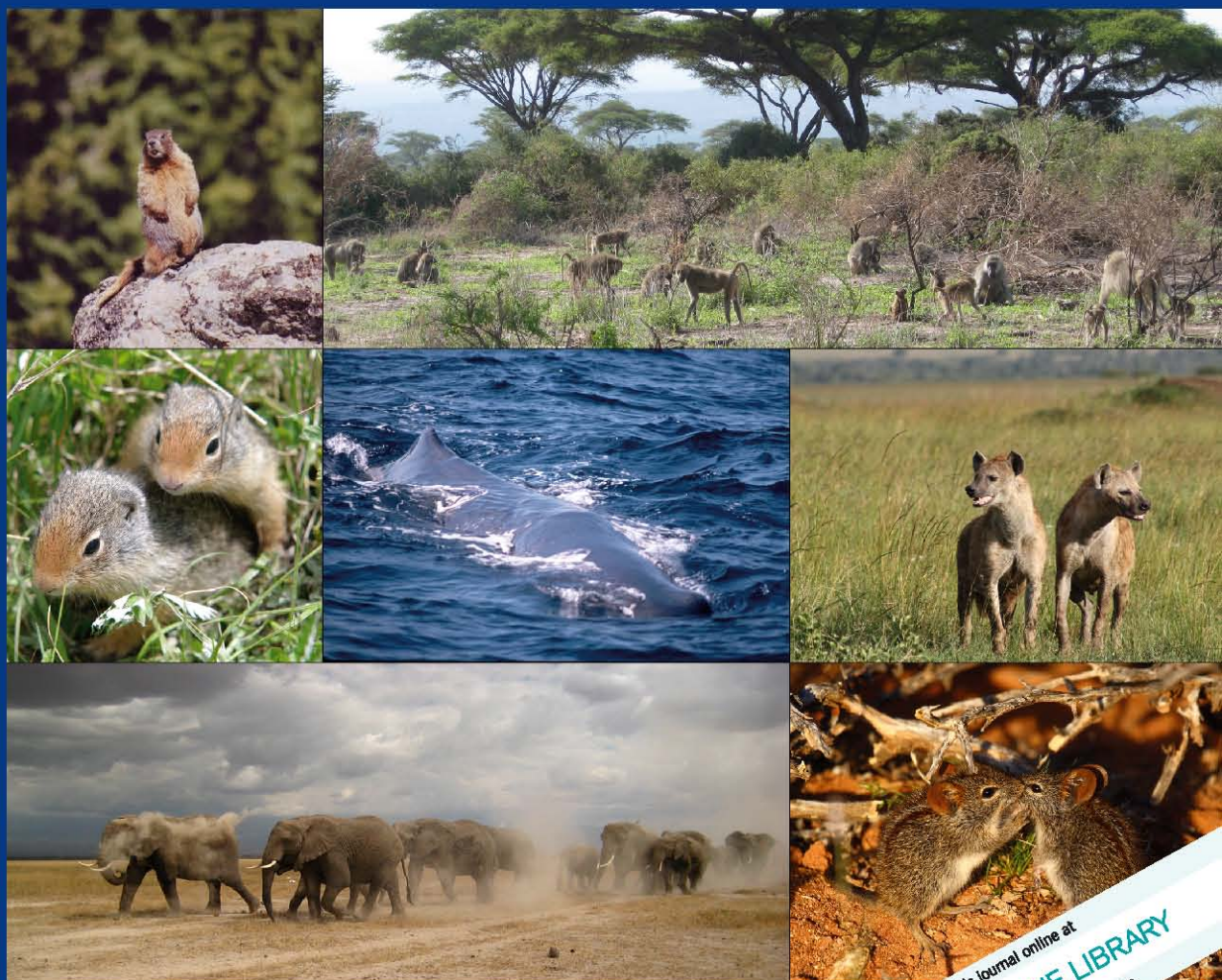


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INVITED REVIEW

Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*)

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Abstract

Environmental change poses challenges to many organisms. The resilience of a species to such change depends on its ability to respond adaptively. Social flexibility is such an adaptive response, whereby individuals of both sexes change their reproductive tactics facultatively in response to fluctuating environmental conditions, leading to changes in the social system. Social flexibility focuses on individual flexibility, and provides a unique opportunity to study both the ultimate and proximate causes of sociality by comparing between solitary and group-living individuals of the same population: why do animals form groups and how is group-living regulated by the environment and the neuro-endocrine system? These key questions have been studied for the past ten years in the striped mouse *Rhabdomys pumilio*. High population density favours philopatry and group-living, while reproductive competition favours dispersal and solitary-living. Studies of genetic parentage reveal that relative fitness of alternative reproductive tactics depends on the prevailing environment. Tactics have different fitness under constrained ecological conditions, when competitive ability is important. Under conditions with relaxed ecological constraints, alternative tactics can yield equal fitness. Both male and female striped mice display alternative reproductive tactics based on a single strategy, i.e. all individuals follow the same decision rules. These changes are regulated by endocrine mechanisms. Social flexibility is regarded as an adaptation to unpredictably changing environments, selecting for high phenotypic flexibility based on a broad reaction norm, not on genetic polymorphism for specific tactics.

Keywords: communal breeding, mate choice, paternal care, prolactin, prairie vole, testosterone

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Social flexibility

Behavioural ecology seeks to understand how animals survive and reproduce in their natural environment. However, the environment is not static, but changes in predictable and unpredictable ways (Wingfield, 2003). Long-term field studies are needed to understand individual responses to changing environments and how these may affect the evolution of social behaviour (Clutton-Brock & Sheldon 2010). Natural environments are predicted to change faster in the future due to anthropogenic induced climate change (Friedlingstein 2008),

testing the limits of behavioural adaptation and resilience of natural populations.

The term *social flexibility* is generally used to describe modifications of individual social behaviours, but its usage differs among authors. A search in the ISI Web of Science for the term 'social flexibility' revealed 276 publications in the field of Zoology for the period 1900 to 2010. Most papers were about 'behavioural flexibility' of non-social behaviours, only 84 papers were about flexibility in social behaviour and no clear difference was made between 'social flexibility', 'intra-specific variation in social behaviour', and 'alternative reproductive tactics'. Used in such a way, the term 'social flexibility' simply means that social behaviour is flexible, which is true for nearly all social behaviours of all species.

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We developed the concept of social flexibility from our long-term field studies on the striped mouse (*Rhabdomys pumilio*; Fig. 1). Here, we define the concept of social flexibility, in which the social organization (the composition of groups) within a population changes facultatively as a function of individuals of both sexes changing their reproductive and social tactics in response to changing environmental conditions (Box 1). As a consequence, the entire social system (comprising of the social organization, the mating system, and the social structure of a population; Kappeler & van Schaik 2002) can change, although this is not a pre-requisite for social flexibility (see examples below).

