1,15} = 0.00$, $P = 0.97$), ambient temperature ($F_{1,15} = 0.02$, $P = 0.90$) and predation ($F_{1,6} = 1.13$, $P = 0.32$) had no significant effect on whether striped mice were solitary or group-living.

The best non-linear fit for the relationship between PD and percentage of group-living striped mice (PGL) during the

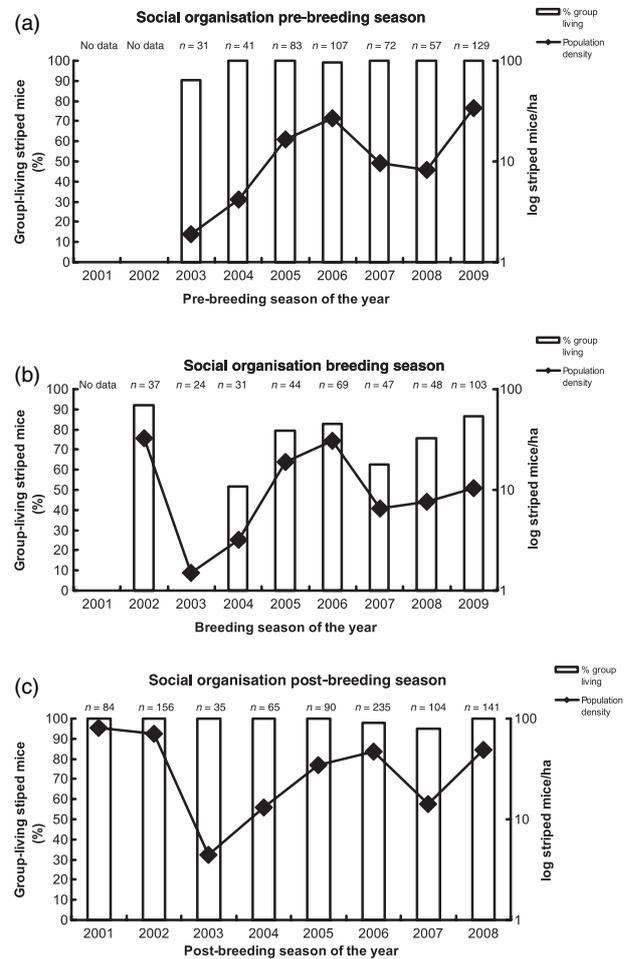


Fig. 1. The relationship between population density and number of striped mice that were group-living during (a) the pre-breeding season, (b) the breeding season and (c) the post-breeding season. Bars indicate the percentage of striped mice of both sexes that were group-living (left y-axis), with sample sizes above bars (both sexes combined). 'No data' means no data were available for that year. Diamonds (linked by a line) indicate the population density in log scale (right y-axis).

breeding season was obtained from a hyperbolic curve ($R = 0.98$, $F_{2,7} = 23.17$, $P < 0.001$, Fig. 2), resulting in $PGL = 91.34 + (-136.03/PD)$. Significantly more striped mice were observed to be group-living both during the post-breeding and pre-breeding season than predicted from the hyperbolic regression obtained from the breeding season ($T = 0$, Wilcoxon matched-pairs signed-ranks test, $P < 0.0001$; Fig. 2).

During the breeding season, the percentage of group-living males increased significantly in relation to the percentage of group-living females ($r_s = 0.88$, $n = 8$, $P < 0.01$).

CAPTIVE STUDY

We observed aggression among adults in two of 37 (5.4%) monogamous pairs but none of these pairs had to be separated as no damaging fights occurred. We observed

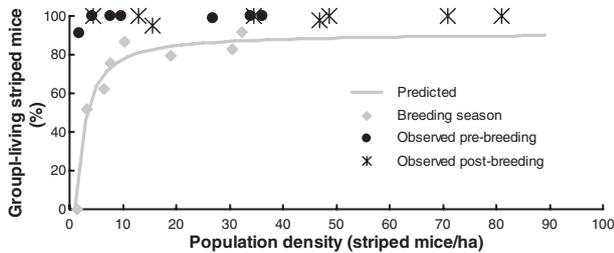


Fig. 2. Hyperbolic regression curve of the relationship between population density and group-living striped mice during the breeding season (grey diamonds). The line indicates the expected percentage of group-living striped mice depending on population densities during the breeding seasons. Crosses show the observed percentages for eight post-breeding seasons, points for seven pre-breeding seasons.