Social plasticity is a similar term, but can include examples where during ontogenetic processes one of several alternative tactics is developed and maintained during adulthood. Social flexibility comprises the cases of social plasticity in which adult individuals can switch back and forth between tactics. Other similar terms have been used, such as 'intra-specific variation social systems' (Lott 1991), which in contrast to social flexibility could also be a result of genetic differences between populations. The term 'flexible social structure' (Randall *et al.* 2005) describes a case where due to low population density (absence of surviving female relatives) individuals might have to live solitarily. To demonstrate social flexibility in the way we define it, its important to show that individuals of both sexes (not only males like in many species with alternative reproductive tactics) can chose their social organization, for example to live solitarily or to live in groups. In contrast to this, one simple explanation for solitary versus group-living could be differences in population density. Individuals may be constrained to live solitarily when population density is very low, and constrained to be group-living when population density is very high, without giving individuals a choice of social organization. However, there is little empirical support for this. Obligate social species form groups even under very low population densities, for example lions in the Kalahari (Bothma & Walker 1999). On the other hand, some species like whistling rats (*Parotomys brantsii*) live solitarily even under very high population densities (Jackson 1999).

Social flexibility can help to understand the evolution of social systems, since social flexibility results from a complex interaction between individuals and their environment, causing physiological and behavioural reactions (Lott 1991). Understanding social flexibility is an important research topic, especially when we consider that our own species is characterized by high social flexibility with monogamous, polygynous and polyandrous societies, and different individuals following alternative tactics within societies.

Box 1 Social flexibility

Social system: The social system of a species comprises the social organization (the composition of groups, e.g. solitary or family groups), the mating system, and the social structure (describing which individuals interact with each other; Kappeler & van Schaik 2002).

Intra-specific variation in social systems: This term was introduced by Lott (1984;1991) who did not provide a precise definition, but used the term very broadly for variation in group size, territoriality, dominance status, parental care, and mating systems. Intra-specific variation can occur between populations and might have a genetic basis, so that individuals following alternative tactics differ genetically.

Social flexibility: Unlike intra-specific variation, social flexibility focuses on individual flexibility. It describes the phenomenon that individuals change their social and reproductive tactic, modify their interactions with other individuals (social structure), with whom they mate (mating system), and consequently the composition of groups (social organization). If this occurs in both sexes, it influences the entire social system of the population, for example from solitary living to single family groups (pair plus offspring) to extended family groups. Within a population, often two forms of social organization might exist, e.g. both solitary and group-living individuals or monogamous and polygynous groups. We predict social flexibility to be an adaptation to unpredictably changing environments, selecting for high phenotypic flexibility that is based on a broad reaction norm, not on genetic polymorphisms for specific tactics.

Definition of social flexibility: Both males and females have alternative reproductive and social tactics based on a single strategy (all individuals have the same decision rules). Depending on environmental as well as individual conditions (e.g. social status, competitive ability) individuals choose to live solitarily, in small or large social groups (though not all individuals might be able to live under the condition of their choice; for an example see Box 3). Consequently, the social system of a species or population can change as a function of individuals changing their tactics.

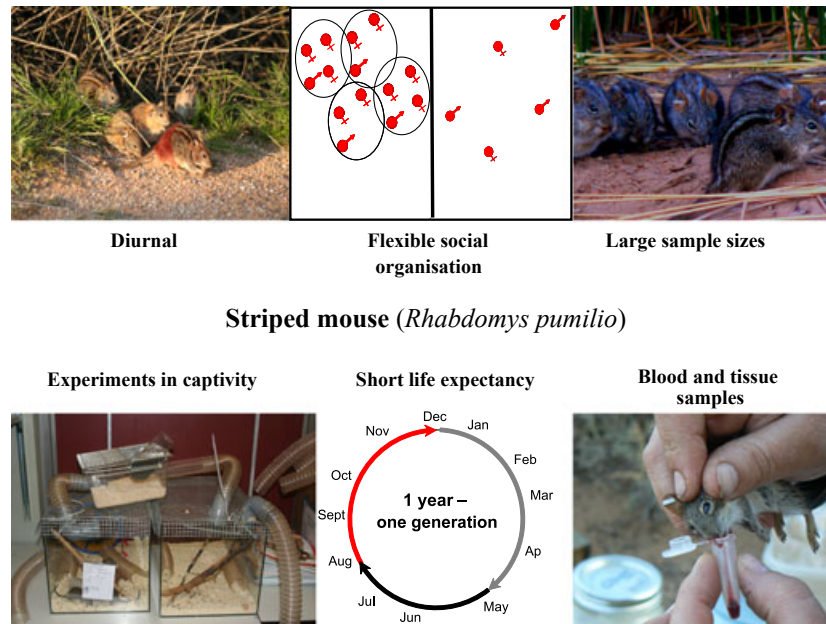


Fig. 1 Advantages of the striped mouse as a study species (from top left to bottom right). 1. It is diurnal, inhabits an open habitat and easily habituates to the presence of observers, making direct behavioural observations possible in the field. 2. High social flexibility, ranging from extended family groups (left) to solitary living (right) in the same population. 3. Large sample sizes. 4. Can be studied in captivity. 5. Short generation time (red: breeding season in spring; grey: hot dry season; black: cold rainy season). 6. Samples for hormone measurements and genetic analyses can be easily collected. Blood samples are taken from a sub-lingual vein, a method less harmful than traditional methods of blood sampling used in mice (Heimann *et al.* 2009).

Social flexibility in the African striped mouse

First studies indicated that the striped mouse of the Succulent Karoo is best characterized as a territorial, group-living, solitary forager with communal breeding, paternal care and helpers at the nest (Schradin & Pillay 2004). Groups of close kin consist of up to 30 adult individuals: a single breeding male, two to four communally breeding females and their adult offspring of both sexes that act as helpers at the nest (Schradin & Pillay 2004). Groups of striped mice sleep together in one nest and share a territory which they defend against neighbouring groups (Schradin 2004). Individuals from the same group forage solitarily during the day but bask and interact with each other amicably in front of their nest at dawn and at dusk (Schradin *et al.* 2007). After a severe drought in 2003, population density declined significantly from 70 mice/ha to 2 mice/ha, but striped mice still formed groups, though these huddling groups consisted of non-related individuals (Schradin *et al.* 2006). With the onset of the breeding season, all individuals switched from group- to solitary-living, but they became group-living again at the end of the breeding season, when their adult offspring remained philopatric (Schradin *et al.* 2010a).

Thus, individuals of both sexes switched from group- to solitary-living and back to group-living, indicating high social flexibility (Schradin *et al.* 2010a), offering a unique opportunity to study ultimate and proximate causes of sociality (Box 2).

Social flexibility occurs in many taxa

Intra-specific variation in the social system has been observed in more than a hundred vertebrate species (Lott 1991), but in most cases it is not known whether this is due to genetic differences between individuals (or populations), or due to social flexibility, i.e. flexibility in the social behaviour of individuals. Indication exists also for invertebrates such as the burying beetle (*Necrophorus vespilloides*). In this species both males and females have alternative reproductive tactics: males can attract females via pheromones either after they searched for and found a carcass (searching tactic) or without having access to a carcass (pure pheromone tactic), or they act as satellite males at carcasses defended by larger males (Eggert, 1992). Each male can use all three tactics (Eggert, 1992), indicating behavioural flexibility. Females either have a carcass for themselves or with one other

female, which could be either a subordinate female (called parasite), or a female of equal status (joint or communal breeding; Müller *et al.*, 2006). The main factors influencing the resulting social system are differences in body mass between individuals and the availability of food resources, i.e. carcass size. Thus, in burying beetles females may breed solitarily (having previously mated with a pheromone secreting male), in monogamous bi-parental pairs, as parasitic subordinate females, or in communally breeding groups with two females and one male sharing a carcass (Eggert and Müller 2000; Müller *et al.* 2006). This system fits our definition of social flexibility where the social system changes as a function of individuals of both sexes changing their tactics depending on environmental conditions.