aggression in 20 of 54 communal groups (37.0%) and 12 of these communal groups had to be separated. In communal groups, aggression occurred exclusively between two full sisters. Female–female aggression occurred significantly more often than female–male aggression in monogamous pairs ($P = 0.0004$) or in communal groups ($P < 0.0001$). We found evidence for infanticide in four of the 32 pairs (12.5%) that produced pups and in 18 of the 46 communal groups (39.1%) that produced pups. Infanticide occurred significantly more often in communal groups than in monogamous pairs ($P < 0.01$).

Discussion

Our 8-year field study revealed that the social organization of striped mice depended on PD during the breeding season. When PD was high, nearly all striped mice lived in family groups, while all striped mice lived solitarily when PD was low. In contrast, PD played no role outside the breeding season, when reproductive competition was absent. During the 8-month non-breeding period, PD declined steadily after breeding, halving by the start of the next breeding season in years with good food availability, and declining by 99% in years of extreme droughts (such as 2003). Two months before breeding started again (the pre-breeding period), PD was so low that available territories were abundant, but the majority of striped mice were still group-living (Table 1). Thus, significantly fewer striped mice lived solitarily during the non-breeding season than predicted from the data collected during the breeding season.

Reproductive competition is an inevitable consequence of group-living (Emlen 1982b), imposing significant costs. Female striped mice were aggressive towards other females and committed infanticide in communal groups in captivity, indicating strong reproductive competition. Group-living can only evolve when its inherent benefits are higher than the costs of reproductive competition, or when ecological constraints limit dispersal and independent reproduction. The concepts of ecological constraints and benefits of group-living (or philopatry) are not mutually exclusive but can complement each other (Koenig *et al.* 1992). This is nicely demonstrated by our results on the social organization of

Table 1. A model to show the predicted relationships between sociality and both reproductive competition and population density. Animals should be solitary living (marked in dark grey) if reproductive competition is high and they have the opportunity to leave when population density is low. If reproductive competition is high but no opportunity to leave exists, animals are forced to be social (top left). If reproductive competition is absent, animals should be social if the benefits of group-living outweigh any costs (right column). In the model, the years and seasons for which these predictions were met for the striped mouse are indicated. B: breeding season; Pre: pre-breeding season; Post: post-breeding season

		Reproductive competition	
		High	Low or absent
Population density	High	Social B 2002	Social Pre 2005–2006, 2009 Post 2001–2002, 2008
	Intermediate	Mixed B 2004–2009	Social Pre 2007–2008 Post 2005–2007
	Low	Solitary B 2003	Social Pre 2003–2004 Post 2003–2004

striped mice. Social groups were unstable only during the breeding season, as predicted by Emlen (1995). High PD may hinder offspring from dispersal because of a lack of empty territories of sufficient quality, which we suggest is the reason that striped mice were group-living during the breeding season. In another study of the same population, home range sizes decreased as the number of direct neighbours and PD increased (from 0.54 to 0.21 ha; Schradin *et al.* in press), supporting our interpretation that high PD resulted in an absence of available territories.

What factors might have caused the observed pattern in the social organization of striped mice? Food availability was highest during the breeding season, when many striped mice were solitary. However, within the breeding season, food availability did not correlate with the percentage of group-living striped mice. Also, food availability was typically high in the pre-breeding season (winter: rainy season) and low in the post-breeding season (summer: dry season), but striped mice were group-living during both seasons. Ambient temperature was also excluded as an explanatory variable, despite the observation that striped mice reduce energetic costs by huddling in the nest and might thus benefit most from group-living in winter (Scantlebury *et al.* 2006). However, they were group-living during the coldest period (pre-breeding season in winter) and the hottest period (post-breeding season in summer), but often solitary living during the period of intermediate temperatures (breeding season in spring). Group-living also can be beneficial for predator avoidance (Schradin 2000), but striped mice were not more likely to live in groups when predation pressure was high. Season, PD and their interaction were the only significant predictors, with solitary living occurring during the breeding season, especially when PD was low. These results support

the hypothesis that reproductive competition and the availability of territories influenced sociality in striped mice.