In several bird species, social flexibility is represented by switching from breeding in monogamous pairs to single families to extended family groups, which has been used to study cooperative breeding (Emlen 1997; Koenig *et al.* 1992). In dunnocks (*Prunella modularis*), social organization includes monogamous pairs, polyandric, polygynous or polygynandrous groups. Females defend exclusive territories, with territory size depending on density of competing females and habitat quality. A single male or groups of unrelated males (depending on competitive ability) defend territories that overlap those of one or more females. Females mate with all resident males, resulting in a mating system that ranges from monogamy to polygyny. Studies on dunnocks have helped to understand the evolution of sexual conflict, mating systems, parental effort and life histories (Davies 1992).

Solitary-living is quite rare in birds, but occurs in many mammalian species. Social flexibility seems to be especially prevalent in short lived rodents that need to quickly respond to changing environmental conditions (Lott 1991). Among rodents, several species that are solitary during summer form huddling groups during winter (Madison *et al.* 1984; Webster & Brooks 1981), which function to save energy (Canals *et al.* 1989). In the great gerbil (*Rhombomys opimus*) the social organization comprises solitary living, pair-living and large social groups (Randall *et al.* 2005). Great gerbil males have reproductive tactics similar to male striped mice, being philopatric, a solitary roamer, or to be the breeding male of a group. Females can also be either solitary or group-living, but it is not clear whether this reflects individual choice or is the result of availability of surviving female kin, as population density is one of the main factors influencing sociality in great gerbils (Randall *et al.* 2005).

Box 2 Social flexibility in African striped mice as a tool for studying social behaviour

Social flexibility in the striped mouse offers the opportunity to study proximate and ultimate aspects of social behaviour by comparing solitary and sociable individuals of the same population and by studying individuals changing their tactics.

1. **Benefits of group living:** individuals sleeping in huddling groups spend 25% less energy than solitary individuals (Scantlebury *et al.* 2006).
2. **Reasons for group versus solitary-living:** reproductive competition during the breeding season leads to solitary living when vacant territories are available, while ecological constraints force individuals to remain in communal groups (Schradin *et al.* 2010a).
3. **Communal breeding:** allo-parental care is shown by breeding females towards the pups of other females in the group (Schradin 2006; Schubert *et al.* 2009), but female infanticide induces high costs. In breeding experiments, males with larger testes were more successful in fertilizing several females synchronously than males with smaller testes (i.e. larger testes reduced the risk of sperm depletion; Schradin *et al.* 2009a). Synchronous mating leads to synchronous births, reduced risk of infanticide (females cannot discriminate between their own and unrelated pups before weaning; Pillay 2000)§ and is thus important for the evolution of communal breeding
4. **Paternal care:** paternal care leads to better pup development due to improved thermoregulation (Schradin & Pillay 2005). Costs of paternal care (missed mating opportunities) are low when males defend several females breeding in communal groups (Schradin & Lindholm 2011).
5. **Extra group paternity:** when population density is high, being a breeding male appears to be the most successful tactic in spite of a ~30% frequency of extra group paternity (Schradin & Lindholm 2011).
6. **Alternative reproductive tactics:** males adopting three alternative reproductive tactics differ in prolactin, corticosterone and testosterone levels (Schradin *et al.* 2009b). By measuring the fitness consequences of each tactic, the distinction between mixed and conditional strategies was not definitive, and instead the term "single strategy" was suggested (see Box 3; Schradin & Lindholm 2011).
7. **Dispersal tactics:** male striped mice have status dependent alternative dispersal tactics (Solmsen *et al.* 2011).

In prairie voles (*Microtus ochrogaster*), individuals of the same population can be socially monogamous, solitary promiscuous or polygynous (McGuire and Getz 1998). While this species has been used as a model to study monogamy (Carter & Getz 1993; Young 2009), its social system is very similar to the one of the striped mouse, as it displays different reproductive tactics in both sexes. Males can be either philopatric, solitary wanderers (=roamers), or resident breeders at a nest with one or more breeding females. Females can be either philopatric, solitary breeders, single or plural breeders within social groups (monogamous pairs or communally breeding groups). This social flexibility has been used as a tool to understand the ecological (Lucia *et al.* 2008), evolutionary (Ophir *et al.* 2008b; Mabry *et al.* 2011), neuro-endocrine (Cushing *et al.* 2004; Young & Wang 2004) and genetic (Ophir *et al.* 2008a; Mabry *et al.* 2011; Solomon *et al.* 2009) bases of group-living and social bonding.

The house mouse (*Mus domesticus*) is another socially flexible species with alternative reproductive tactics in both sexes (Beery *et al.* 2008). Males can be subordinate philopatrics, monogamously mated paternal males (Elwood & Kennedy 1991), roaming males, or polygynous males defending a territory with a group of cooperatively breeding females. Similarly, females can be non-breeding subordinate philopatrics, or solitary or cooperative breeders (Latham & Mason 2004). Individuals can change their tactics. The factors influencing these decisions are at the moment not well understood, but population density and individual competitive ability are probably important. As a result of these individual tactics, the social system of a population can be primarily either solitary, small family groups or extended family groups with communal breeding.

Reasons for group *vs.* solitary living and the regulation of social flexibility

Group-living can yield significant benefits, as revealed by studies comparing solitary with sociable species (Pulliam & Caraco 1984; Krebs & Davies 1993) or by studying groups of different sizes in obligate group-living species (Dunbar 2002; Taborsky 1984; Clutton-Brock 2005). However, in the former case, phylogeny may confound comparisons between species, whereas in the latter case, it is difficult to determine which benefits of group-living have led to its evolution and which became prevalent only *after* complex social groups had evolved. Social flexibility avoids such confounding effects since comparisons are made between solitary and group living individuals of the same population and within individuals switching their tactics.

Group-living striped mice are solitary foragers and do not share information about food locations in their

territory (Schradin 2007). However, they benefit from sharing a nest, which might lead to increased vigilance against nocturnal predators (Schradin 2005). Huddling yields significant energy savings: striped mice sleeping alone spend about 25% more energy than striped mice sleeping in huddling groups (Scantlebury *et al.* 2006). Thermoregulatory benefits of huddling are probably the main reason for group-living in striped mice and many other small mammals (Canals *et al.* 1989).

Group-living also induces costs, explaining why individuals disperse from their natal group and become solitary. Two hypotheses have been proposed to explain this change in social system. 1. The ecological constraints (habitat saturation) hypothesis predicts that individuals remain in their natal group when no opportunities for independent breeding exist, or when the costs of dispersal are higher than the costs of remaining philopatric (Koenig *et al.* 1992; Emlen 1997). 2. The reproductive competition hypothesis predicts that individuals leave their social group and breed solitarily to avoid competition for reproduction within groups, often expressed as infanticide or sexual suppression (Dobson 1982; Emlen 1997; Clutton-Brock 2005). Benefits of group-living promote philopatry, ecological constraints increase costs of dispersal also promoting philopatry, while reproductive competition increases costs of remaining philopatric. The net costs or benefits of these different factors will ultimately determine whether an individual remains philopatric or disperses.

Ecological conditions can be easily manipulated experimentally by removing individuals and thus changing population density. Several experimental studies provide support for the ecological constraints hypothesis (Pruett-Jones & Lewis 1990; Komdeur 1992; Bergmüller *et al.* 2005; Lucia *et al.* 2008). In contrast, experimental manipulation of reproductive competition is difficult, even though we know that reproductive competition has significant costs and can lead to reproductive skew (Kokko 2003).

Field data collected over eight years indicated that striped mice of both sexes were group-living during the breeding season when population density was high, but solitary living when population density was low (due to high predation pressure or low food availability), supporting the ecological constraints hypothesis (Fig. 2; Schradin *et al.* 2010a). Reproductive competition is prevalent during the breeding season in the form of reproductive suppression in males (Schradin *et al.* 2009c) and female infanticide (Schradin *et al.* 2010a). This can explain why females leave the communal group and start breeding alone when free territories become available. Communal groups often break apart at the start of the breeding season if population density is low. Female distribution seems to determine male reproductive

tactics: males join existing groups of communally breeding females, but if females are singly dispersed, males adopt a solitary roaming tactic (Schradin *et al.* 2010a). To study the effect of reproductive competition on sociality, comparisons were made of the social system between periods with and without reproductive competition. After the breeding season, in the absence of reproductive competition, the positive correlation between population density and percentage of group-living striped mice was absent and striped mice lived in groups, even under very low population densities (Fig. 2). Striped mice thus prefer to live in groups and gain benefits of group living outside the breeding season when costs of reproductive competition are absent. During the breeding season, however, they avoid reproductive competition by living solitarily when free territories are available, but are forced to live in groups when population density is high.

The degree of reproductive competition in a group can be measured by reproductive skew, and a low level of reproductive competition is believed to favour group-living (Ragsdale, 1999; Kokko, 2003; Clutton-Brock, 2005). A few previous studies have reported that groups might grow larger after the breeding season when reproductive competition is absent (Kraaijeveld & Dickinson 2001), and many bird and fish species become non territorial after the breeding season and form anonymous flocks or swarms in which members do not establish individualized relationships (Krause & Ruxton 2002). However, these species are not solitary during the breeding season, but instead form smaller social groups. Few other studies have provided comparisons between solitary-living and group-living individuals of the same species and population (but see Wcislo *et al.*, 1997; Randall *et al.* 2005; Purcell & Aviles, 2007). While reproductive competition has been observed in many taxa (Koenig *et al.* 1995; Faulkes & Bennett 2001; Wingfield & Sapolsky 2003; Clutton-Brock, 2005;), our study was the first to provide empirical evidence that reproductive competition can lead to solitary-living.

Alternative reproductive tactics

In species with social flexibility individuals of both sexes are able to switch between alternative reproductive tactics (ARTs). The phenomenon of alternative reproductive tactics has been analysed by game theory, where a tactic refers to a specific behaviour resulting from individual decision rules, so-called strategies (Gross 1994; Tomkins & Hazel 2007; Box 3). Adult female striped mice have the following ARTs: they can remain in their natal group and breed communally, or leave the group and start solitary breeding (Schradin *et al.* 2010a). The different factors influencing which tactic

a female chooses and the resulting consequences are currently under research. ARTs are better understood in male striped mice which can follow one of three tactics (Fig. 3; Schradin *et al.* 2009b): (1) Philopatric males that might sneak copulations with females from neighbouring groups, but do not breed with the females of their natal group. These males show allo-parental care. (2) Solitary living roaming males that attempt to copulate with single breeding females or with females from communal groups, and do not show paternal care. (3) Territorial breeding males that defend groups of communally breeding females. These males show high levels of paternal care. Breeding males always originate from other groups, because males cannot obtain the breeding position in their natal group.

Box 3 Tactic and strategy

Tactic: the behaviour of an individual. For example the tactic of defending a group of communally breeding females *or* the tactic of solitary roaming.

Strategies: a strategy describes the decision rules of an individual, determining which tactic it will follow. Gross (1996) defined three categories of strategies:

1. *Alternative strategies:* genetically polymorphic, based on frequency dependent selection. Different tactics yield the same average fitness. Examples are male ruffs (*Philomachus pugnax*) and males of the isopod *Paracerceis sculpta* (Lank *et al.*, 1995; Shuster and Sassaman, 1997).
2. *Mixed strategies:* genetically monomorphic, based on frequency dependent selection. Different tactics yield the same average fitness. No good empirical examples exist (Gross 1996). Mixed strategies have also been characterized by a probabilistic basis, i.e. a probability x to play tactic X and probability $1-x$ to play tactic Y (Tomkins & Hazel 2007).
3. *Conditional strategies:* genetically monomorphic, based on status dependent selection. Different tactics yield different fitness. The tactic that an individual chooses depends on its competitive abilities. The most competitive individuals follow the tactic that yields the greatest fitness payoff, called the bourgeois tactic. Less competitive males (often called sneaker or satellite), that are often smaller and younger than the bourgeois males, make the best of a bad job (Dawkins 1980), following a tactic with

lower fitness that is still better than no reproductive success at all. These males change to the bourgeois tactic when they grow larger. Many examples exist in both vertebrates and invertebrates (Gross 1996).

Criticism of Gross definitions: The definition by Gross (1996) has been criticized on theoretical grounds because of its focus on genetic polymorphism *versus* genetic monomorphism: even if different animals follow very similar decisions rules and show flexibility, i.e. they can change between tactics, they still might differ genetically, e.g. in their decision when to switch tactics (Shuster & Wade 2003; Taborsky *et al.* 2008; Tomkins & Hazel 2007). Tomkins & Hazel (2007) further concluded that mathematical models can neither prove that fitness must be unequal (as was proposed by Gross 1996) nor that fitness must be equal (as was proposed by Shuster & Wade 2003). Our empirical study contributes data to this criticism.

Single strategy: this is a new term introduced by Schradin & Lindholm (2011) to replace the terms mixed and conditional strategy, which differ mainly in the predicted fitness consequences (equal *versus* different fitness payoffs for alternative tactics). Single strategies are not based on genetic polymorphisms, but all individuals follow the same or very similar decision rules when choosing a tactic. Individuals have plastic tactics, which means they can switch tactics, often repeatedly. Environmental conditions determine whether the different tactics yield similar or different fitness.

Unfortunately, studies on strategies underlying ARTs typically lack a formulation of the decision rules. Formulating the strategy for male striped mice has helped to explain why a single strategy can yield different fitness payoffs (Schradin & Lindholm 2011):

1. Decision: remain philopatric or disperse?

- I. Remain a philopatric male if all females breed in communal groups defended by breeding males and your body mass is below the population mean.
- II. Disperse from natal group:
 - a. If population density is low and more singly than communally breeding females are present in the population.

- b. If your body mass at the beginning of the breeding season is above the population mean, independent of population density.