The 'safe haven hypothesis' (Kokko & Ekman 2002) suggests that offspring benefit from staying in their parents' territory due to increased access to limited resources. Natal philopatry during the non-breeding season is only possible in year round territorial species. In birds, year round territoriality is correlated with delayed dispersal and cooperative breeding (Brown 1987; Arnold & Owens 1999; Baglione *et al.* 2005). For striped mice, the safe haven may provide increased vigilance against predators in the group nest at night (Schradin 2005b), a territory and a nest defended by all group members (Schradin 2004), and reduced costs of thermoregulation due to huddling (Scantlebury *et al.* 2006). However, groups break up at the onset of the breeding season at low PD, suggesting that during the breeding season, the costs can exceed the benefits of group-living.

Reproductive competition is a cost for both sexes in group-living species. In striped mice, several adult females in a group can reproduce (Schradin & Pillay 2004), but we found reproductive competition within communal groups in our captive study. Female–female aggression occurred in one-third of the communal groups and infanticide was common. Nearly 50% of females suffered reproductive costs either due to failed breeding (likely because of female–female aggression) or due to infanticide. Reproductive competition between females is strong and is the most parsimonious explanation for females preferring to breed singly when free territories are available.

Reproductive skew among males is greater than among females, as only one male per group breeds (Schradin & Pillay 2004). Male striped mice follow a conditional strategy with the largest males becoming breeding males, the smallest males remaining philopatric, and males of medium body size following a solitary roaming strategy (Schradin *et al.* 2009a,b). Sociality of males was closely correlated with female sociality. When females formed groups, the largest males became the breeding males of these multi-female groups (Schradin *et al.* 2009b), defending harems within a relatively small territory (Schradin & Pillay 2005c). By contrast, when females lived solitarily, males preferred to roam, occupying large home ranges, overlapping with the home ranges of several single breeding females, which they only visited for copulation (Schradin *et al.* 2009a,b). Thus, as predicted for mammals in general (Orians 1969; Ostfeld 1990), whether males were group or solitary living was mainly determined by the spatial distribution of females.

The formation of groups after the breeding season has been reported in other taxa. In facultatively cooperative breeding birds, such as western bluebirds (*Sialia mexicana*), groups are larger during the post-breeding season due to immigration by unrelated females and due to delayed dispersal by philopatric males (Kraaijeveld & Dickinson 2001). Many bird and fish species become non-territorial after the breeding season and form anonymous flocks or swarms (Krause & Ruxton 2002). However, these species are not solitary during the breeding season, but instead form smaller

social groups, such as monogamous pairs without or with helpers. In contrast, family groups of striped mice consist of related individuals that defend their territories against other groups even outside the breeding season, which is different from non-territorial anonymous groups. Few other studies have provided comparisons between solitary living and group-living individuals of the same species and population (for invertebrates see Purcell & Aviles 2007; Weislo & Danforth 1997), but our study indicates that this will be a fruitful avenue of research.

Surprisingly, little direct empirical evidence exists for the concept that reproductive competition results in solitary living. Our analysis of sociality in both the presence and absence of reproductive competition helps us to understand why animals live alone and not in groups. Solitary living is preferred during periods of reproductive competition, but high PD can prevent individuals from becoming solitary. Habitat saturation decreases the costs of philopatry by increasing the costs of dispersal, while reproductive competition increases the costs of philopatry and group-living. Thus, with increasing habitat saturation and decreasing reproductive competition, the costs of cooperative breeding for subdominants decrease, because both factors influence the *c* (cost) term in Hamilton's rule (Hamilton, 1964), determining the social organization of a species.

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