2. Decision: become a roamer or attempt to be a territorial breeder?

- I. Become a roaming male if all females breed solitarily.
- II. Become a breeding male if you find a group of communally breeding females that are not defended by a male that is larger than you.

By formulating the single strategy (=decision rules) for striped mice, it becomes evident that fitness outcomes depend on the prevailing environment. To become a roamer can be the result of a male choosing to disperse and to roam, as the tactic yields high fitness. Alternatively, it can be the result of a male which chooses to disperse and attempts to become a territorial breeder, but was not competitive enough. In the latter case, being a roamer would be a sub-optimal tactic.

To understand the evolution of male ARTs in striped mice, the first step was to determine their strategy. Traditionally, behavioural studies distinguish among three strategies for ARTs. In alternative strategies, males of different tactics are genetically polymorphic but have the same fitness (Gross 1996). Male striped mice can switch their tactic within their lifetime (Fig. 3), which is in contrast to alternative strategies based on genetic polymorphisms. To distinguish between mixed or con-

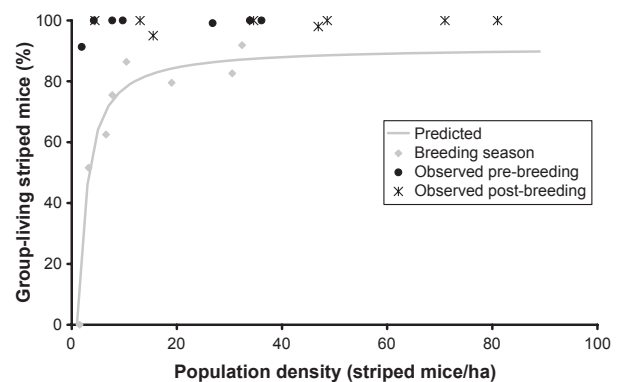


Fig. 2 Effect of population density on social organization during the breeding and the non-breeding season. Hyperbolic regression curve of the relationship between population density and percentage of group-living striped mice during the breeding season (grey diamonds; best fit, $P < 0.001$). Crosses give the observed percentages for eight post-breeding seasons and points for seven pre-breeding seasons. Figure from (Schradin *et al.* 2010a).

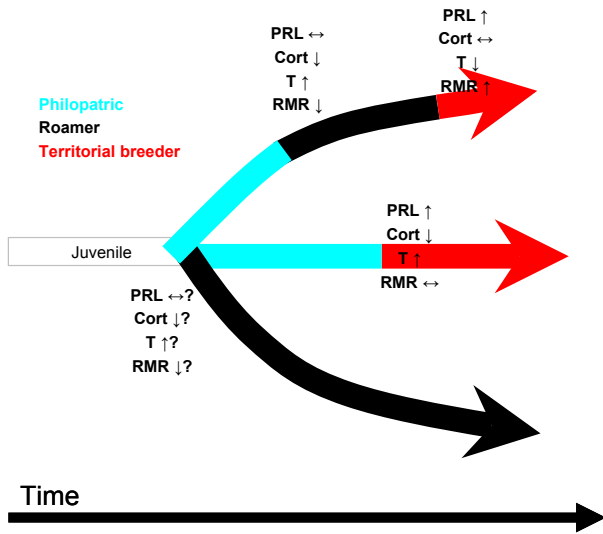


Fig. 3 Alternative male reproductive tactics in striped mice and correlated physiological changes. When reaching adulthood, male striped mice in the Succulent Karoo typically remain philopatric in their natal group (top and middle arrows). In the subsequent breeding season, philopatrics can become roamers first (black, top arrow), which is associated with an increase in testosterone (T) and a decrease in corticosterone (Cort) and resting metabolic rate (RMR), before becoming territorial breeders and experiencing an increase in prolactin (PRL) and RMR and a decrease in T. If philopatrics gain sufficient body mass during the dry season and winter, they can directly become territorial breeders the subsequent breeding season (middle arrow), which is associated with a decrease in Cort and an increase in T and PRL. If population density is very low, males can become roamers in the season of their birth, which is predicted to be associated with an increase in T and a decrease in Cort and RMR. ↓ decrease; ↑: increase; ↔: stays the same; ?: predicted change. Figure from (Schradin *et al.* 2009b).

ditional strategies, one needs to know whether the males adopting different tactics differ in competitive ability, which would indicate status dependent selection and a conditional strategy (Box 3). For conditional strategies, males with the highest competitive ability follow the dominant bourgeois tactic with much greater fitness than males with a low competitive ability doing the best of a bad job. In contrast, under mixed strategies, alternative tactics yield on average the same fitness.

Males adopting different tactics differed significantly in body weight, with territorial breeders being the heaviest males, philopatrics being the smallest males and roamers occupying an intermediate position (Schradin *et al.* 2009b). Furthermore, philopatrics can switch to roamers when they increase body mass, and roamers can switch into breeders when they become heavier (Schradin *et al.* 2009b). As heavier males are better in winning territorial encounters (Schradin 2004), these results indicated that male striped mice follow a

conditional strategy. This was supported in a study of the paternities of 125 pups from 10 groups using nine microsatellite loci. The reproductive success of territorial breeding males was ten times higher than that of solitary roaming males, and a hundred times higher than that of philopatrics (Fig. 4A; Schradin & Lindholm 2011). This was one of the first studies using molecular markers to measure fitness consequences of male ARTs, with similar results in other species, where roaming males (=wanderers in prairie voles, *Microtus ochrogaster*, Ophir *et al.* 2008) or subordinates (in meerkats, *Suricata suricatta*, Young *et al.* 2007) have significantly lower reproductive success.

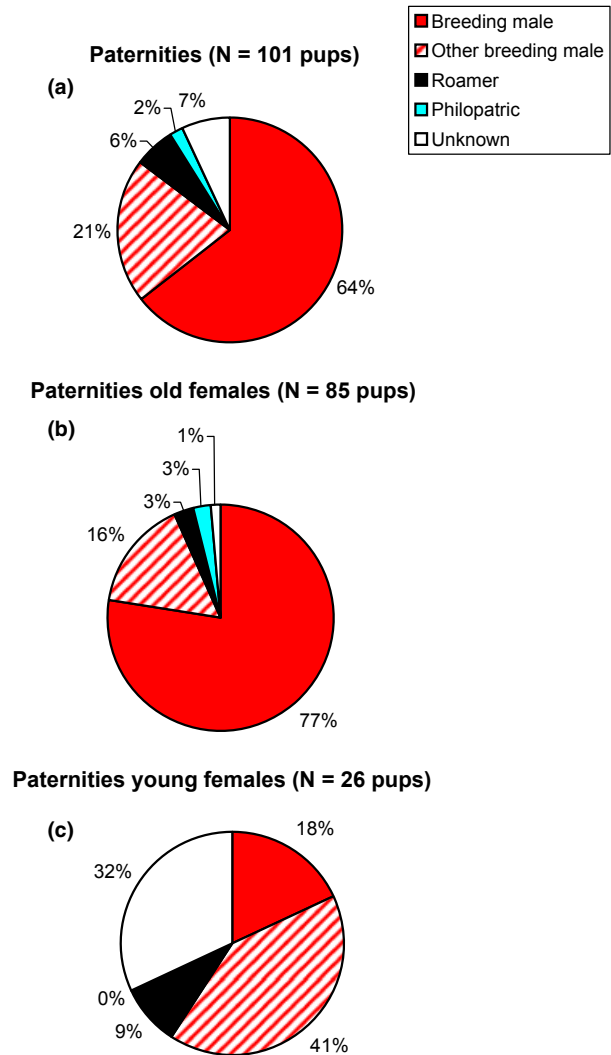


Fig. 4 Paternity within groups by the breeding male of the group, neighbouring breeding males, roamers, philopatrics and unknown males during a year with high population density, for (a) entire groups, (b) pups from old breeding females born the previous breeding season, (c) pups from young philopatric females born during the same breeding season. Figure from (Schradin *et al.* 2010b).

Genetic parentage studies have significantly increased our knowledge of natural mating systems, but few have collected data for different generations. The above-mentioned study was performed in a year of high population density, i.e. when ecological constraints were high. We repeated the study, measuring male fitness for another generation living under intermediate population density (with relaxed ecological constraints). In this generation, breeding males and roamers had similar body mass and similar fitness (Schradin & Lindholm 2011). These results were in agreement with the theory of mixed strategies and thus in contrast to the conclusion of conditional strategy derived from the results obtained from the generation living under high population density.

Do male striped mice follow a mixed or a conditional strategy? Conditional strategies are believed to arise from status dependent selection, predicting a positive correlation between fitness and status (status is typically measured as the condition of the individual). Status is often measured as body mass, a correlate of competitive ability. In theory, the slopes of the predicted fitness lines differ between tactics, leading to switch points at which individuals should switch tactics (see graphs in Taborsky *et al.* 2008). However, we did not find correlations between body mass and fitness for any of the tactics in the two years studied. Our empirical study demonstrates that the differentiation between conditional and mixed strategies is not absolute, which gives empirical support to theoretical work criticising the categorization provided by Gross (Shuster & Wade 2003; Tomkins & Hazel 2007; Taborsky *et al.* 2008). In many other species, environmental conditions might fluctuate temporally and spatially so that the usually sub-optimal tactic yields similar fitness to the dominant tactic, or that only a single tactic prevails (see for example Müller *et al.* 2006). We therefore suggest replacing the terms mixed and conditional strategy by the term single strategy for studies on ARTs (Box 3). The term single strategy indicates that all individuals follow a single set of decision rules determining their tactic, while the environmental conditions determine relative fitness outcomes (Schradin & Lindholm 2011).

Sex-biased dispersal and indication for alternative dispersal tactics

In striped mice, males are the dispersing sex while females are mainly philopatric, as demonstrated by the fine-scale genetic structure (Solmsen *et al.* 2011). A population genetic study identified male migrants between sub-populations and provided an indication for alternative male dispersal tactics (Solmsen *et al.* 2011): (1) highly competitive males (i.e. heavy males) have short dispersal distances, becoming the breeding males of

neighbouring groups while minimizing costs of dispersal; (2) less competitive males have to disperse greater distances and become roamers in their natal sub-population; and (3) males of even lower competitive ability might not be able to disperse into areas occupied by other territorial striped mice. These males make the best of a bad job, leaving their sub-population to avoid territorial encounters, dispersing several kilometres across areas unoccupied by striped mice, until they reach another sub-population. While males migrating across unoccupied habitats can potentially create gene flow between sub-populations, this tactic is likely to be very costly in terms of energy expenditure, increased predation risk, and the peril of not finding another sub-population.

Endocrine mechanisms of alternative male reproductive tactics

Social flexibility as a response to changing environmental conditions needs physiological mechanisms that enable individuals to change their reproductive and social behaviour. The relative plasticity hypothesis predicts that changes and differences in sex steroid hormone levels regulate the expression of alternative reproductive tactic (Moore *et al.* 1998). In species with alternative male reproductive tactics, the highest androgen levels have usually been reported in dominant males (Oliveira *et al.* 2008). However, in sociable species, amicable behaviours may conflict with high testosterone levels. In the striped mouse, territorial breeders show highly amicable behaviours towards other group members (Schradin & Pillay 2004; Schubert *et al.* 2009), and have lower testosterone levels than solitary roamers, which might reflect a trade-off between low testosterone amicable behaviour and high testosterone dominance behaviour (Schradin *et al.* 2009b). Territorial breeders are heavier than roamers, and territory holding potential may be related more to body mass than to testosterone levels. The high testosterone levels of roamers, on the other hand, might promote risky behaviour, such as invading territories defended by territorial males. Philopatric males have the highest corticosterone but lowest testosterone levels, indicating that they are sexually suppressed and potentially stressed by being forced (by ecological constraints) to remain philopatric instead of breeding independently. Prolactin, a hormone associated with paternal care (Schradin & Anzenberger 1999), was highest in territorial breeders (Schradin 2008a), which show high levels of paternal care (Schradin & Pillay 2003). Interestingly, the differences in hormone levels between tactics disappeared during the non-breeding season (Schradin 2008a, b), suggesting that they were rather due to differences in reproductive

behaviour than in dominance rank. Important differences were also found in resting metabolic rate (RMR), which was higher in the two group-living tactics than in the solitary roamers. Energy savings due to huddling in a social group by males adopting social tactics might enable higher energy expenditure during the day and a higher RMR, which could lead to a better reaction potential, enabling for example a faster response towards predators (Schradin *et al.* 2009b).

The endocrine differences found in the field were also demonstrated in the laboratory (Schradin *et al.* 2009c). When brothers were separated at an age of 21 days (weaning is at day 16), with one brother remaining in the family (representing a philopatric male) and the other male housed singly (representing a solitary roamer), the singly housed male reached puberty earlier (became scrotal with descended testes) than his family living brother. After both males were sexually mature, they differed hormonally in the same way as do philopatrics and roamers in the field, with the family housed males exhibiting higher corticosterone but lower testosterone levels. Furthermore, family-housed males had smaller testes and lower sperm counts. This only occurred in families where the father was present, but not when the father was removed, indicating sexual suppression by the breeding male. This was supported by field data from 170 individuals: males were found to become sexually mature at a younger age when no breeding male was present in their group and when food was abundant (Schradin *et al.* 2009c). Onset of puberty in male striped mice is therefore flexible, with environmental cues providing the relevant information on resource availability and opportunities for reproduction (Schradin *et al.* 2009c).

Extra-group paternity and female choice

Extra-group paternity is common in striped mice, and it is more common for pups from young compared to old females (87% *vs.* 20%; compare Fig. 4B with C), indicating inbreeding avoidance by young females. While territorial breeding males have high reproductive success, they nevertheless lose more than 30% of within-group paternity to other males, mainly neighbouring territorial breeders (Schradin *et al.* 2010b; Fig. 4A). In neutral arena experiments, territorial breeders were found to be especially aggressive towards their direct neighbours, the so-called 'nasty neighbour phenomenon' (Schradin *et al.* 2010b). This is in contrast to the 'dear enemy phenomenon', where neighbours show reduced levels of aggression towards each other, while being more aggressive towards strangers (Temeles 1994). Aggression in male striped mice seems to be a

response to the high risk of extra-pair copulations, and we predicted that with increasing rate of extra-pair fertilizations by neighbours, animals will rather show the 'nasty neighbour' instead of the 'dear enemy phenomenon' (Schradin *et al.* 2010b).

Synthesis: why is social flexibility important?

In species in which both males and females have alternative reproductive tactics based on a single strategy, the entire social system can switch, a phenomenon we refer to as social flexibility. Thus, when studying social flexibility, the focus is consistently on the individual and how its decisions affect the social system of a population. Social flexibility is one of the hallmarks of humans, and its understanding will provide insights into our own behaviour. We focused on social flexibility in African striped mice to study aspects of group living by comparing solitary and social individuals of the same population, without confounding phylogenetic differences. By using molecular tools and studying several generations, we demonstrated important differences in fitness outcomes, mate choice and dispersal tactics, depending on prevailing environmental conditions and individual responses to the environment, helping us to understand many different aspects of social behaviour (Box 2) and developing new concepts (Boxes 1 and 3).

Social flexibility is in itself an interesting and important phenomenon that needs scientific explanation. When does social flexibility evolve and why is it not present in many more species? At the moment we can merely speculate about the evolutionary forces. Social flexibility might be a coping mechanism for individuals to survive and reproduce in unpredictably fluctuating environments (Randall *et al.* 2005). Cooperative breeding in birds, an alternative to breeding in pairs, has been found to occur more often in unstable environments (Jetz & Rubenstein 2011). We predict that unpredictably recurring environmental changes lead to selection for genotypes that enable high phenotypic flexibility (a broad reaction norm). Regarding social behaviour, individuals must have genotypes enabling them to tolerate other individuals for long periods (longer than mating) and the motivation to seek their company (leading to group-living), and a switch to a motivational state to avoid other individuals (leading to solitary-living). This might be especially important in short living species such as the striped mouse, where one generation lives for 1 year and has to maximize its lifetime reproductive success under the prevailing environmental conditions, which might differ significantly from the conditions experienced by previous and succeeding generations. Thus, if environmental conditions

change faster than genetic adaptations can occur, social flexibility allows for an immediate response. While social flexibility enables adaptation to a certain range of a fluctuating environment, anthropogenic (climate) change might induce conditions to which individuals can no longer adapt behaviourally and physiologically. In a period of accelerated climate change it is important to know the limits of social flexibility to predict the range of conditions to which individuals can respond adaptively.

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References

- 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 B*, **272**, 325–331.
- Berry RJ, Tattersall FH, Hurst J (2008) Genus *Mus*. In: *Mammals of the British Isles Handbook*, 4th edn (eds Harris S, Yalden DW), pp. 141–149. The Mammal Society, Southampton, UK.
- Bothma J du P, Walker C (1999) *Larger Carnivores of the African Savannas*. pp. 277. J.L. van Schaik, Pretoria.
- Canals M, Rosenmann M, Bozinovic F (1989) Energetics and geometry of huddling in small mammals. *Journal of theoretical Biology*, **141**, 181–189.
- Carter CS, Getz LL (1993) Monogamy and the prairie vole. *Scientific American*, **6**, 70–76.
- Clutton-Brock TH, Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, **25**, 562–573.
- Clutton-Brock TH (2005) Cooperative breeding in mammals. In: *Cooperation in Primates and Human* (eds Kappeler PM, van Schaik CP). pp. 173–190, Springer, Heidelberg.
- Cushing BS, Razzoli M, Murphy AZ, et al. (2004) Intraspecific variation in estrogen receptor alpha and the expression of male sociosexual behavior in two populations of prairie voles. *Brain Research*, **1016**, 247–254.
- Davies NB (1992) *Dunnock Behaviour and Social Evolution*. Oxford University Press, Oxford.
- Dawkins R (1980) In: *Good strategy or evolutionary stable strategy? In: Sociobiology: Beyond Nature/Nurture* (eds Barlow GW, Silverberg J). pp. 331–367, Westview, Boulder, CO.
- Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, **30**, 1183–1192.
- Dunbar RIM (2002) Modelling primate behavioral ecology. *International Journal of Primatology*, **23**, 785–819.
- Eggert A-K (1992) Alternative male mate-finding tactics in burying beetles. *Behavioral Ecology*, **3**, 243–254.
- Eggert A-K, Müller JK (2000) Timing of oviposition and reproductive skew in cobreeding female burying beetles (*Nicrophorus vespilloides*). *Behavioral Ecology*, **11**, 357–366.
- Elwood RW, Kennedy HF (1991) Selectivity in paternal and infanticidal responses by male mice effects of relatedness location and previous sexual partners. *Behavioural and Neural Biology*, **56**, 129–147.
- Emlen ST (1997) Predicting family dynamics in social vertebrates. In: *Behavioural Ecology* (eds Krebs JR, Davies NB), pp. 228–253. Blackwell Science, Oxford.
- Faulkes CG, Bennett NC (2001) Family values: group dynamics and social control of reproduction in African mole-rats. *Trends in Ecology and Evolution*, **16**, 184–190.
- Friedlingstein P (2008) A steep road to climate stabilization. *Nature*, **451**, 297–298.
- Gross MR (1996) Alternative reproductive strategies and tactics: diversity within the sexes. *Trends in Ecology and Evolution*, **11**, 92–98.
- Heimann M, Kasermann HP, Pfister R, Roth DR, Burki K (2009) Blood collection from the sublingual vein in mice and hamsters: a suitable alternative to retrobulbar technique that provides large volumes and minimizes tissue damage. *Laboratory Animals*, **43**, 255–260. doi: 10.1258/la.2008.007073.
- Jackson TP (1999) The social organisation and breeding system of Brants' whistling rat (*Parotomys brantsii*). *Journal of Zoology*, **247**, 323–331.
- Jetz W, Rubenstein DR (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, **21**, 72–78.
- Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. *International Journal of Primatology*, **23**, 707–740.
- Koenig WD, Mumme RL, Stanback MT, Pitelka FA (1995) Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. *Animal Behaviour*, **50**, 607–621.
- Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology*, **67**, 111–150.
- Kokko H. (2003) Are reproductive skew models evolutionary stable? *Proceedings Royal Society of London B*, **270**, 265–270.
- Komdeur J (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, **358**, 493–495.
- Kraaijeveld K, Dickinson JL (2001) Family-based winter territoriality in western bluebirds, *Sialia mexicana*: the structure and dynamics of winter groups. *Animal Behaviour*, **61**, 109–117.
- Krause J, Ruxton GD (2002) *Living in Groups*. Oxford University Press, Oxford.
- Krebs JR, Davies NB (1993) *An Introduction to Behavioural Ecology*, 3rd edn. Blackwell Science Ltd, Oxford.
- Lank DB, Smith CM, Hanotte O, Burke T, Cooke F (1995) Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature*, **378**, 59–62.
- Latham N, Mason G (2004) From house mouse to mouse house: the behavioural biology of free-living *Mus musculus*

- and its implications in the laboratory. *Applied Animal Behaviour Science*, **86**, 261–289.
- Lott DF (1984) Intraspecific variation in the social systems of wild vertebrates. *Behaviour*, **88**, 266–325.
- Lott DF (1991) *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge University Press, New York.
- Lucia KE, Keane B, Hayes LD, Lin YK, Schaefer RL, Solomon NG (2008) Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behavioral Ecology*, **19**, 774–783.
- Mabry KE, Streatfeild CA, Keane B, Solomon NG (2011) *avpr1a* length polymorphism is not associated with either social or genetic monogamy in free-living prairie voles. *Animal Behaviour*, **81**, 11–18.
- Madison DM, FitzGerald RW, McShea WJ (1984) Dynamics of social nesting in overwintering meadow voles (*Microtus pennsylvanicus*): possible consequences for population cycling. *Behavioral Ecology and Sociobiology*, **15**, 9–17.
- Moore MC, Hews DK, Knapp R (1998) Hormonal control and evolution of alternative male phenotypes: generalizations of models for sexual differentiation. *American Zoologist*, **38**, 133–151.
- Müller JF, Braunisch V, Hwang W, Eggert A-K (2006) Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*. *Behavioral Ecology*, **18**, 196–203.
- Oliveira RF, Canario AVM, Ros AFH (2008) Hormones and alternative reproductive tactics in vertebrates. In: *Alternative Reproductive Tactics* (eds Oliveira RF, Taborsky M, Brockmann HJ), pp. 132–174. Cambridge University Press, Cambridge.
- Ophir AG, Campbell P, Hanna K, Phelps SM (2008a) Field tests of cis-regulatory variation at the prairie vole *avpr1a* locus: Association with V1aR abundance but not sexual or social fidelity. *Hormones and Behavior*, **54**, 694–702.
- Ophir AG, Phelps SM, Sorin AB, Wolff JO (2008b) Social but not genetic monogamy is associated with greater breeding success in prairie voles. *Animal Behaviour*, **75**, 1143–1154.
- Pillay N. (2000) Fostering in the African striped mouse: implications for kin recognition and dominance. *Acta Theriologica*, **45**, 193–200.
- Pruett-Jones SG, Lewis MJ (1990) Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature*, **348**, 541–542.
- Purcell J, Aviles L (2007) Smaller colonies and more solitary living mark higher elevation populations of a social spider. *Journal of Animal Ecology*, **76**, 590–597.
- Randall JA, Rogovin K, Parker PG, Eimes JA (2005) Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behavioral Ecology*, **16**, 961–973.
- Ragsdale JE (1999) Reproductive skew theory extended: the effect of resource inheritance on social organisation. *Evolutionary Ecology Research*, **1**, 859–874.
- Scantlebury M, Bennett NC, Speakman JR, 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**(suppl.), 77–82.
- Schradin C (2006) Whole day follows of the striped mouse. *Journal of Ethology*, **24**, 37–43.
- Schradin C (2007) Information transfer about food locations is not a benefit of group living in the solitary foraging striped mouse (*Rhabdomys pumilio*). *Journal of Ethology*, **25**, 83–86.
- Schradin C (2008a) Differences in prolactin levels between three alternative male reproductive tactics in striped mice (*Rhabdomys pumilio*). *Proceedings of the Royal Society of London B*, **275**, 1047–1052.
- Schradin C (2008b) Seasonal changes in testosterone and corticosterone levels in four social categories of a desert dwelling sociable rodent. *Hormones and Behavior*, **53**, 573–579.
- Schradin C, Anzenberger G (1999) Prolactin, the hormone of paternity. *News in Physiological Sciences*, **14**, 223–231.
- Schradin C, Kinahan AA, Pillay N (2009a) Cooperative breeding in groups of synchronously mating females and evolution of large testes to avoid sperm depletion in African striped mice. *Biology of Reproduction*, **81**, 111–117.
- Schradin C, König B, Pillay N (2010a) Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology*, **79**, 515–521.
- Schradin C, Krackow S, Schubert M, Keller C., Schradin B., Pillay N (2007) Regulation of activity in desert-living striped mice: The importance of basking. *Ethology*, **113**, 606–614.
- Schradin C, Lindholm AK (2011) Relative fitness of alternative male reproductive tactics in a mammal varies between years. *Journal of Animal Ecology*, **80**, 908–917. Doi: 10.1111/j.1365-2656.2011.01831.x
- Schradin C, Pillay N (2003) Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): laboratory and field evidence. *Journal of Comparative Psychology*, **117**, 317–324.
- Schradin C, Pillay N (2004) The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of South Africa: A territorial group living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology*, **118**, 37–47.
- Schradin C, Pillay N (2005) The influence of the father on offspring development in the striped mouse. *Behavioral Ecology*, **16**, 450–455.
- Schradin C, Scantlebury M, Pillay N, König B (2009b) 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, Schneider C, Lindholm AK (2010b) The nasty neighbour in the striped mouse (*Rhabdomys pumilio*) steals paternity and elicits aggression. *Frontiers in Zoology*, **7**, 19.
- Schradin C, Schneider C, Yuen CH (2009c) 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, Schubert M, Pillay N (2006) Winter huddling groups in the striped mouse. *Canadian Journal of Zoology*, **84**, 693–698.
- Schubert M, Pillay N, Schradin C (2009) Parental and alloparental care in a polygynous mammal. *Journal of Mammalogy*, **90**, 724–731.

- Shuster SM, Sassaman C (1997) Genetic interaction between male mating strategy and sex ratio in a marine isopod. *Nature*, **388**, 373–376.
- Shuster SM, Wade MJ (2003) *Mating Systems and Strategies*. Princeton University Press, Princeton.
- Solmsen N, Johannesen J, Schradin C (2011) Highly asymmetric fine-scale genetic structure between sexes of African striped mice and indication for condition dependent alternative male dispersal tactics. *Molecular Ecology*, **20**, 1624–1634.
- Solomon NG, Richmond AR, Harding PA, *et al.* (2009) Polymorphism at the *avpr1a* locus in male prairie voles correlated with genetic but not social monogamy in field populations. *Molecular Ecology*, **18**, 4680–4695.
- Taborsky M (1984) Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Animal Behaviour*, **32**, 1236–1252.
- Taborsky M, Oliveira RF, Brockmann HJ (2008). The evolution of alternative reproductive tactics: concepts and questions. In: *Alternative Reproductive Tactics* (eds Oliveira RF, Taborsky M, Brockmann HJ), pp. 1–22. Cambridge University Press, Cambridge.
- Temeles EJ (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? *Animal Behaviour*, **47**, 339–350.
- Tomkins JL, Hazel W (2007) The status of the conditional evolutionary stable strategy. *Trends in Ecology and Evolution*, **22**, 522–528.
- Wcislo WT, Danforth BN (1997) Secondly solitary: the evolutionary loss of social behavior. *Trends in Ecology & Evolution*, **12**, 468–474.
- Webster AB, Brooks RJ (1981) Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy*, **62**, 738–751.
- Wingfield JC (2003) Control of behavioural strategies for capricious environments. *Animal Behaviour*, **66**, 807–816.
- Wingfield JC, Sapolsky RM (2003) Reproduction and Resistance to stress: when and how. *Journal of Neuroendocrinology*, **15**, 711–724.
- Young L, Wang Z (2004) The neurobiology of pair bonding. *Nature Neuroscience*, **7**, 1048–1054.
- Young L (2009) Love: Neuroscience reveals all. *Nature*, **457**, 148.
- Young AJ, Spong G, Clutton-Brock T (2007) Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society of London B*, **274**, 1603–1609.